

TREATISE ON INVERTEBRATE PALEONTOLOGY

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Part R ARTHROPODA 4

Volume 3: Superclass Hexapoda

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TREATISE ON INVERTEBRATE PALEONTOLOGY

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VOLUMES ALREADY PUBLISHED

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- Part H. BRACHIPODA, xxxii + 927 p., 5,198 fig., 1965.
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- Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 1,762 fig., 1969.
- Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), xxx + 650 p., 2,868 fig., 1967 [1968].
- Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1-3, xxxviii + 1027 p., 4,833 fig., 1978.
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- Part W, Revised. MISCELLANEA, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 858 fig., 1981.

THIS VOLUME

Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 1,489 fig., 1992.

VOLUMES IN PREPARATION

Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).

Part E, Revised. PORIFERA. Volume 2.

Part G, Revised. BRYOZOA (additional volumes).

Part H, Revised. BRACHIOPODA.

Part I. Introduction to MOLLUSCA (part).

Part J. MOLLUSCA 2 (Caenogastropoda, Streptoneura exclusive of Archaeogastropoda, Euthyneura).

Part L, Revised. MOLLUSCA 4 (Ammonoidea).

Part M. MOLLUSCA 5 (Coleoidea).

Part O, Revised. ARTHROPODA 1 (Trilobita).

Part Q, Revised. ARTHROPODA 3 (Ostracoda).

EDITORIAL PREFACE

FROM THE outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a single specialist with a synoptic view of the group being monographed. More rarely, two or perhaps three specialists worked together. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. Part R, Hexapoda, prepared by Professor Frank M. Carpenter, is certainly the last of the volumes that will be written by a single author rather than by a team of specialists. Few paleontologists have ever had such an all-encompassing command of a major group of fossils as Professor Carpenter's of the fossil insects. We are indeed privileged that he has found both the time and the energy over the years to compile this information and share it with the paleontological and entomological communities.

These volumes on the Hexapoda, the final section of Part R, are not a revision of previous work but are one of four remaining parts of the *Treatise* project that have not yet been covered for the first time. The others remaining to be done are Part B, Protista; Part J, Caenogastropoda; and Part M, Coleoidea, all of which are presently in preparation.

The fourth part of the arthropod *Treatise* has had a long history. Volumes 1 and 2, forming one unit, were published in 1969 and comprise an introduction to Hexapoda and an introduction and systematics sections on Onychophora, Crustacea other than Ostracoda, and Myriapoda. Volumes 3 and 4, originally planned for a single volume, cover the Hexapoda including, of course, the fossil insects, taxonomy of which fills most of the two volumes. The introduction to the insects is brief. The insects and their hexapod relatives are morphologically, physiologically, and ecologically quite complex organisms that abound in the modern world. Numerous excellent introductions are avail-

able. To reintroduce them here would require extensive duplication, and an adequate introductory section would be beyond the scope of the *Treatise on Invertebrate Paleontology*.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1985 in the *International Code of Zoological Nomenclature*, hereinafter referred to as the *Code*, provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code*, but under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, is undertaking a revision of the *Code* that will enhance nomenclatorial stability. Nevertheless, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient

attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*, especially in these two volumes. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnean, hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are not regulated by the *Code*. It is both natural and convenient to discuss nomenclatorial matters in general terms first and then to consider each of these three, recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

All zoological names can be considered on the basis of their spelling. The first form of a name to be published is defined as the original spelling (*Code*, Article 32), and any form of the same name that is published later and is different from the original spelling is designated a subsequent spelling (Article 33). Not all original spellings are correct, just as is true of subsequent spellings.

Original Spellings

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some

stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code*, or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Articles 11 and 24 to 34).

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names; and they call for correction. For example, a name originally published with a diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary purpose of zoological nomenclature as an information retrieval system. One looks forward with hope to a revised *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

Subsequent Spellings

If a subsequent spelling differs from an original spelling in any way, even by the

omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name. Exceptions include such changes as altered terminations of adjectival specific names to agree in gender with associated generic names; changes of family-group names to denote assigned taxonomic rank; and corrections that eliminate originally used diacritical marks, hyphens, and the like. Such changes are not regarded as spelling changes conceived to produce a different name. In some instances, however, species-group names having variable spellings are regarded as homonyms as specified in the *Code*, Article 58.

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If “demonstrably intentional” (*Code*, Article 33, p. 73), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication. They are junior, objective synonyms of the name in its original form.

Subsequent spellings, if unintentional, are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Editorial prefaces of previous volumes of the *Treatise* have discussed in appreciable detail the availability of the many kinds of zoological names that have been proposed under a variety of circumstances. Much of that information, while important, does not pertain to the present volumes in which the

author has used only *nomen nudum* (plural *nomina nuda*, naked names). The reader is referred to *Part G Bryozoa (Revised)* of the *Treatise* and to the *Code* (Articles 10 to 20) for further details on availability of names. Here, besides the discussion of *nomina nuda* below, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the *Code*. All zoological names that fail to comply with mandatory provisions of the *Code* are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the *Treatise*, although not explicitly differentiated in the *Code*. Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code*, which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (Articles 12 and 16) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen substitutum*) of a preexisting available name (Article 13a), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (Article 13b). *Nomina nuda* have no status in nomenclature and are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

Important considerations distinguish valid from available names on the one hand and invalid from unavailable names on the other. Whereas determination of availability is based entirely on objective considerations guided by articles of the *Code*, conclusions as to validity of zoological names may be partly subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct, hence valid, name, which is generally the oldest. Obviously, no valid name can also be an unavailable name, but invalid names may be either available or unavailable. It follows that any name for a given taxon other than the valid name, whether available or unavailable, is an invalid name.

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, invalid but available names persist in the literature.

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

Species-Group Names

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the *Treatise* deals with genus-group names and higher categories. When the form of an adjectival specific name is changed to agree with the gender of a generic

name in transferring a species from one genus to another, one need never label the changed name as *nomen correctum*. Similarly, transliteration of a letter accompanied by a diacritical mark in the manner now called for by the *Code*, as in changing originally *bröggeri* to *broeggeri*, or eliminating a hyphen, as in changing originally published *cornu-oryx* to *cornuoryx*, does not require the designation *nomen correctum*.

Genus-Group Names

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct.

As has been pointed out above, difficulty typically arises when one tries to decide whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has often to be made arbitrarily.

Family-Group Names: Authorship and Date

All family-group taxa having names based on the same type genus are attributed to the author who first published the name of any of these assemblages, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Also, every family containing differ-

entiated subfamilies must have a nominotypical subfamily (*sensu stricto*), which is based on the same type genus as the family; and the author and date set down for the nominotypical subfamily invariably are identical with those of the family, irrespective of whether the author of the family or some subsequent author introduced subdivisions.

Corrections in the form of family-group names do not affect authorship and date of the taxon concerned, but in the *Treatise* recording the authorship and date of the correction is desirable because it provides a pathway to follow the thinking of the systematists involved.

Family-Group Names: Use of *nomen translatum*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) names, but all family-group taxa are defined as coordinate (Article 36, p. 77): "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix [Art. 34a]." Such changes of rank and concomitant changes of endings as elevation of a tribe to subfamily rank or of a subfamily to family rank, if introduced subsequent to designation of a subfamily or family based on the same nominotypical genus, are *nomina translata*. In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum*, abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration. This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the super-

family as defined by the *Code*. The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

An example of the use of *nomen translatum* is the following.

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* DEMOULIN, 1954, p. 566, *ex* Hexagenitinae LAMEERE, 1917, p. 74]

**Family-Group Names: Use of
*nomen correctum***

Valid name changes classed as *nomina correctum* do not depend on transfer from one category of family-group units to another but most commonly involve correction of the stem of the nominotypical genus. In addition, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

Family STREPTELASMATIDAE Nicholson, 1889

[*nom. correct.* WEDEKIND, 1927, p. 7, *pro* Streptelasmidae NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 297]

Family PALAEOSCORPIDAE Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, 1955, p. P73, *pro* Palaescorpionidae LEHMANN, 1944, p. 177]

Family-Group Names: Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for family and subfamily, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but

among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (Article 39, p. 79), in which case “. . . it must be replaced either by the next oldest available name from among its synonyms, including those of its subordinate taxa, or, if there is no such name, by a new replacement name based on the valid name of the former type genus.” Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name; but, for subsequent application of the rule of priority, the name takes the date of the replaced name (see Recommendation 40A). Many family-group names that have been in use for a long time are *nomina nuda*, since they fail to satisfy criteria of availability (Article 11f). These demand replacement by valid names.

The aim of family-group nomenclature is to yield the greatest possible stability and uniformity, just as in other zoological names. Both taxonomic experience and the *Code* (Article 40) indicate the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of the same worker may change from time to time. The retention of first-published, family-group names that are found to be based on junior objective synonyms, however, is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. To displace a widely used, family-group name based on the senior objective synonym by disinterring

a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

A family-group name may need to be replaced if the nominotypical genus is transferred to another family-group. If so, the first-published of the generic names remaining in the family-group taxon is to be recognized in forming a replacement name.

Suprafamilial Taxa: Taxa above Family-Group

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to phylum) are either unmentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th International Congress of Zoology convened in 1958, thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision that was supported by a wide majority

of the participants in the Colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, a class or order defined by an author at a given date, using chosen morphologic characters (e.g., gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (e.g., hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. No basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this publication. Some uniformity is needed, especially for the guidance of *Treatise* authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

1. The name of any suprafamilial taxon must be a Latin or latinized, uninominal noun of plural form, or treated as such, with a capital initial letter and without diacritical mark, apostrophe, diaeresis, or hyphen. If a component consists of a numeral, numerical adjective, or adverb, this must be written in full.

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (e.g., Yuania); none of these, however, can end in -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatural distinction between suprafamilial and family-group taxa that, respectively, are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina ULRICH & SCOFIELD, 1897; superfamily Bellerophon-tacea McCoy, 1851; family Bellerophontidae McCoy, 1851). Family-group names are not coordinate with suprafamilial names.

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatural stability and to avoid confusion these rules are widely applied by zoologists to taxa above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4. Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such changes cannot rationally be judged to alter the authorship and date of the taxon as published originally. A name revised from its previously published rank is a transferred name (*nomen translatum*), as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935
[*nom. transl.* MOORE, 1959, p. O217, *ex* suborder Corynexochida KOBAYASHI, 1935, p. 81]

A name revised from its previously published form merely by adoption of a different termination without changing taxonomic rank is an altered name (*nomen correctum*).

Order DISPARIDA Moore & Laudon, 1943
[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *pro* order Disparata MOORE & LAUDEN, 1943, p. 24]

A suprafamilial name revised from its previously published rank with accompanying change of termination, which signal the change of rank, is recorded as a *nomen translatum et correctum*.

Order HYBOCRINIDA Jackel, 1918
[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, *ex* suborder Hybocrinites JAEKEL, 1918, p. 90]

5. The authorship and date of nominotypical subordinate and supraordinate taxa among suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

Subclass ENDOCERATOIDEA Teichert, 1933
[*nom. transl.* TEICHERT in TEICHERT *et al.*, 1964, p. K128, *ex* order Endoceroidea TEICHERT, 1933, p. 214]

Order ENDOCERIDA Teichert, 1933
[*nom. correct.* TEICHERT in TEICHERT *et al.*, 1964, p. K165, *pro* order Endoceroidea TEICHERT, 1933, p. 214]

Suborder ENDOCERINA Teichert, 1933
[*nom. correct.*, TEICHERT in TEICHERT *et al.*, 1964, p. K165, *ex* Endoceratina SWEET, 1958, p. 33, suborder]

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are (1) alteration of a name itself in various ways for various reasons, as has been reviewed, and (2) alteration of the taxonomic scope or concept for which a name is used. The *Code*

(Article 33a and Glossary, p. 148) concerns itself only with the first type of emendation, applying the term to either justified or unjustified changes, both intentional, of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names, refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *emend.* then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other assemblage of animals is incorporated into or removed from the coverage of a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat radical revisions are put forward, generally with published statement of reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as aid to subsequent workers in taking account of the altered nomenclatural usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation.

Examples from *Treatise* volumes follow.

Order ORTHIDA Schuchert & Cooper, 1932
[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, *ex* suborder Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.*, WILLIAMS & WRIGHT, 1965, p. H299]

Subfamily ROVEACRININAE Peck, 1943
[Roveacrininae PECK, 1943, p. 465; *emend.*, PECK in MOORE & TEICHERT, eds. 1978, p. T921]

STYLE IN GENERIC DESCRIPTIONS

Citation of Type Species

The name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (*), with notation of the author and date of original publication. An exception in this procedure is made, however, if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type; in this instance, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

Orionastraea SMITH, 1917, p. 294 [**Sarcinula philipsi* MCCOY, 1849, p. 125; OD]

Schoenophyllum SIMPSON, 1900, p. 214 [**S. aggregatum*; OD]

If the cited type species is a junior synonym of some other species, the name of this latter also is given, as follows.

Actinocyathus D'ORBIGNY, 1849, p. 12 [**Cyathophyllum crenulate* PHILLIPS, 1836, p. 202; M; =*Lonsdalaeia floriformis* (MARTIN), 1809, pl. 43; validated by ICZN Opinion 419]

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication except that diacritical marks have been removed. Where other

mandatory changes are required, these are introduced later in the text, typically in a figure caption.

Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code*, may be fixed in various ways in the original publication; or it may be fixed in ways specified by the *Code* (Article 68) and described in the next section. Type species fixed in the original publication include (1) *original designation* (in the *Treatise* indicated by "OD") when the type species is explicitly stated or (before 1931) indicated by "n. gen., n. sp." (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as "M"), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

Fixation of Type Species Subsequently

The type species of many genera are not determinable from the publication in which the generic name was introduced and therefore such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus. In the *Treatise*, fixation of the type species in this manner is indicated by the letters "SD" accompanied by the name of the subsequent author (who may be the same

person as the original author) and the date of publishing the subsequent designation. Some genera, as first described and named, included no mentioned species (for such genera established after 1930, see below); these necessarily lack a type species until a date subsequent to that of the original publication when one or more species are assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later "SD" designation is necessary. Examples of the use of "SD" as employed in the *Treatise* follow.

Hexagonaria GÜRICH, 1896, p. 171 [**Cyathophyllum hexagonum* GOLDFUSS, 1826, p. 61; SD LANG, SMITH, & THOMAS, 1940, p. 69]
Mesephepera HANDLIRSCH, 1906, p. 600 [**Tineites lithophilus* GERMAR, 1842, p. 88; SD CARPENTER, herein]

Another mode of fixing the type species of a genus is action of the International Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters "ICZN," accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication, is invalid (*Code*, Article 13b). Effort of a subsequent author to validate such a name by subsequent

designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

Homonyms

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to two or more distinct taxonomic units, however, it is necessary to differentiate such homonyms. This calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, *Callophora* HALL, 1852, introduced for Paleozoic trepostomate bryozoans, is invalid because GRAY in 1848 published the same name for Cretaceous-to-Holocene cheilostomate bryozoans. BASSLER in 1911 introduced the new name *Hallophora* to replace Hall's homonym. The *Treatise* style of entry is given below.

Hallophora BASSLER, 1911, p. 325, *nom. subst. pro*
Callophora HALL, 1852, p. 144, *non* GRAY, 1848

In like manner, a needed replacement generic name may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

Mysterium DE LAUBENFELS, herein, *nom. subst. pro*
Mystrium SCHRAMMEN, 1936, p. 183, *non* ROGER,
1862 [**Mystrium porosum* SCHRAMMEN, 1936, p.
183; OD]

Otherwise, no mention of the existence of a junior homonym generally is made.

Synonymous Homonyms

An author sometimes publishes a generic name in two or more papers of different date,

each of which indicates that the name is new. This is a bothersome source of errors for later workers who are unaware that a supposed first publication that they have in hand is not actually the original one. Although the names were separately published, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymous homonyms. In the *Treatise* the junior of one of these is indicated by the abbreviation "jr. syn. hom."

Not infrequently, identical family-group names are published as new names by different authors, the author of the later-introduced name being ignorant of previous publication(s) by one or more other workers. In spite of differences in taxonomic concepts as indicated by diagnoses and grouping of genera and possibly in assigned rank, these family-group taxa are nomenclatural homonyms, based on the same type genus; and they are also synonyms. Wherever encountered, such synonymous homonyms are distinguished in the *Treatise* as in dealing with generic names.

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae R. & E. RICHTER, 1925, based on *Scutellum* PUSCH, 1833, a trilobite. This name is a junior homonym of Scutellidae GRAY, 1825, based on the echinoid genus *Scutella* LAMARCK, 1816. The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

Synonyms

In the *Treatise*, citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are

indicated by accompanying designation "obj.," others being understood to constitute subjective synonyms, of which the types are also indicated. Examples showing *Treatise* style in listing synonyms follow.

Mackenziophyllum PEDDER, 1971, p. 48 [**M. insolitum*; OD] [= *Zonastraea* TSYGANKO in SPASSKIY, KRAVTSOV, & TSYGANKO, 1971, p. 85, *nom. nud.*; *Zonastraea* TSYGANKO, 1972, p. 21 (type, *Z. graciosa*, OD)]

Kodonophyllum WEDEKIND, 1927, p. 34 [**Streptelasma Milne-Edwardsi* DYBOWSKI, 1873, p. 409; OD; = *Madrepora truncata* LINNÉ, 1758, p. 795, see SMITH & TREMBERTH, 1929, p. 368] [= *Patropontes* LANG & SMITH, 1927, p. 456 (type, *Madrepora truncata* LINNÉ, 1758, p. 795, OD); *Codonophyllum* LANG, SMITH, & THOMAS, 1940, p. 39, obj.]

Some junior synonyms of either the objective or the subjective sort may take precedence desirably over senior synonyms whenever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a genus. This requires action of ICZN, which may use its plenary powers to set aside the unwanted name and validate the wanted one, with placement of the concerned names on appropriate official lists.

MATTERS OF STYLE SPECIFIC TO THESE VOLUMES

The Fossil Record of Hexapods

In spite of their being the most diverse group of organisms, the insects have a surprisingly poor fossil record. Their dominantly terrestrial mode of life and lack of mineralized skeletons have contributed to extensive taphonomic loss. Thus, whereas such *Treatise* volumes as Part Q, Ostracoda have sought to include all genera in the group whether or not they have a fossil record because of their potential for fossilization, to attempt to do so with the insects would be both beyond the scope of the *Treatise on Invertebrate Paleontology* and doomed to failure. Most of the recent genera of insects are not included

herein. In fact, a recent genus with no fossil record is included only if it is the type genus of a family that contains fossil forms. Moreover, for recent genera that have a fossil record, we do not indicate type species or give diagnoses. Instead, we give only the last name of their author, the date of publication, and the page number. Although full citations of these author-date combinations are not in the bibliography, subsequent references to the literature are included.

Names of Taxa, Places, and Authors

Several matters relate specifically to the style of generic descriptions. Names of type species have been corrected only by having diacritical marks removed. For example, *Corydaloïdes* has been changed to *Corydaloides*. Throughout the text the author has used the solidus to indicate uncertainty with respect to age. "Oligo./Mio.," for example, indicates that the age of the genus is uncertain but is one of the two ages noted. The question mark is used when the age is still more uncertain.

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past two years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change. Throughout the text, the author has used the letters RSFSR to refer to the Russian Socialist Federated Soviet Republic with two parts, European and Asian, separated by the Ural Mountains. The RSFSR, of course, no longer exists as a political or geographical entity, but the strata containing fossil insects remain where they were. One expects confusion among readers in the future as they try to decipher such geographical terms as U.S.S.R. or Yugoslavia. Such confusion is unavoidable, as books must be completed

and published at some time. Our libraries would be small indeed if publication were always delayed until the world had settled down.

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause English-language bibliographers headaches for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into Roman letters. Thus, a Chinese author may change the Roman-letter spelling of his name from one publication to another. For example, the name Chang, which is the most common family name in the world, might also be spelled Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the Roman spelling that the Chinese author used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations to his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names, but people with Chinese names who study in the West often reverse the order, putting the family name last. Thus, for example, Dr. Yi-Maw Chang, now on the staff of the Paleontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang, and his subsequent bibliographic citations are listed as "Chang, Yi-Maw." The *Treatise* staff has adopted the convention of listing family names first, inserting a comma, and following this with given names or initials. We do this even for Chinese authors who have not reversed their names in the Western fashion.

Several specific systems exist for transliterating the Cyrillic alphabet into the Roman alphabet, so that this problem need not occur, for example, with names of Russian authors. We have adopted System II from J. Thomas Shaw's *Transliteration of Modern Russian for English-Language Publications*, which is the same as the Library of Congress system for transliteration of modern Russian with diacritical marks omitted.

Stratigraphical Range Charts

Readers may notice that stratigraphical range charts in this volume are somewhat different from those in previous volumes. Charts in this volume were prepared using RangeChart, an unpublished computer-software program developed by Kenneth C. Hood and David W. Foster, both now with Exxon, when they were graduate students at The University of Kansas. RangeChart sorts the taxa by their ranges and the degree of certainty of those ranges and uses different weights of lines for different categories. A revised version of the program, RangeChart 2.0, is in preparation.

Acknowledgments

The *Treatise* volumes on the Hexapoda have had a long history of development, having been the focus of Professor Carpenter's efforts with varying degrees of intensity since the early stages of the *Treatise* project. The staff of the Paleontological Institute has remained remarkably stable during the ensuing decades, but given the length of time quite a number of people have been involved with the volumes. They deserve special mention here, for without their efforts the *Treatise* project as a whole and these volumes specifically would not be what they are today. Not the least of these are the three previous Editors and Directors of the Paleontological Institute: the late Raymond C. Moore as well

as Curt Teichert and Richard A. Robison. The two previous Assistant Editors for Text, Lavon McCormick and Virginia Ashlock, and the previous Assistant Editor for Illustrations, Roger B. Williams, worked closely with Professor Carpenter on the volumes. The present Assistant Editor for Text, Elizabeth Brosius, and the Assistant Editor for Illustrations, Jane Priesner, have faced admirably the formidable task of moving the volumes through the final stages of editing and into and beyond the production phase. In this they have been ably assisted by Jill Hardesty with word processing; Jill Krebs with editorial backup; and Jack Keim with photography, layout, and preparation of range charts. Yi-Maw Chang, the remaining member of the Paleontological Institute staff, is involved with preparation of PaleoBank, the paleon-

tological data base for future *Treatise* volumes, and has not been closely involved with the hexapod *Treatise*. Margery Rowell edited the Russian titles in the bibliography, and Richard A. Leschen and George W. Byers, respectively, drew figures 173 and 204.

This Editorial Preface is an extensive revision of prefaces prepared for previous *Treatise* volumes by former editors, including the late Raymond C. Moore, Curt Teichert, and Richard A. Robison. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Roger L. Kaesler
Lawrence, Kansas
May 1, 1992

AUTHOR'S PREFACE

Nearly thirty years ago Professor Raymond Moore, then editor of the *Treatise on Invertebrate Paleontology*, invited me to prepare the volume on the Hexapoda. Following considerable correspondence with him, I decided to undertake that assignment, although no definite date was set for its completion. My start on the project was slow, mainly because I was shortly asked to serve in several administrative positions at Harvard University, in addition to my regular teaching schedule. Not until 1974, when I became professor *emeritus*, was I able to devote full time to the preparation of the volume. At that time previously submitted manuscript was revised, and the first draft of the manuscript was sent to the editorial office of the *Treatise* in 1982. It was decided to set the end of 1983 as the terminal date for literature citations, since there had been an unusual amount of literature on fossil insects published during the preceding twenty years

(1963 to 1983), and since a large part of that was in Russian and needed to be translated. In this connection I should mention that a bibliography of fossil insects, covering the years 1980 to 1990, is now in preparation by E. A. Jarzembowski and A. J. Ross (Booth Museum, Brighton, U. K.) and will be published in 1992 in *The Fossil Record* (eds., M. J. Benton & M. A. Whyte, Chapman & Hall, London).

I am deeply grateful to the editorial staff of the *Treatise*, especially to Elizabeth Brosius and Jane Priesner, for their indispensable assistance, particularly regarding the bibliography. I am equally indebted to Helen Vaitaitis, who has done all of the translating of the numerous Russian articles for me these many years. Dr. Laurie Burnham assisted me for several years with the preparation of the illustrations for the *Treatise*, and Dr. Curtis Sabrosky has provided helpful advice pertaining to special taxonomic problems. My

wife, Ruth Carpenter, has been very supportive in many ways and especially with the preparation of an index to the genera in the early stages of the manuscript. I acknowledge with gratitude the cooperation of the following museums in the United States and Europe that have placed type material at my disposal at the institutions or have loaned such specimens when needed: the United States National Museum (Washington), the Field Museum (Chicago), the British Museum,

Natural History (London), Museum d'Histoire Naturelle (Paris), and the Paleontological Institute (Moscow). Finally, I am indebted to our National Science Foundation for research grants that made these investigations possible.

Frank M. Carpenter
Cambridge, Massachusetts
January, 1992

SOURCES OF ILLUSTRATIONS

Some illustrations in this volume are new. Where previously published illustrations are used, the author and date of publication are given in parentheses in the figure explanation. Full citation of the publication is provided in the references.

In addition to the citation of the publication, additional credit was requested by those who supplied the following illustrations. Figure 10 is reproduced with permission, from the Annual Review of Entomology, Vol. 26, ©1981 by Annual Reviews Inc. Figure 193,2 is reproduced with permission, from the Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College. The artists responsible for the illustrations reproduced from *The Insects of Australia* are F. Nanninga (Figure 79,2), N. Key (Figure 82,2), B. Rankin (Figure 132), S. Curtis (Figure 134), and T. Binder (Figure 217).

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., substages, stages, and subseries) are more likely to be provincial in application. The stratigraphical units listed here show the fairly coarse time resolution that is characteristic of the study of fossil hexapods.

CENOZOIC ERATHEM

Quaternary System

Holocene Series

Pleistocene Series

Tertiary System

Pliocene Series

Miocene Series

Oligocene Series

Eocene Series

Paleocene Series

MESOZOIC ERATHEM

Cretaceous System

Jurassic System

Triassic System

PALEOZOIC ERATHEM

Permian System

Carboniferous System

Upper Carboniferous Subsystem

Lower Carboniferous Subsystem

Devonian System

Silurian System

Ordovician System

Cambrian System

PRECAMBRIAN (undifferentiated herein)

PART R
ARTHROPODA 4

HEXAPODA

VOLUMES 3, 4

By FRANK M. CARPENTER

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SYSTEMATIC DESCRIPTIONS OF THE SUPERCLASS HEXAPODA

Superclass HEXAPODA

Latreille, 1825

[Hexapoda LATREILLE, 1825, p. 328]

Six-legged, tracheate arthropods, with thorax more or less demarcated from abdomen; head typically with 1 pair of antennae, and with mandibles, maxillae, and a labium; thorax usually strongly sclerotized, the coxa-body mechanisms diverse; abdomen with from 6 to 11 segments. Species mainly terrestrial, but some secondarily aquatic. Reproduction and life histories very diverse. *Dev.—Holo.*

The status of this group as a taxon is uncertain. MANTON (1969a, 1977, 1979), following her extensive investigations on functional morphology of the arthropods, was convinced that the classes she included in the Hexapoda were more akin to one another than to any other arthropod classes. At the same time, however, she was also convinced that there could not have been any one type of ancestral hexapod capable of giving rise to the existing hexapod classes. Although in recent years an unprecedented amount of literature has been published on arthropod evolution (see SCUDDER, 1973; BOUDREAUX, 1979; GUPTA, 1979; HENNIG, 1981), the relationships of the classes of Hexapoda seem as obscure as ever. In all probability this situation will not improve until we have a truly extensive record of the terrestrial arthropods in Lower Carboniferous (Mississippian) and Devonian strata. The four or five existing classes of six-legged arthropods have had a long history, apparently extending that far back; but as the present record stands only one species of hexapod is known earlier than the Late Carboniferous—*Rhytniella praecursor*, a collembolon from the Devonian of Scotland (see Fig. 2). Numerous fragments of other arthropods have been found in freshwater deposits of the Devonian, but for the most part they cannot be

associated with any of the existing hexapod classes. It seems likely that the diversity of the wingless, noninsect hexapods during the Devonian was far greater than that represented by the few classes now in existence.

In the present treatment of the Hexapoda, I follow the classification proposed by MANTON (1969a) in the Introduction to the Arthropoda in this series of volumes, except that the Thysanura (*sensu lato*) are here included within the Insecta, as orders Archaeognatha and Zygentoma, instead of being separated into a distinct class.

Class and Order COLLEMBOLA

Lubbock, 1871

[Collembola LUBBOCK, 1871, p. 295]

Mostly very small hexapods, body usually covered with hairs or, more rarely, with scales; head prognathous, with mandibulate, entognathous mouthparts; mandibles slender; maxillae and labium much reduced; antennae typically with 4 segments, the first 3 with intrinsic muscles; eyes consisting of a few ommatidia on each side of head, or entirely absent. Thorax diversely formed, pronotum usually much reduced; in some species, thorax fused with abdomen, the segmentation being obsolescent; legs lacking a distinct tarsal segment. Abdomen with only 6 segments, the first bearing a ventral, tubular, adhesive organ (collophore); fourth segment bearing a jumping organ (furcula), which at rest folds back under abdomen. Sperm transfer indirect, as in members of the Diplura. Adults and young occurring mostly in decaying vegetation; a few on foliage. *Dev.—Holo.*

This is a relatively small order of about 2,000 widely distributed species. Presumably because of their small size, Collembola are rarely preserved as fossils except in amber. All of the Baltic amber (Oligocene) species appear to belong to recent genera (HANDSCHIN, 1926a), but the only known

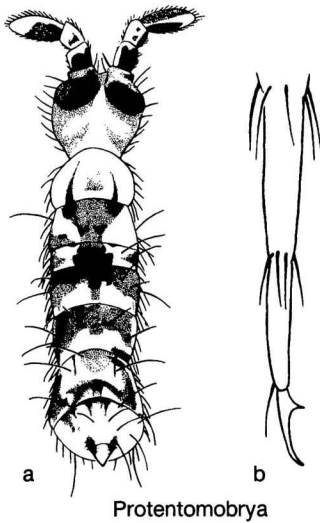


FIG. 1. Protentomobryidae (p. 2).

species in Cretaceous amber represents an extinct genus and family (Protentomobryidae), somewhat intermediate between certain existing families (DELAMARE DEBOUTTEVILLE & MASSOUD, 1968). The genus *Rhyniella* from the Rhynie chert of Scotland, apparently without question a collembolon (WHALLEY & JARZEMBOWSKI, 1981), is the only hexapod now known from the Devonian.

OLFFERS in his 1907 article named several other genera in the Collembola, but, as HANDSCHIN (1926a) has shown, each of these was based on a mixed series of specimens belonging to several genera; no type species or specimens were designated, and HANDSCHIN felt compelled to reject the names. Also, MARI MUTT (1983) has reported the presence of several existing genera (*Cryptopygus*, *Isotomus*, *Lepidocyrtus*, *Pseudosinella*, *Seira*, *Salina*, *Paronella*, *Cyphoderus*, and *Sphyrotheca*) in the Miocene amber of the Dominican Republic but has not identified or named any species.

Family PROTENTOMOBRYIDAE Folsom, 1937

[Protentomobryidae FOLSOM, 1937, p. 15]

Antennae short and stout, with 4 segments; body elongate, setose; pronotum

weakly formed, concealed by mesonotum; first abdominal segment reduced; furcula consisting of a pair of long, simple stylets. *Cret.*

Protentomobrya FOLSOM, 1937, p. 15 [**P. walkeri*; OD]. Third abdominal segment almost as long as fourth; fifth abdominal segment not reduced. DELAMARE DEBOUTTEVILLE & MASSOUD, 1967, 1968. *Cret.*, Canada (Manitoba).—FIG. 1. **P. walkeri*; a, dorsal view, $\times 100$; b, distal portion of left arm of furcula, ventral view, $\times 650$ (both Delamare Deboutteville & Massoud, 1968).

Family ISOTOMIDAE Schaeffer, 1896

[Isotomidae SCHAEFFER, 1896, p. 177]

Pronotum reduced and without setae; rest of body with scales or hairs; furcula usually present. *Oligo.—Holo.*

Isotoma BOURLET, 1839, p. 401. HANDSCHIN, 1926a; CHRISTIANSEN, 1971. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Isotomorus BÖRNER, 1903, p. 171. CHRISTIANSEN, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Family HYPOGASTRURIDAE Börner, 1913

[Hypogastruridae BÖRNER, 1913, p. 315]

Pronotum well developed, bearing setae; rest of body with scales; head prognathous. *Oligo.—Holo.*

Hypogastrura BOURLET, 1839, p. 404. HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*

Family TOMOCERIDAE Schaeffer, 1896

[Tomoceridae SCHAEFFER, 1896, p. 177]

Pronotum reduced; body with scales; antennae long. *Oligo.—Holo.*

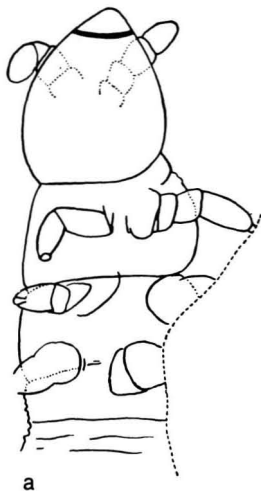
Tomocerus NICOLET, 1841, p. 67. HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*

Family ENTOMOBRYIDAE Schaeffer, 1896

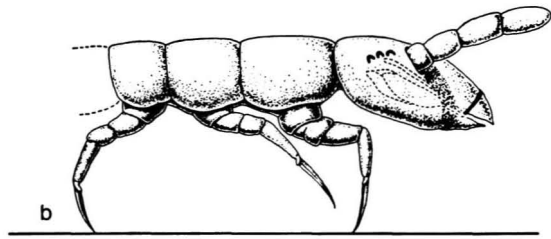
[Entomobryidae SCHAEFFER, 1896, p. 177]

Pronotum reduced; body usually with scales; antennae short; furca well developed. *Perm.—Holo.*

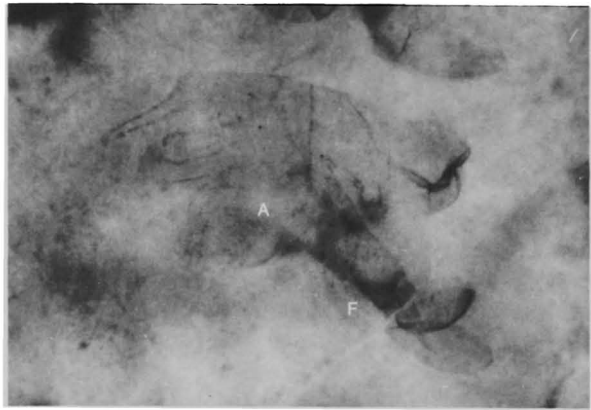
Entomobrya RONDANI, 1861, p. 40 [= *Stylonotus* OLFFERS, 1907, p. 20 (type, *S. lanuginosus*); *Omo-*



a
Rhyniella



b



c

FIG. 2. Uncertain (p. 3).

phora OLFERS, 1907, p. 21 (type, *O. tricuspidata*); *Cuculliger* OLFERS, 1907, p. 24 (type, *C. longistylus*). CHRISTIANSEN, 1971. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*
Lepidocyrtinus BÖRNER, 1903, p. 154. CHRISTIANSEN, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*
Lepidocyrtus BOURLET, 1839, p. 391. KOCH & BERENDT, 1854; HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*
Orchesella TEMPLETON, 1835, p. 92. HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*
Permobrya RIEK, 1977, p. 141 [**P. mirabilis*; OD]. Similar in general appearance to *Lepidocyrtus*, but legs short and stout, and fourth antennal segment annulated. [Family assignment uncertain.] *Perm.*, South Africa.
Salina MACGILLIVRAY, 1894, p. 107. PIERCE, 1960; CHRISTIANSEN, 1971. *Oligo./Mio.*, Mexico (Chiapas); *Mio.*, USA (Colorado)—*Holo.*

Family SMINTHURIDAE
Lubbock, 1862

[Sminthuridae LUBBOCK, 1862, p. 430]

Antennae at least as long as head; thorax and the 4 basal abdominal segments fused into single unit. *Oligo.*—*Holo.*

Sminthurus LATREILLE, 1802, p. 71. STACH, 1923; HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*

Allacma BÖRNER, 1906, p. 183. HANDSCHIN, 1926a. *Oligo.*, Europe (Baltic)—*Holo.*

Family UNCERTAIN

The genus described below, apparently belonging to the class and order Collembola, is too poorly known to permit family assignment.

Rhyniella HIRST & MAULIK, 1926, p. 69 [**R. praecursor*; OD]. Little-known genus; furcula well developed. TILLYARD, 1928c; SCOURFIELD, 1940a, 1940b; DELAMARE DEBOUTTEVILLE & MASSOUD, 1967; MASSOUD, 1967; WHALLEY & JARZEMBOWSKI, 1981. *Dev.*, Scotland.—FIG. 2. **R. praecursor*; a, head and thorax, ventral view, $\times 55$ (Massoud, 1967); b, head and thorax, lateral view, reconstruction, $\times 55$ (Delamare Deboutteville & Massoud, 1967); c, lateral view of abdomen (A) with furcula (F), $\times 100$ (photograph courtesy of P. E. S. Whalley).

Class and Order PROTURA
Silvestri, 1907

[Protura SILVESTRI, 1907, p. 296]

Very small, slender hexapods; head prognathous, with entognathous mouthparts;

antennae and eyes absent; maxillary and labial palpi well developed; prothorax small; forelegs of moderate length, meso- and metathoracic legs short; abdomen with 12 segments in adult; small styli present on sterna; immature forms with anamorphic development, abdominal segments increasing from 9 to 12. Adults and young usually occurring in damp soil or leaf litter. TUXEN, 1964. *Holo.*

Class and Order DIPLURA Börner, 1904

[Diplura BÖRNER, 1904, p. 524]

Small to large hexapods, with entognathous mouthparts. Antennae moniliform, with at least 20 segments, flagellar members with intrinsic muscles; mandibles elongate; maxillary and labial palpi much reduced; hypopharynx well developed; compound eyes and ocelli absent; thoracic segments slightly separated and free, prothorax smallest, meso- and metathorax nearly equal; tarsi consisting of a single segment; abdomen with 11 segments, the last bearing cerci; sterna of segments 2 through 7 with a pair of small, lateral, styliform appendages; cerci diversely formed, either multisegmented or modified to stout, heavily sclerotized forceps. So far as known, sperm transfer indirect, the male depositing stalked spermatophores on the substrate and the female taking up the sperm. Some species (Campodeidae) phytophagous, others (Japygidae) carnivorous. *Paleoc.-Holo.*

Family CAMPODEIDAE Meinert, 1865

[Campodeidae MEINERT, 1865, p. 400]

Cerci long and multisegmented; thorax with 3 pairs of spiracles; abdominal styli soft. *Paleoc.-Holo.*

Campodea WESTWOOD, 1842, p. 71. SILVESTRI, 1913a; PACLT, 1957. *Oligo.*, Europe (Baltic)-*Holo.*
Onychocampodea PIERCE, 1951, p. 48 [**O. onychis*; OD]. Little-known genus; body length about 10 mm. [Family position doubtful.] PACLT, 1957. *Paleoc.-Plio.*, USA (Arizona).

Family UNCERTAIN

The following genera, apparently belonging to the class and order Diplura, are too poorly known to permit family assignment.

Onychojapyx PIERCE, 1950, p. 104 [**O. schmidtii*; OD]. Little-known genus, with short, unsegmented cerci. PIERCE, 1951; PACLT, 1957; REDDELL, 1983. *Paleoc.-Plio.*, USA (Arizona).

Plioprojapyx PIERCE, 1951, p. 48 [**P. primitivus*; OD]. Little-known genus; cerci very short, apparently with only 3 segments. PACLT, 1957. *Paleoc.-Plio.*, USA (Arizona).

Class INSECTA Linné, 1758

[Insecta LINNÉ, 1758, p. 339]

Very small to large ectognathous hexapods; body composed of 20 embryonic segments, grouped into 3 main regions: head consisting of 6 segments, thorax of 3, and abdomen of 11; no abdominal segments added after embryonic stages; one pair of antennae, 2 compound eyes, and 3 ocelli usually present; mouthparts typically mandibulate but diversely modified in several orders; thoracic segments each bearing a pair of segmented legs; eleventh abdominal segment with a pair of segmented cerci, commonly much reduced or absent. Immature stages of primitive insects similar to adults, but those of most existing species greatly modified. *U. Carb.-Holo.*

INTRODUCTION TO THE INSECTS

GENERAL MORPHOLOGY

The class Insecta is not only the largest of all the existing classes of animals but is larger than all other classes combined. As a consequence, there is very great morphological diversity within the class. The following survey is concerned with those structures that are generally used in the higher classification of the insects. Detailed accounts of insect morphology are available in such basic works as *The Principles of Insect Morphology* by R. E. SNODGRASS (1935), *The Insects of Australia* by the Commonwealth Scientific and

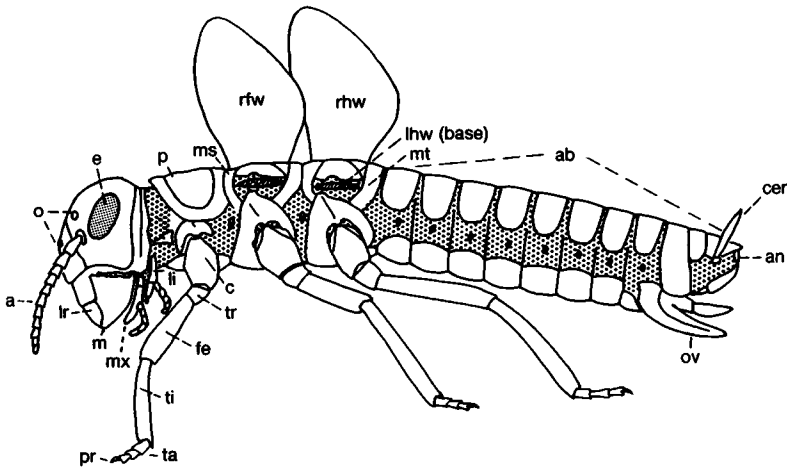


FIG. 3. Lateral view of typical female insect. Head: antenna (a); compound eye (e); labium (li); labrum (lr); mandible (m); maxilla (mx); ocelli (o). Thorax: coxa (c); femur (fe); left hind wing, base (lhw); mesonotum (ms); metanotum (mt); pronotum (p); pretarsus (pr); right fore wing (rfw); right hind wing (rhw); tarsus (ta); tibia (ti). Abdomen: anus (an); cercus (cer); ovipositor (ov) (Carpenter, new).

Industrial Research Organization (CSIRO), Canberra (1970), and *Imms' General Text-book of Entomology*, tenth edition, edited by O. W. RICHARDS and R. G. DAVIES (1977), as well as in many more specialized works on insects. Basic elements in the external morphology of a typical insect are diagrammed in Figure 3.

HEAD

The antennae are usually the most conspicuous structures on the head. In generalized insects, the antennae are usually long and filamentous, the numerous segments showing little differentiation. In most insects, however, the basal segment (scape) is at least a little longer than the others, and in many species the distal segments are much enlarged, forming club-shaped or comb-shaped antennae. In a few orders, such as the Odonata, the antennae are very small to minute.

The mouthparts of the primitive insects were obviously used for chewing, consisting in part of two pairs of plates articulated to the head capsule and controlled by muscles. In several orders, such as the Lepidoptera, however, they have been modified for sucking liquid food (haustellate), the mandibles

and maxillae forming stylets through which the food is drawn. In others, such as the Hemiptera and Diptera, the mouthparts are adapted for both piercing and sucking.

Three types of heads are usually recognized, based on the position of the mouthparts relative to the longitudinal axis of the head. A head is termed hypognathous when its longitudinal axis is vertical and the mouthparts ventral. This is the commonest and probably the most generalized type, occurring among foliage feeders, such as nearly all Orthoptera and Dermaptera, and many Coleoptera. A prognathous head has the longitudinal axis of the head horizontal and the mouthparts anterior. This usually occurs in predaceous species. An opisthognathous head has its axis nearly horizontal but the mouthparts are posterior, the mouthparts arising near the base of the prothoracic legs. This occurs chiefly among some of the Hemiptera.

The two compound eyes are the main visual organs of insects. Each eye is usually divided into numerous visual units (ommatidia), ranging in number from a few to over 20,000. The eyes are usually located dorsally on the sides of the head. The 3 ocelli, each of which comprises a single visual unit, are located on

the front area of the head; the median ocellus lies near the center of the frons, and the other two are positioned slightly more dorsally.

THORAX

The three thoracic segments, termed the prothorax, mesothorax, and metathorax, are very similar in the primitively wingless insects (subclass Apterygota), but in most of the winged species (subclass Pterygota) there is a marked differentiation. The prothorax, which bears no functional wings, is much smaller than the mesothorax and the metathorax. The two latter segments may be different from each other, depending on the relative sizes of their wings. Such insects as the Diptera, in which hind wings are greatly reduced, have a small metathorax. On the other hand, the metathorax of the Coleoptera and Dermaptera, in which the hind wings are the main organs of flight, is much larger than the mesothorax.

The legs typically consist of 5 segments: coxa, the basal segment, followed by the trochanter, femur, tibia, and tarsus. The coxa and trochanter are usually very short, but the other segments are diversely modified. The basic function of the legs was presumably walking (gressorial) or running (cursorial). One or more pairs of the legs are often modified for special functions, such as jumping, swimming, burrowing, or seizing prey. The tarsus is typically further subdivided into 5 segments, the last of which is the pretarsus, usually consisting of a pair of claws.

The wings are the most notable structures of the insects. They develop laterally on the meso- and metathoracic segments in the immature stages (nymphs or larvae) as expansions of the integument and resemble flat pouches with an upper and lower layer (HOLDSWORTH, 1940, 1941, 1942). Spaces (lacunae) containing blood are formed in the wing pads, and the integument near the lacunae produces the veins. In the final stages of development, as the adult insect emerges, the wings are inflated by increased blood pressure in the veins, the cuticle hardens, and the

wings become functional in a surprisingly short time.

The venational patterns of the wings are of much importance in the systematics of most orders of insects, especially in the study of fossil insects, since the cuticle of the wings is usually much better preserved than the soft parts of the insects' bodies. Early attempts to use the venation in systematics were unsuccessful, mainly because there was no generally accepted concept of the evolution and homology of the veins in the several orders. (See, for example, the *Principles of Zoology*, by LOUIS AGASSIZ and A. A. GOULD, 1871, second edition, p. 237–239.) HAGEN (1870) tried in a preliminary way to homologize the wing veins of insects, but REDTENBACHER (1886) followed with the most significant contribution to the subject. He recognized six main veins, termed the costa, subcosta, radius, media, cubitus, and anal vein, a terminology that is still used. He based his homologies in part on the topographic positions of the veins, having noted that some of the veins were on ridges (convex) and others in depressions (concave). In 1895, COMSTOCK and NEEDHAM began their studies of wing venation, using REDTENBACHER's terminology for the main veins (COMSTOCK, 1918). Their homology of the veins, however, was based on the assumption that the venational pattern was determined by the tracheal pattern in the developing wing pads, and this led to some erroneous conclusions (COMSTOCK & NEEDHAM, 1898–1899). Actually, as later shown by HOLDSWORTH (1940, 1941), HENKE (1951), and LESTON (1962), the tracheae do not enter the wing pads until the lacunae have already determined the positions of the veins.

In 1922, LAMEERE, while studying the Carboniferous insects from Commeny, France, was impressed by the alternate convexity and concavity of the main wing veins, and he was convinced that COMSTOCK and NEEDHAM had included two distinct veins in their media and two in their cubitus, one of each being convex and the other concave. He accordingly termed the convex media the *anterior*

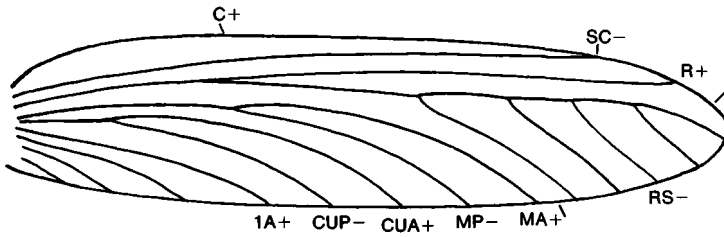


FIG. 4. Fore wing of *Stenodictya* sp., Palaeodictyoptera, Upper Carboniferous of France (Carpenter, new).

media (MA) and the concave media the *posterior media* (MP). Similarly, he termed the convex cubitus the *anterior cubitus* (CUA) and the concave cubitus the *posterior cubitus* (CUP). His studies led a large number of entomologists interested in insect evolution to their own investigations of venation, which ultimately fully supported LAMEERE's conclusions (TILLYARD, 1923d; MARTYNOV, 1924a; SPIETH, 1932; HOLDSWORTH, 1940, 1941). Among such primitive pterygotes as the Ephemeroptera, the convex veins are formed on the dorsal membrane of the wing pouch, and the concave veins on the ventral membrane. Among more specialized insects, at least most of the cuticular material forming the convex veins is produced on the dorsal layer, and most of that of the concave veins on the ventral layer. This results in the alternation of the convex and concave veins when the two layers are fused together.

The venational interpretation and terminology advocated by WOOTTON (1979) are followed here: costa (C, convex), subcosta (SC, concave), radius (R, convex), radial sector (RS, concave), anterior media (MA, con-

vex), posterior media (MP, concave), anterior cubitus (CUA, convex), posterior cubitus (CUP, concave), anal vein (1A, convex) (Figs. 4 and 5). Thickened wings, such as tegmina and elytra, tend to lose the convexity or concavity of the media veins. If both veins of the median system are flat, they are simply designated as the media (M). In addition to these main longitudinal veins, there are often many small veins, such as crossveins, that occur in various parts of the wings, especially the anterior areas; but these are not part of the system of main longitudinal veins discussed above (Fig. 6).

In many insects the hind wings have been secondarily lost, as in the Diptera, or much reduced, as in many Hymenoptera. In some others, the fore wings have been lost, the hind wings being much enlarged, as in the Strepsiptera. In two orders, Siphonaptera and Grylloblattodea, all existing species have lost their wings, and it is noteworthy that at least some secondarily wingless species occur in all existing orders of insects except the Ephemeroptera and the Odonata, both of which are members of the Palaeoptera.

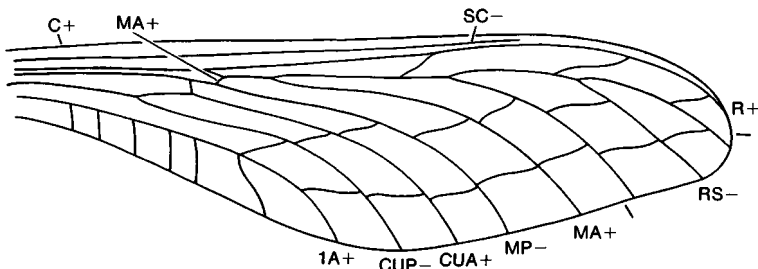


FIG. 5. Fore wing of *Psilotborax* sp., Megasecoptera, Upper Carboniferous of France (Carpenter, 1951).

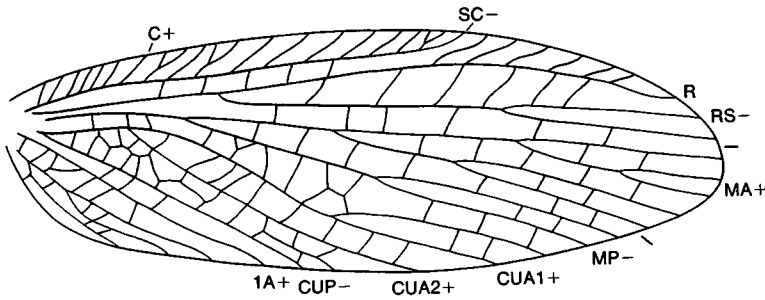


FIG. 6. Fore wing of *Liometopum* sp., Protorthoptera, Permian of Kansas (Carpenter, 1950).

ABDOMEN

Evidence from embryos indicates that the primitive insects had 11 abdominal segments, but in most existing species the 3 terminal segments are commonly much reduced or modified. In some insects, the eleventh segment is represented by a pair of segmented appendages, the cerci, which are very prominent in some orders, as in Ephemeroptera, but much reduced in most others. In a very few species (some Apterygota and Ephemeroptera) a median process or style also arises from the eleventh segment. The female abdomen typically has three pairs of unsegmented processes arising from the eighth and ninth segments and forming an ovipositor. The male abdomen has a pair of claspers, apparently arising from the ninth segment and used for holding the female during mating.

REPRODUCTION AND DEVELOPMENT

Among the most primitive of the living insects, the order Archaeognatha of the subclass Apterygota, the transfer of sperm to the female is indirect, the sperm being deposited in droplets, usually on the ground. These are picked up by the females and inserted into their genital tracts. In all other existing insects the sperm is transferred directly into the female tract, usually after a specific pattern of courtship behavior. The eggs are deposited in environments appropriate for the species concerned, as in soil, on foliage, in water, or,

in the case of parasitic species, on the bodies of host species. Parthenogenesis does occur in several orders. In some of these the unfertilized eggs produce males, as in certain Hymenoptera and Hemiptera (Homoptera), the cycle of parthenogenesis and normal mating being involved with their social behavior (ALEXANDER, 1964; ENGLEMANN, 1970).

The postembryonic development of insects is characterized by a series of cuticular molts. The newly hatched young of the Apterygota closely resemble the adults, except in size, but they molt many times, even after the adult stage has been attained (DELANY, 1961). The immature stages of the Pterygota differ, at least in form, from the adults, and in most species they are strikingly different (Fig. 7).

The great majority of insects are terrestrial in their immature stages, but aquatic species occur in several orders, such as Diptera, Coleoptera, Hemiptera, and all species are aquatic in a few orders, such as Ephemeroptera, Odonata, Trichoptera, and Perlaria. The food of immature forms is very diverse; in some it is similar to that of the adults, but in most species it is very different.

ORIGIN OF INSECTS

Although more than two hundred research papers have been published on this subject, there is still no convincing evidence regarding the ancestral stock that produced the insects. TIEGS and MANTON (1958) have provided a very useful discussion of the subject, and MANTON (1969a, 1969b, 1977, 1979) has summarized her conclusions, after many years

of research, on the evolution of the Arthropoda, including the insects. The present account is a brief synopsis of the diverse views of zoologists and entomologists on the subject.

The most unlikely theories are those of WALTON (1927) and HANDLIRSCH (1908a). WALTON was of the opinion that the insects had evolved from the polychete annelids, and HANDLIRSCH proposed that the pterygotes were directly evolved from the trilobites, the apterygotes having subsequently developed from the pterygotes. MÜLLER (1864), HANSEN (1893), and CARPENTER (1903, 1905) believed that the insects arose from the larvae of decapod crustaceans; and CRAMPTON (1920, 1938) was convinced that they were descended from adult Crustacea allied to the Syncarida. TILLYARD (1930) was of the opinion, from his own research, that they were derived from the Collembola, through the Protura. PACKARD (1873), IMMS (1936), SNODGRASS (1952, 1958), WILLE (1960), and SHAROV (1966b) favored the Symphyla as the ancestors of all the hexapods, including the insects, whereas MANTON (1979) concluded that the Hexapoda and Symphyla could not have shared an immediate, common ancestor, and that the present myriopod and insect faunas represent the isolated descendants of a once widespread, early radiation of terrestrial arthropods. Unfortunately, the present geological record of the insects is no help in this connection, since the earliest insects now known (Late Carboniferous) are true insects, belonging to the subclasses Apterygota and Pterygota.

EVOLUTION OF INSECTA

The present concept of the evolution of insects after the appearance of the Apterygota recognizes two major events: the development of wings and the acquisition of a complicated metamorphosis during the immature stages.

The literature on the origin of wings is nearly as extensive as that on the origin of the insects. The several theories have been proposed and discussed by WIGGLESWORTH

and others (1963), WIGGLESWORTH (1963, 1973, 1976), WOOTTON (1976), KUKALOVÁ-PECK, (1978, 1983) and RASNITSYN (1981). Although there are obvious differences in opinions, the theory generally accepted assumes that the wings were derived from small meso- and metathoracic, paraxonal lobes, which may have originally functioned as sex attractants (ALEXANDER & BROWN, 1963), as thermoregulators (DOUGLAS, 1980), or as stationary aids in aerial migrations of small insects (RASNITSYN, 1981). There is some experimental evidence that such lobes, even without muscular movements, could have had selective survival value. Once formed, the lobes could have been modified to wings. Unfortunately, the geological record of the insects provides no actual record of the evolution of wings, although some species of Paleozoic orders, such as the Palaeodictyoptera, Protorthoptera, and Ephemeroptera, had small prothoracic lobes similar to those postulated above on the meso- and metathoracic segments.

Whatever their origin, the development of wings, which obviously occurred before the beginning of the Late Carboniferous, must be regarded as the most significant event in the evolution of the insects, which so far as we know, were the first animals to develop organs of flight. They provided a unique means of dispersal and of escape from predators. It is not surprising that the winged insects, comprising the subclass Pterygota, have been the predominate insects since the beginning of the Late Carboniferous, at least.

From their first appearance in the Carboniferous, the pterygotes have included two groups of orders, which MARTYNOV (1924) designated the infraclasses Palaeoptera and Neoptera. The first of these includes species that have a somewhat limited articulation of the wings with the thorax, with the result that they are unable to fold their wings back over the abdomen at rest. The evolutionary significance of this was first noted by WOODWORTH (1907) and was much later extensively discussed by MARTYNOV (1924, 1925e, 1938b), CRAMPTON (1924), and

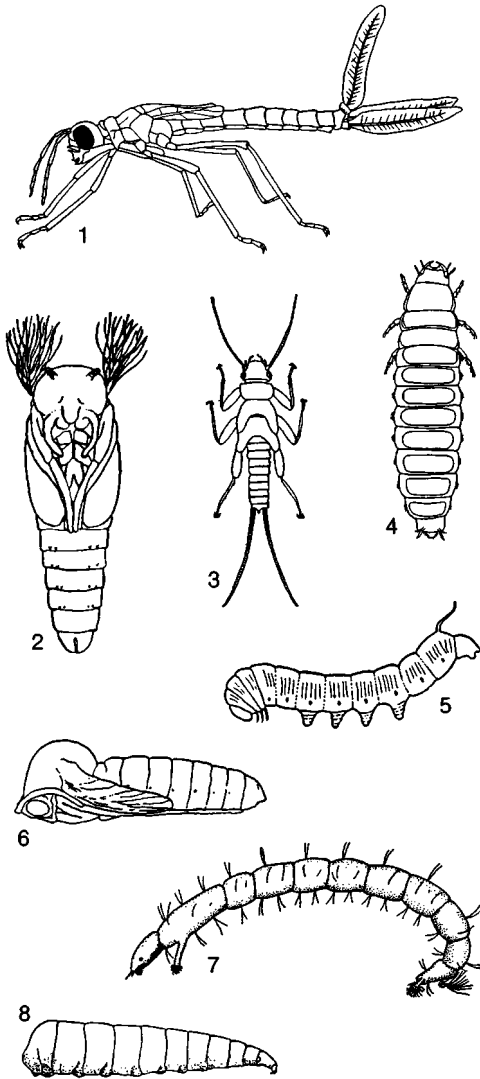


FIG. 7. Immature stages of diverse insects, all Holocene.—1. Nymph of *Lestes* sp., Odonata, lateral view (Essig, 1942).—2. Pupa of *Simulium* sp., Diptera, ventral view (Brues, Melander, & Carpenter, 1954).—3. Nymph of *Perla* sp., Perlaria, dorsal view (Brues, Melander, & Carpenter, 1954).—4. Larva of *Calosoma* sp., Coleoptera, dorsal view (Brues, Melander, & Carpenter, 1954).—5. Larva of *Acherontia* sp., Lepidoptera, lateral view (Brues, Melander, & Carpenter, 1954).—6. Pupa of *Leia* sp., Diptera, lateral view (Brues, Melander, & Carpenter, 1954).—7. Larva of *Tanytus* sp., Diptera, lateral view (Brues, Melander, & Carpenter, 1954).—8. Larva of *Musca* sp., Diptera, lateral view (Brues, Melander, & Carpenter, 1954).

SNODGRASS (1935). Two existing orders, Ephemeroptera and Odonata, belong in the infraclass Palaeoptera along with several extinct orders, including the Palaeodictyoptera, Protodonata, and Megasecoptera. The remaining orders of the Pterygota, which constitute the infraclass Neoptera, have a more complicated wing articulation that allows the wings to be placed back over the abdomen when the insect is at rest. Since these insects are not hindered in their activities by outstretched wings, they are able to crawl among dense foliage, under stones, and even in tunnels in the soil. This was apparently a significant development in the evolution of the insects, since 99 percent of all living species of the Pterygota belong to the infraclass Neoptera. In this connection it is interesting to note that the extinct order Diaphanopteroidea, known only from the Upper Carboniferous and Permian, apparently developed wing folding independently of the Neoptera, as shown by the position of the wings in the fossils. The Diaphanopteroidea, however, have the venational features and the long haustellate mouthparts characteristic of the Palaeodictyoptera and Megasecoptera, both members of the Palaeoptera. The articular plates of their wings are very different from those of the Neoptera (KUKALOVÁ-PECK, 1974a, 1974b).

The more primitive members of the Neoptera are characterized by having the wings develop externally in the immature stages. With few exceptions, the nymphs resemble the adults closely, live in the same environments, and feed on similar foods (Fig. 7, 1, 3). Most of the existing orders of insects belong in this category, termed the division Exopterygota (CARPENTER & BURNHAM, 1985). However, the interrelationships of some of these orders are uncertain, and the exopterygotes may not constitute a monophyletic group.

The development of a complicated metamorphosis in the postembryonic stages apparently occurred within the Neoptera. This involved major changes. The wings, instead of developing externally, are invag-

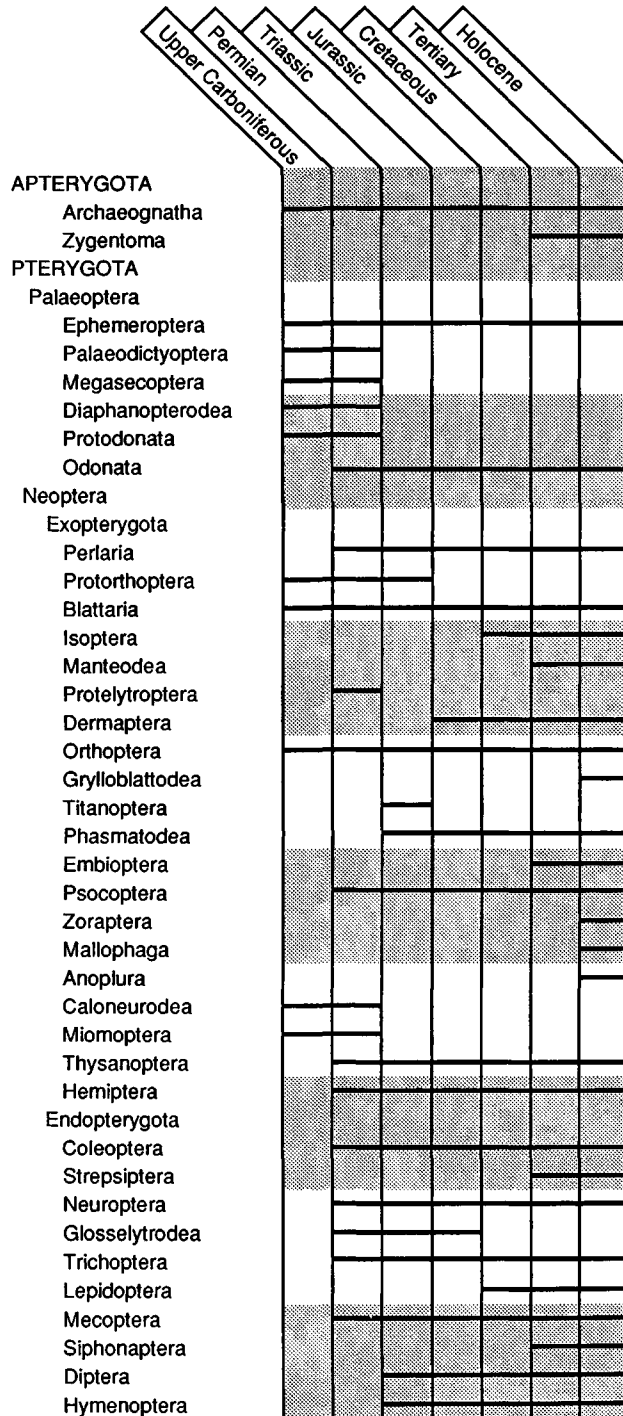


FIG. 9. Geological ranges of orders of insects (Carpenter, new).

knowledge of the geological history of the class is actually very limited. This is apparent from the analysis by MULLER & CAMPBELL (1954) of the relative numbers of known species, both existing and extinct, in all animal phyla, and the percentage of those known as fossils (Fig. 8). For most existing phyla, at least 35 percent of the total species known are extinct. For the insects, however, the number of extinct species in the record is only one percent. Since most of insects are terrestrial, they are ordinarily preserved as fossils only under special environmental conditions.

At this time, insects are unknown in deposits older than the Upper Carboniferous, but the presence of eleven orders in those rocks, including representatives of the Apterygota, Palaeoptera, and Neoptera as well as of four existing orders, indicates that the class existed at least in the Lower Carboniferous and possibly in the Devonian (Fig. 9). Apart from the Carboniferous, the least known of the extinct insect faunas is that of the Cretaceous, a very long and unusually important period in the history of the existing insect families. The Tertiary fossils are the most numerous, but their generic and even family identifications, as recorded, are not always reliable. Many of them were named a century or more ago and placed into existing genera, long before the current concepts of those genera were reached. Restudy of the early type collections by specialists in the families concerned is probably the most urgent need in paleoentomology. There are also many differences of opinion about the systematic positions of some of the extinct genera, especially those based on fragmented specimens. Restudy of additional material is essential, and, until more is known about them, such genera are best assigned to the category of family Uncertain.

In citing the geological ranges of the Cenozoic genera, I have recorded the names of the series, but for the Mesozoic and Paleozoic genera, I have intentionally omitted the series. In many cases the precise ages of the insect deposits within those systems are not defi-

nately known. The one exception to this policy is my use of the series term Upper Carboniferous; this is done because there is at present no record of insects in the Lower Carboniferous. The precise ages of some of the insect-bearing ambers, mostly Tertiary, are not certain. In general I have followed the ages cited by BURLEIGH and WHALLEY (1983). In referring to the insects in the Baltic amber, I have used the term "Baltic," as is usually done, without specifying the several countries in western Europe in which the resin occurs.

The number of existing orders of insects currently recognized by entomologists varies considerably, although the range is usually between twenty-five and thirty. In the present account I recognize twenty-eight, all but four (Grylloblattodea, Zoraptera, Mallophaga, Anoplura) being represented in the fossil record. In contrast, fifty-five extinct orders have been named, most of them from the Carboniferous and Permian. The majority of these extinct orders, however, were based on small fragments or otherwise poorly preserved specimens that have subsequently been placed in other orders or in the category of order unknown. In this treatise I recognize ten extinct orders as valid (Table 1). Additional extinct orders will almost certainly become known as new collections of fossils are studied.

The relationships of the existing orders have been extensively discussed in the literature. In the past there have been many differences of opinion but in recent years the main lines of insect evolution, discussed above, have been generally accepted; and in most respects the more detailed concept of the phylogeny of existing orders proposed by KRISTENSEN (1981) has been widely adopted (Fig. 10). Although the phylogeny of the endopterygote orders is apparently clear, that of the more primitive exopterygotes remains uncertain. The relationships of most of the ten extinct orders seem obvious. Four of these are palaeopterous, five exopterygote, and one endopterygote. Their relationships are discussed below in detail.

TABLE 1. *Extinct Orders of Insects*. Chronological list of extinct orders of insects recorded in the literature. The ordinal names printed in boldface are accepted as valid in this publication; the rest are included in other orders or as indicated.

-
1. **Palaeodictyoptera** GOLDENBERG, 1877
 2. **Megasecoptera** BRONGNIART, 1885a
 3. **Protodonata** BRONGNIART, 1893
 4. Palaeohemiptera HANDLIRSCH, 1904b (Hemiptera)
 5. Protoblattoidea HANDLIRSCH, 1906a (Protorthoptera)
 6. Hadentomoidea HANDLIRSCH, 1906a (Protorthoptera)
 7. Mixotermiotoidea HANDLIRSCH, 1906a (Neoptera uncertain)
 8. Reculoidea HANDLIRSCH, 1906b (Protorthoptera)
 9. Hapalopteroidea HANDLIRSCH, 1906a (Protorthoptera)
 10. Prophemeroidea HANDLIRSCH, 1906b (Ephemeroptera)
 11. Protohemiptera HANDLIRSCH, 1906b (Palaeodictyoptera)
 12. **Protorthoptera** HANDLIRSCH, 1906a
 13. Sypharopteroidea HANDLIRSCH, 1911 (Palaeoptera uncertain)
 14. Protomecoptera TILLYARD, 1917a (Neoptera uncertain)
 15. Paratrichoptera TILLYARD, 1919a (Mecoptera)
 16. Paramecoptera TILLYARD, 1919b (Mecoptera)
 17. Synarmogoidea HANDLIRSCH, 1919b (Palaeodictyoptera)
 18. **Diaphanopteroidea** HANDLIRSCH, 1919b
 19. Aeroplanoptera TILLYARD, 1923b (Phasmatodea)
 20. Protohymenoptera TILLYARD, 1924a (Megasecoptera)
 21. Protocoleoptera TILLYARD, 1924b (Protelytroptera)
 22. **Miomoptera** MARTYNOV, 1927d
 23. Protoperlaria TILLYARD, 1928b (Protorthoptera)
 24. Pruvosticoptera M. D. ZALESSKY, 1928b (Orthoptera)
 25. Permodonata G. M. ZALESSKY, 1931 (Odonata)
 26. **Protelytroptera** TILLYARD, 1931
 27. Archodonata MARTYNOV, 1932 (Palaeodictyoptera)
 28. Meganisoptera MARTYNOV, 1932 (Protodonata)
 29. Hemipsocoptera ZALESSKY, 1937e (Hemiptera)
 30. **Caloneuroidea** HANDLIRSCH, 1937
 31. Cnemidolestoidea HANDLIRSCH, 1937 (Protorthoptera)
 32. Strephocladodea MARTYNOV, 1938b (Protorthoptera)
 33. Paraplecoptera MARTYNOV, 1938b (Protorthoptera)
 34. **Glosselytroidea** MARTYNOV, 1938c
 35. Protocicadida HAUPT, 1941 (Palaeodictyoptera, Protorthoptera)
 36. Protofulgorida HAUPT, 1941 (Protorthoptera, Blattaria)
 37. Archaehymenoptera HAUPT, 1941 (Palaeodictyoptera)
 38. Palaeohymenoptera HAUPT, 1941 (Diaphanopteroidea)
 39. Perielytroidea ZALESSKY, 1943 (Neoptera uncertain)
 40. Anisaxia FORBES, 1943 (Palaeodictyoptera)
 41. Permodictyoptera ZALESSKY, 1944a (Palaeoptera uncertain)
 42. Aphelophlebia PIERCE, 1945 (Ephemeroptera)
 43. Hemiodonata ZALESSKY, 1946a (Palaeodictyoptera)
 44. Breyerida HAUPT, 1949 (Palaeodictyoptera)
 45. Eopalaeodictyoptera LAURENTIAUX, 1952a (Palaeodictyoptera)
 46. Syntonopteroidea LAURENTIAUX, 1953 (Palaeodictyoptera)
 47. Permoneuroidea LAURENTIAUX, 1953 (Palaeoptera uncertain)
 48. Paracoleoptera LAURENTIAUX, 1953 (Neoptera uncertain)
 49. Eubleptidodea LAURENTIAUX, 1953 (Palaeodictyoptera)
 50. Campylopteroidea ROHDENDORF, 1962a (Palaeoptera uncertain)
 51. **Titanoptera** SHAROV, 1968
 52. Dictyoneurida ROHDENDORF, 1977 (Palaeodictyoptera)
 53. Permothemistida SINITSHEKOV, 1980a (Palaeodictyoptera)
 54. Hypoperlida RASNITSYN, 1980f (Neoptera uncertain)
 55. **Blattinopseida** RASNITSYN, 1980f (Neoptera uncertain)
-

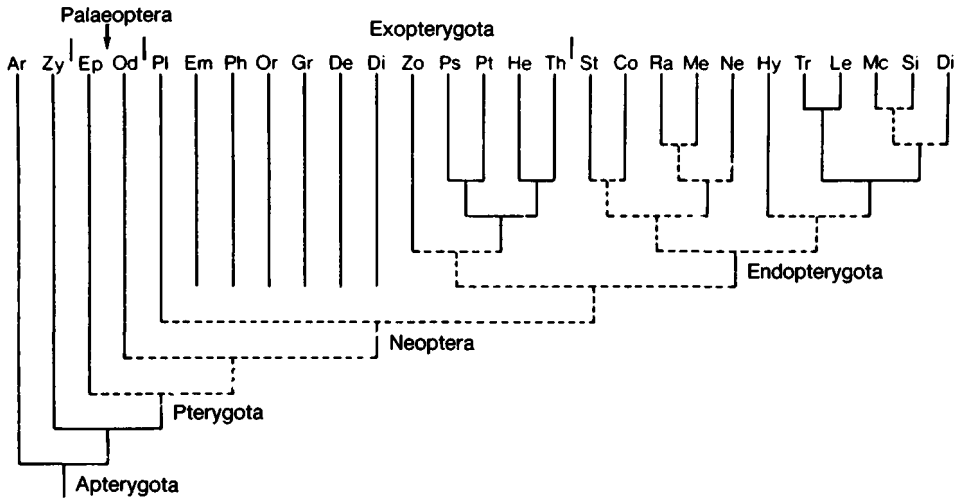


FIG. 10. Phylogeny of existing orders of insects. Higher categories: Apterygota; Pterygota; Palaeoptera; Neoptera; Exopterygota; Endopterygota. Orders: Archaeognatha (Ar); Zygentoma (Zy); Ephemeroptera (Ep); Odonata (Od); Perlaria (Plecoptera) (Pl); Embioptera (Em); Phasmatodea (Ph); Orthoptera (Or); Grylloblattodea (Gr); Dermaptera (De); Dictyoptera (Manteodea, Blattaria, Isoptera) (Di); Zoraptera (Zo); Psocoptera (Ps); Phthiaptera (Mallophaga, Anoplura) (Pt); Hemiptera (He); Thysanoptera (Th); Strepsiptera (St); Coleoptera (Co); Raphidioptera (Ra); Megaloptera (Me); Neuroptera (Ne); Hymenoptera (Hy); Trichoptera (Tr); Lepidoptera (Le); Mecoptera (Mc); Siphonaptera (Si); Diptera (Di) (adapted from Kristensen, 1981).

Subclass APTERYGOTA

Brauer, 1885

[Apterygota BRAUER, 1885, p. 290]

Primitively wingless insects. Antennae usually well developed; mouthparts mandibulate; thoracic segments not united, similar in size and form; ventral styli commonly present on abdominal segments 2 through 9; cerci prominent, typically very long, rarely reduced or absent; median caudal process usually well developed. Reproduction indirect. Ecdysis and molting occurring throughout life. *U. Carb.—Holo.*

Order ARCHAEOGNATHA

Börner, 1904

[Archaeognatha BÖRNER, 1904, p. 523]

Body cylindrical, with a covering of hairs, scales, or both; head usually hypognathous; compound eyes large; mandibles with a single articulation; antennae filiform, usually long and multisegmented, rarely short; maxillary palpi long to very long, with 7 segments

in the Machiloidea (and probably in the Monura); thorax strongly arched dorsally; tarsi with from 1 to 3 segments; abdomen with 11 segments, the last bearing a median caudal process (appendix dorsalis) and in the Machiloidea bearing a pair of cerci, usually somewhat shorter than median caudal process; eighth and ninth abdominal segments of females each with a pair of prominent gonopophyses, combining to form an ovipositor; abdominal segments 2 through 9 with ventral styli. Reproduction indirect, sperm deposited on substrate (often in a spermatophore) by male and then gathered by female, with transference to her spermatheca. Postembryonic development involving only minor external changes; sexual maturity reached after about 10 molts, but ecdyses continuing throughout life, the number of molts often reaching 60.

Nocturnal insects, feeding mainly on algae and vegetable debris, they are fast runners and they can also jump by a downward flexing of the abdomen. *U. Carb.—Holo.*

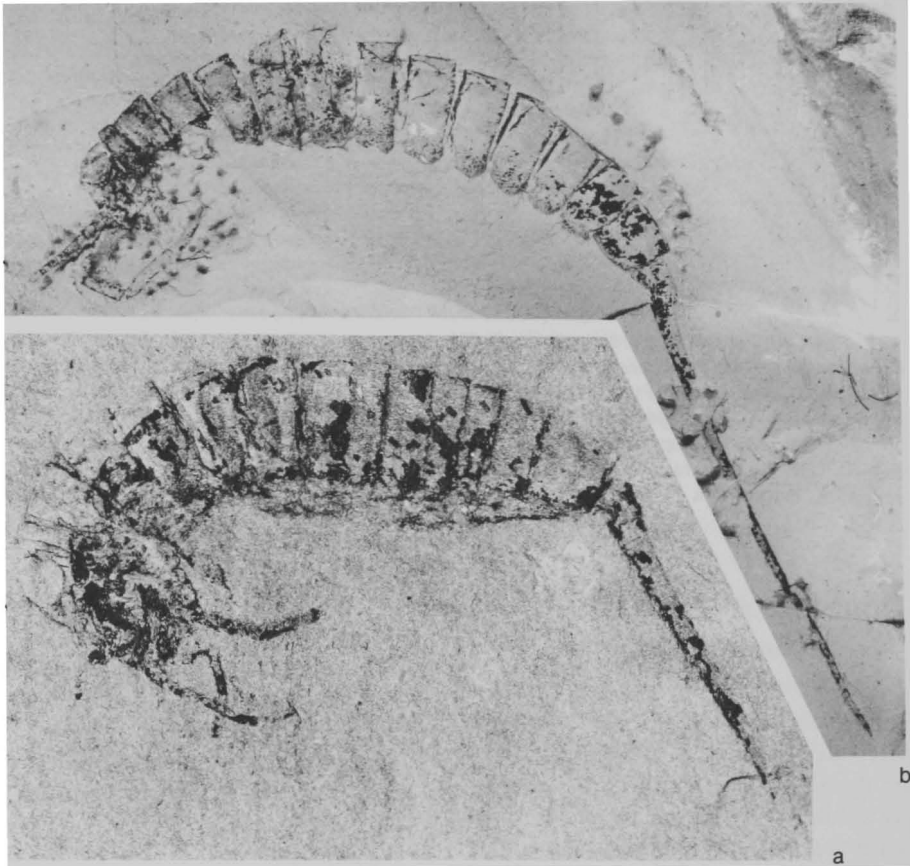
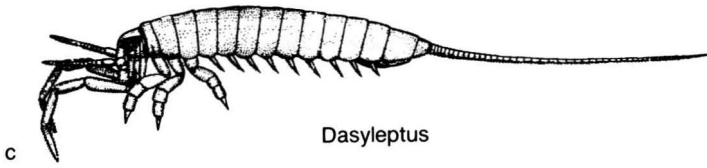


FIG. 11. Dasyleptidae (p. 16–17).

Suborder MONURA Sharov, 1957

[Monura SHAROV, 1957c, p. 796]

Antennae well developed but may be relatively short; maxillary palpi with at least 5 segments (incompletely known); thoracic segments showing little differentiation dorsally from abdominal segments; cerci absent; median caudal process stout and about as long as body; legs relatively short, tarsi unsegmented, bearing only a single claw. *U. Carb.–Perm.*

Family DASYLEPTIDAE Sharov, 1957

[Dasyleptidae SHAROV, 1957c, p. 797]

Antennae short, with only a few segments; ovipositor short, extending only to level of hind margin of eleventh segment. *U. Carb.–Perm.*

Dasyleptus BRONGNIART, 1885b, p. cii [**D. lucasi*; OD]. Compound eyes with upper margin nearly straight and lower margin convex; prothorax about half as long as mesothoracic segment; body with an extensive covering of short hairs. SHAROV, 1957c; ROHDENDORF, 1962a. *U. Carb.*, Europe

(France); *Perm.*, USSR (European RSFSR).—FIG. 11, *a*. **D. lucasi*, U. Carb.; lateral view, $\times 10$ (Carpenter, new).—FIG. 11, *b, c*. *D. brongniarti* SHAROV, *Perm.*; *b*, lateral view, $\times 10$ (Carpenter, new); *c*, reconstruction, lateral view, $\times 7$ (Sharov, 1957c).

Lepidodasyus DURDEN, 1978, p. 1 [**L. sharovi*; OD]. Similar to *Dasyleptus* but with scales apparently present, in addition to hairs, on body and appendages. *Perm.*, USA (Kansas).

Suborder MACHILOIDEA

Handlirsch, 1904

[Machiloidea HANDLIRSCH, 1904c, p. 758]

Antennae long, multisegmented; thoracic segments clearly differentiated dorsally from abdominal segments; tarsi usually with 3 segments (rarely only 2) and bearing 2 claws; cerci present but usually shorter than median caudal process. *Trias.*—*Holo.*

Family MACHILIDAE Grassi, 1888

[Machilidae GRASSI, 1888, p. 582] [=Triassomachilidae SHAROV, 1948, p. 517]

Abdominal sterna large. *Trias.*—*Holo.*

Machilis LATREILLE, 1802, p. 70 [= *Lepismodion* OLFERS, 1907, p. 16 (type, *L. machilops*); *Machilodes* OLFERS, 1907, p. 11 (type, *M. diastatica*)]. GADEAU DE KERVILLE, 1893; SILVESTRI, 1913a; PACLT, 1972. *Oligo.*, Europe (Baltic)—*Holo.*

Praemachilis SILVESTRI, 1905, p. 8. SILVESTRI, 1913a. *Oligo.*, Europe (Baltic)—*Holo.*

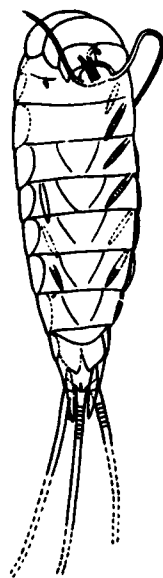
Triassomachilis SHAROV, 1948, p. 517 [**T. uralensis*; OD]. Little-known genus, similar to *Machilis*. PACLT, 1972. *Trias.*, USSR (European RSFSR).—FIG. 12. **T. uralensis*; dorsal view, $\times 7$ (Sharov, 1948).

Order ZYGENTOMA

Börner, 1904

[Zygentoma BÖRNER, 1904, p. 524]

Body distinctly flattened dorsoventrally, with or without a covering of scales; compound eyes small or absent; mandibles with both anterior and posterior articulations; maxillary palpi with 5 segments; cerci and median caudal process present, but cerci usually longer than median process; styli usually present on abdominal segments 2 through 9, rarely absent from segments 8 and 9. Reproduction and postembryonic development much as in Archaeognatha. Nocturnal,



Triassomachilis

FIG. 12. Machilidae (p. 17).

omnivorous apterygotes (silverfish), capable of running with extreme rapidity but without jumping ability of Archaeognatha. *Oligo.*—*Holo.*

Family LEPIDOTRICHIDAE

Silvestri, 1913

[*nom. transl. et correct.* ANDER, 1942, p. 57, ex Lepidotrichinae SILVESTRI, 1913a, p. 51]

Body lacking scales; tarsi with 5 segments. *Oligo.*—*Holo.*

Lepidotrix MENGE, 1854, p. 117, footnote [**L. pilifera*; OD] [= *Lepidotrix* SILVESTRI, 1913a, p. 49, unjustified emend.; *Lepidion* MENGE, 1854, p. 117 (type, *L. pisciculus*); *Klebsia* OLFERS, 1907, p. 8 (type, *K. horrens*); *Micropa* OLFERS, 1907, p. 8 (type, *M. stylifera*)]. Similar to *Tricholepidion* (recent) but lacking ocelli. KOCH & BERENDT, 1854; SILVESTRI, 1913a; WYGODZINSKY, 1961a; PACLT, 1967. *Oligo.*, Europe (Baltic).—FIG. 13. **L. pilifera*; dorsal view of whole insect as preserved, $\times 10$ (Silvestri, 1913a).

Family LEPISMATIDAE

Latreille, 1802

[Lepismatidae LATREILLE, 1802a, p. 70]

Compound eyes present; body covered with scales; tarsi with 3 or 4 segments. *Oligo.*—*Holo.*

Lepisma LINNÉ, 1758, p. 608. *Holo.*

Allocrotelsa SILVESTRI, 1935, p. 307, *nom. subst.*
pro Lampropholis MENGE, 1854, p. 117, *non*
 FITZINGER, 1843. SILVESTRI, 1913a; COCKERELL,
 1917g; WYGODZINSKY, 1961b; PAULT, 1967.
Oligo., Europe (Baltic); *Mio.*, Burma-*Holo.*

Subclass PTERYGOTA

Brauer, 1885

[Pterygota BRAUER, 1885, p. 290]

Wings present or secondarily absent. Antennae usually long, rarely short; mouth-parts mandibulate or haustellate; prothorax much smaller than the meso- or metathorax, the latter two united to form the pterothorax; abdominal segments 2 through 9 without styli; cerci prominent in more primitive orders but much reduced or absent in others; median caudal process well developed in Ephemeroptera but absent in other orders. Reproduction direct. Ecdysis and molting occurring only in nymphal or larval stages. *U. Carb.-Holo.*

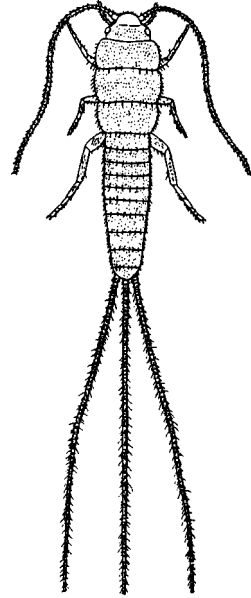
Infraclass PALAEOPTERA

Martynov, 1923

[Palaeoptera MARTYNOV, 1923, p. 89]

Wings articulated to thorax by sclerotized plates (axillaries) fused to bases of main veins; flexor muscles absent; wings with main veins forming a complete alternation of convexities and concavities; vein MA distinctly convex; cerci commonly well developed and long; median caudal process present only in Ephemeroptera. Nymphs diversely formed, some aquatic; wings developing in cuticular sheaths, much as in exopterygote Neoptera. Subimaginal stage or stages present in some orders. *U. Carb.-Holo.*

This infraclass, now represented by only two orders (Ephemeroptera and Odonata), was apparently much more diverse in the Paleozoic. The fusion of the axillary sclerites to the bases of the main veins and the absence of wing-flexing muscles prevent the placing of the wings back along the abdomen at rest. Consequently, complete palaeopterous fossils, with wings and body, are nearly always



Lepidotrix

FIG. 13. Lepidotrichidae (p. 17).

preserved with the wings outstretched (see Figs. 26,3c and 39). The exceptions to this are of unusual interest. Members of the extinct order Diaphanopterodea are consistently preserved with the wings resting back along the abdomen. The structural mechanisms that make this possible are not known, but the wing axillaries were apparently not arranged as they are in the Neoptera (KUKALOVÁ-PECK, 1975), indicating that the wing flexing in the Diaphanopterodea was developed independently of that in the Neoptera. The known members of the Triassic odonate suborder Triadophlebiomorpha are likewise preserved with their wings placed along the abdomen, but the wing axillaries are unknown (PRITYKINA, 1981). In this connection it is noteworthy that the members of the existing odonate suborder Zygoptera also hold their wings along the abdomen at rest. However, this posture has been achieved by tilting of the pterothorax at an obtuse angle with reference to the abdomen.

Six orders are considered to belong to the Palaeoptera: Palaeodictyoptera, Megasecop-

tera, Diaphanopteroidea, Ephemeroptera, Protodonata, and Odonata. With the single exception of the Odonata, all of these are known as far back as the Late Carboniferous.

Order EPHEMEROPTERA

Hyatt & Arms, 1890

[Ephemeroptera HYATT & ARMS, 1890, p. 69] [=Protephemeroidea HANDLIRSCH, 1906b, p. 311; Aphelophlebia PIERCE, 1945, p. 4] [Several names have been proposed for this order. Ephemeroptera is the term consistently used now by specialists in the order.]

Delicate insects with short, filiform antennae; mouthparts vestigial in existing families, mandibulate and functional in Paleozoic families; compound eyes large, 3 ocelli present; abdomen slender, terminating in a pair of long, segmented cerci and usually with a long, median caudal process; legs usually weak in recent species, the mesothoracic and metathoracic pairs often much reduced, but all legs well developed in Paleozoic families; wings very delicate, with a complete set of all main veins in addition to intercalary veins (indicated by an I prefix) and crossveins; base of costal area supported in some families by a stout crossvein or a series of crossveins (costal brace; see Figs. 14,4a and 15,a); in all recent and Tertiary species, as well as those from the Mesozoic, hind wings much smaller than fore pair and in some genera completely absent; in known Paleozoic species, pairs of wings similar in size and venation; digestive tract modified to form aerostatic organ; reproductive ducts paired in both sexes. Nymphs aquatic, occurring in ponds and streams, usually with at least 7 pairs of abdominal tracheal gills; cerci and median caudal process present; mostly herbivorous. Postembryonic development slow, with 20 or more ecdyses and a single molt from winged subimago to imago. *U. Carb.—Holo.*

The Ephemeroptera is a relatively small order of about 2,000 species. Although basically primitive, the recent members are highly adapted to living in aquatic environments in the nymphal stages and to a very brief imaginal life. The nymphal gills are unusually large compared with those of other aquatic insects

and are capable of rapid movements, aiding the circulation of water. Nymphal development is slow, taking at least a few months and commonly as long as three years. In contrast, most imagoes live for only a few hours to a few days. The process of mating is hastened by swarming.

The earliest record of the Ephemeroptera is a single imago of *Triplosoba pulchella* (BRONGNIART) from the Upper Carboniferous of Commentry, France, but representatives of five extinct families, including nymphs as well as adults, are known from the Permian. The peak of diversity appears to have been reached in the Jurassic, from which nine families have been obtained, including the existing families Siphonuridae, Leptophlebiidae, Palingeniidae, Behningiidae, and possibly the Ephemereidae. So far as known, the imagoes of all the Permian species had fully developed mouthparts with functional, dentate mandibles, normally developed legs, and similar fore and hind wings. These imagoes appear to be the most primitive of the known pterygote insects. The nymphs, however, were apparently as well adapted to an aquatic life as those now existing.

The classification of the Ephemeroptera has been discussed by several specialists in the order in recent years (TSHERNOVA, 1970; LANDA, 1979; McCAFFERTY & EDMUNDS, 1979; RIEK, 1979), mainly with reference to the existing families. There seems to be general agreement that division of the order into the suborders Permopteroptera and Euplectoptera, separating the Permian families from the later ones, as proposed by TILLYARD (1932b), is unsatisfactory. In the following account the sequence of families follows that of McCAFFERTY and EDMUNDS (1979) and TSHERNOVA (1970).

Family TRIPLOSOBIDAE

Handlirsch, 1906

[Triplosobidae HANDLIRSCH, 1906b, p. 312]

Fore and hind wings apparently similar in form and venation; crossveins numerous; costal brace apparently absent; vein SC extending to wing apex; RS arising directly from

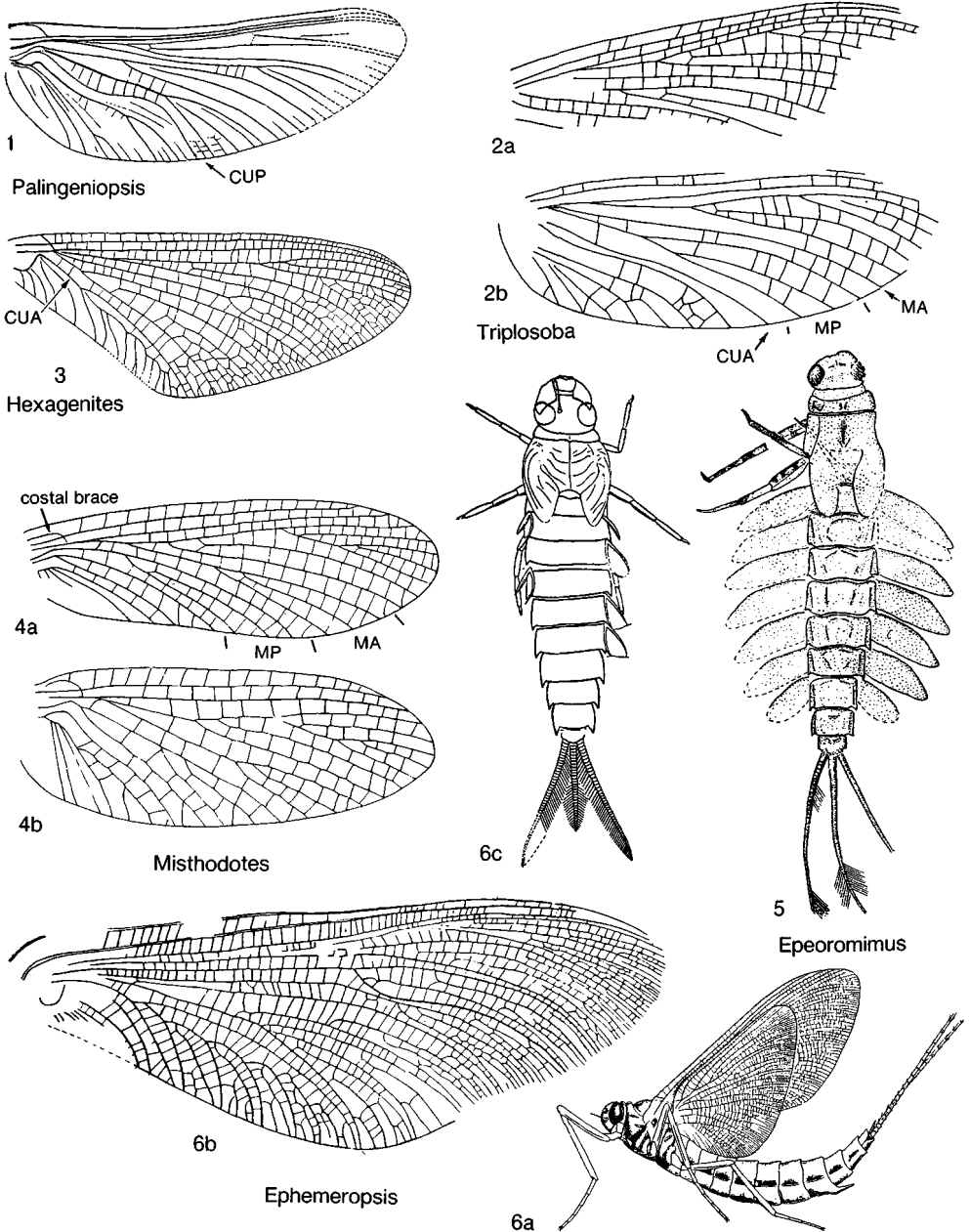


FIG. 14. Triplosobidae, Misthodotidae, Palingeniopsidae, Hexagenitidae, and Epeoromimidae (p. 20–24).

R, free from MA and including 2 intercalary veins; abdomen slender, with prominent cerci and a median caudal process. *U. Carb.*

Triplosoba HANDLIRSCH, 1906b, p. 312, *nom. subst.* *pro Blanchardia* BRONGNIART, 1893, p. 325, *non*

CASTELNAU, 1875 [*Blanchardia pulchella* BRONGNIART, 1893, p. 325; OD]. MA and CUA unbranched in both wings; MP branched. CARPENTER, 1963c. *U. Carb.*, Europe (France).— FIG. 14.2. **T. pulchella* (BRONGNIART); a, fore and b, hind wings, $\times 2.5$ (Carpenter, new).

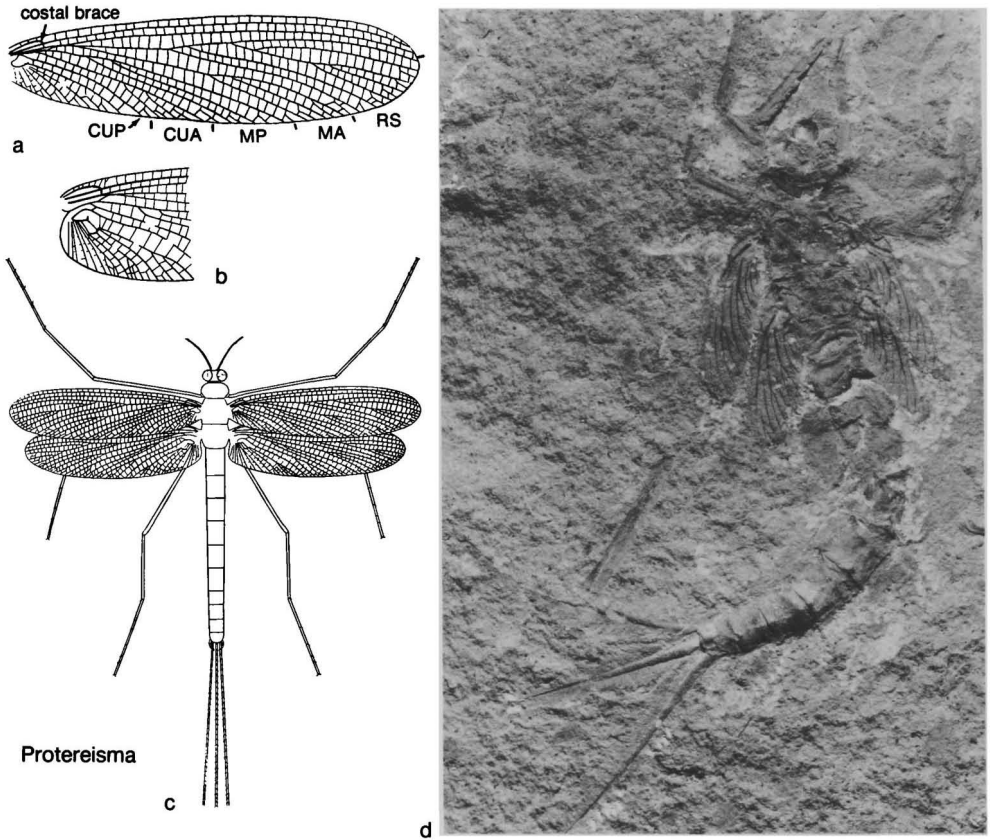


FIG. 15. Prottereismatidae (p. 21–22).

Family PROTTEREISMATIDAE Lameere, 1917

[*nom. correct.* TILLYARD, 1932b, *ex* Prottereismidae LAMEERE, 1917a, p. 45] [=Kukalovidae DEMOULIN, 1970b, p. 6]

Adults moderate to large in size. Wings elongate-oval; fore and hind wings similar in form and venation, hind pair only slightly shorter; crossveins numerous; costal brace strongly developed in both wings (Fig. 15,*a*); vein SC extending almost to wing apex; RS coalesced with MA immediately after its origin, and including 3 intercalary veins; MP and CUA each with a single triad; antennae short but longer than in existing mayflies; mandibles sclerotized and dentate; compound eyes large; legs very long and slender, with 5 tarsal segments; cerci and median caudal process elongate; males with prominent claspers. Nymphs with well-developed man-

dibles; legs subequal, with 5 tarsal segments; cerci and median caudal process well developed; abdomen with 9 pairs of tracheal gills; wing pads independent of each other, attached to thorax only along equivalent of the articular area of adult wings, projecting obliquely.
Perm.

Prottereisma SELLARDS, 1907, p. 347 [**P. permianum*; OD] [=*Protechma* SELLARDS, 1907, p. 349 (type, *P. acuminatum*); *Prodromus* SELLARDS, 1907, p. 349 (type, *P. rectus*); *Bantiska* SELLARDS, 1907, p. 349 (type, *B. elongata*); *Pinctodia* SELLARDS, 1907, p. 352 (type, *P. curia*); *Recter* SELLARDS, 1909, p. 151, *pro* *Rekter* SELLARDS, 1907, p. 349 (type, *R. arcuatus*); *Esca* SELLARDS, 1909, p. 151 (type, *Therates planus* SELLARDS, 1907, p. 354); *Mecus* SELLARDS, 1909, p. 151 (type, *Scopus gracilis* SELLARDS, 1907, p. 352); *Loxophlebia* MARTYNOV, 1928b, p. 8, *non* BUTLER, 1876 (type, *L. apicalis*)]. MP forked more deeply than RS. TILLYARD, 1932b; CAR-

PENTER, 1933a, 1979; ROHDENDORF, 1962a; GUTHÖRL, 1965; DEMOULIN, 1970b. *Perm.*, USA (Kansas, Oklahoma), ?Europe (Germany).—FIG. 15, *a-c*. **P. permianum*, Kansas; *a*, fore wing, *b*, base of hind wing, both $\times 3.5$; *c*, reconstruction, dorsal view, $\times 1.5$ (all Carpenter, 1933a).—FIG. 15, *d*. *P. americanum* DEMOULIN, Oklahoma; photograph of nymph, dorsal view, $\times 5$ (Carpenter, new).

Family MISTHODOTIDAE Tillyard, 1932

[Misthodotidae TILLYARD, 1932b, p. 260] [=Eudoteridae DEMOULIN, 1954c, p. 561]

Adults small to moderate in size. Wings broadly oval; fore and hind wings similar in venation but hind wings distinctly broader; vein CUA unbranched, lacking a triad; crossveins less numerous than in Protereismatidae; legs of moderate length; tarsi with 4 segments; cerci and median caudal process very long. Nymphs with 9 pairs of tracheal gills. *Perm.*

Misthodotes SELLARDS, 1909, p. 151, *nom. subst. pro Dromeus* SELLARDS, 1907, p. 351, *non* REICHE, 1854 [**Dromeus obtusus* SELLARDS, 1907, p. 351; OD] [=Eudoter TILLYARD, 1936, p. 443 (type, *E. delicatulus*)]. Posterior margin of hind wing strongly convex. LAMEERE, 1917a; TILLYARD, 1932b; CARPENTER, 1933a, 1979; DEMOULIN, 1954c; TSHERNOVA, 1965. *Perm.*, USA (Kansas, Oklahoma), USSR (Asian RSFSR).—FIG. 14, *4a*. **M. obtusus* (SELLARDS), Kansas; fore wing, $\times 5.5$ (Carpenter, 1933a).—FIG. 14, *4b*. *M. edmundsi* CARPENTER, Oklahoma; hind wing, $\times 5.5$ (Carpenter, 1979).

Family JARMILIDAE Demoulin, 1970

[Jarmilidae DEMOULIN, 1970b, p. 7]

Little-known family (nymph only); mesothorax and metathorax nearly twice as broad as long; mesonotum larger than metanotum; tracheal gills narrow and elongate. *Perm.*

Jarmila DEMOULIN, 1970b, p. 7 [**J. elongata*; OD]. Diagnostic characters same as for family. *Perm.*, Europe (Czechoslovakia).

Family OBORIPHEBIIDAE Hubbard & Kukalová-Peck, 1980

[Oboriphebiidae HUBBARD & KUKALOVÁ-PECK, 1980, p. 29]

Little-known family (nymph only); mesothorax slightly larger than metathorax; wing pads divergent. *Perm.*

Oboriphebia HUBBARD & KUKALOVÁ-PECK, 1980, p. 30 [**O. tertia*; OD]. Diagnostic characters same as for family. *Perm.*, Europe (Czechoslovakia).

Family PALINGENIOPSIDAE Martynov, 1938

[Palingeniopsidae MARTYNOV, 1938b, p. 35]

Little-known family, based on hind wing only; vein CUP strongly sigmoidal. *Perm.*

Palingeniopsis MARTYNOV, 1932, p. 10 [**P. praecox*; OD]. Little-known genus; intercalary veins incompletely known. MARTYNOV, 1938b; ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 14, *1*. **P. praecox*; hind wing, $\times 1.7$ (Martynov, 1932).

Family MESEPHEMERIDAE Lameere, 1917

[Mesephemeridae LAMEERE, 1917a, p. 47]

Little-known family. Fore and hind wings apparently similar in size and venation; inner and outer margins of fore wing forming a smooth curve; costal brace apparently absent. *Jur.*

Mesephemera HANDLIRSCH, 1906b, p. 600 [**Tineites lithophilus* GERMAR, 1842, p. 88; SD CARPENTER, herein]. Little-known genus; hind wings apparently at least as broad as fore wings. CARPENTER, 1932a; DEMOULIN, 1955b; TSHERNOVA, 1970. *Jur.*, Europe (Germany).

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* DEMOULIN, 1954c, p. 566, *ex* Hexagenitinae LAMEERE, 1917a, p. 74] [=Paedephemeridae LAMEERE, 1917a, p. 49; Ephemeropsidae COCKERELL, 1927a, p. 1; Stenodicranidae DEMOULIN, 1954c, p. 567]

Mayflies of moderate to very large size. Fore wing triangular owing to well-developed tornus of hind margin; vein CUA of fore wing forked, one of its branches with a series of loop-shaped veinlets leading to wing margin. Nymphs with 7 pairs of gills along sides of abdomen. *Jur.—Cret.*

Hexagenites SCUDDER, 1880, p. 6 [**H. weyenberghi*; OD; =*Ephemera cellulosa* HAGEN, 1862, p. 115] [=Paedephemera HANDLIRSCH, 1906b, p. 601 (type, *Ephemera multivenosa* OPPENHEIM, 1888, p. 225)]. Adults of moderate size. Fore wing about twice as long as wide; MA1 and MA2

- forming a symmetrical fork; few crossveins. CARPENTER, 1932a; TSHERNOVA, 1961; DEMOULIN, 1970c; TSHERNOVA & SINITSHENKOVA, 1974. *Jur.*. Europe (Germany).—FIG. 14,3. **H. weyenberghi*; fore wing, $\times 3.5$ (Carpenter, 1932a).
- Ephemeropsis** EICHWALD, 1864, p. 21 [**E. tristalis*; OD] [= *Phacelobranchnus* HANDLIRSCH, 1906b, p. 604 (type, *P. braueri*)]. Adults very large. Fore wing more than 2.5 times as long as its width; hind wing more than half as long as fore wing. PING, 1928; UENO, 1935; DEMOULIN, 1954a, 1956d; MESHKOVA, 1961; TSHERNOVA, 1961; SINITSHENKOVA, 1975. *Cret.*, USSR (Asian RSFSR).—FIG. 14,6. **E. tristalis*; *a.* restoration, $\times 0.8$ (Tshernova, 1961); *b.* fore wing, $\times 2.0$ (Tshernova & Sinitshenkova, 1974); *c.* nymph, restoration, dorsal view, $\times 2.0$ (Meshkova, 1961).
- Hexameropsis** TSHERNOVA & SINITSHENKOVA, 1974, p. 131 [**H. selini*; OD]. Similar to *Hexagenites*, but MA1 and MA2 forming asymmetrical fork; hind wing less than half length of fore wing. SINITSHENKOVA, 1975. *Cret.*, USSR (Ukraine), Africa (Algeria).

Family SIPHLONURIDAE

Banks, 1900

[Siphonuridae BANKS, 1900, p. 246]

Fore wings narrow and triangular; hind wings relatively large; crossveins numerous in both wings; vein CUA of fore wing connected to hind margin by several veinlets; forks of MP and CUA almost symmetrical. *Jur.*—*Holo.*

- Siphonurus** EATON, 1868, p. 89. DEMOULIN, 1968c. *Oligo.*. Europe (Baltic)—*Holo.*
- Baltameletus** DEMOULIN, 1968c, p. 238 [**B. oligocaenicus*; OD]. Little-known genus, based on subimago; apparently related to *Ameletus* (recent). *Oligo.*. Europe (Baltic).
- Balticophlebia** DEMOULIN, 1968c, p. 237 [**B. benigni*; OD]. Based on female imago; similar to *Chaquibua* (recent) but with hind wings more elongate. *Oligo.*. Europe (Baltic).
- Cronicus** EATON, 1871, p. 133 [**Baetis anomala* PICTET in PICTET & HAGEN, 1856, p. 75; OD]. Gonostyle of male subimago with 5 segments, the third about twice as long as the second and as long as segments 4 and 5 combined. DEMOULIN, 1955a, 1968c, 1974. *Oligo.*. Europe (Baltic).—FIG. 16,2. **C. anomalus* (PICTET); fore and hind wings and part of body, dorsal view, $\times 3.5$ (Demoulin, 1968c).
- Isonychia** EATON, 1871, p. 33. LEWIS, 1977b. *Oligo.*. USA (Montana)—*Holo.*
- Oligisca** DEMOULIN, 1970c, p. 6 [**Paedephemera schuertschlagerei* HANDLIRSCH, 1906b, p. 602;

- OD]. Little-known genus, based on poorly preserved wing; similar to *Stackelbergisca*, but branches of CUA simple; MP with long branches. *Jur.*, Europe (Germany).
- Proameletus** SINITSHENKOVA, 1976, p. 86 [**P. caudata*; OD]. Imago: fore wing similar to that of *Oligisca* but with an intercalary vein between RS1 and RS2; median caudal process long, with 10 segments. Nymph: legs long and slender; 7 pairs of oval gills along abdomen. *Cret.*, USSR (Asian RSFSR).
- Siphurites** COCKERELL, 1923d, p. 170 [**S. explanatus*; OD]. Little-known genus, apparently related to *Murphyella* (recent). DEMOULIN, 1970d, 1974. *Oligo.*. USA (Colorado).
- Stackelbergisca** TSHERNOVA, 1967, p. 323 [**S. sibirica*; OD]. Imago: fore wing triangular; anal margin long; CUA straight and connected to wing margin by a series of veinlets; CUP slightly curved. Nymph: with 7 pairs of foliate gills along sides of abdomen. DEMOULIN, 1968a. *Jur.*, USSR (Asian RSFSR).—FIG. 16,3. **S. sibirica*; *a.* fore wing, *b.* nymph, dorsal view, both $\times 3.5$ (Tshernova, 1967).

Family AMETROPODIDAE

Bengtsson, 1913

[Ametropodidae BENGTSSON, 1913, p. 305]

Fore tarsi of male very long; hind tarsi with 4 segments; basal tarsal segment fused to tibia; fore wing with only 1 or 2 unattached cubital intercalaries; vein 1A of fore wing connected to hind margin by several veinlets. *Oligo.*—*Holo.*

- Ametropus** ALBARDA, 1878, p. 129. *Holo.*
- Brevitibia** DEMOULIN, 1968c, p. 245 [**B. intricans*; OD]. Similar to *Ametropus* (recent), with shorter median caudal process. *Oligo.*. Europe (Baltic).
- Metretopus** EATON, 1901, p. 253. DEMOULIN, 1968c. *Oligo.*. Europe (Baltic)—*Holo.*
- Siphloplecton** CLEMENS, 1915, p. 245. DEMOULIN, 1968c, 1970a. *Oligo.*. Europe (Baltic)—*Holo.*

Family BAETIDAE Leach, 1815

[Baetidae LEACH, 1815, p. 137]

Eyes of males divided; fore wing with veins IMA, MA2, IMP, and MP2 detached basally; hind wing reduced or absent; median caudal process absent. *Plio.*—*Holo.*

- Baetis** LEACH, 1815, p. 137. *Holo.*
- Cleon** LEACH, 1815, p. 137. [Generic assignment of fossil (nymph) doubtful.] RIEK, 1954b. *Plio.*. Australia (New South Wales)—*Holo.*

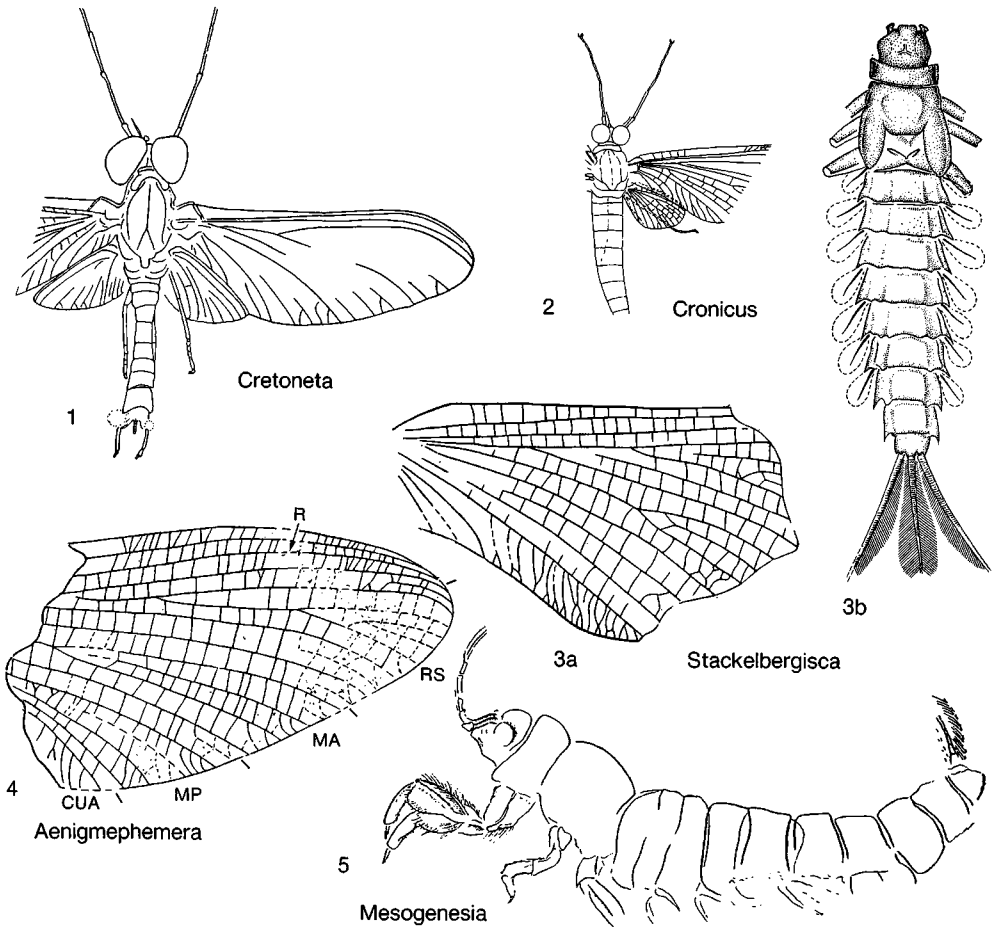


FIG. 16. Siphonuridae, Aenigmephemeridae, Leptophlebiidae, and Palingeniidae (p. 23–26).

Family EPEOROMIMIDAE
Tshernova, 1969

[Epeoromimidae Tshernova, 1969, p. 154]

Known only from nymphs, apparently related to the Heptageniidae. Head and thorax strongly concave; gill plates long and foliaceous; abdomen elongate; legs thin and short; abdomen 3 times as long as thorax; fifth abdominal segment 2 or 3 times as wide as long; 7 pairs of gill plates along sides of abdomen. *Jur.–Cret.*

Epeoromimus Tshernova, 1969, p. 155 [*E. kuzlauskasi*; OD]. Anterior margin of pronotum strongly concave; gill plates long and foliaceous. Sinitschenkova, 1976. *Jur.–Cret.*, USSR (Asian RSFSR).—FIG. 14, 5. **E. kuzlauskasi*; dorsal view of nymph, $\times 5.5$ (Tshernova, 1969).

Family HEPTAGENIIDAE
Needham, 1901

[Heptageniidae Needham in Needham & Betten, 1901, p. 419]

Cubitus of fore wing with 2 pairs of intercalary veins; MP1 and MP2 forming symmetrical fork; hind tarsi with 5 segments; median caudal process absent. *Oligo.–Holo.*

Heptagenia Walsh, 1863, p. 197. Demoulin, 1968c, 1970a. *Oligo.*, Europe (Baltic)–*Holo.*

Cinygma Eaton, 1885, p. 236. [Generic assignment of fossil doubtful.] Demoulin, 1968c. *Oligo.*, Europe (Baltic)–*Holo.*

Electrogenia Demoulin, 1956a, p. 95 [*E. dewalschei*; OD]. MA of hind wing unbranched; crossveins dense over fore wing; third tarsi with first segment longer than second; gonostyle with 4 segments. *Oligo.*, Europe (Baltic).

Miocoenogenia Tshernova, 1962, p. 943 [**M. gorbunovi*; OD]. Little-known genus, nymph only; similar to *Heptagenia* but with relatively small head; pronotum broad, with anterior angles projecting forward. *Mio.*, USSR (Asian RSFSR).

Rhithrogena Eaton, 1881, p. 23. DEMOULIN, 1968c. *Oligo.*, Europe (Baltic)—*Holo.*

Succinogenia DEMOULIN, 1965, p. 151 [**S. larssoni*; OD]. Little-known genus, based on young nymph. *Oligo.*, Europe (Baltic).

Family AENIGMEPHEMERIDAE Tshernova, 1968

[Aenigmephemeridae Tshernova, 1968, p. 23]

Apparently related to the Heptageniidae. Fore wing narrow, inner and outer margins forming a smooth curve; longitudinal veins straight, almost equidistant from each other; fork of MA very deep. *Jur.*

Aenigmephemera Tshernova, 1968, p. 23 [**A. demoulini*; OD]. Fore wing with forking of MA at level of origin of RS; 5 longitudinal veins between MA2 and CUA; crossveins numerous. DEMOULIN, 1969a. *Jur.*, USSR (Kazakh).—FIG. 16.4. **A. demoulini*; fore wing, $\times 3$ (Tshernova, 1968).

Family LEPTOPHLEBIIDAE Banks, 1900

[Leptophlebiidae Banks, 1900, p. 246]

Eyes of male divided; 2 to 4 long intercalary veins between veins CUA and CUP; CUP usually strongly curved; median caudal process present. *Jur.*—*Holo.*

Leptophlebia Westwood, 1840, p. 31. *Holo.*

Atalophlebia Eaton, 1881, p. 193. Etheridge & Olliff, 1890; Riek, 1954b. *Plio.*, Australia (New South Wales)—*Holo.*

Blasturophlebia DEMOULIN, 1968c, p. 268 [**B. birsuta*; OD]. Little-known genus, based on a subimaginal exuvium of a male. [Family assignment doubtful.] HUBBARD & SAVAGE, 1981. *Oligo.*, Europe (Baltic).

Cretoneta Tshernova, 1971, p. 614 [**C. zherichini*; OD]. Fore wing with MA about half length of stem M; base of MP2 connected to MP1; cubital area very narrow; eyes of male not divided. HUBBARD & SAVAGE, 1981. *Cret.*, USSR (Asian RSFSR).—FIG. 16.1. **C. zherichini*; dorsal view, male, $\times 10$ (Tshernova, 1971).

Lepismophlebia DEMOULIN, 1968b, p. 7 [**Lepisma platymera* Scudder, 1890, p. 102; OD]. Little-

known nymph. [Family assignment doubtful.] DEMOULIN, 1956b. *Oligo.*, USA (Colorado).

Mesoneta Brauer, Redtenbacher, & Ganglbauer, 1889, p. 4 [**M. antiqua*; OD]. Little-known genus, nymph only. Head small, thorax very short; femur longer than tibia; 7 pairs of tracheal gills along sides of abdomen. Tshernova, 1971; Sinitsheknova, 1976. *Jur.*—*Cret.*, USSR (Asian RSFSR).

Paraleptophlebia Lestage, 1917, p. 340 [= *Oligophlebia* DEMOULIN, 1965, p. 146 (type, *O. callicarys*)]. DEMOULIN, 1968c, 1970a; Hubbard & Savage, 1981. *Oligo.*, Europe (Baltic)—*Holo.*

Xenophlebia DEMOULIN, 1968c, p. 267 [**X. aenigmatica*; OD]. Only male adult known. Forking of MA and MP in fore wing symmetrical; median caudal process absent. DEMOULIN, 1970a; Hubbard & Savage, 1981. *Oligo.*, Europe (Baltic).

Family EPHEMERELLIDAE Klapálek, 1909

[Ephemerellidae Klapálek, 1909, p. 13]

Fore wing with 1 or 2 long intercalary veins between veins MP and CUA and usually with detached marginal intercalary veins; crossveins usually absent or very weak. *Jur.*—*Holo.*

Ephemerella Walsh, 1862, p. 377. *Holo.*

Philolimnias Hong, 1979, p. 336 [**P. sinica*; OD]. Similar to *Ephemerella* (recent), but costal area narrower and CUA1 with 5 branches. *Eoc.*, China (Liaoning).

Turfanerella DEMOULIN, 1954a, p. 324 [**Ephemeropsis tingi* Ping, 1935, p. 107; OD]. Little-known genus, based on nymph. *Jur.*, China (Sichiang).

Family BEHNINGIIDAE Motas & Bocasco, 1938

[Behningiidae Motas & Bocasco, 1938, p. 25]

Legs of adults much reduced; forelegs of nymphs resembling palpi; middle and hind legs modified to protect the tracheal gills; gills ventral. *Jur.*—*Holo.*

Behningia Lestage, 1930, p. 436. *Holo.*

Archaeobehningia Tshernova, 1977, p. 94 [**A. edmundsi*; OD]. Little-known genus, based on nymph. Similar to *Protobehningia* (recent) but with claws present on all tarsi, and forelegs not functionally part of trophi. *Jur.*, USSR (Asian RSFSR).

Family NEOEPHEMERIDAE

Needham, 1935

[Neophemeridae NEEDHAM in NEEDHAM, TRAYER, & HSU, 1935, p. 288]

Adults resembling those of ephemerids, but crossveins in basal half of fore wing weak or atrophied; costal angle of hind wing acute. Nymphs as in caenids but gills operculate, fused medially. *Oligo.-Holo.*

Neophemera McDUNNOUGH, 1925, p. 168. *Holo.*
Potamanthellus LESTAGE, 1930, p. 120. LEWIS, 1977b. *Oligo.*, USA (Montana)—*Holo.*

Family EPHEMERIDAE Leach, 1815

[Ephemeridae LEACH, 1815, p. 137]

Legs well developed; veins MP2 and CUA abruptly diverging from MP1 basally; 1A unbranched but connected to hind margin of wing by at least 3 veinlets. *Oligo.-Holo.*

Ephemera LINNÉ, 1758, p. 546. COCKERELL, 1908e. *Oligo.*, USA (Colorado)—*Holo.*

Family POLYMITARCIDAE

Banks, 1900

[Polymitarciidae BANKS, 1900, p. 246]

Adults as in Euthyplociidae (recent) but with veins MP2 and CUA strongly divergent from MP1 basally; middle and hind legs weakly developed. Nymphs with fossorial legs; gills dorsal. *Mio.-Holo.*

Ephoron WILLIAMSON, 1802, p. 71. *Holo.*

Asthenopodichnium THENIUS, 1979, p. 185 [**A. xylobiontum*; OD]. Trace fossils; burrows in fossil wood, resembling those now made by polymitarcid nymphs. *Mio.*, Europe (Austria).

Family PALINGENIIDAE

Selys-Longchamps, 1888

[Palingeniidae SELYS-LONGCHAMPS, 1888, p. 147]

Main veins of fore wings arranged in pairs, converging at wing margin; crossveins numerous; forelegs of nymphs flattened and fossorial in nature; tibiae toothed. *Jur.-Holo.*

Palingenia BURMEISTER, 1839, p. 802. *Holo.*

Mesogenesia TSHERNOVA, 1977, p. 92 [**M. petersae*; OD]. Little-known genus, nymph only; similar to *Heterogenesia* (recent), with very short mandibles and lacking a distinct frontal process. *Jur.*, USSR (Asian RSFSR).—FIG. 16,5. **M.*

petersae; lateral view of nymph, $\times 7.5$ (Tshernova, 1977).

Family UNCERTAIN

The following genera, apparently belonging to the order Ephemeroptera, are too poorly known to permit assignment to families.

Aphelophlebodes PIERCE, 1945, p. 3 [**A. stocki*; OD]. Little-known genus, based on small fragment of wing. [Type of family Aphelophlebiidae and order Aphelophlebia PIERCE, 1945.] CARPENTER, 1960b; DEMOULIN, 1962. *Mio.*, USA (California).

Mesobaetis BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 5 [**M. sibirica*; OD]. Little-known nymph. DEMOULIN, 1954a, 1968b; ROHDENDORF, 1962a; TSHERNOVA, 1970; HUBBARD & SAVAGE, 1981. *Jur.*, USSR (Asian RSFSR).

Mesopteopteron HANDLIRSCH, 1918, p. 112 [**M. longipes*; OD]. Little-known genus, based on nymph. *Trias.*, Europe (Germany).

Parabaetis HAUPT, 1956, p. 32 [**P. eocaenicus*; OD]. Little-known genus, based on small fragment of wing. DEMOULIN, 1957. *Eoc.*, Europe (Germany).

Phthartus HANDLIRSCH, 1904b, p. 6 [**P. rossicus* HANDLIRSCH, 1904b, p. 6; SD CARPENTER, herein]. Little-known genus, based on nymph. HANDLIRSCH, 1906b. *Perm.*, USSR (Asian RSFSR).

Protoligoneuria DEMOULIN, 1955d, p. 270 [**P. limai*; OD]. Little-known genus, based on nymph only, possibly related to Oligoneuridae. COSTA LIMA, 1950. *Paleoc.-Plio.*, Brazil.

Order PALAEODICTYOPTERA

Goldenberg, 1877

[Palaeodictyoptera GOLDENBERG, 1877, p. 8] [=Protohemiptera HANDLIRSCH, 1906b, p. 387; Synarmogoida HANDLIRSCH, 1919b, p. 28; Protocicadida HAUPT (in part), 1941, p. 75; Archaeymenoptera HAUPT, 1941, p. 102; Archodonata MARTYNOV, 1932, p. 12; Anisaxia FORBES, 1943, p. 403; Hemiodonata ZALESKY, 1946a, p. 63; Breyerida HAUPT, 1949, p. 23; Eopalaeodictyoptera LAURENTIAUX, 1952a, p. 234; Eubleptidodea LAURENTIAUX, 1953, p. 423; Syntonopteroidea LAURENTIAUX, 1953, p. 425; Dictyoneurida ROHDENDORF, 1977, p. 20; Permothemistida SINITSHENKOVA, 1980a, p. 49]

Palaeoptera of moderate to very large size. Wings containing all main veins, including MA, MP, CUA, and CUP, with alternation of convexities and concavities; main veins usually without coalescence and always arising independently; area between veins with a delicate, irregular network (archedictyon) or with true crossveins, or with a combination of both; intercalary veins present in a very few families (e.g., Syntonopteridae); fore and

hind wings similar in form and venation in some families (e.g., Dictyoneuridae); in others (e.g., Spilapteridae) hind wings much broader than fore pair with basic venational pattern remaining the same; in some others (e.g., Eugereonidae and Megaptilidae) hind wings only about half as long as fore wings; in one family (Diathemidae) hind wings minute, in a related family (Permothemistidae) hind wings completely absent; front margin of wing commonly serrate, costa with or without setae; wings in some families with prominent pigment markings. Antennae setaceous, usually of moderate length but may be long and threadlike; head typically small, hypognathous (in some slightly prognathous), with prominent eyes, and with well-developed haustellate beak, enclosing 5 stylets derived from mandibles, maxillae, and presumably hypopharynx; maxillary palpi usually well developed, labial palpi apparently absent. Thoracic segments typically subequal, but prothorax in most species with a pair of lateral winglike lobes, usually membranous and commonly with veinlike supports; legs (known in very few genera) short, with 5 tarsal segments; abdomen of moderate length, slender, segments showing little differentiation; in some species pleurites apparently separated from tergites by longitudinal ridges; in others tergites strongly sclerotized and bearing lateral extensions; cerci long and multisegmented in both sexes, densely covered with hairs; ovipositor broad and short, strongly curved. Nymphs apparently terrestrial, without indications of aquatic modifications; mouthparts haustellate like those of adults; wing pads of nymphs held in an oblique-lateral position, independent of each other in all stages (so far as known), and articulated to thorax like wings of adult.

The food of nymphs and adults of the Palaeodictyoptera has been the subject of much speculation (SHAROV, 1973). It seems virtually certain that their mouthparts were adapted for obtaining liquid food from plants. Those with short beaks could have fed on the juices of foliage; those with longer beaks may have fed on contents of the developing

inflorescences of the Cordaitales, which were abundant in Late Carboniferous and Permian forests. *U. Carb.—Perm.*

The Palaeodictyoptera comprise one of the major orders of the Upper Carboniferous (beginning with the Namurian) and to a lesser extent of the Permian. During the past 20 years our knowledge of the order has been greatly extended, and our present concept of the group is far different from that given by HANDLIRSCH in 1920. However, the classification of the Palaeodictyoptera is necessarily an arbitrary one to a large extent. Eighty-one genera, placed in twenty families, are recognized here, along with another forty-odd genera that are too poorly known for assignment to family. Most of these genera are based almost entirely on wings, details of the body structures being only rarely preserved. The chief difficulty in developing a satisfactory phylogenetic classification is the lack of enough material (specimens and species) to permit evaluation of the characteristics of the several levels of taxa within the order. A few groups of related families can readily be recognized (e.g., the Eugereonidae, Archaeomegaptilidae, and Calvertiellidae, for one group; and the Permothemistidae and Diathemidae, for another), but there is not enough evidence to support the designation of a series of suborders or superfamilies. For the same reason it is difficult to determine with confidence the evolutionary level of the families within the order. The Dictyoneuridae, which have homonomous wings with a dense archdictyon, and which are known almost exclusively from the Upper Carboniferous (including the Namurian), appear to be the least specialized of the families now known. The most obvious specialization among the Palaeodictyoptera is the reduction of the hind wings, which occurs in the Eugereonidae and the Megaptilidae, as well as in the Diathemidae and Permothemistidae.

The Palaeodictyoptera are obviously closely related to the Megasecoptera, which have similar haustellate beaks and many other morphological features of the Palaeodictyoptera. Indeed, as more genera of these orders

become known, distinctions between them are increasingly difficult to find, except for the nature of the articular plates (peralialia). Ultimately, these two orders will probably be merged into one, without even subordinal separation. The Diaphanopteroidea also share the haustellate mouthparts and several other structural characters with the Palaeodictyoptera and Megasecoptera but are isolated from them by their unique ability, as Palaeoptera, to fold their wings over the abdomen at rest (CARPENTER & RICHARDSON, 1971; SHAROV, 1973; KUKALOVÁ-PECK, 1974b).

Family DICTYONEURIDAE Handlirsch, 1906

[Dictyoneuridae HANDLIRSCH, 1906a, p. 670]

Fore wing moderately slender, apex slightly pointed; costal area often broad up to midwing; main veins without coalescence; vein SC terminating well beyond midwing; R ending near apex; RS with several branches; MA unbranched, usually strongly curved; MP with or without branches; CUA unbranched; CUP with or without branches; archedictyon well developed over most of wing, usually dense but rarely coarse. Hind wing usually similar to fore wing but costal area narrower. Head small; antennae multisegmented; prothoracic lobes relatively large; legs short, with 5 tarsal segments; cerci long and multisegmented; ovipositor short and curved; males with claspers. *U. Carb.*—*Perm.*

Dictyoneura GOLDENBERG, 1854, p. 33 [**D. libelluloides*; OD]. Hind wing broad, with strongly curved hind margin; RS dichotomously branched; MP with 4 branches. HANDLIRSCH, 1906b; GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 17.9. **D. libelluloides*; hind wing, $\times 0.8$ (Guthörl, 1934).

Cleffia GUTHÖRL, 1931, p. 91 [**C. sarana*; OD] [= *Pseudocleffia* GUTHÖRL, 1940, p. 48 (type, *P. palatina*)]. Little-known genus. Wings slender; CUP with 2 branches. GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 17.12. **C. sarana*; wing, $\times 1.5$ (Guthörl, 1934).

Dictyoneurula HANDLIRSCH, 1906b, p. 75 [**Dictyoneura gracilis* KLIVER, 1886, p. 107; SD HANDLIRSCH, 1922, p. 30]. Little-known genus, apparently similar to *Microdictya* but anal area narrower. GUTHÖRL, 1934. *U. Carb.*, Europe

(Germany).—FIG. 17.8. **D. gracilis* (KLIVER); wing, $\times 1$ (Guthörl, 1934).

Goldenbergia SCUDDER, 1885a, p. 170 [**Dictyoneura elongata* GOLDENBERG, 1877, p. 50; SD HANDLIRSCH, 1906b, p. 71]. Fore wing elongate; costal margin moderately curved; SC extending nearly to wing apex; R and RS contiguous at wing base but apparently not fused; MA separating from MP at basal one-fourth of wing; MP deeply forked; CUA and CUP unbranched; several anal veins; dense archedictyon over wing surface. GUTHÖRL, 1934; SHAROV & SINITSHEKOVA, 1977. *U. Carb.*, Europe (Germany); *Perm.*, USSR (Kazakh).

Kallenbergia GUTHÖRL, 1930, p. 147 [**K. handlirschi*; OD]. Little-known genus, based on wing fragment. Wing broad, but narrowed basally; posterior margin strongly curved; RS pectinately branched. GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 17.4. **K. handlirschi*; wing, $\times 1.5$ (Guthörl, 1934).

Macrodictya GUTHÖRL, 1940, p. 46 [**M. stenomediali*; OD]. Little-known genus, based on wing fragment. RS with 5 terminal branches; MA very close to MP. *U. Carb.*, Europe (Germany).

Microdictya BRONGNIART, 1893 (atlas), p. 28, *nom. subst. pro Heeria* BRONGNIART, 1893, p. 388, *non* SCUDDER, 1890 [**Heeria vaillantii* BRONGNIART, 1893, p. 399; SD HANDLIRSCH, 1922, p. 25]. Fore and hind wings similar, broadest at about middle; posterior margin of hind wing smoothly curved; RS dichotomously forked; MP forked at least once; CUP usually branched; archedictyon nearly uniform over wings. LAURENTIAUX & TEIXEIRA, 1958a; KUKALOVÁ, 1970. *U. Carb.*, Europe (France).—FIG. 17.1. *M. hamyi* BRONGNIART; fore wing, $\times 0.8$ (Kukalová, 1970).

Polioptenus SCUDDER, 1885a, p. 170 [**Dictyoneura elegans* GOLDENBERG, 1877, p. 9; OD] [= *Acanthodictyon* HANDLIRSCH, 1906b, p. 72 (type, *Termes decheni* GOLDENBERG)]. Similar to *Stenodictyoneura*, but RS with 4 terminal branches. GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 17.10. **P. elegans* (GOLDENBERG); wing, $\times 1$ (Guthörl, 1934).

Rotundopteris GUTHÖRL, 1940, p. 44 [**R. multimediali*; OD]. Little-known genus. RS with only 3 branches; MA and branches of MP strongly curved. *U. Carb.*, Europe (Germany).—FIG. 17.11. **R. multimediali*; wing, $\times 1$ (Guthörl, 1940).

Sagenoptera HANDLIRSCH, 1906b, p. 72 [**Termes formosus* GOLDENBERG, 1854, p. 30; OD] [= *Arlitia* GUTHÖRL, 1934, p. 56 (type, *Dictyoneura schmitzi* GOLDENBERG)]. Little-known genus. Posterior margin of wing smoothly curved; RS dichotomously branched in distal third of wing; MP dichotomously branched. BRAUCKMANN & HAHN, 1983. *U. Carb.*, Europe (Germany).—

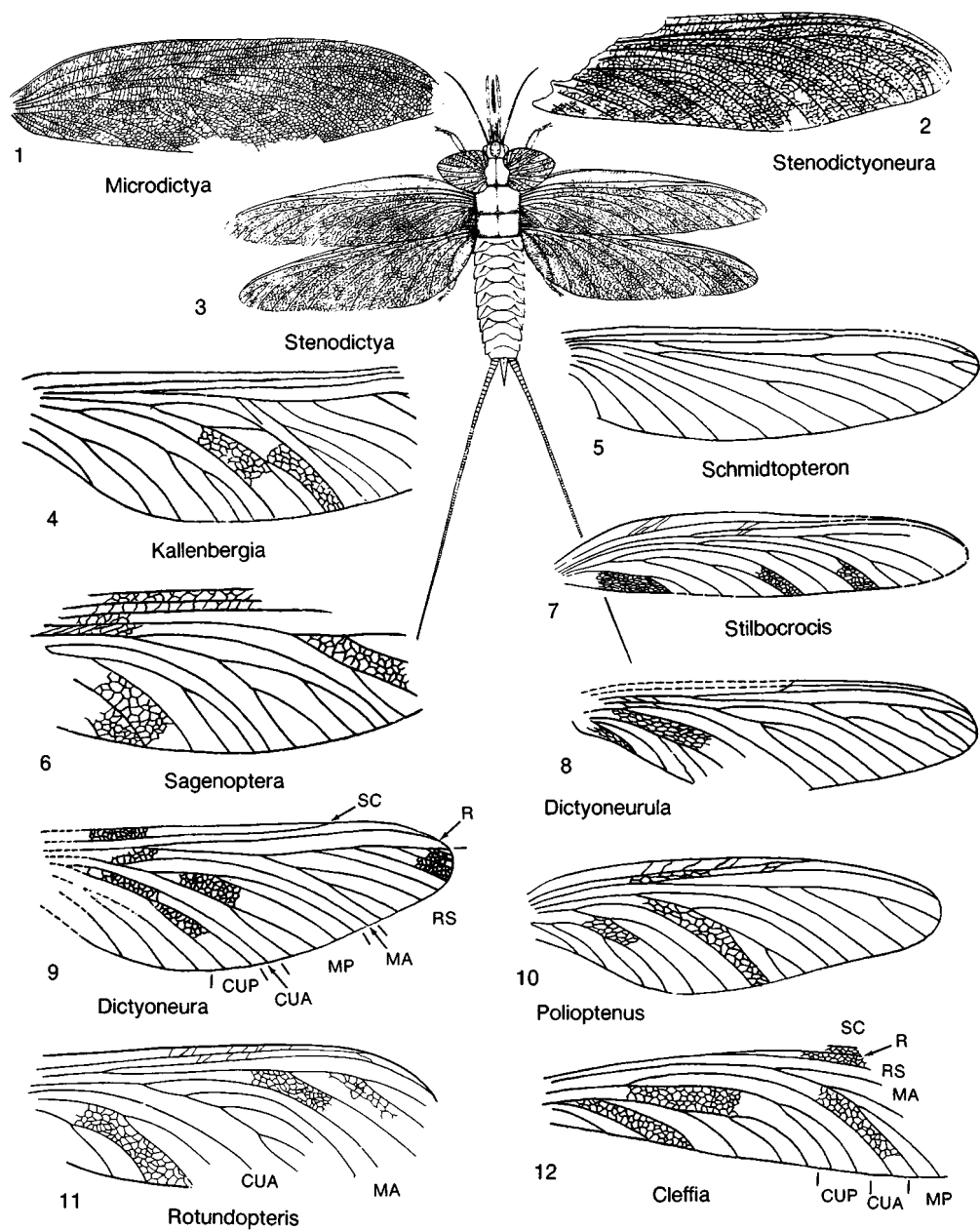


FIG. 17. Dictioneuriidae (p. 28-30).

FIG. 17.6. **S. formosa* (GOLDENBERG); wing, $\times 1$ (Guthörl, 1934).

SCHMIDTOPTERON BRAUCKMANN & HAHN, 1978, p. 14 [*S. adictyon*; OD]. Hind(?) wing with costal area very narrow; SC terminating about two-thirds wing length from base, just beyond level

of first fork of RS; RS arising in basal quarter of wing, with 3 dichotomous forks in distal area; MA and MP separating at about level of origin of RS; MA, CUA, and CUP unbranched; MP forked at about half of its length; CUA and CUP nearly straight, not strongly curved toward hind

- margin; 3 to 4 anal veins. *U. Carb.*, Europe (Germany).—FIG. 17.5. **S. adictyon*; hind(?) wing, $\times 1.8$ (Brauckmann & Hahn, 1978).
- Siberiodictya** SHAROV & SINITSHEKOV, 1977, p. 51 [**S. gigas*; OD]. Little-known genus, apparently similar to *Stenodictya*. Origin of RS, separation of MA and MP, and division of CUA and CUP occurring near wing base and at almost same level. *U. Carb.*, USSR (Asian RSFSR).
- Stenodictya** BRONGNIART, 1893, p. 383, *nom. subst. pro Scudderia* BRONGNIART, 1885a, p. 61, *non GROTE*, 1873 [**Scudderia lobata* BRONGNIART, 1885a, p. 61; SD HANDLIRSCH, 1922, p. 24]. Wings: RS arising at about midwing, its branches pectinate; MA, CUA, and CUP unbranched; MP usually unbranched; anal area broad; archidictyon irregular; costal area with thin but dense, regular crossveins. LAURENTIAUX, 1952a; KUKALOVÁ, 1970. *U. Carb.*, Europe (France).—FIG. 17.3. *Stenodictya*; reconstruction, $\times 0.8$ (Kukalová, 1970).
- Stenodictyoneura** LERICHE, 1911, p. 195 [**S. belgica*; OD]. Little-known genus. RS with 8 terminal branches; MP and CUP with 4 branches. *U. Carb.*, Europe (Belgium).—FIG. 17.2. **S. belgica*; wing, $\times 0.7$ (Leriche, 1911).
- Stilbocrocis** HANDLIRSCH, 1906b, p. 74 [**Termes heeri* GOLDENBERG, 1854, p. 29; OD] [= *Longivenapteris* GUTHÖRL, 1940, p. 52 (type, *L. pulchra*)]. Little-known genus. Wings very slender; RS dichotomously branched; CUP with 3 branches. *U. Carb.*, Europe (Germany).—FIG. 17.7. *S. lanceolata* GUTHÖRL; fore wing, $\times 1$ (Guthörl, 1940).

Family LITHOMANTEIDAE Handlirsch, 1906

[*nom. correct.* CARPENTER in BRUES, MELANDER, & CARPENTER, 1954, p. 790, *pro* Lithomantidae HANDLIRSCH, 1906a, p. 673] [= Macropterae LAURENTIAUX, 1949b, p. 217; Lusiellidae LAURENTIAUX & TEIXEIRA, 1958a, p. 6]

Fore wing: anterior margin and stems of main veins strongly curved basally; veins MA and CUA unbranched; crossveins slightly irregular, but mostly unbranched. Hind wing much broader than fore wing basally. *U. Carb.*

Lithomantis WOODWARD, 1876, p. 63 [**L. carbonaria*; OD] [= *Hadroneuria* HANDLIRSCH, 1906b, p. 84 (type, *Gryllacris bohémica* NOVÁK, 1880, p. 69); *Lithosialis* SCUDDER, 1881a, p. 167 (type, *Corydalis brongniarti* MANTELL, 1839, p. 680)]. Fore wing with CUP more extensive than MP. KUKALOVÁ, 1969c. *U. Carb.*, England, Europe (Holland, Czechoslovakia).—FIG. 18.1. **L. carbonaria*, England; dorsal view, $\times 0.6$ (Woodward, 1876).

Lusiella LAURENTIAUX & TEIXEIRA, 1958a, p. 6, *nom. subst. pro Macroptera* LAURENTIAUX, 1949b, p.

217, *non* LIOY, 1863 [**Lusiella fariai*; OD]. Similar to *Lithomantis*, but hind wing much broader than fore wing and crossveins in both wings fewer and more regular. KUKALOVÁ, 1969c. *U. Carb.*, Europe (France, Portugal).—FIG. 18.2. **L. fariai*, Portugal; hind wing, $\times 0.6$ (Laurentiaux & Teixeira, 1958a).

Synarmoge HANDLIRSCH, 1910d, p. 250 [**S. ferrarii*; OD] [= *Climacoptera* LAURENTIAUX, 1949b, p. 214, *non* REDTENBACHER, 1895 (type, *C. antiqua*)]. Fore wing with posterior margin of anal area concave; crossveins diversely formed but mostly unbranched. HANDLIRSCH, 1919b; LAURENTIAUX, 1953; KUKALOVÁ, 1969c. *U. Carb.*, Europe (Germany, France).—FIG. 18.3. **S. ferrarii*; wing, $\times 0.6$ (Laurentiaux, 1953).

Family MEGAPTILIDAE Handlirsch, 1906

[Megaptilidae HANDLIRSCH, 1906b, p. 80] [= Lithoptilidae HANDLIRSCH, 1922, p. 44]

Fore wing large and broad; vein SC apparently extending nearly to wing apex; RS with at least 5 terminal branches; branches of M and CU strongly curved toward posterior wing margin; MA unbranched; CUP with at least one fork; crossveins very dense and reticulate. Hind wing apparently much shorter than fore wing, with reduced branching of RS and MP. *U. Carb.*

Megaptilus BRONGNIART, 1885a, p. 61 [**M. blanchardi*; SD HANDLIRSCH, 1906b, p. 80]. Fore wing with RS3+4 arising before level of midwing; M more extensively branched than CU. BRONGNIART, 1893; LAMEERE, 1917b; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Lithoptilus LAMEERE, 1917b, p. 157 [**Archaoptilus boulei* MEUNIER, 1909a, p. 131; OD] [= *Anaxion* HANDLIRSCH, 1919b, p. 529, obj.]. Little-known genus, based on distal part of hind wing. Wing apparently short and broad; costal area broad; RS short, with only 6 terminal branches; MP with 2 forks; crossveins numerous, coarsely reticulate. KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).—FIG. 18.4. **L. boulei*; hind wing, $\times 0.8$ (Kukalová, 1969c).

Family ARCHAEMEGAPTILIDAE Handlirsch, 1919

[Archaemegaptilidae HANDLIRSCH, 1919b, p. 523]

Little-known family, based on a hind(?) wing fragment. Vein SC long, extending almost to wing apex; R very close to SC except at wing base; RS arising about one-quarter wing length from base; M dividing

a short distance from level of origin of RS.
U. Carb.

Archaeomegaptilus MEUNIER, 1908g, p. 174 [**A. kiefferi*; OD]. Hind(?) wing: RS with 5 terminal branches; MA unbranched; MP with 6 terminal branches; CUP with at least 3 terminal branches; crossveins coarsely reticulate. LAMEERE, 1917b; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Family EUGEREONIDAE

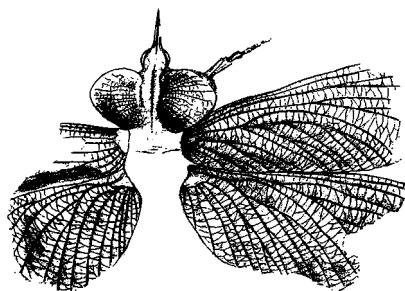
Handlirsch, 1906

[Eugereonidae HANDLIRSCH, 1906b, p. 389] [=Peromapteridae HANDLIRSCH, 1906b, p. 79; Dictyoptilidae LAMEERE, 1917b, p. 191]

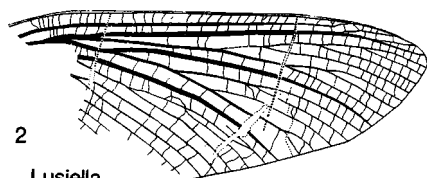
Fore wing long and narrow; precostal area present; furrow extending from anal area to vein R; SC ending at or nearly at wing apex; stems of R and M independent at base of wing but coalesced for short distance beyond that; MA unbranched; MP usually with 4 branches; CUA typically unbranched; CUP with one fork; anal area extending about one-third wing length from base; crossveins forming dense pattern with much reticulation. Hind wing distinctly shorter than fore wing, with stem of M strongly curved toward posterior margin; CUA recurved toward anal area. Beak long; pronotal lobes small but distinct. *U. Carb.*—*Perm.*

Eugereon DOHRN, 1866, p. 333 [**E. boeckingi*; OD]. Little-known genus, represented by bases of wings and details of head and thorax. Fore wing with 1A not strongly curved toward posterior wing margin. Hind wing with area between stem RS and MA relatively broad. HANDLIRSCH, 1906b; GUTHÖRL, 1934; LAMEERE, 1935; CARPENTER, 1964a; KUKALOVÁ, 1969c; MÜLLER, 1978a. *Perm.*, Europe (Germany).—FIG. 19. **E. boeckingi*; a, dorsal view of head, thorax, and wing bases, $\times 0.5$ (Laurentiaux, 1953); b, fore wing base, $\times 1$; c, hind wing base, $\times 1$ (both Carpenter, 1964a).

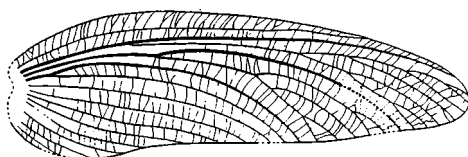
Dictyoptilus BRONGNIART, 1893, p. 390 [**D. renaulti*; OD] [= *Cockerelliella* MEUNIER, 1909a, p. 132, *nom. subst. pro Cockerelliella* MEUNIER, 1908b, p. 154, *non* ASHMEAD, 1898 (type, *C. peromapteroides*)]. Fore wing similar to that of *Eugereon*, but 1A strongly curved toward posterior wing margin. Hind wing with area between stems of RS and M narrow. LAMEERE, 1917b; HANDLIRSCH, 1919b; CARPENTER, 1964a; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).—FIG. 20,2a. *D. sepultus* (MEUNIER); fore wing, $\times 1$ (Kukalová, 1969c).—FIG. 20,2b. *D. per-*



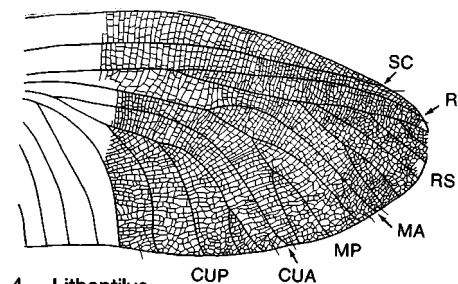
1 Lithomantis



2 Lusiella



3 Synarmoge



4 Lithoptilus

FIG. 18. Lithomanteidae and Megaptilidae (p. 30).

omapteroides (MEUNIER); fore and hind wings, $\times 0.8$ (Kukalová, 1969c).

Peromaptera BRONGNIART, 1893, p. 391 [**P. filiboli*; OD]. Fore wing with CUA forked; MP with 3 terminal branches. Hind wing only about half as long as fore wing and much broader. MARTYNOV, 1931a; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Sandiella CARPENTER, 1970, p. 405 [**S. readi*; OD]. Similar to *Dictyoptilus* but with a coarser reticulation of crossveins and without rows of crossveins between R and RS, and R and SC; SC ending well before apex of wing. *U. Carb.*, USA (New Mexico).—FIG. 20,1. **S. readi*; fore wing, $\times 2$ (Carpenter, 1970).

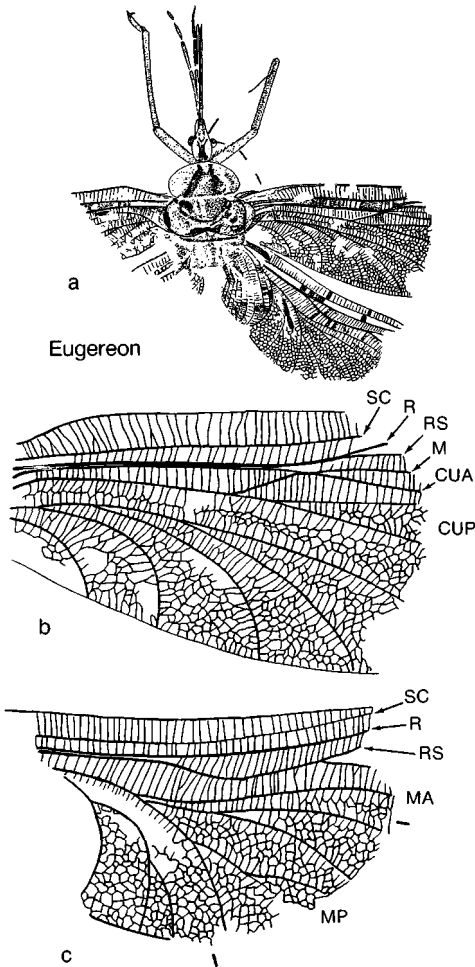


FIG. 19. Eugereonidae (p. 31).

Valdeania TEIXEIRA, 1941, p. 15 [**V. medeirosi*; OD]. Little-known genus. Fore wing elongate, front and hind margins nearly parallel for most of their lengths; R terminating at apex of wing; RS with 6 terminal branches; MA unbranched; MP with 3 terminal branches. Hind wing only half as long as fore wing but much broader; all veins, including R, strongly curved toward hind margin. LAURENTIAUX, 1953. *U. Carb.*, Europe (Portugal).

Family CALVERTIELLIDAE Martynov, 1931

[Calvertiellidae MARTYNOV, 1931b, p. 146]

Fore wing with vein SC terminating on R just beyond midwing; RS originating in basal third of wing, with 3 or 4 main branches;

stem R and M separate at wing base but contiguous near origin of RS; M forking near level of RS; MA unbranched, MP branched; stem CU independent of M; CUA diverging toward M near origin of RS and then running close to posterior branch of MP; 6 anal veins; crossveins numerous, with some reticulation. Hind wing very broad basally; anterior margin concave; venation essentially as in fore wing except for modifications associated with wing shape. Body unknown. *U. Carb.-Perm.*

Calvertiella TILLYARD, 1925b, p. 43 [**C. permiana*; OD]. Fore wing moderately slender; CUA coalesced with M for short distance just before origin of MP; MP forked twice, with 3 branches; crossveins in distal part of wing coarsely reticulate. KUKALOVÁ, 1964a. *Perm.*, USA (Kansas).—FIG. 21,2. **C. permiana*; fore wing, $\times 2$ (Kukalová, 1964a).

Carrizopteryx KUKALOVÁ-PECK in KUKALOVÁ-PECK & PECK, 1976, p. 87 [**C. arroyo*; OD]. Hind wing apparently similar to that of *Moravia*, but stems of R, M, and CU fused from base to point of divergence of the three veins, just before origin of RS. *U. Carb.*, USA (New Mexico).

Moravia KUKALOVÁ, 1964a, p. 159 [**M. convergens*; OD]. Fore wing broad, nearly oval, apex broadly rounded, anterior margin convex; MP forked 3 or 4 times, with at least 4 branches; crossveins in distal area finely reticulate. Hind wing much broader basally than fore wing; crossveins reticulate in basal region also. Nymphal wings and presumed subimaginal wings with venation like that of imaginal forms. KUKALOVÁ-PECK & PECK, 1976; CARPENTER, 1979. *Perm.*, Europe (Czechoslovakia), USA (Oklahoma).—FIG. 21,7. **M. convergens*; a, fore and b, hind wings, $\times 1.5$ (Kukalová, 1964a).

Moraviptera KUKALOVÁ, 1955a, p. 547 [**M. reticulata*; OD]. Little-known genus, based on apical wing fragment. Similar to *Moravia*, but wing much narrower and with pointed apex. KUKALOVÁ, 1964a. *Perm.*, Europe (Czechoslovakia).

Sharovia SINITSHENKOVA in SHAROV & SINITSHENKOVA, 1977, p. 61 [**S. sojanica*; OD]. Little-known genus, based on apical portions of fore and hind wings. Apex of wing more pointed than in *Moravia*; anterior border of wing more nearly straight; MP with 4 branches; CUA only slightly curved distally. *Perm.*, USSR (European RSFSR).—FIG. 21,9. **S. sojanica*; fore wing, $\times 1.2$ (Sharov & Sinitschenkova, 1977).

Family LYCOCERCIDAE Handlirsch, 1906

[Lycocercidae HANDLIRSCH, 1906a, p. 675] [=Polycraegridae HANDLIRSCH, 1906b, p. 110; Apopappidae LAMEERE, 1917a, p. 42; Patreiskiyidae LAURENTIAUX, 1958, p. 302]

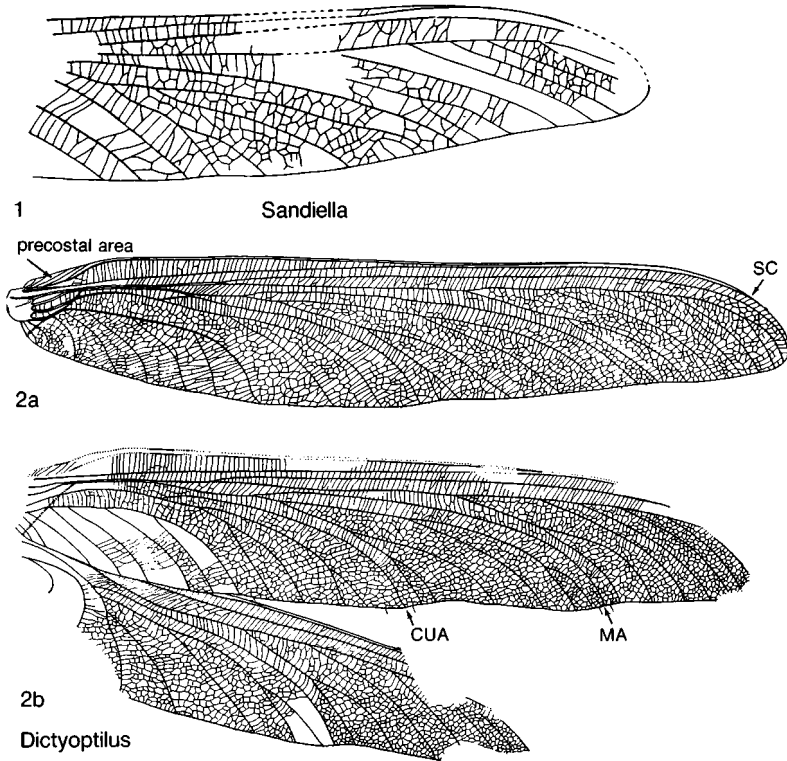


FIG. 20. Eugereonidae (p. 31).

Fore wing with anterior margin nearly straight for most of its length; vein SC extending nearly to wing apex; RS with many branches; MA unbranched, apparently arising from anterior branch of MP; MP with many branches, mostly arising distally; CUA unbranched; CUP with at least 2 branches; anal area extensive; crossveins very numerous, commonly reticulate. Hind wing apparently similar to fore wing. Head small, with prominent eyes; beak broad basally. *U. Carb.*

Lycocercus HANDLIRSCH, 1906b, p. 89 [**Dictyoneura goldenbergi* BRONGNIART, 1883, p. 268; SD HANDLIRSCH, 1922, p. 39] [= *Patteiskya* LAURENTIAUX, 1958, p. 302 (type, *P. bouckaerti*)]. Fore wing: RS with at least 10 terminal branches; MP with 10 to 20 forks; usually 8 anal veins. DEMOULIN, 1958a; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France, Germany).—FIG. 21,6. **L. goldenbergi* (BRONGNIART); fore wing, $\times 0.75$ (Kukalová, 1969c).

Apopappus HANDLIRSCH, 1906b, p. 100 [**Spilaptera guernei* BRONGNIART, 1893, p. 463; OD]. Little-known genus, based on apical fragment of

wing. Similar to *Lycocercus* but with CUP more extensively branched and with crossveins more regularly arranged. LAMEERE, 1917b; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Lycodemus CARPENTER & RICHARDSON, 1971, p. 268 [**L. adolescens*; OD]. Little-known genus, based on nymphs; venation similar to that of *Lycocercus*, but MP with fewer branches. *U. Carb.*, USA (Illinois).

Madera CARPENTER, 1970, p. 402 [**M. mamayi*; OD]. Similar to *Lycocercus*, but fore and hind wings relatively broad; MA arising in both wings at about level of origin of RS; CUP consisting of 2 large branches, without marginal forks. *U. Carb.*, USA (New Mexico).—FIG. 21,5. **M. mamayi*; fore wing, $\times 3.5$ (Carpenter, 1970).

Notorachis CARPENTER & RICHARDSON, 1971, p. 272 [**N. wolfforum*; OD]. Pronotal lobes heavily sclerotized and bearing long spines. Venation similar to that of *Lycocercus*; MA arising before origin of RS; MP with 5 terminal branches. *U. Carb.*, USA (Illinois).—FIG. 21,3. **N. wolfforum*; dorsal view, $\times 1.6$ (Carpenter & Richardson, 1971).

Polycreagra HANDLIRSCH, 1906a, p. 678 [**P. elegans*; OD]. Hind(?) wing: RS and MP with numerous, fine branches; about 15 terminal anal veins. KUKALOVÁ, 1969c. *U. Carb.*, USA (Rhode

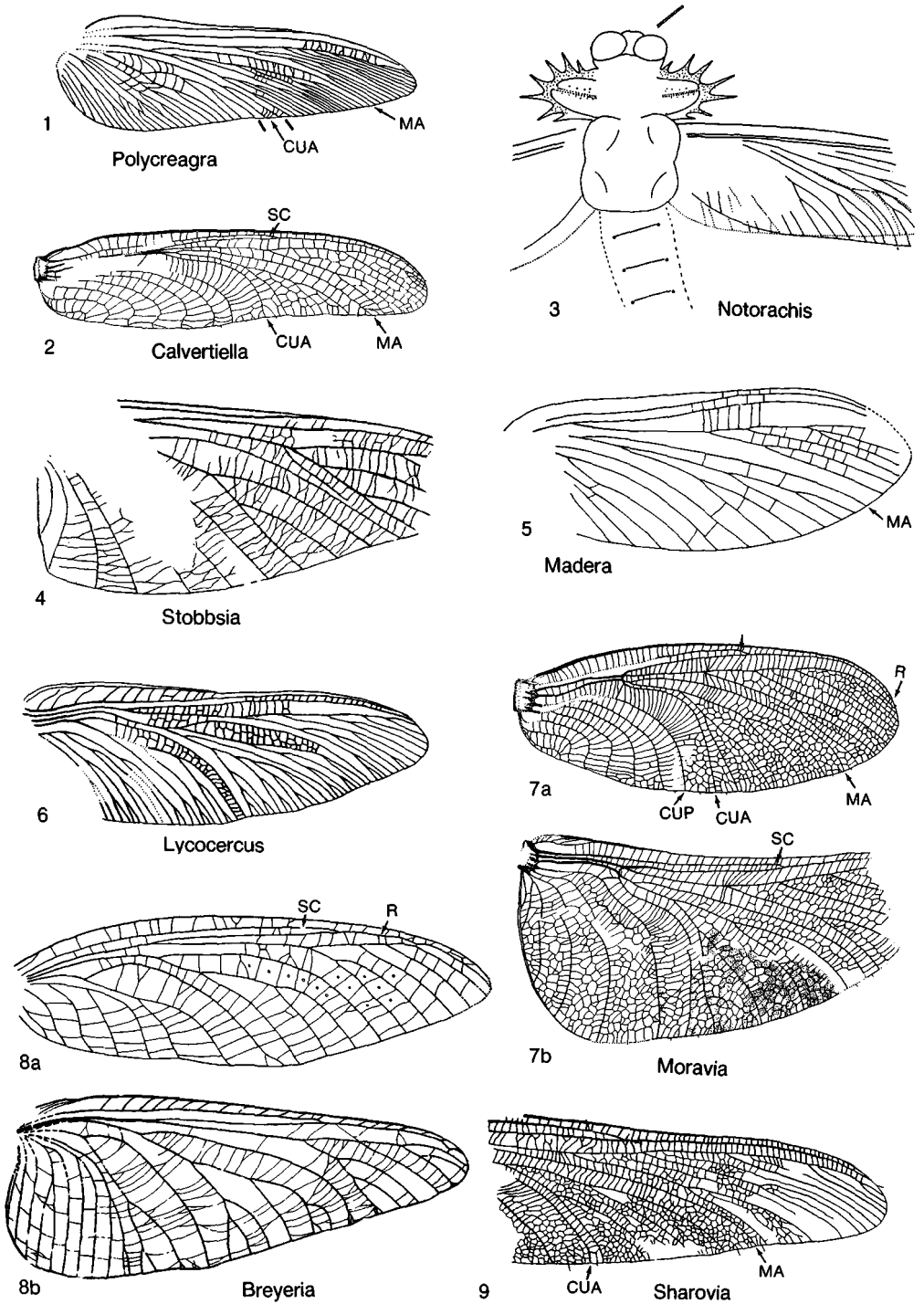


FIG. 21. Calvertiellidae, Lycocercidae, and Breyeriidae (p. 32-35).

Island).—FIG. 21, 1. **P. elegans*; hind(?) wing, $\times 0.7$ (Handlirsch, 1906a).

Family GRAPHIPTILIDAE

Handlirsch, 1906

[Graphiptilidae HANDLIRSCH, 1906b, p. 99] [=Rhabdoptilidae HANDLIRSCH, 1919b, p. 525]

Little-known family. Hind(?) wing with vein SC extending nearly to apex of wing; RS with several pectinate branches; M forking just before level of midwing; MA usually unbranched; MP with 3 branches; CUA unbranched; CUP with 3 branches; crossveins numerous and fine. *U. Carb.*

Graphiptilus BRONGNIART, 1893, p. 348 [**G. heeri*; OD] [= *Graphiptiloides* HANDLIRSCH, 1906b, p. 92 (type, *Graphiptilus williamsoni* BRONGNIART, 1893, p. 349)]. Little-known genus. RS with 5 terminal branches, the first ending at wing apex; MP forking shortly after its separation from MA. KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Rhabdoptilus BRONGNIART, 1893, p. 364 [**R. edwardsi*; OD]. Little-known genus. Hind(?) wing with RS arising in basal third of wing, with at least 5 terminal branches; MP with 6 terminal branches; crossveins more irregular than in *Graphiptilus*. HANDLIRSCH, 1906b, 1919b; LAMEERE, 1917b; KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).

Family BREYERIIDAE

Handlirsch, 1906

[Breyeriidae HANDLIRSCH, 1906b, p. 95]

Fore wing broad; costal margin strongly curved; vein SC terminating at midwing or well before wing apex; stems of R and M very close or in contact basally; R extending almost to apex; RS with 5 or 6 terminal branches, widely separated; MA unbranched; CUA usually unbranched, at most with a marginal fork; CUP usually forked at least once; crossveins very fine, irregular, and numerous, commonly anastomosed. Hind wing much broader than fore wing, posterior margin strongly curved. *U. Carb.*

Breyeria BORRE, 1875b, p. lxvi [**Pachyrylopsis borinensis* BORRE, 1875a, p. xli; OD]. Fore wing with SC terminating on R; branches of M and CU strongly curved toward hind margin of wing. BRONGNIART, 1893; MEUNIER, 1910a; HANDLIRSCH, 1919b; STRAND, 1929; KELLER, 1935; LAURENTIAUX, 1949a; KUKALOVÁ, 1959a, 1969c;

LAURENTIAUX-VIEIRA & LAURENTIAUX, 1963; CARPENTER, 1967a. *U. Carb.*, Europe (France, Belgium, Germany, Czechoslovakia, Holland), England, USA (Tennessee).—FIG. 21, 8a. *B. rappi* CARPENTER, Tennessee; fore wing, $\times 0.8$ (Carpenter, 1967a).—FIG. 21, 8b. *B. barborae* KUKALOVÁ, Czechoslovakia; hind wing, $\times 0.7$ (Kukalová, 1959a).

Megaptiloides HANDLIRSCH, 1906b, p. 97 [**Megaptilus brodiei* BRONGNIART, 1893, p. 375; OD]. Little-known genus, based on wing fragment; similar to *Breyeria*, but crossveins numerous and more irregular. KUKALOVÁ, 1969c. [Family assignment doubtful.] *U. Carb.*, Europe (France).

Stobbsia HANDLIRSCH, 1908a, p. 1347 [**S. woodwardiana*; OD]. Similar to *Breyeria*, but SC terminating on costa; branches of M and CU not strongly curved toward posterior margin of wing. [Family assignment doubtful.] LAMEERE, 1917b; LAURENTIAUX & LAURENTIAUX-VIEIRA, 1951; KUKALOVÁ, 1969c. *U. Carb.*, England.—FIG. 21, 4. **S. woodwardiana*; wing, $\times 1$ (Handlirsch, 1908a).

Family TCHIRKOVAEIDAE

Sinitshenkova, 1979

[Tchirkovaeidae SINITSHENKOVA, 1979, p. 74]

Similar to Breyeriidae, but vein MP unbranched or with only a short fork; branches of M and CU only slightly curved distally. *U. Carb.*

Tchirkovaea M. D. ZALESSKY, 1931, p. 403 [**T. guttata*; OD]. Fore wing with anterior margin strongly convex; SC extending well beyond two-thirds of wing length; MP forked to about half its length; crossveins forming coarse reticulation in several areas. Hind wing with anterior margin almost straight. ZALESSKY, 1932a; SINITSHENKOVA, 1979, 1981a. *U. Carb.*, USSR (Asian RSFSR).

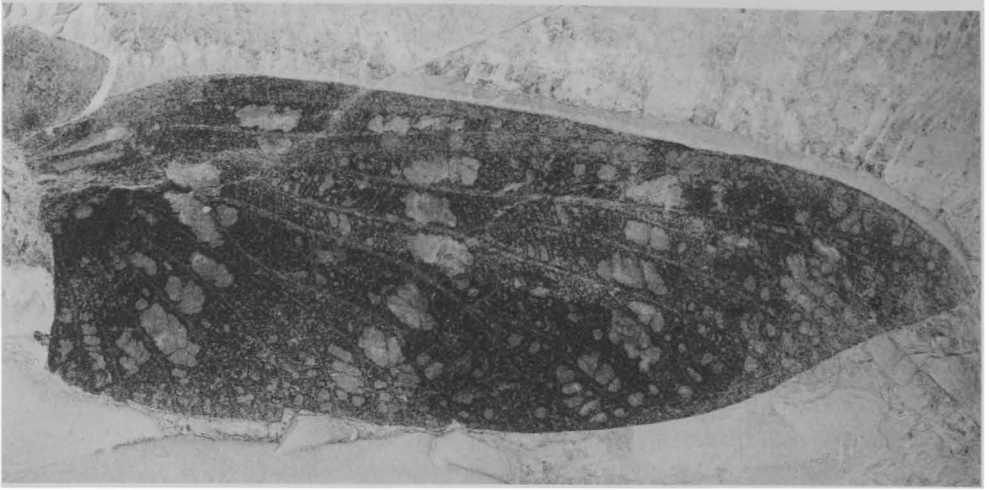
Paimbia SINITSHENKOVA, 1979, p. 82 [**P. fenestrata*; OD]. Similar to *Tchirkovaea*, but fore wing with anterior margin straight and costal area narrow. Hind wing with concave anterior margin. SINITSHENKOVA, 1981a. *U. Carb.*, USSR (Asian RSFSR).

Family HOMOIOPTERIDAE

Handlirsch, 1906

[Homoiopteridae HANDLIRSCH, 1906b, p. 91] [=Rocklingiidae GUTHÖRL, 1934, p. 188; Thesoneuridae CARPENTER, 1944, p. 10]

Large insects. Fore wing with stems of veins SC, R, and M distinctly curved basally; SC long, terminating near wing apex; RS with relatively few branches; MA unbranched or



Homioiptera

FIG. 22. Homioipteridae (p. 36).

with very few short branches; MP with several branches; CUA with several short branches; stems of CUA and CUP more or less parallel for most of their lengths. Hind wing somewhat broader than fore wing, with narrow costal area. Head apparently small, eyes bulging; prothoracic lobes well developed. *U. Carb.*

Homioiptera BRONGNIART, 1893, p. 353 [**H. woodwardi*; OD] [= *Homioephlebia* HANDLIRSCH, 1906b, p. 92 (type, *Homioiptera gigantea* AGNUS, 1902, p. 259); *Anthracentomon* HANDLIRSCH, 1904a, p. 6 (type, *A. latipenne*)]. Fore wing: RS with only 3 main branches; M dividing near level of midwing; MA usually unbranched or with distal twig; MP with 3 or 4 branches; 6 to 8 anal veins. Crossveins numerous, weak, and with much reticulation. HANDLIRSCH, 1906a; MEUNIER, 1908f, 1910a; KUKALOVÁ, 1969c; BRAUCKMANN & KOCH, 1982. *U. Carb.*, Europe (France, Belgium, Germany).—FIG. 22. *H. gigantea* AGNUS, France; fore wing and pronotal lobe, $\times 0.7$ (Carpenter, new).

Adolaryria KUKALOVÁ-PECK & RICHARDSON, 1983, p. 1677 [**A. bairdi*; OD]. Little-known genus, based on nymph consisting of thoracic segments and partially developed wings. *U. Carb.*, USA (Illinois).

Boltopruvostia STRAND, 1929, p. 20, *nom. subst. pro Boltonia* PRUVOST, 1919, p. 284, *non* KOENIG, 1820 [**Boltonia robusta* PRUVOST; OD] [= *Ostrava* KUKALOVÁ, 1960, p. 241 (type, *O. nigra*)]. Little-known genus. Similar to *Homioiptera* but wings longer; RS more extensively branched and with

much more extensive anal area. GUTHÖRL, 1934; HAUPT, 1949; KUKALOVÁ, 1969c. *U. Carb.*, Europe (Germany, France, Czechoslovakia).

Larryia KUKALOVÁ-PECK & RICHARDSON, 1983, p. 1678 [**L. osterbergi*; OD]. Little-known genus, based on the metathorax and a hind wing with distinct bend in costal margin near midwing. *U. Carb.*, USA (Illinois).

Mazonopterum KUKALOVÁ-PECK & RICHARDSON, 1983, p. 1674 [**M. wolfforum*; OD]. Hind wing similar to that of *Boltopruvostia*, but costal margin straight and costal area narrow; space between CUA and CUP conspicuously wide. *U. Carb.*, USA (Illinois).

Mazothairos KUKALOVÁ-PECK & RICHARDSON, 1983, p. 1672 [**M. enormis*; OD]. Little-known genus, based on single thoracic segment. *U. Carb.*, USA (Illinois).

Parathesoneura SINITSHENKOVA in SHAROV & SINITSHENKOVA, 1977, p. 48 [**P. carpenteri*; OD]. Hind wing similar to *Thesoneura*, but M dividing nearer wing base; CUA unbranched; arched-ictyon coarse. *U. Carb.*, USSR (Kazakh).

Thesoneura CARPENTER, 1944, p. 10 [**T. americana*; OD]. Hind wing with MA unbranched; MP with only 3 short branches; CUA with several long branches, arising pectinately and directed anteriorly; CUP sinuously curved; several anal veins, mostly unbranched. KUKALOVÁ, 1969c. *U. Carb.*, USA (Illinois).—FIG. 23. **T. americana*; hind wing, $\times 0.6$ (Carpenter, 1944).

Turneropterum KUKALOVÁ-PECK & RICHARDSON, 1983, p. 1680 [**T. turneri*; OD]. Little-known genus, based on thorax and basal parts of fore and hind wings. Fore wing with costal margin strongly concave basally; stems of R, M, and CU

separating close to base of wing and dividing early. *U. Carb.*, USA (Illinois).

Family MECYNOSTOMATIDAE

Kukalová, 1969

[Mecynostomatidae KUKALOVÁ, 1969b, p. 208]

Fore wing with costal area very broad basally; vein SC short, terminating on R at about midwing; branches of RS curving posteriorly; MA, MP, CUA, and CUP branched; crossveins numerous, many irregular. Hind wing similar to fore wing, but costal area much narrower. Head small, with prominent eyes; beak elongate. *U. Carb.*

Mecynostomata METCALF, 1952, p. 230, *nom. subst. pro Mecynostoma* BRONGNIART, 1893, p. 451, *non* GRAFF, 1882 [**Mecynostoma dobrni* BRONGNIART, 1893, p. 452; OD]. Fore wing: MA with 2 terminal branches, MP with 3; CUA more deeply forked than CUP. HANDLIRSCH, 1906b; KUKALOVÁ, 1969b. *U. Carb.*, Europe (France). —FIG. 24,2. **M. dobrni* (BRONGNIART); fore wing, head, and foreleg, $\times 1$ (Kukalová, 1969b).

Family FOUQUEIDAE

Handlirsch, 1906

[Fouqueidae HANDLIRSCH, 1906b, p. 98]

Wing venation similar to that of Spilapteridae, but crossveins very numerous and reticulate over entire wing. *U. Carb.*

Fouquea BRONGNIART, 1893, p. 372, *nom. subst. pro Oustaletia* BRONGNIART, 1885a, p. 66, *non* TROUSSERT, 1885 [**Oustaletia lacroixi*; OD] [= *Archaeocomponeura* MEUNIER, 1909b, p. 139 (type, *A. superba*)]. Fore wing: RS with 4 to 7 branches; MA with a long fork; MP with several branches; CUP with 4 terminal branches; at least 3 branched anal veins. Hind wing much broader than fore wing, with similar venation. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France). —FIG. 24,3. **F. lacroixi* (BRONGNIART); fore wing, $\times 1$ (Kukalová, 1969b).

Neofouquea CARPENTER, 1967a, p. 62 [**N. suzanneae*; OD]. Little-known genus. Hind(?) wing similar to *Fouquea*, but CUP with single long fork. *U. Carb.*, USA (Illinois).

Family EUBLEPTIDAE

Handlirsch, 1906

[Eubleptidae HANDLIRSCH, 1906a, p. 679]

Small Palaeodictyoptera with slender, pointed wings. Fore wing with vein SC

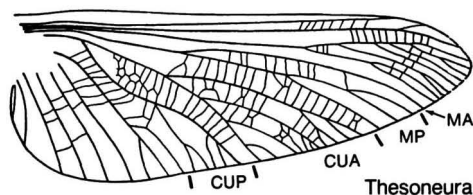


FIG. 23. Homiopteridae (p. 36).

extending nearly to wing apex; RS dichotomously forked, usually with 4 branches; M forking just before origin of RS; MA with long fork; MP with 3 terminal branches; CUA with short fork; CUP usually with 3 terminal branches; relatively few crossveins, forming distinct pattern. Hind wing similar to fore wing in venation, but slightly broader. Body slender, pronotal lobes small. *U. Carb.*

Eubleptus HANDLIRSCH, 1906a, p. 681 [**E. danielsi*; OD]. Fork of MA nearly at level of first fork of RS; first fork of MP well before midwing, its posterior branch forked near wing margin. CARPENTER, 1983. *U. Carb.*, USA (Illinois). —FIG. 24,1. **E. danielsi*; dorsal view, $\times 2.5$ (Carpenter, 1983).

Family SPILAPTERIDAE

Handlirsch, 1906

[Spilapteridae HANDLIRSCH, 1906b, p. 101] [= *Lamproptiliidae* HANDLIRSCH, 1906b, p. 109; *Dunbartiidae* HANDLIRSCH, 1937, p. 81; *Doropteridae* ZALESSKY, 1946a, p. 64; *Neuburgiidae* ROHDENDORF, 1961a, p. 72]

Fore wing: anterior margin more or less concave; vein SC long, usually extending to wing apex; RS with 3 to 6 terminal branches, usually pectinate; MA and MP with at least 2 branches; CUA with several branches, CUP with few or, rarely, unbranched; several anal veins. Hind wing: broader than fore wing, with larger anal area; venation similar to that of fore wing. Both wings commonly marked with spots or bands. Body structure: head broad, with bulging eyes; beak long; antennae long, multisegmented; pronotal lobes usually well developed and with radiating support veins; metathorax usually slightly longer than mesothorax; legs short, cursorial; abdomen usually slender, female with 10 visible segments and a short, curved ovipositor, male apparently with 11 abdominal segments; cerci well developed. *U. Carb.*—*Perm.*

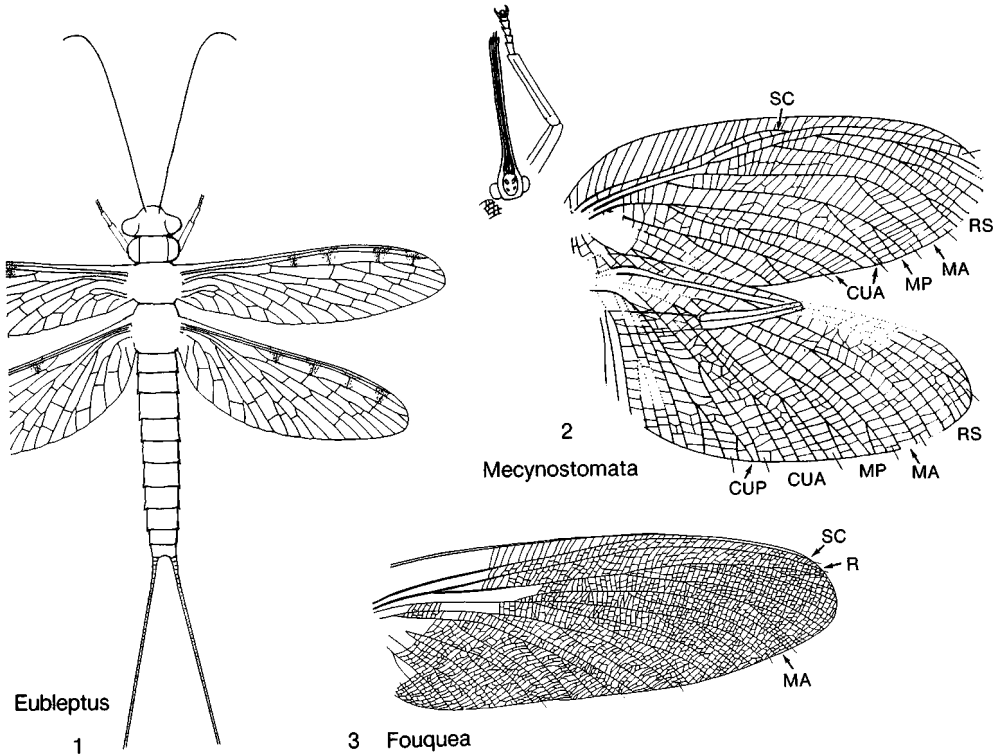


FIG. 24. Mecynostomatidae, Fouqueidae, and Eubleptidae (p. 37).

Spilaptera BRONGNIART, 1885a, p. 63 [**S. packardii*; SD HANDLIRSCH, 1922, p. 45]. Fore wing: R without terminal branches; RS with 4 to 6 terminal branches; area between R and RS with several strong, oblique crossveins; M free from RS; MP with several forks; CUA pectinately branched; CUP usually forked; relatively few crossveins, commonly forming distinct pattern. BRONGNIART, 1893; HANDLIRSCH, 1906b; KUKALOVÁ, 1969b; CARPENTER & RICHARDSON, 1971; SHAROV & SINITSHENKOVA, 1977. *U. Carb.*, Europe (France), USSR (Ukraine), USA (Illinois). —FIG. 25.4. **S. packardii*; fore wing, $\times 0.9$ (Kukalová, 1969b).

Abaptilon ZALESSKY, 1946c, p. 58 [**A. sibiricum*; OD]. Little-known genus, based on apical fragment of hind(?) wing. MA and MP each with 3 terminal branches; RS apparently originating near midwing. [Family assignment doubtful.] ROHDENDORF, 1962a. *U. Carb.*, USSR (Asian RSFSR).

Baeoneura SINITSHENKOVA in SHAROV & SINITSHENKOVA, 1977, p. 58 [**B. obscura*; OD]. RS of hind wing with pectinate branches as in *Dunbaria* but with several branches forked. *U. Carb.*, USSR (Asian RSFSR).

Becquerelia BRONGNIART, 1893, p. 356 [**B.*

superba; SD HANDLIRSCH, 1922, p. 46] [= *Pseudobecquerelia* HANDLIRSCH, 1919b, p. 534 (type, *Becquerelia elegans* BRONGNIART)]. Similar to *Homaloneura*, but MA apparently coalesced with RS for considerable interval; CUA pectinate; R with short terminal branches. HANDLIRSCH, 1919b; KUKALOVÁ, 1969b. *U. Carb.*, Europe (France). —FIG. 25.3. **B. superba*; hind wing, $\times 0.6$ (Kukalová, 1969b).

Dunbaria TILLYARD in DUNBAR & TILLYARD, 1924, p. 203 [**D. fasciipennis*; OD] [= *Doropteron* ZALESSKY, 1946a, p. 64 (type, *D. mirum*)]. Fore wing with anterior margin serrate and distinctly concave; branches of RS without forks; MA and MP arising close to wing base, MA with single fork, MP with 2 or 3 branches; CUA with several branches; CUP unbranched; cuticular thickenings between CUP and 1A. Hind wing venation as in fore wing; anterior margin more deeply concave than that of fore wing; anal area very broad. ROHDENDORF, 1962a; KUKALOVÁ-PECK, 1971; SHAROV & SINITSHENKOVA, 1977. *Perm.*, USA (Kansas), USSR (European RSFSR). —FIG. 26.3. **D. fasciipennis*; a, fore wing, $\times 3.6$; b, hind wing, $\times 3.7$; c, dorsal view, $\times 1.7$ (all Kukalová-Peck, 1971).

Epitethe HANDLIRSCH, 1906b, p. 103 [**Spilaptera*

meunieri BRONGNIART, 1893, p. 343; OD]. Similar to *Palaeoptilus*, but R without terminal branches; area between R and RS with straight (not sigmoidal) crossveins. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).

Homaloneura BRONGNIART, 1885a, p. 66 [**H. elegans*; OD] [= *Homaloneurina* HANDLIRSCH, 1906b, p. 106 (type, *Homaloneura bonnieri* BRONGNIART); *Homaloneurites* HANDLIRSCH, 1906b, p. 107 (type, *Homaloneura joannae* BRONGNIART)]. Anterior margins of wings usually with only slight concavity; venation very similar to that of *Spilaptera*; a cuticular ridge extending from near base to 1A to R. BRONGNIART, 1893; HANDLIRSCH, 1922; CARPENTER, 1964b; KUKALOVÁ, 1969b; CARPENTER & RICHARDSON, 1971. *U. Carb.*, Europe (France), USA (Illinois).—FIG. 27, a. **H. elegans*, France; dorsal view of wings, head, and part of thorax, $\times 1.3$ (Kukalová, 1969b).

—FIG. 27, b. *H. dabasinskasi* CARPENTER, Illinois; fore and hind wings, $\times 1.5$ (Carpenter, new).

Lamproptilia BRONGNIART, 1885a, p. 63 [**L. grandeuryi*; OD]. Fore wing unusually broad; hind wing broader than fore; cubital-anal area forming distinct lobe; R without terminal branches; cuticular thickenings near wing base apparently absent. BRONGNIART, 1893; HANDLIRSCH, 1906b; KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).

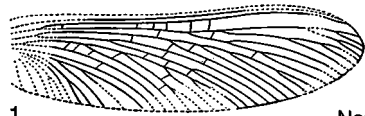
—FIG. 25, 5. **L. grandeuryi*; a, fore and b, hind wings, $\times 0.8$ (Kukalová, 1969b).

Mcluckiepteron RICHARDSON, 1956, p. 20 [**M. luciae*; OD]. Little-known genus, based on isolated hind wing. Costal margin serrate and strongly concave; SC and R very close together distally; RS with pectinate branching; MA with only small fork; MP more extensively branched; CUA with many branches; CUP unbranched. [Family assignment doubtful.] *U. Carb.*, USA (Illinois).—FIG. 26, 2. **M. luciae*; hind wing, $\times 0.8$ (Richardson, 1956).

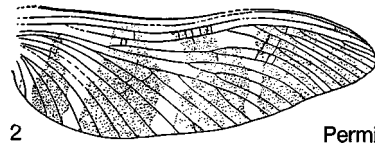
Neuburgia MARTYNOV, 1931a, p. 74 [**N. altaica*; OD]. Fore wing unusually slender; RS arising near wing base and M forked at level of origin of RS; CUP unbranched. [Family assignment uncertain.] ROHDENDORF & others, 1961; ROHDENDORF, 1962a; KUKALOVÁ, 1969b; SHAROV & SINITSHEKOVÁ, 1977. *U. Carb.*, USSR (Asian RSFSR).—FIG. 25, 1. **N. altaica*; fore wing, $\times 1.3$ (Martynov, 1931a).

Palaeoptilus BRONGNIART, 1893, p. 352 [**P. brullei*; OD]. Similar to *Becquerelia*, but MA apparently not coalesced with RS. [Probably a synonym of *Becquerelia*.] HANDLIRSCH, 1906b; KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).

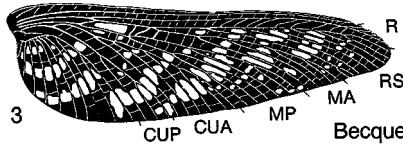
Paradunbaria SHAROV & SINITSHEKOVÁ, 1977, p. 54 [**P. pectinata*; OD]. Similar to *Dunbaria*, but RS and CUA with more extensive branching. *Perm.*, USSR (Asian RSFSR).—FIG. 26, 1. **P. pectinata*; ventral view, $\times 1.5$ (Sharov & Sinitshechkova, 1977).



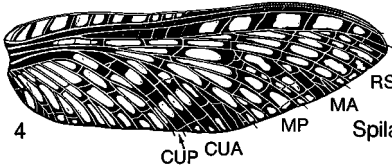
Neuburgia



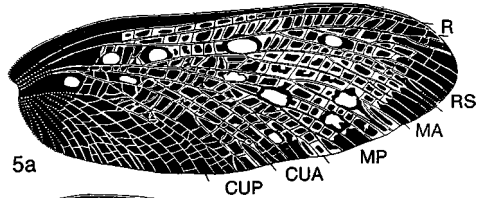
Permiakovia



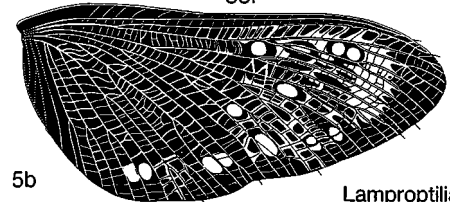
Becquerelia



Spilaptera



5a



5b

Lamproptilia

FIG. 25. Spilapteridae (p. 38–39).

Permiakovia MARTYNOV, 1940, p. 7 [**P. quinquefasciata*; OD]. Similar to *Dunbaria* but with several branches of RS deeply forked. ROHDENDORF, 1962a; SHAROV & SINITSHEKOVÁ, 1977. *Perm.*, USSR (European and Asian RSFSR).—FIG. 25, 2. **P. quinquefasciata*; fore wing, $\times 1.3$ (Martynov, 1940).

Spiloptilus HANDLIRSCH, 1906b, p. 100 [**Graphiptilus ramondi* BRONGNIART, 1893, p. 351; OD]. Little-known genus. RS originating almost at level of midwing; M dividing much nearer to wing base. [Family assignment doubtful.] KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).

Tectoptilus KUKALOVÁ, 1969b, p. 193 [**Becquer-*

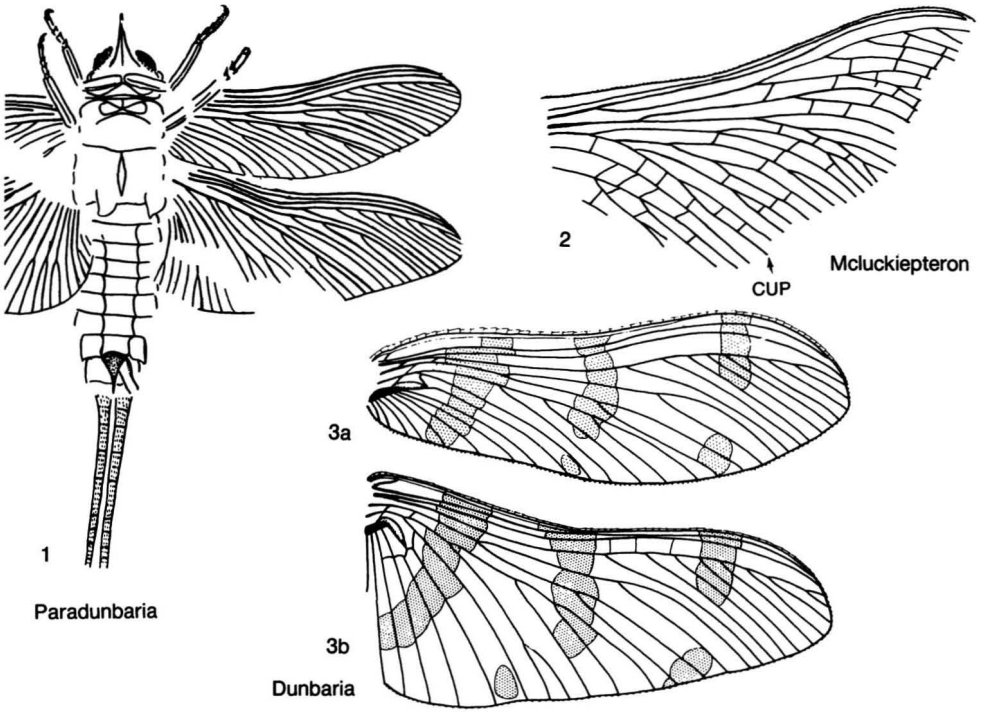


FIG. 26. Spilapteridae (p. 38–39).

elia grebanti BRONGNIART, 1893, p. 359; OD]. Wings without cuticular thickenings between 1A and CUP, with fewer branches than in *Epitetbe* and *Palaeoprilus*. HANDLIRSCH, 1906b. *U. Carb.*, Europe (France).

Vorkutoneura SINITSHENKOVA in SHAROV & SINITSHENKOVA, 1977, p. 60 [**V. variabilis*; OD]. Hind wing very broad basally; RS, MA, MP, and CUA multibranching. *Perm.*, USSR (European RSFSR).

Family ELMOBORIIDAE Carpenter, 1976

[Elmoberiidae CARPENTER, 1976, p. 349]

Fore wing slender, at least 4 times as long as wide, broadest distally; vein R close to and parallel to SC, except distally; RS with several long branches; M forking nearly at same level as origin of RS; MP forking almost immediately after its origin from M, with 2 or 3 branches; CU forking near base of wing; CUA and CUP deeply forked; crossveins weak, apparently generally distributed over wing area. Hind wing and body unknown. *Perm.*

Elmoberia CARPENTER, 1976, p. 350 [**E. piperi*; OD]. Fore wing with R extending almost to wing apex; RS dichotomously branched, with 4 terminal branches; MA unbranched; MP₃₊₄ deeply forked. *Perm.*, USA (Kansas).—FIG. 28,2. **E. piperi*; fore wing, (Carpenter, 1976).

Oboeria KUKALOVÁ, 1960, p. 245 [**O. longa*; OD]. Similar to *Elmoberia*, but RS apparently with 7 or 8 terminal branches and MA deeply forked. CARPENTER, 1976. *Perm.*, Europe (Czechoslovakia).

Family SYNTONOPTERIDAE Handlirsch, 1911

[Syntonopteridae HANDLIRSCH, 1911, p. 299]

Fore wing broadest near midwing; anterior margin with slight curvature basally; vein RS arising near wing base and forking just before midwing; stem of M independent of R basally; MA and MP separating a short interval from wing base, with MA diverging at about 45° angle toward RS and coalescing with it for short interval; MA and MP forked; CUA and CUP diverging near wing base; CUA forked; CUP unbranched; 3 anal veins; crossveins numerous, with some reticulation basally; intercalary veins present between some

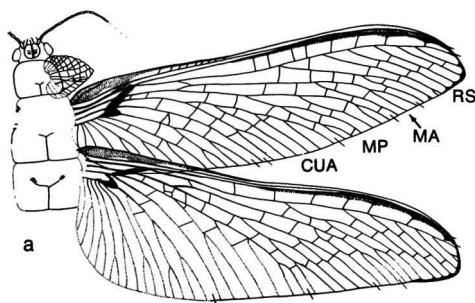


FIG. 27. Spilapteridae (p. 39).

branches of RS, MA, MP, and CUA. Hind wing much broader basally than fore wing, hind margin strongly curved; vein SC terminating just before wing apex; stem of M coalesced with basal part of CUA near wing base; immediately after its origin, MA coalescing with RS for short interval, as in fore wing; CUP with prominent bend directed toward hind margin of wing; crossveins and intercalary veins present as in fore wing. Body little known; antennae very thin and pronotal lobes apparently small. *U. Carb.*

[The Syntonopteridae are considered by some investigators (EDMUNDS & TRAVER, 1954; EDMUNDS, 1972; WOOTTON, 1981) to

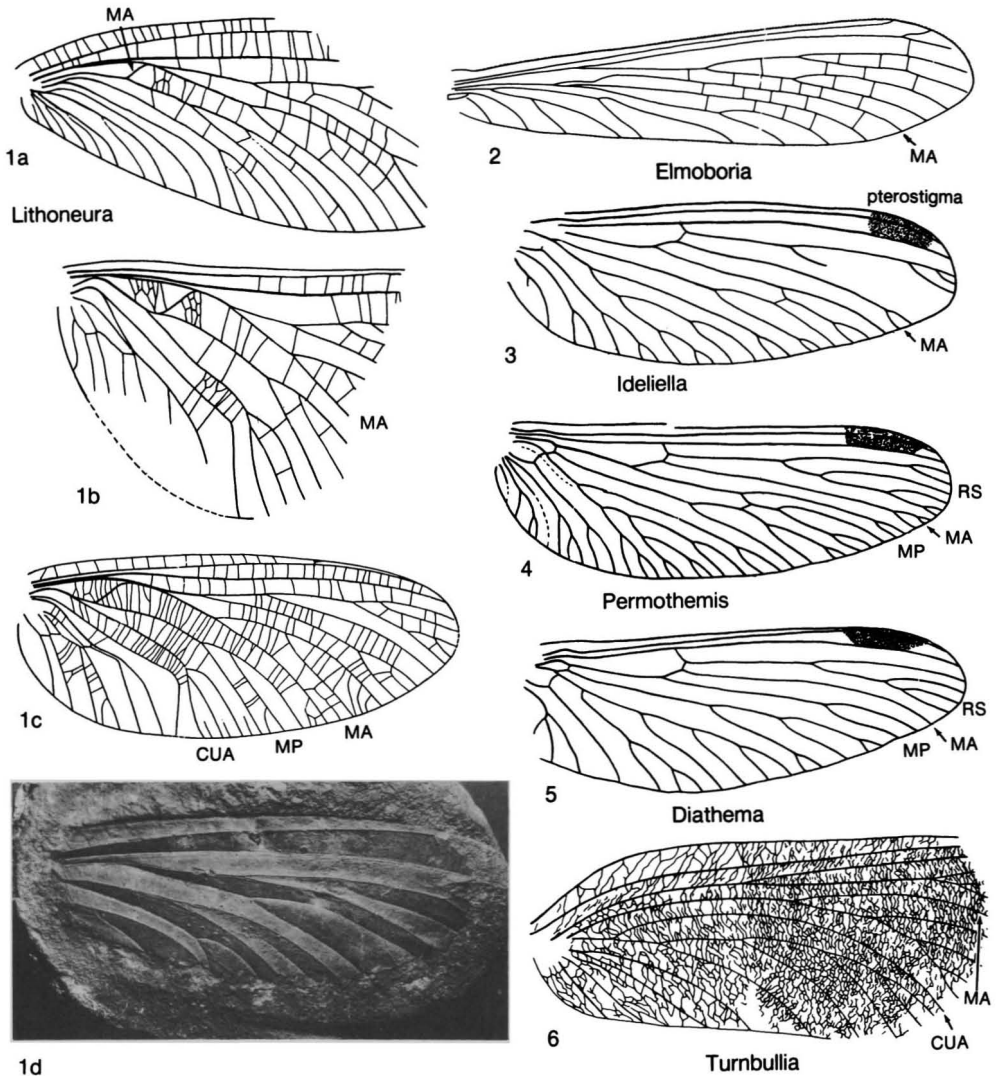


FIG. 28. Elmoboriidae, Syntonopteridae, Permothemistidae, Diathemidae, and Uncertain (p. 41–45).

belong to the order Ephemeroptera, chiefly because of the presence of intercalary veins. However, KUKALOVÁ-PECK (HUBBARD & KUKALOVÁ-PECK, 1980) has reported the presence of a haustellate beak in the type specimen of the syntonopterid genus *Lithoneura*. All the Paleozoic Ephemeroptera known had normal, dentate mandibles.]

Syntonoptera HANDLIRSCH, 1911, p. 299 [**S. schuberti*; OD]. Little-known genus, based on fragment of fore wing. Costal area broad basally, narrowed near midwing; RS coalesced with MA

near wing base. CARPENTER, 1938, 1944; LAURENTIAUX, 1953. *U. Carb.*, USA (Illinois). **Lithoneura** CARPENTER, 1938, p. 446 [**L. lameerei*; OD]. Fore wing similar to that of *Syntonoptera*, but costal area much narrower basally; coalescence of MA and RS more remote from wing base. Hind wing broadly oval; RS with 1 long and 3 short intercalary sectors; MA, MP, and CUA each with 1 intercalary vein. CARPENTER, 1944; RICHARDSON, 1956. *U. Carb.*, USA (Illinois).—FIG. 28, 1a, b. **L. lameerei*; a, fore and b, hind wings, $\times 1.6$ (Carpenter, 1938).—FIG. 28, 1c. *L. mirifica* CARPENTER; hind wing, $\times 0.7$ (Carpenter, 1944).—FIG. 28, 1d. *L. carpenteri* RICHARDSON; fore wing, $\times 1.5$ (Carpenter, new).

Family PERMOTHEMISTIDAE

Martynov, 1938

[*nom. correct.* ROHDENDORF, 1962a, p. 55, ex Permothemidae MARTYNOV, 1938b, p. 37]

Fore wing with vein SC long, extending to wing apex; pterostigma present; RS arising in basal third of wing; CUA and CUP separating at base of wing; RS, MP, CUA, and CUP branched and usually with marginal forks. Hind wings absent. Antennae long and slender; eyes large; prothoracic lobes apparently absent; cerci long; ovipositor short, curved. *Perm.*

Permothemis MARTYNOV, 1934, p. 995, *nom. subst. pro Palaeothemis* MARTYNOV, 1932, p. 12, *non* FRASER, 1923 [**Palaeothemis libelluloides*; OD]. Fore wing: pterostigma at least 3 times as long as wide; MP with several dichotomous branches; CUA with 3 or 4 branches. ROHDENDORF, 1962a; SINITSHENKOVA, 1980b. *Perm.*, USSR (European RSFSR).—FIG. 28,4. **P. libelluloides*; fore wing, $\times 3$ (Sinitschenkova, 1980b).

Ideliella ZALESSKY, 1937c, p. 107 [**I. decora*; OD]. Fore wing: pterostigma broader than in *Permothemis*; MP and CUA each with only 1 long fork. ROHDENDORF, 1962a; SINITSHENKOVA, 1980b. *Perm.*, USSR (Asian RSFSR).—FIG. 28,3. **I. decora*; fore wing, $\times 4.5$ (Sinitschenkova, 1980b).

Pauciramus SINITSHENKOVA, 1980b, p. 99 [**P. demoulini*; OD]. Similar to *Permothemis*, but pterostigma longer; MA unbranched, MP forked once. *Perm.*, USSR (Asian RSFSR).

Permothemidia ROHDENDORF, 1940b, p. 109 [**P. caudata*; OD] [= *Uralothemis* ZALESSKY, 1951c, p. 270 (type, *U. bellus*)]. Fore wing with pterostigma short, about twice as long as wide; RS with 5 to 6 branches directed posteriorly. SINITSHENKOVA, 1980b. *Perm.*, USSR (Asian RSFSR).

Family DIATHEMIDAE

Sinitschenkova, 1980

[Diathemidae SINITSHENKOVA, 1980b, p. 101]

Fore wing with pterostigma about 4 times as long as wide; veins MP and CUA not anastomosed; 3 anal veins. Hind wing present but greatly reduced, with little venation. *Perm.*

DiatHEMA SINITSHENKOVA, 1980b, p. 102 [**D. tenerum*; OD]. MP of fore wing with 2 branches. *Perm.*, USSR (Asian RSFSR).—FIG. 28,5. **D. tenerum*; fore wing, $\times 4$ (Sinitschenkova, 1980b).

DiatHEMIDIA SINITSHENKOVA, 1980b, p. 105 [**D. monstruosa*; OD]. Fore wing similar to *Dia-*

thema, but MP with 3 branches. *Perm.*, USSR (Asian RSFSR).

Family PSYCHROPTILIDAE

Riek, 1976

[Psychroptilidae RIEK, 1976c, p. 230]

Palaeodictyoptera of moderate size; hind wing slightly broader than fore wing. Vein RS with 3 branches; MA, CUA, CUP unbranched; MP branched. Body structure little known; pronotal lobes apparently absent. *U. Carb.*

Psychroptilus RIEK, 1976c, p. 230 [**P. burrettiae*; OD]. SC ending on costa about two-thirds wing length from base. [Ordinal assignment uncertain; the family was originally placed in the Megasecoptera.] *U. Carb.*, Tasmania.

Family UNCERTAIN

The following genera, apparently belonging to the order Palaeodictyoptera, are too poorly known to permit family assignments.

Althansia GUTHÖRL, 1934, p. 61 [**A. sabneri*; OD]. Fragment of wing with archedictyon. *U. Carb.*, Europe (Germany).

Ametretus HANDLIRSCH, 1911, p. 303 [**A. laevis*; OD]. Little-known genus, based on basal fragment of large wing. KUKALOVÁ, 1969c. *U. Carb.*, USA (Illinois).

Amosus HANDLIRSCH, 1911, p. 301 [**A. mazonus*; OD]. Little-known genus, based on basal fragment of large wing. KUKALOVÁ, 1969c. *U. Carb.*, USA (Illinois).

Anagesthes HANDLIRSCH, 1906b, p. 70 [**Termes affinis* GOLDENBERG, 1854, p. 31; OD]. Small fragment of wing with archedictyon. GOLDENBERG, 1873. *U. Carb.*, Europe (Germany).

Anthracosta PRUVOST, 1930, p. 147 [**A. dubois*; OD]. Small fragment of large wing. *U. Carb.*, Europe (Germany).

Asiodictya ROHDENDORF, 1961a, p. 70 [**A. rossica*; OD]. Apical fragment of wing with archedictyon. ROHDENDORF, 1962a. *U. Carb.*, USSR (Asian RSFSR).

Bathytaptus HANDLIRSCH, 1906a, p. 686 [**B. falcipennis*; OD]. Apical wing fragment. HANDLIRSCH, 1906b. *U. Carb.*, USA (Alabama).

Bojoptera KUKALOVÁ, 1958c, p. 235 [**B. colorata*; OD]. Fore wing with costal area very broad basally; SC terminating well before apex of wing; RS arising before midwing, with many branches; MA with only 3 branches; MP extensively branched; CUA and its branches strongly curved, forming prominent loop toward CU; CUP also curved but with only 2 terminal branches. Hind wing little known; costal area narrower than in

- fore wing; CUA and CUP more nearly normal in form. *U. Carb.*, Europe (Czechoslovakia).
- Boltonocosta** CARPENTER, 1986, p. 575, *nom. subst. pro Orthocosta* BOLTON, 1912, p. 310, *non* FRITSCH, 1879 [**Orthocosta splendens*; OD]. Little-known genus, based on wing fragment. RS with first fork well beyond midwing; M dividing just beyond point of origin of RS. *U. Carb.*, England.
- Catadyesthus** HANDLIRSCH, 1906b, p. 87 [**Acridites priscus* ANDREE, 1864, p. 163; OD]. Basal fragment of wing. AGNUS, 1902. *U. Carb.*, Europe (Czechoslovakia).
- Componeura** BRONGNIART, 1893, p. 334, *nom. subst. pro Zeilleria* BRONGNIART, 1885a, p. 63, *non* BAYLE, 1878 [**C. fusca*; OD]. Little-known genus, based on wing fragment. RS, MP, and CUA with several branches; MA with 1 fork; crossveins numerous, curved and anastomosed, especially dense distally. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).
- Diexodus** HANDLIRSCH, 1911, p. 302 [**D. debilis*; OD]. Basal fragment of wing. *U. Carb.*, USA (Illinois).
- Eumecoptera** HANDLIRSCH, 1906b, p. 73 [**Termes laxus* GOLDENBERG, 1877, p. 50; OD]. Fragment of wing with archedictyon. *U. Carb.*, Europe (Germany).
- Eurydictyella** CARPENTER, 1986, p. 575, *nom. subst. pro Eurydictya* GUTHÖRL, 1934, p. 49, *non* ULRICH, 1889 [**Eurydictya richteri*; OD]. Little-known genus, based on wing fragment. *U. Carb.*, Europe (Germany).
- Eurythmopteryx** HANDLIRSCH, 1906a, p. 675 [**E. antiqua*; OD]. Little-known genus, based on poorly preserved wing; SC ending on costal margin before apex; crossveins numerous over entire wing, without reticulation. *U. Carb.*, USA (Alabama).
- Gegenemene** HANDLIRSCH, 1906b, p. 76 [**Dictyoneura sinuosa* KLIVER, 1883, p. 259; OD]. Little-known genus, based on poorly preserved wing. BRONGNIART, 1893; GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).
- Haplophlebium** SCUDDER, 1867, p. 151 [**H. barnesii*; OD]. Wing fragment with archedictyon. HANDLIRSCH, 1906b. *U. Carb.*, Canada (Nova Scotia).
- Heolus** HANDLIRSCH, 1906b, p. 94 [**H. providentiae*; OD]. Little-known genus, based on small wing fragment. [Type of family Heolidae HANDLIRSCH.] *U. Carb.*, USA (Rhode Island).
- Idoptilus** WOOTTON, 1972, p. 666 [**I. onisciformis*; OD]. Little-known genus, based on nymph. Similar to *Rochdalia* but with different venational pattern in wing pads. [Ordinal assignment uncertain.] *U. Carb.*, England.
- Jongmansia** LAURENTIAUX, 1950, p. 18 [**Mecynoptera tuberculata* BOLTON, 1921, p. 37; OD]. Little-known genus, based on wing fragment. RS much reduced, apparently with series of short branches extending anteriorly toward wing apex and R; MA unbranched; MP with long branches, extending apically only; CUP apparently branched distally. [Type of family Jongmansiidae LAURENTIAUX.] ROHDENDORF, 1962a. *U. Carb.*, England, Europe (Holland).
- Kansasia** TILLYARD, 1937a, p. 85 [**K. pulchra*; OD]. Little-known genus, based on apical fragment; probably related to Diathemidae. [Type of family Kansasiidae DEMOULIN, 1954b, p. 334.] SINITSHENKOVA, 1980b. *Perm.*, USA (Kansas).
- Mammia** HANDLIRSCH, 1906a, p. 671 [**M. alutacea*; OD]. Little-known genus, based on wing fragment. HANDLIRSCH, 1906b. *U. Carb.*, USA (Illinois).
- Mecynoptera** HANDLIRSCH, 1904a, p. 7 [**M. splendida*; OD]. Little-known genus, based on poorly preserved wing. [Type of family Mecynopteridae HANDLIRSCH (1904a); placed in Dictyoneuridae by LAMEERE (1917b), and in new order, Archaeohymenoptera, by HAUPT (1941).] *U. Carb.*, Europe (Belgium).
- Mecynostomites** HANDLIRSCH, 1919b, p. 535 [**M. brongniarti*; OD]. Little-known genus, based on wing fragment. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).
- Monsteropterum** KUKALOVÁ-PECK, 1972, p. 259 [**M. moravicum*; OD]. Little-known genus, based mainly on body structures and wing bases, including details of beak and legs. *Perm.*, Europe (Czechoslovakia).
- Palaioptus** HANDLIRSCH, 1906a, p. 687 [**P. mazonus*; OD]. Apical wing fragment with archedictyon. HANDLIRSCH, 1906b. *U. Carb.*, USA (Illinois).
- Palapteris** GUTHÖRL, 1940, p. 41 [**P. stenodictyus*; OD]. Little-known genus, based on wing fragment. MA, MP, CUA, and CUP apparently unbranched. [Ordinal assignment doubtful.] *U. Carb.*, Europe (Germany).
- Paramecynostoma** HANDLIRSCH, 1919b, p. 535 [**P. dobrnianum*; OD]. Little-known genus, based on small fragment of wing. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).
- Paramegaptilus** HANDLIRSCH, 1906b, p. 118 [**Megaptilus scudderi* BRONGNIART, 1893, p. 325; OD]. Small fragment of wing. KUKALOVÁ, 1969c. *U. Carb.*, Europe (France).
- Platephemera** SCUDDER, 1867, p. 151 [**P. antiqua*; OD]. Little-known genus, based on small fragment of wing. [Ordinal assignment doubtful.] SCUDDER, 1868c, 1880; HANDLIRSCH, 1906a. *U. Carb.*, Canada (New Brunswick).
- Propalingenia** HANDLIRSCH, 1906b, p. 86 [**Palalingenia feistmanteli* FRITSCH, 1880, p. 241; OD]. Small fragment of wing. FRITSCH, 1889. *U. Carb.*, Europe (Czechoslovakia).
- Pseudomecynostoma** HANDLIRSCH, 1919b, p. 535 [**P. dubium*; OD]. Little-known genus, based on small fragment of wing. KUKALOVÁ, 1969b. *U. Carb.*, Europe (France).
- Pteronidia** BOLTON, 1912, p. 314 [**P. plicatula*;

- OD]. Little-known genus, based on wing fragment. [Type of family Pteronidiidae BOLTON, 1912.] HANDLIRSCH, 1919b. *U. Carb.*, England.
- Rochdalia** WOODWARD, 1913, p. 352 [**R. parkeri*; OD]. Little-known genus, based on nymph. Pronotum extended laterally; fore wing with very broad triangular costal area; cerci prominent. [Ordinal assignment uncertain.] ROLFE, 1967; WOOTTON, 1972. *U. Carb.*, England.
- Saarlandia** GUTHÖRL, 1930, p. 154 [**S. flexsubcostata*; OD]. Little-known genus, based on poorly preserved wing fragment. [Type of family Saarlandiidae GUTHÖRL, 1930.] *U. Carb.*, Europe (Germany).
- Sabitaptus** PRUVOST, 1930, p. 149 [**S. lagagei*; OD]. Little-known genus, based on poorly preserved hind wing. *U. Carb.*, Europe (Belgium).
- Scepasma** HANDLIRSCH, 1911, p. 302 [**S. gigas*; OD]. Little-known genus, based on small fragment of large wing. KUKALOVÁ, 1969c. *U. Carb.*, USA (Illinois).
- Schedoneura** CARPENTER, 1963b, p. 62 [**Brodioptera amii* COPELAND, 1957, p. 54; OD]. Little-known genus, based on incomplete hind wing. *U. Carb.*, Canada (Nova Scotia).
- Severinopsis** KUKALOVÁ, 1958c, p. 232 [**S. vetusta*; OD]. Little-known genus, based on wing fragment with strongly concave anterior margin. [Possibly a spilapterid.] *U. Carb.*, Europe (Czechoslovakia).
- Titanodictya** HANDLIRSCH, 1906a, p. 671 [**Titanophasma jucunda* SCUDDER, 1885a, p. 169; OD]. Distal fragment of wing, with archidictyon. HANDLIRSCH, 1906b. *U. Carb.*, USA (Pennsylvania).
- Turnbullia** RICHARDSON, 1956, p. 27 [**T. luciae*; OD]. Little-known genus, based on basal portion of large wing, probably a fore wing. Costal margin strongly arched basally, costal area relatively wide; RS arising before separation of MA and MP; MP with at least 4 branches; CUA arising near wing base, unbranched and strongly arched; crossveins forming fine network over entire wing, except for basal part of costal area. [Possibly related to the Megaptilidae.] *U. Carb.*, USA (Illinois). — FIG. 28,6. **T. luciae*; fore(?) wing. X0.9 (Carpenter, new).

Order MEGASECOPTERA

Brongniart, 1885

[*nom. correct.* HANDLIRSCH, 1906a, p. 691, *pro* Megasecoptera BRONGNIART, 1885a, p. 65] [=Protohymenoptera TILLYARD, 1924a, p. 111]

Small to large palaeopterous insects; wings homonomous or nearly so; all main longitudinal veins present, forming an alternation of convexities and concavities; archidictyon only rarely present; crossveins usually well

developed, numerous, and evenly distributed in some families (e.g., Aspidothoracidae) but reduced in number and arranged in rows in others (e.g., Protohymenidae); wing membrane hyaline, macrotrichia rarely well developed (e.g., Bardohymenidae); maculations may be present; veins SC and R very close together and usually close to costal margin. Body structure known in very few genera; head small; antennae setaceous, of moderate length; mouthparts haustellate, as in the Palaeodictyoptera; legs and abdomen usually slender, cerci very long, usually longer than body proper; prothoracic lobes and median caudal process absent. Nymphs, best known in the Mischopteridae, with haustellate mouthparts like those of adults; tracheal gills and other aquatic modifications absent. *U. Carb.—Perm.*

The order Megasecoptera, as treated here, comprises only the families formerly included in the suborder Eumegasecoptera (CARPENTER, 1947); the others, previously contained in the suborder Paramegasecoptera (BRUES, MELANDER, & CARPENTER, 1954), are placed in the order Diaphanopteroidea. The separation of these two taxa into orders is based mainly on the palaeopterous condition of the wings in the Megasecoptera (i.e., Eumegasecoptera) and the flexed or folded condition in the Diaphanopteroidea (i.e., Paramegasecoptera). The palaeopterous condition of the wings in the Megasecoptera is conclusively shown in whole insects by the consistent preservation of the wings in outstretched position, as in the Palaeodictyoptera.

Wings of the Megasecoptera are diverse in both form and venation. In the evolution of the order there have apparently been several lines of change: (1) veins SC and R have become closer together and have finally merged with the costa along the anterior margin of the wings (e.g., Aspidothoracidae, Protohymenidae, Bardohymenidae); (2) veins MA and MP have coalesced for varying intervals with their neighboring veins (e.g., Corydaloididae, Mischopteridae, Protohymenidae); (3) crossveins became fewer and

developed in definite rows (e.g., Mischopteridae, Protohymenidae); (4) the wings became slender and petiolate (e.g., Brodiidae and Sphecopteridae). These changes obviously took place several times quite independently. The Corydaloididae appear to have had the most generalized wing form and venation, although the coalescence of RS with MA and of MP with CUA had already started.

The body structure, except for general features, is known in only a few genera, chiefly *Mischoptera* and *Protohymen*. The presence of a haustellate beak, in the nymphs as well as the adults, has now been definitely established, although details are not so well known as in the Palaeodictyoptera. None of the Megasecoptera seem to have had pronotal lobes comparable to those of the Palaeodictyoptera.

The nymphs are known in the Mischopteridae and Brodiidae, as well as in *Lameerites* (family uncertain). Their most striking features are found in the wing pads: the divergent position, the nature of their articulation to the thorax, and the advanced state of the venation. Unlike the developing wings in nymphs of existing insects, those of the Megasecoptera are joined to the thorax only at the articular areas of the adult wing, and they extend obliquely to the sides. The wings appear to have had some freedom of movement and the early development of the venation enhances that view. None of the nymphs appears to have had tracheal gills, swimming legs, or other modifications for an aquatic existence.

The Megasecoptera are obviously close relatives of the Palaeodictyoptera. In fact, during the past thirty years, as the Megasecoptera have become better known, separation of the Palaeodictyoptera and Megasecoptera, on wing venation alone, has become increasingly difficult (CARPENTER, 1962; SINITSHEKOV, 1980a). Eventually, we may come to recognize these two taxa as representing one order, although KUKALOVÁ-PECK (1974b) has indicated that the articular sclerites at the bases of the wings are different in the two groups. In any case, it seems advisable to continue to recognize the two taxa as separate

orders until we know more about the body structure and its diversity in both groups.

Family ASPIDOTHORACIDAE Handlirsch, 1919

[Aspidothoracidae HANDLIRSCH, 1919b, p. 579]

Venation of fore and hind wings similar; vein SC terminating well before wing apex; SC and R very close together and submarginal; stem of M very close to R basally, but separate from it; MA free from RS and not diverging toward it; stem of CU very close to that of M but not fused with it; 1 anal vein. Crossveins numerous and nearly uniformly distributed over wings. Prothorax with a conspicuous, thickened notum armed with stout spines. *U. Carb.*

Aspidothorax BRONGNIART, 1893, p. 304 [**A. triangularis*; SD HANDLIRSCH, 1922, p. 202] [= *Protocapnia* BRONGNIART, 1885a, p. 63, *nom. nud.*]. RS arising slightly basad of midwing, with 3 to 5 terminal branches; MA and CUA unbranched, MP forked. HANDLIRSCH, 1906b, 1919b; CARPENTER, 1951. *U. Carb.*, Europe (France).—FIG. 29,8. **A. triangularis*; a, fore and b, hind wings, $\times 1.7$ (Carpenter, 1951).

Family ANCHINEURIDAE Carpenter, 1963

[Anchineuridae CARPENTER, 1963a, p. 44]

Wing elongate-oval (base unknown), anterior margin smoothly curved; vein SC very close to costal margin and terminating near wing apex; R parallel and close to SC; RS with numerous branches; MA free from RS and CUA free from MP; crossveins numerous, irregular, in some areas forming a reticulation; costal margin serrate, with setae; hind margin and some veins with small setae. *U. Carb.*

Anchineura CARPENTER, 1963a, p. 46 [**A. hispanica*; OD]. RS with 6 main branches; MA and CUP unbranched; MP and CUA branched. *U. Carb.*, Europe (Spain).—FIG. 29,10. **A. hispanica*; wing, $\times 1.5$ (Carpenter, 1963a).

Family ASPIDOHYMENIDAE Martynov, 1930

[Aspidohymenidae MARTYNOV, 1930a, p. 80]

Veins SC and R close together; costal space very narrow; MA not anastomosed with RS; anterior branch of RS apparently coalesced

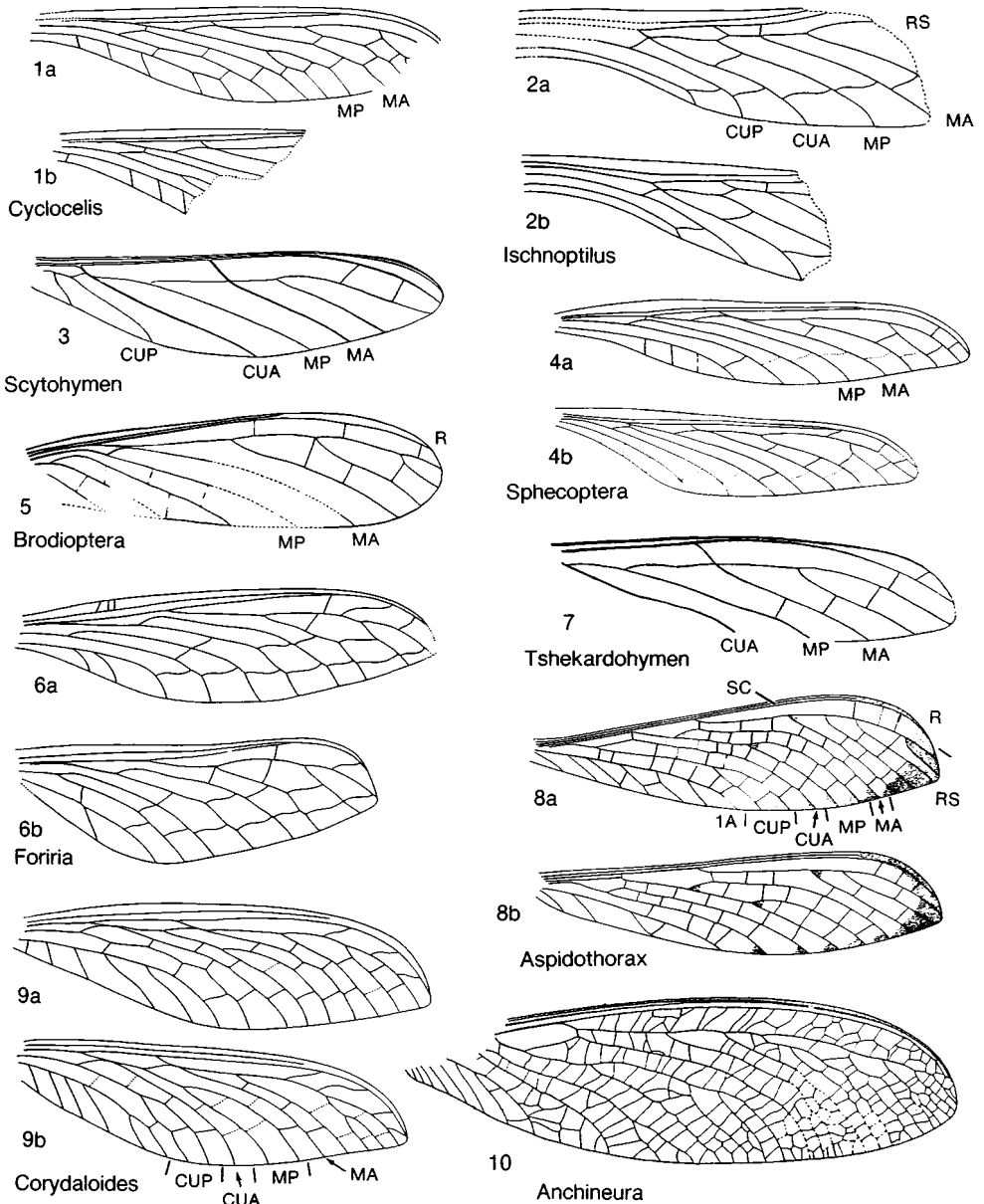


FIG. 29. Aspidothoracidae, Anchineuridae, Corydaloididae, Brodiopteridae, Foririidae, Sphecopteridae, Ischnoptilidae, and Scytohymenidae (p. 46-51).

with R for a short interval; few crossveins, arranged in 2 rows. *Perm.*

Aspidothymen MARTYNOV, 1930a, p. 80 [**A. extensus*; OD]. MA and MP unbranched. CARPENTER, 1930d; MARTYNOV, 1937b; ZALESKY, 1937c. *Perm.*, USSR (European RSFSR).—FIG. 30,2. **A. extensus*; distal half of wing, X2 (Martynov, 1930a).

Family CORYDALOIDIDAE
Handlirsch, 1906

[Corydaloididae HANDLIRSCH, 1906b, p. 314]

Wings broad, as in Mischopteridae. Vein MA anastomosed for very short distance with RS, and CUA anastomosed with M for longer distance. *U. Carb.*

Corydaloides BRONGNIART, 1885a, p. 64 [**C. scuderi*; SD HANDLIRSCH, 1922, p. 201] [= *Corydaloides* HANDLIRSCH, 1919b, p. 579 (type, *Corydaloides simplex* BRONGNIART, 1893, p. 476, pl. 32, fig. 8,9)]. MA unbranched, MP deeply forked; crossveins in main part of wing arranged in 3 rows. HANDLIRSCH, 1906b; CARPENTER, 1951. *U. Carb.*, Europe (France).—FIG. 29,9. **C. scuderi*; *a*, fore and *b*, hind wings, $\times 1$ (Carpenter, 1951).

Family BRODIOPTERIDAE Carpenter, 1963

[Brodiopteridae CARPENTER, 1963b, p. 59]

Little-known family, probably related to the Corydaloididae. Wing broad basally, but vein SC clearly terminating on costa and MA not fused with RS. *U. Carb.*

Brodioptera COPELAND, 1957, p. 53 [**B. cumberlandensis*; OD]. SC terminating a little beyond midwing; RS with several branches; MA, MP, CUA, and CUP unbranched. CARPENTER, 1963b. *U. Carb.*, Canada (Nova Scotia).—FIG. 29,5. **B. cumberlandensis*; wing, $\times 3.5$ (Carpenter, 1963b).

Family FORIRIIDAE Handlirsch, 1919

[Foririidae HANDLIRSCH, 1919b, p. 577]

Vein SC clearly terminating on R; MA free from RS, and CUA free from MP. *U. Carb.*

Foriria MEUNIER, 1908g, p. 172 [**F. maculata*; OD]. RS with 3 terminal branches; other main veins unbranched; crossveins mainly sigmoidal, arranged in 2 rows. HANDLIRSCH, 1919b; CARPENTER, 1951. *U. Carb.*, Europe (France).—FIG. 29,6. **F. maculata*; *a*, fore and *b*, hind wings, $\times 1.5$ (Carpenter, 1951).

Family SPHECOPTERIDAE Carpenter, 1951

[Sphecopteridae CARPENTER, 1951, p. 345]

Wings slender, petiolate; vein SC clearly terminating on R; MA anastomosing with RS for very short distance in fore wing and usually in hind wing; crossveins fewer than in Mischopteridae and forming only 1 complete row in main part of wing. *U. Carb.*

Sphecoptera BRONGNIART, 1893, p. 294 [**S. gracilis*; SD HANDLIRSCH, 1922, p. 205]. Crossveins slightly sigmoidal; MP unbranched. HANDLIRSCH, 1906b; CARPENTER, 1951; ROHDENDORF, 1962a. *U. Carb.*, Europe (France).—FIG. 29,4. **S.*

gracilis; *a*, fore and *b*, hind wings, $\times 1$ (Carpenter, 1951).

Cyclocelis BRONGNIART, 1893, p. 290 [**C. chatini*; SD HANDLIRSCH, 1922, p. 204]. Crossveins straight; MP deeply forked. HANDLIRSCH, 1906b; CARPENTER, 1951. *U. Carb.*, Europe (France).—FIG. 29,1. **C. chatini*; *a*, fore and *b*, hind wings, $\times 1$ (Carpenter, 1951).

Family ISCHNOPTILIDAE Carpenter, 1951

[Ischnoptilidae CARPENTER, 1951, p. 349]

Wings slender, petiolate; vein MA anastomosed with RS for much greater interval than in Sphecopteridae; CUA anastomosed with MP for short interval. *U. Carb.*

Ischnoptilus BRONGNIART, 1893, p. 296 [**I. elegans*; OD]. Crossveins sigmoidal, forming single row. HANDLIRSCH, 1906b; CARPENTER, 1951; ROHDENDORF, 1962a. *U. Carb.*, Europe (France).—FIG. 29,2. **I. elegans*; *a*, fore and *b*, hind wings, $\times 2.6$ (Carpenter, 1951).

Family MISCHOPTERIDAE Handlirsch, 1906

[Mischopteridae HANDLIRSCH, 1906b, p. 316]

Vein SC more remote from margin of wing than in Aspidothoracidae; MA anastomosed for very short interval with RS; crossveins regularly arranged, forming 2 or 3 rows over most of wing. Prothorax very short, with or without lateral spines. *U. Carb.*

Mischoptera BRONGNIART, 1893, p. 283, *nom. subst. pro Woodwardia* BRONGNIART, 1885a, p. 64, *non* CROSSE & FISCHER, 1861 [**Woodwardia nigra* BRONGNIART, 1885a, p. 64; SD HANDLIRSCH, 1922, p. 203]. Both fore and hind wings falcate; most crossveins strongly sigmoidal; circular, cuticular thickenings regularly distributed over each wing. Prothorax with lateral spines. Nymph with similar lateral spines and similar venation in wing buds. CARPENTER, 1951. *U. Carb.*, Europe (France), USA (Illinois).—FIG. 30,3a-c. **M. nigra* (BRONGNIART); *a*, whole insect, $\times 0.4$, *b*, fore wing, $\times 0.7$, *c*, hind wing, $\times 0.7$ (Carpenter, 1951).—FIG. 30,3d,e. *M. douglassi* CARPENTER & RICHARDSON, Illinois; nymph, *d*, $\times 1.5$, *e*, $\times 1.9$ (Carpenter & Richardson, 1968).

Psilothorax BRONGNIART, 1893, p. 288 [**Woodwardia longicauda* BRONGNIART, 1885a, p. 64; OD]. Fore wing with an evenly rounded posterior margin, not falcate; crossveins only slightly sigmoidal; cuticular thickenings absent. HANDLIRSCH, 1906b; CARPENTER, 1951; ROHDENDORF, 1962a. *U. Carb.*, Europe (France).

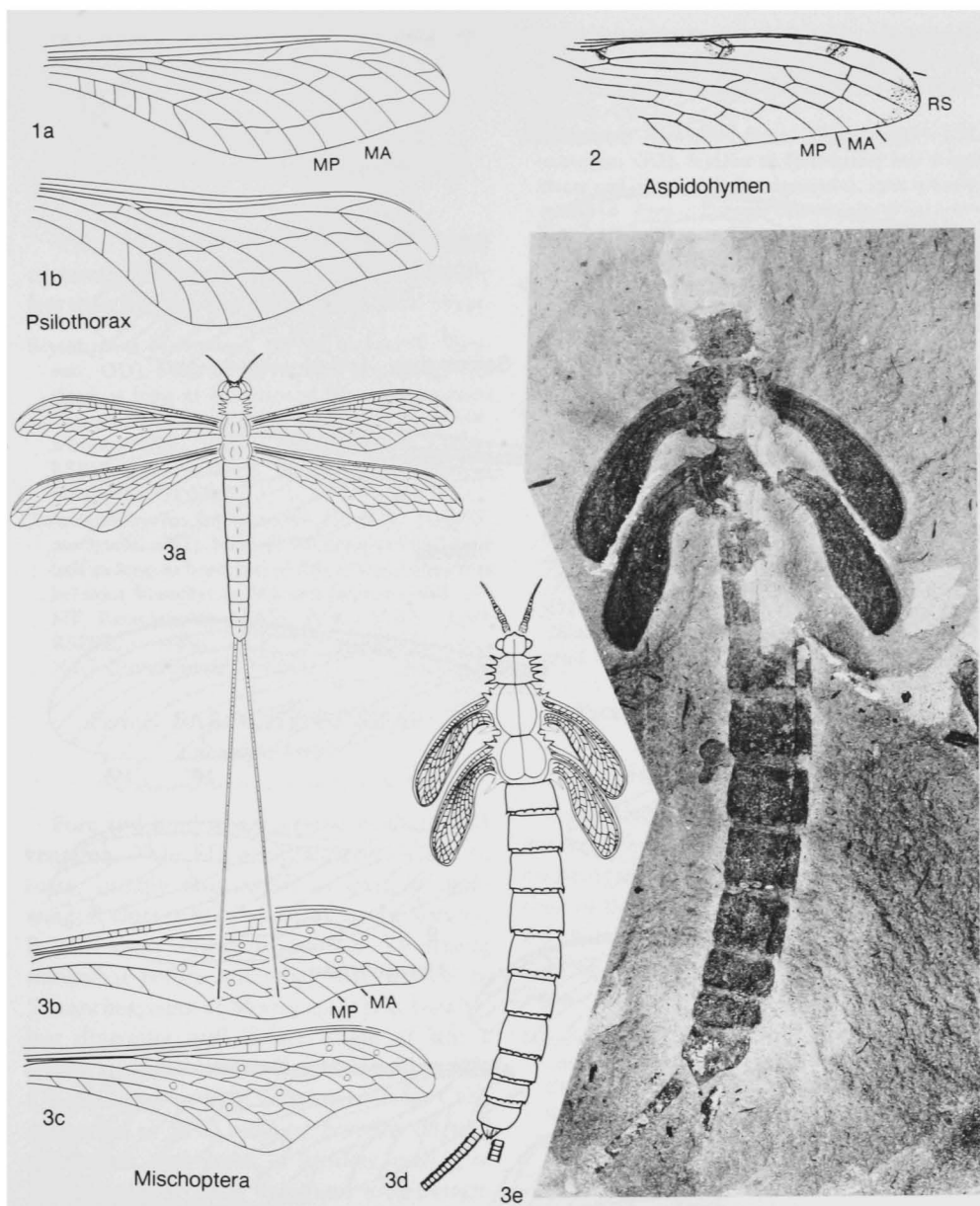


FIG. 30. Aspidohymenidae and Mischoptera (p. 47–49).

—FIG. 30,1. **P. longicauda* (BRONGNIART); *a*, fore and *b*, hind wings, $\times 0.8$ (Carpenter, 1951).

Family PROTOHYMENIDAE
Tillyard, 1924

[Protohymenidae TILLYARD, 1924a, p. 112]

Veins SC and R close to one another and to costal margin; several crossveins (usually

10 to 12) present; MA and RS anastomosed. Perm.

Protohymen TILLYARD, 1924a, p. 113 [**P. permianus*; OD] [= *Pseudohymen* MARTYNOV, 1932, p. 5 (type, *P. angustipennis*); *Pseudohymenopsis* ZALESSKY, 1956b, p. 1089 (type, *P. concinna*)]. Wings petiolate or subpetiolate; crossvein between 1A and hind margin remote from wing

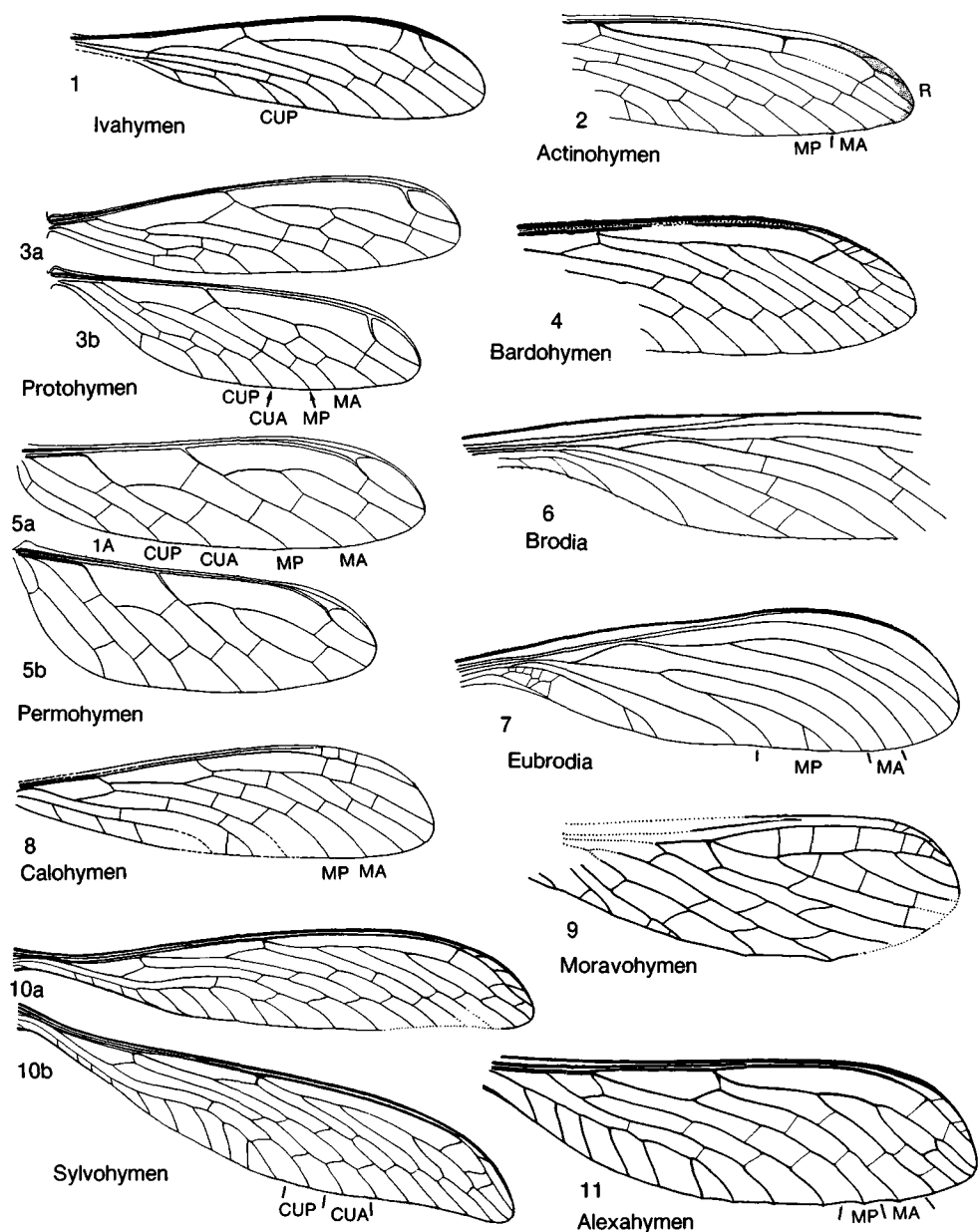


FIG. 31. Protohymenidae, Bardohymenidae, Moravohymenidae, and Brodiidae (p. 49–52).

base; CUP unbranched. CARPENTER, 1947; ROHDENDORF, 1962a. *Perm.*, USA (Kansas, Oklahoma), USSR (Asian RSFSR).—FIG. 31.3. **P. permianus*; a, fore and b, hind wings, $\times 4$ (Carpenter, 1947).
Ivahymen MARTYNOV, 1932, p. 9 [*I. constrictus*; OD]. Wings petiolate; CUP forked distally.

ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 31.1. **I. constrictus*; wing, $\times 3$ (Martynov, 1932).
Permohymen TILLYARD, 1924a, p. 115 [*P. schucherti*; OD]. Wings broad basally; crossveins between 1A and margin near base of wing; CUP unbranched. CARPENTER, 1930d, 1947. *Perm.*,

USA (Kansas, Oklahoma).—FIG. 31,5. **P. schuchberti*; *a*, fore and *b*, hind wings, $\times 4$ (Carpenter, 1930d).

Family SCYTOHYMENIDAE Martynov, 1937

[Scytohymenidae MARTYNOV, 1937b, p. 58]

Veins SC and R close to one another and to costal margin; crossveins very few (usually less than 6); MA and RS anastomosed. *Perm.*

Scytohymen MARTYNOV, 1937b, p. 58 [**S. extremus*; OD]. Stem of RS beyond MA about one-third as long as branches of RS; no crossveins between branches of RS or between MA and MP. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).—FIG. 29,3. **S. extremus*; wing, $\times 1.3$ (Martynov, 1937b).

Tshekardohymen ROHDENDORF, 1940a, p. 106 [**T. martynovi*; OD]. Stem of RS beyond MA about half as long as branches of RS; a single crossvein between branches of RS and between MA and MP. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).—FIG. 29,7. **T. martynovi*; wing, $\times 1.7$ (Rohdendorf, 1962a).

Family BARDOHYMENIDAE Zalessky, 1937

[Bardohymenidae ZALESSKY, 1937a, p. 601]

Fore and hind wings similar in shape and venation. Vein SC weak and very close to costa, usually obsolescent at least by midwing; R close to SC and costa, except distally; R with short terminal branches; RS arising somewhat before midwing, with from 2 to 5 branches; stem of M very close to R basally, but diverging well before origin of RS; a strong crossvein connecting MA to R or RS; CU coalesced at base with stem of M; CUA connected to M by strong crossvein; 1A well developed, with series of veinlets leading to hind margin of wing; veins and wing margin bearing rows of setae or setal sockets. Head apparently short and broad; antennae long, setaceous; meso- and metathorax large; female with prominent ovipositor. *Perm.*

Bardohymen ZALESSKY, 1937a, p. 602 [**B. magnipennifer*; OD]. RS with 5 terminal branches. ROHDENDORF, 1962a; KUKALOVÁ-PECK, 1972. *Perm.*, USSR (Asian RSFSR).—FIG. 31,4. **B. magnipennifer*; wing, $\times 1$ (Zalessky, 1937a).

Actinohymen CARPENTER, 1962, p. 37 [**A. russelli*;

OD]. RS with 3 terminal branches; wing broadest near midwing. *Perm.*, USA (Texas).—FIG. 31,2. **A. russelli*; apical half of wing, $\times 1.7$ (Carpenter, 1962).

Alexahymen KUKALOVÁ-PECK, 1972, p. 254 [**A. maruska*; OD]. Similar to *Sylvohymen* but wings short and broad; 1A not sigmoidal; apex broadly rounded. *Perm.*, Europe (Czechoslovakia).—FIG. 31,11. **A. maruska*; hind wing, $\times 2$ (Kukalová-Peck, 1972).

Calohymen CARPENTER, 1947, p. 30 [**C. permianus*; OD]. RS with 3 terminal branches; wing broadest apically. *Perm.*, USA (Oklahoma).—FIG. 31,8. **C. permianus*; wing, $\times 2$ (Carpenter, 1947).

Sylvohymen MARTYNOV, 1940, p. 10 [**S. robustus*; OD]. Wings long and slender, tapered markedly in basal third; hind margin of fore wing nearly straight, that of hind wing smoothly curved; RS with 4 terminal branches; 1A sigmoidal in both wings; thorax and abdomen with prominent spines. CARPENTER, 1947, 1962; KUKALOVÁ-PECK, 1972; ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR), USA (Oklahoma).—FIG. 31,10. *S. sibiricus* KUKALOVÁ-PECK, USSR; *a*, fore and *b*, hind wings, $\times 1.3$ (Kukalová-Peck, 1972).

Family MORAVOHYMENIDAE Kukalová-Peck, 1972

[Moravohymenidae KUKALOVÁ-PECK, 1972, p. 256]

Little-known family, apparently related to Bardohymenidae. Hind wing broadest beyond midwing; vein SC more remote from costa than in Bardohymenidae and R remote from RS distally; MA, MP, and branches of RS curving slightly anteriorly in distal portions. *Perm.*

Moravohymen KUKALOVÁ-PECK, 1972, p. 256 [**M. vitreus*; OD]. Little-known genus; MA, MP, CUA, and CUP unbranched; 1A not parallel to hind margin of wing. *Perm.*, Europe (Czechoslovakia).—FIG. 31,9. **M. vitreus*; hind wing, $\times 4$ (Kukalová-Peck, 1972).

Family BRODIIDAE Handlirsch, 1906

[Brodiidae HANDLIRSCH, 1906b, p. 113]

Wings petiolate; entire wing margin serrate, costal margin more distinctly so; vein SC close to R basally and parallel to it for most of its length, apparently merging with costa beyond midwing, but retaining its identity until near wing apex; R nearly straight to level of midwing, unbranched, and curv-

ing slightly away from costal margin distally; RS arising before midwing, with 3 or 4 branches; M independent of R basally; MA unbranched, diverging anteriorly toward RS but not coalescing with it; MP dividing shortly after level of origin of RS, with at least 2 terminal branches; CUA unbranched; 1A present. Only a few distinct crossveins on wing, but a fine archedictyon present in some genera over much of wing. Differences between fore and hind wings unknown, body structure unknown. *U. Carb.*

Brodia SCUDDER, 1881b, p. 293 [**B. priscocincta*; OD]. Wings broadest at midwing; several distinct, transverse crossveins present, but most of wing surface with uniform pattern of weak crossveins, very close together, not forming an archedictyon. CARPENTER, 1967a. *U. Carb.*, England. —FIG. 31.6. **B. priscocincta*; wing, $\times 1.2$ (Carpenter, 1967a).

Eubrodia CARPENTER, 1967a, p. 73 [**E. dabasin-skasi*; OD]. Similar to *Brodia*, but wing broadest beyond middle; no distinct transverse crossveins present, but archedictyon covering most of wing surface. CARPENTER & RICHARDSON, 1971. *U. Carb.*, USA (Illinois). —FIG. 31.7. **E. dabasin-skasi*; wing, $\times 1.2$ (Carpenter & Richardson, 1971).

Family ANCOPTERIDAE Kukulová-Peck, 1975

[Ancopteridae KUKALOVÁ-PECK, 1975, p. 10]

Wings slender, but apparently not petiolate; hind margin slightly undulated; vein SC extending well beyond midwing; bases of R and M not coalesced; RS arising well before midwing; MA and CUA unbranched; MP and CUP branched; crossveins numerous, sometimes reticulate and forming intercalary veins. *Perm.*

Ancoptera KUKALOVÁ-PECK, 1975, p. 12 [**A. permiana*; OD]. Apex of wing broadly rounded; SC and R close to costal margin of wing distally. *Perm.*, Europe (Czechoslovakia). —FIG. 32.1. **A. permiana*; wing, $\times 1.8$ (Kukulová-Peck, 1975).

Family VORKUTIIDAE Rohdendorf, 1947

[Vorkutiidae ROHDENDORF, 1947, p. 391]

Little-known family, based on wing fragments. Vein SC coalesced with R beyond

level of origin of RS; 2 crossveins between RS and MA. *U. Carb.—Perm.*

Vorkutia ROHDENDORF, 1947, p. 391 [**V. tsbernovi*; OD]. Little-known genus. No crossvein between stem of RS and MA. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).

Sibiriohymen ROHDENDORF, 1961a, p. 76 [**S. asiaticus*; OD]. One crossvein between stem of RS and MA. *U. Carb.*, USSR (Asian RSFSR).

Family ALECTONEURIDAE Kukulová-Peck, 1975

[Alectoneuridae KUKALOVÁ-PECK, 1975, p. 15]

Little-known family, based on wing fragment. Wings narrow basally but not petiolate; vein SC extending beyond midwing; RS arising before midwing; MA coalescing briefly with RS just after its origin; 1A with long branches. *Perm.*

Alectoneura KUKALOVÁ-PECK, 1975, p. 15 [**A. europaea*; OD]. Subcostal area relatively broad in basal half of wing, with oblique veinlets to wing margin; MA and MP separating at about level of origin of RS. *Perm.*, Europe (Czechoslovakia). —FIG. 32.3. **A. europaea*; wing, $\times 5$ (Kukulová-Peck, 1975).

Family HANIDAE Kukulová-Peck, 1991

[Hanidae KUKALOVÁ-PECK, 1991, p. 193]

Little-known family, based on wing fragments. Wings apparently very slender and petiolate, broadest near midwing; hind margin undulated beyond midwing; vein RS arising at about midwing; CUA apparently unbranched; crossveins very numerous, forming a network in posterior area of wing. *Perm.*

Hana KUKALOVÁ-PECK, 1991, p. 193 [**H. filia*; OD]. RS with 3 or 4 branches distally; 1A closely following posterior margin of wing; wing membrane with a dense covering of tubercles. *Perm.*, Europe (Czechoslovakia). —FIG. 32.7a. **H. filia*; distal part of fore wing, $\times 1.4$ (Kukulová-Peck, 1975). —FIG. 32.7b. *H. lineata* KUKALOVÁ-PECK; basal part of wing, $\times 1.4$ (Kukulová-Peck, 1975).

Family ARCIONEURIDAE Kukulová-Peck, 1975

[Arcioneuridae KUKALOVÁ-PECK, 1975, p. 8]

Little-known family, based on nymphal wing pad and fragments of adult wing. Wing

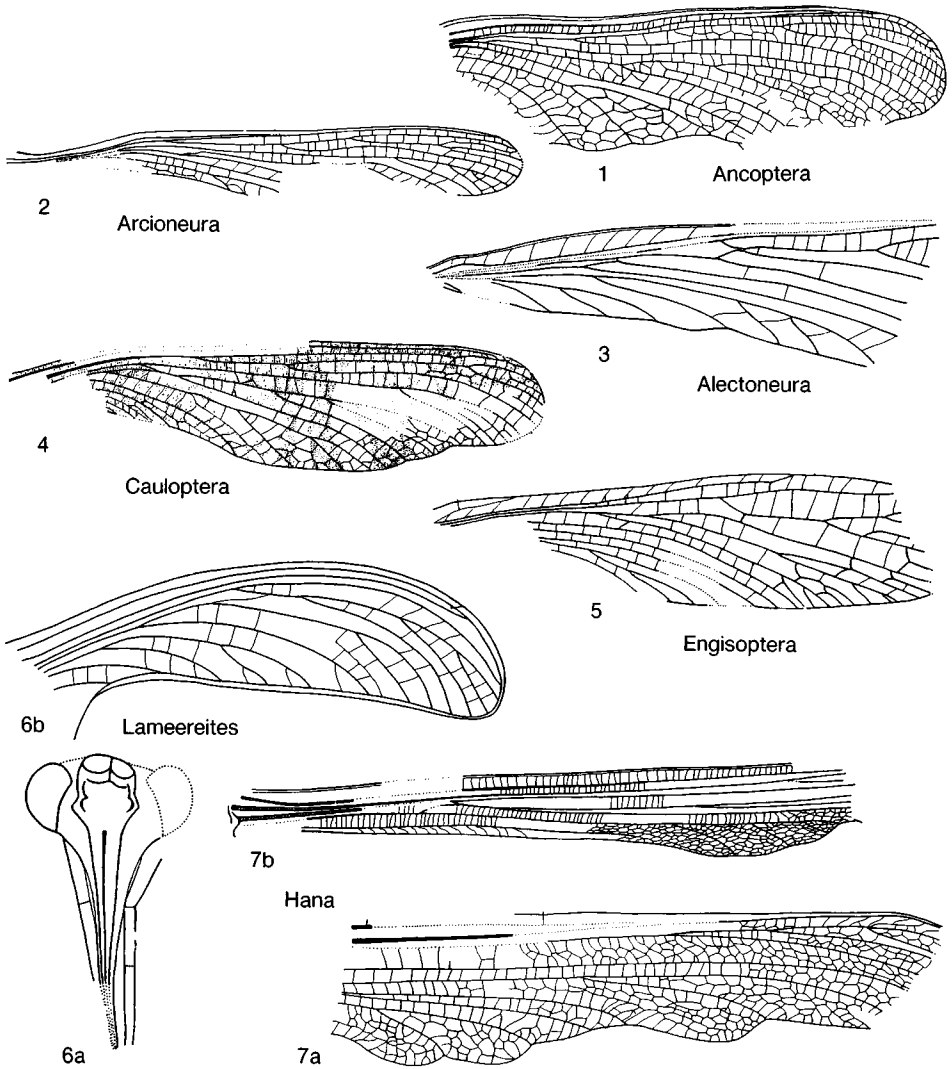


FIG. 32. Ancopteridae, Alectoneuridae, Hanidae, Arcioneuridae, Caulopteridae, Engisopteridae, and Uncertain (p. 52-54).

slender, petiolate; vein SC short; RS arising before midwing; MA and MP with several branches; CUA and CUP with few branches; crossveins numerous, forming intercalary veins. *Perm.*

Arcioneura KUKALOVÁ-PECK, 1975, p. 9 [**A. juveniles*; OD]. Little-known genus, based on nymphal wing pad. R close to costal margin of wing distally; MA with short branches; MP forked at about level of origin of RS. *Perm.*, Europe (Czechoslovakia). — FIG. 32,2. **A. juveniles*; nymphal wing pad, $\times 3.6$ (Kukalová-Peck, 1975).

Anconeura KUKALOVÁ-PECK, 1975, p. 10 [**A. havlatai*; OD]. Little-known genus, based on isolated adult wing. Similar to *Arcioneura* but with more branches on RS and CUA. *Perm.*, Europe (Czechoslovakia).

Family CAULOPTERIDAE
Kukalová-Peck, 1975

[Caulopteridae KUKALOVÁ-PECK, 1975, p. 4]

Little-known family, based on nymphal wing pad; wing slender, probably petiolate; hind margin slightly undulated; vein SC long

extending nearly to apex of wing; bases of R and M apparently not coalesced; RS arising before midwing; both MA and MP branched; MP coalesced with CUA for short distance, just before level of origin of RS; CUA unbranched; CUP branched; crossveins numerous, irregular, forming in some areas short intercalary veins. *Perm.*

Cauloptera KUKALOVÁ-PECK, 1975, p. 4 [**C. colorata*; OD]. RS with 2 long branches; MA with several short branches. *Perm.*, Europe (Czechoslovakia).—FIG. 32.4. **C. colorata*; nymphal wing pad, $\times 1.8$ (Kukalová-Peck, 1975).

Family ENGISOPTERIDAE Kukalová-Peck, 1975

[Engisopteridae KUKALOVÁ-PECK, 1975, p. 13]

Little-known family, based on wing fragment. Wing elongate-oval; vein SC extending well beyond midwing; RS arising just beyond midwing; MA with numerous branches; CUA unbranched, CUP with long branches; crossveins numerous. *Perm.*

Engisoptera KUKALOVÁ-PECK, 1975, p. 13 [**E. simplices*; OD]. RS remote from R for most of its length, with 2 main branches. *Perm.*, Europe (Czechoslovakia).—FIG. 32.5. **E. simplices*; wing, $\times 4$ (Kukalová-Peck, 1975).

Family UNCERTAIN

The genus described below, apparently belonging to the order Megasecoptera, is too poorly known to permit family assignment.

Lameereites HANDLIRSCH, 1911a, p. 375 [**L. curvipennis*; OD]. Little-known genus, based on nymphal wing pads and parts of body; crossveins not arranged in rows. CARPENTER & RICHARDSON, 1968. *U. Carb.*, USA (Illinois).—FIG. 32.6. **L. curvipennis*; a, head, front view, $\times 6$; b, wing pad, $\times 3.8$ (Carpenter & Richardson, 1968).

Order DIAPHANOPTEROIDEA Handlirsch, 1919

[*nom. correct.* ROHDENDORF, 1962a, p. 69, *pro* Diaphanopteroidea HANDLIRSCH, 1919b, p. 575] [=Palaeohymenoptera HAUPT, 1941, p. 99]

Palaeoptera resembling Megasecoptera but with wings held backward along abdomen at rest; fore and hind wings similar in general form and venation; all main longitudinal veins

present, with alternation of convexities and concavities; archidictyon absent, crossveins distinct; in most families, stems of veins R and M very close together, even contiguous, forming a distinct curve; at distal end of this curve MA and MP separating from R, MA nearly bisecting the angle formed by R and MP; head with haustellate beak; cerci very long, as in Megasecoptera; ovipositor present and well developed. Immature stages unknown. *U. Carb.*—*Perm.*

The ordinal relationships of this series of families have been problematical. Most of the species included have previously been assigned to the Megasecoptera because of their very similar wing venation and body structure (e.g., the haustellate beak and long cerci). However, specimens of all families of Diaphanopteroidea in which both wings and body are known (i.e., Diaphanopteridae, Prochopteridae, Martynoviidae, and Asthenohymenidae) are preserved with the wings placed backward along the abdomen, much as in the neopterous insects. On the other hand, the similarity of their wing venation and haustellate mouthparts to those of the Megasecoptera shows that they are actually members of the Palaeoptera that developed a mechanism for flexing the wings back along the abdomen when at rest. That this mechanism was developed independently of the Neoptera seems virtually certain; their haustellate mouthparts eliminate them as ancestral stock of the primitive Neoptera (i.e., Perlaria and Orthopteroidea). Also, the articular plates (pteralia) of the wing bases of the Diaphanopteroidea lack the third axillary characteristic of the wing-flexing mechanism of the Neoptera (KUKALOVÁ-PECK, 1974b).

The wing venation seems to have evolved along similar lines in the Diaphanopteroidea and Megasecoptera, as shown in the Protohymenidae of the Megasecoptera and the Asthenohymenidae of the Diaphanopteroidea. Consequently, specimens consisting of isolated wings or especially of fragments of wings cannot be assigned to either order with confidence. The most characteristic feature of the diaphanopteroidean venation is the cur-

vature of R+M basally and the separation of MA and MP just beyond that point.

Family DIAPHANOPTERIDAE Handlirsch, 1906

[Diaphanopteridae HANDLIRSCH, 1906b, p. 313] [=Diaphanopteritidae HANDLIRSCH, 1919b, p. 575]

Fore and hind wings similar. Vein SC terminating on R slightly beyond midwing; MA diverging from MP directly after its origin and just touching RS before continuing as an independent vein; CUA coalesced with base of M. Several large, thickened, circular spots on membrane of both wings. *U. Carb.*

Diaphanoptera BRONGNIART, 1893, p. 308 [**D. munieri*; SD HANDLIRSCH, 1922, p. 200] [=Diaphanopterites HANDLIRSCH, 1919b, p. 576 (type, *Diaphanoptera superba* MEUNIER, 1908b); *Pseudanthracotbremma* HANDLIRSCH, 1906b, p. 324 (type, *Anthracotbremma scudderi* BRONGNIART, 1893, p. 329)]. RS3+4 and distal part of MA nearly parallel. CARPENTER, 1963d; CARPENTER & RICHARDSON, 1978. *U. Carb.*, Europe (France).—FIG. 33,5a,b. *D. superba*; a, fore and b, hind wings, $\times 1.5$ (Carpenter, 1963d).—FIG. 33,5c. **D. munieri*; fore wing, $\times 1.5$ (Carpenter, 1963d).—FIG. 34. *D. superba*; dorsal view, $\times 1.8$ (Carpenter, new).

Philiasptilon ZALESSKY, 1932a, p. 217 [**P. maculosum*; OD]. Apparently similar to *Diaphanoptera*, but RS3+4 and distal part of MA convergent. [Family assignment uncertain.] PINTO & ORNELLAS, 1978a. *U. Carb.*, USSR (Asian RSFSR), Argentina (Province San Luis).—FIG. 33,8. **P. maculosum*; wing, $\times 1$ (Zalessky, 1932a).

Family PROCHOROPTERIDAE Handlirsch, 1911

[Prochoropteridae HANDLIRSCH, 1911, p. 375]

Little-known family. Wings slender; fore wing with vein SC terminating on R well beyond origin of RS; MA anastomosed with RS for short interval; MP with 3 short, terminal branches; crossveins numerous. Hind wing slightly broader than fore wing, but with similar venation basally. Ovipositor long; cerci about twice as long as entire body. *U. Carb.*

Prochoroptera HANDLIRSCH, 1911, p. 376 [**P. calopteryx*; OD]. Fore wing broadest distally. CARPENTER & RICHARDSON, 1978. *U. Carb.*, USA (Illinois).—FIG. 33,2. **P. calopteryx*; a, fore and

b, hind wings, $\times 2.5$ (Carpenter & Richardson, 1978).

Euchoroptera CARPENTER, 1940b, p. 638 [**E. longipennis*; OD]. Fore wing broadest near midwing. *U. Carb.*, USA (Kansas).—FIG. 33,6. **E. longipennis*; wing, $\times 2.5$ (Carpenter, 1940b).

Family ELMOIDAE Tillyard, 1937

[Elmoidae TILLYARD, 1937a, p. 82]

Fore wing narrow; costal margin slightly arched basally; vein SC terminating on R; RS with 3 terminal branches; MA not coalesced with RS; MP with deep fork; CUA and CUP unbranched; 2 anal veins. Hind wing oval, shorter than fore wing but with similar venation. *Perm.*

Elmoa TILLYARD, 1937a, p. 82 [**E. trisecta*; OD]. SC terminating only slightly beyond level of origin of RS; MP forked to about half its length. ZALESSKY, 1937b; CARPENTER, 1943a, 1947. *Perm.*, USA (Kansas, Oklahoma).—FIG. 33,1. **E. trisecta*; a, fore and b, hind wings, $\times 2.2$ (Carpenter, 1943a).

Family PARELMOIDAE Rohdendorf, 1962

[Parelmoidae ROHDENDORF, 1962a, p. 71]

Vein SC terminating on costal margin a short distance beyond midwing; costal margin strongly curved basally; MA not coalesced with RS; RS with 3 long branches; MP deeply forked; CUA unbranched; 3 anal veins; hind margin of wing angular basally. *Perm.*

Parelmoa CARPENTER, 1947, p. 28 [**P. revelata*; OD]. MA and MP diverging just beyond level of origin of RS. ROHDENDORF, 1962a. *Perm.*, USA (Oklahoma).—FIG. 33,3. **P. revelata*; fore wing, $\times 3.5$ (Carpenter, 1947).

Pseudelmoa CARPENTER, 1947, p. 29 [**P. ampla*; OD]. MA and MP diverging far beyond level of origin of RS and nearly at level of first fork of RS. ROHDENDORF, 1962a. *Perm.*, USA (Oklahoma).—FIG. 33,7. **P. ampla*; fore wing, $\times 2.5$ (Carpenter, 1947).

Family MARTYNOVIIDAE Tillyard, 1932

[Martynoviidae TILLYARD, 1932a, p. 13]

Fore wing moderately slender; costal area broad as far as midwing, much narrowed distally; vein SC terminating on R at about

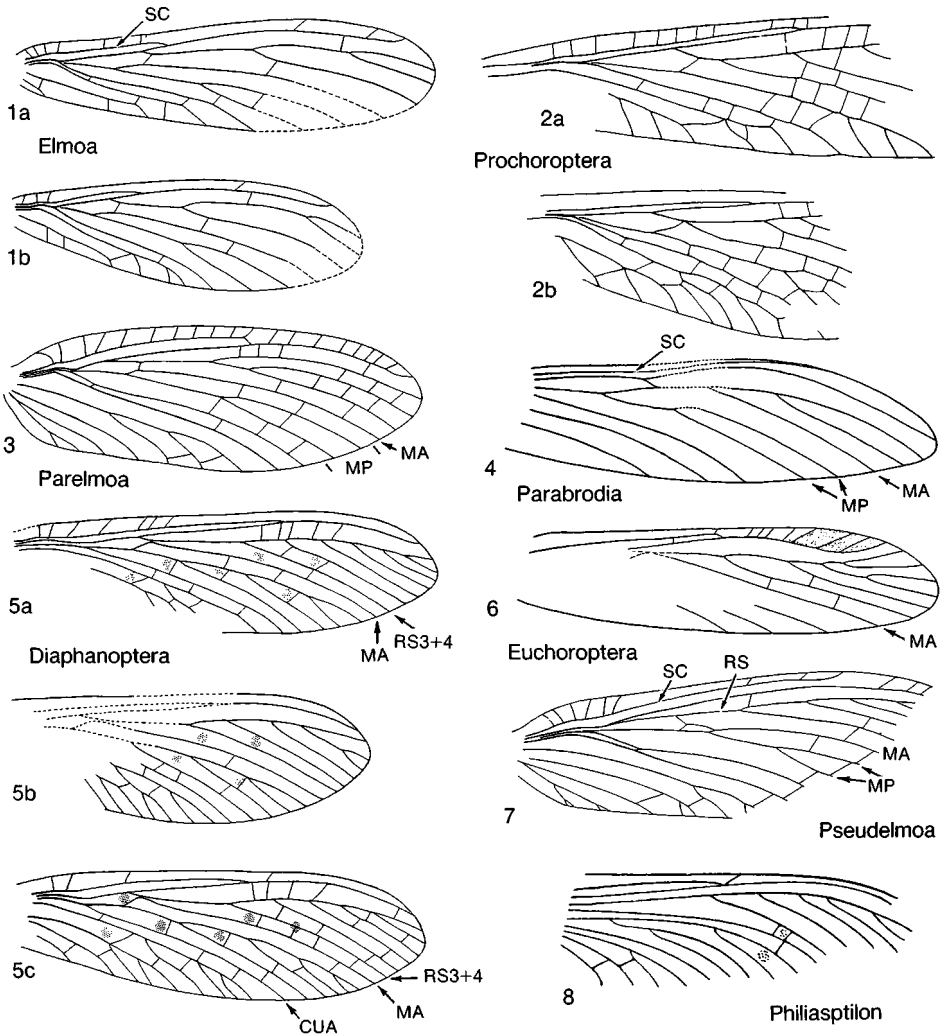


FIG. 33. Diaphanopteridae, Prochoropteridae, Elmoidae, Parelmoidae, and Parabrodiidae (p. 55–58).

midwing; RS with 3 to 5 terminal branches; MA coalesced basally with R or RS or both; MP, CUA, and CUP unbranched; 2 or 3 anal veins. Hind wing similar to fore wing in venation but broader, with strongly curved posterior margin. *Perm.*

Martynovia TILLYARD, 1932a, p. 14 [**M. insignis*; OD] [= *Martynoviella* TILLYARD, 1932a, p. 17 (type, *M. protohymenoides*)]. MA coalesced with RS only, not with R. CARPENTER, 1931b, 1943a, 1947. *Perm.*, USA (Kansas, Oklahoma). — FIG. 35.5. **M. insignis*; a, fore and b, hind wings, $\times 3.5$ (Carpenter, 1943a).

Eumartynovia CARPENTER, 1947, p. 33 [**E. raaschi*; OD]. MA coalesced with stem of R and with RS

for similar lengths. *Perm.*, USA (Oklahoma). — FIG. 35.1. **E. raaschi*; fore wing, $\times 2.5$ (Carpenter, 1947).

Phaneroneura CARPENTER, 1947, p. 33 [**P. martynovae*; OD]. MA coalesced with R for a much greater interval than with RS. *Perm.*, USA (Oklahoma). — FIG. 35.3. **P. martynovae*; fore wing, $\times 4.3$ (Carpenter, 1947).

Family BIARMOHYMENIDAE Zalesky, 1937

[Biarmohymenidae ZALESKY, 1937b, p. 609]

Little-known family. Vein SC remote from R; costal space very broad; MA coalesced with RS from origin of RS nearly to its mid-



Diaphanoptera

FIG. 34. Diaphanopteridae (p. 55).

point; M coalesced with CUA proximally; RS with 2 dichotomous forks. *Perm.*

Biarmohymen ZALESSKY, 1937b, p. 609 [**B. bardense*; OD]. MA and MP unbranched; pterostigma very long. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).—FIG. 35,4. **B. bardense*; wing, $\times 2.2$ (Zalessky, 1937b).

Family ASTHENOHYMENIDAE

Tillyard, 1924

[Asthenohymenidae TILLYARD, 1924a, p. 117]

Small species, with similar fore and hind wings. Stems of all main veins crowded together toward anterior margin of wing base; MA coalesced with R and part of RS; MP coalesced with CUA. Antennae long, with about 24 segments; ovipositor short; cerci

very long, about twice as long as body proper, consisting of about 85 segments. *Perm.*

Asthenohymen TILLYARD, 1924, p. 117 [**A. dunbari*; OD] [= *Karooohymen* RIEK, 1976a, p. 757 (type, *K. delicatulus*)]. RS with 2 branches; MA, MP, CUA, and CUP unbranched. CARPENTER, 1930d, 1931b, 1933a, 1939, 1943a, 1947. *Perm.*, USA (Kansas, Oklahoma), South Africa (Natal).—FIG. 35,2. *A. apicalis* CARPENTER, Oklahoma; fore wing, $\times 12.0$ (Carpenter, 1947).—FIG. 36. **A. dunbari*, Kansas; dorsal view of complete insect, $\times 4.5$ (Carpenter, 1939).

Family RHAPHIDIOPSIDAE

Handlirsch, 1906

[Rhaphidiopsidae HANDLIRSCH, 1906b, p. 319]

Vein SC close to costal margin, apparently terminating at wing apex; MA coalesced with

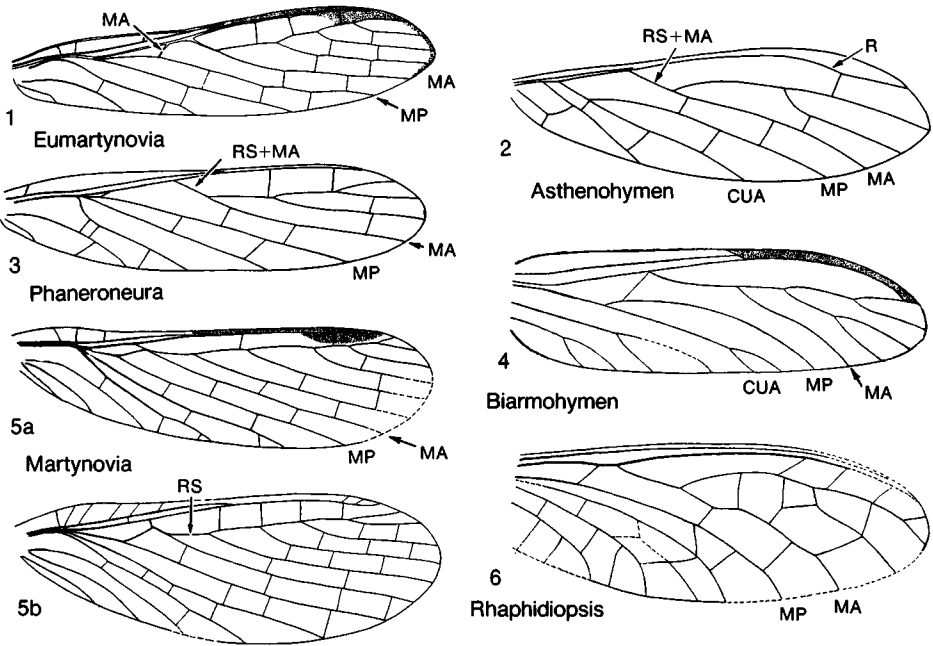


FIG. 35. Martynoviidae, Biarmohymenidae, Asthenohymenidae, and Rhaphidiopsidae (p. 56–58).

RS for short interval; crossveins few, irregular. *U. Carb.*

Rhaphidiopsis SCUDDER, 1893b, p. 11 [**R. diversipenna*; OD]. MA and MP unbranched; RS with deep fork. CARPENTER, 1933a. *U. Carb.*, USA (Rhode Island).—FIG. 35,6. **R. diversipenna*; wing, $\times 1.6$ (Carpenter, 1933a).

Family PARABRODIIIDAE Carpenter, 1933

[Parabrodiidae CARPENTER, 1933b, p. 365]

Vein SC terminating well before apex of wing; MA anastomosed with RS. RS with a single long fork. [Ordinal position uncertain.] *U. Carb.*

Parabrodia CARPENTER, 1933b, p. 366 [**P. carbonaria*; OD]. MA unbranched; MP deeply forked. *U. Carb.*, USA (Kansas).—FIG. 33,4. **P. carbonaria*; wing, $\times 2$ (Carpenter, 1933b).

Family UNCERTAIN

The following genera, which were originally placed in the family Elmoidae, show so much diversity in wing venation and wing form that their separation into a distinct family (or families) seems advisable. Most are

based on isolated wings, virtually nothing being known of their body structure.

Diapha KUKALOVÁ-PECK, 1974a, p. 323 [**P. candida*; OD]. Fore wing slender and long; SC terminating on R just beyond midwing; MA coalesced for a short distance with RS; RS with 6 or 7 terminal branches. *Perm.*, Europe (Czechoslovakia).—FIG. 37,2. **P. candida*; fore wing, $\times 3$ (Kukalová-Peck, 1974a).

Elmodiapha KUKALOVÁ-PECK, 1974a, p. 320 [**E. ovata*; OD]. Fore wing broadly rounded; SC terminating on R beyond midwing; RS with 6 terminal branches; RS and MA not coalesced. *Perm.*, Europe (Czechoslovakia).—FIG. 37,1. **E. ovata*; fore wing, $\times 3$ (Kukalová-Peck, 1974a).

Paradiapha KUKALOVÁ-PECK, 1974a, p. 329 [**P. delicatula*; OD]. Fore wing little known. Hind wing moderately slender, broadest beyond midwing; SC terminating on R beyond midwing; RS with 3 terminal branches; MA very slightly coalesced with RS. *Perm.*, Europe (Czechoslovakia).—FIG. 37,4. **P. delicatula*; hind wing, $\times 4$ (Kukalová-Peck, 1974a).

Permodiapha KUKALOVÁ-PECK, 1974a, p. 323 [**P. carpenteri*; OD]. Fore wing broad; SC terminating on R well beyond midwing; MA coalesced with RS for short interval; RS apparently with 4 terminal branches. Hind wing much broader than fore wing. *Perm.*, Europe (Czechoslovakia).—FIG. 37,6. **P. carpenteri*; hind wing, $\times 3.75$ (Kukalová-Peck, 1974a).

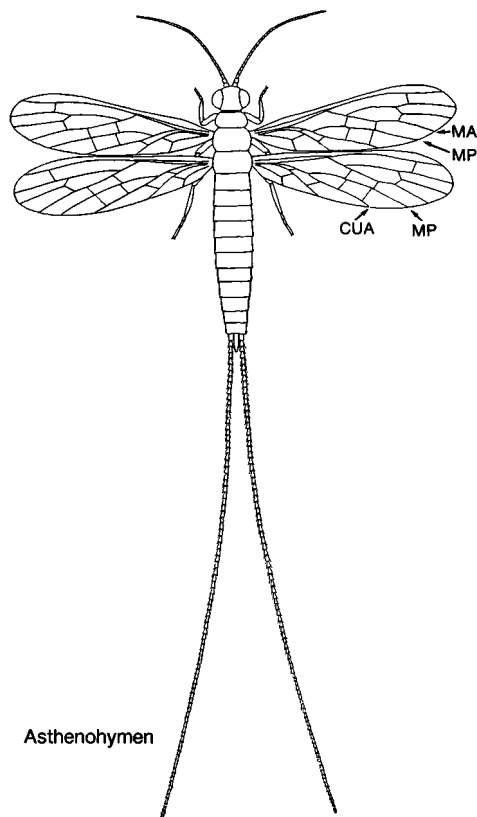


FIG. 36. Asthenohymenidae (p. 57).

Protodiapha KUKALOVÁ-PECK, 1974a, p. 321 [**P. maculifera*; OD]. Hind wing very broad; SC terminating on R beyond midwing; MA and RS not coalesced but connected by very short cross-vein; RS with 5 terminal branches. *Perm.*, Europe (Czechoslovakia).—FIG. 37,5. **P. maculifera*; hind wing, $\times 3.7$ (Kukalová-Peck, 1974a).

Stenodiapha KUKALOVÁ-PECK, 1974a, p. 327 [**S. angusta*; OD]. Fore wing elongate and slender; SC terminating on R well beyond midwing; RS and MA coalesced for short interval; RS with 4 terminal branches. *Perm.*, Europe (Czechoslovakia).—FIG. 37,3. **S. angusta*; fore wing, $\times 3$ (Kukalová-Peck, 1974a).

Order PROTODONATA

Brongniart, 1893

[Protodonata BRONGNIART, 1893, p. 394] [=Meganisoptera MARTYNOV, 1932, p. 17] [FRASER'S erroneous comment (1957, p. 21) on the name of this order has caused much confusion. For a full account of this subject, see CARPENTER, 1960b.]

Large to very large insects. Wings subequal, with similar venation; fore wing usu-

ally more slender and slightly longer than hind wing; setal bases rarely present on wing membrane of some Meganeuridae; anterior margin of wings usually serrate; nodus and pterostigma absent; precostal area present, usually well developed; vein SC extending at least to midwing, usually nearly to wing apex; R long, extending to apex, unbranched; RS arising near wing base and forking before or near midwing, with many branches, including intercalary veins; MA coalesced with R basally, separating from R along with RS (Fig. 38,4a) or fused with RS for a short distance, forming an incipient arculus (Fig. 38,3); MA with numerous branches and intercalary veins; MP apparently absent; CUA also absent or reduced to a short vestigial vein at wing base; CUP strong, sinuously curved, unbranched; 1A long, extending to about midwing, with numerous branches extending to hind margin of wing. Body structure known only in a few Meganeuridae; head globose, with large, dentate mandibles; thorax large, legs stout and spinous; abdomen long and slender, apparently similar to that of the Odonata in general form. Immature stages unknown. *U. Carb.—Perm.*

The Protodonata are obviously closely related to the Odonata and are considered by some entomologists to comprise a sub-order of that order. However, the absence from the protodonate wing of a pterostigma, nodus, and a well-developed arculus justifies the separation of the two orders. Detailed structure of the abdomen, which is highly modified in the Odonata, is not known in the Protodonata, and, since the immature stages of the Protodonata are also not known, there is no evidence that the immature stages were similar in the two groups.

The large, dentate mandibles and the spinous legs, with the fore pair extending anteriorly, strongly indicate that the protodonate adults were predaceous, like those of the Odonata. As such, they were probably important predators on other insects. All known Protodonata were large and some species of the family Meganeuridae, from both the Upper Carboniferous and Permian, had a wing span of about 700 mm.

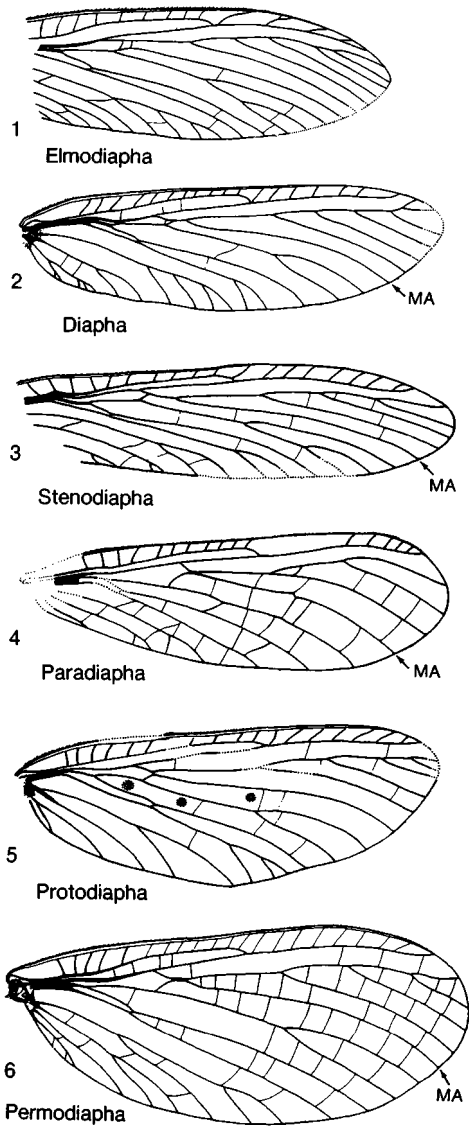


FIG. 37. Uncertain (p. 58–59).

The Protodonata and Odonata share two venational peculiarities. One of these is the presence of intercalary veins, which are also found in some other insects, notably the Ephemeroptera. The other is the absence of two main veins, which have consistently been identified as MP and CUA. The regular alternation of convexities and concavities of the main veins, characteristic of other palaeopterous insects, has been retained. In some pro-

tonates and Palaeozoic odonates, one or two very short veins can be seen near the wing bases and these have been interpreted as vestiges of the missing veins. It seems probable that the venational patterns of the Protodonata and Odonata were derived from common ancestral stock, presumably during the Early Carboniferous, since the Protodonata are known from the Namurian of the Upper Carboniferous.

As defined above, the Protodonata are unknown after the Permian. Several Triassic odonates, recently described by PRITYKINA (1981) from the Soviet Union, had certain features suggestive of the Protodonata, but all had a well-developed nodus.

Family MEGANEURIDAE Handlirsch, 1906

[Meganeuridae HANDLIRSCH, 1906b, p. 306] [=Typidae HANDLIRSCH, 1919b, p. 572; Kohlwaldiidae GUTHÖRL, 1962b, p. 51]

Crossveins very numerous; vein SC long, extending nearly to wing apex; RS1+2 and RS3+4 gradually divergent after their origins. *U. Carb.–Perm.*

Meganeura BRONGNIART, 1885a, p. 60 [**Dictyoneura monyi* BRONGNIART, 1884, p. 833; OD] [=*Meganeurella* HANDLIRSCH, 1919b, p. 569 (type, *M. rapax*)]. Precostal area long, extending nearly to wing apex; very large species. BRONGNIART, 1893; HANDLIRSCH, 1906a; CARPENTER, 1943a; GUTHÖRL, 1962b. *U. Carb.*, Europe (France).—FIG. 38,5. **M. monyi* (BRONGNIART); base of fore wing, $\times 1$ (Carpenter, new).

Boltonites HANDLIRSCH, 1919b, p. 571 [**Meganeura radstockensis* BOLTON, 1914, p. 125; OD]. Little-known genus, based on wing fragment. Precostal area short; anal crossing a short, heavy, oblique vein; 2A arising independently, not as a branch of 1A. *U. Carb.*, England.

Kohlwaldia GUTHÖRL, 1962b, p. 52 [**K. kubni*; OD]. Little-known genus, based on wing fragment, similar to *Tupus*. *U. Carb.*, Europe (Germany).

Meganeuropopsis CARPENTER, 1939, p. 39 [**M. permiana*; OD]. Precostal area much narrower than in *Meganeura*. CARPENTER, 1947. *Perm.*, USA (Kansas, Oklahoma).—FIG. 38,6. *M. americana* CARPENTER, Oklahoma; fore wing, $\times 0.4$ (Carpenter, 1947).

Megatypus TILLYARD, 1925b, p. 52 [**M. schucherti*; OD]. Precostal area as in *Tupus*; anal crossing, at least in hind wing, strongly developed. CAR-

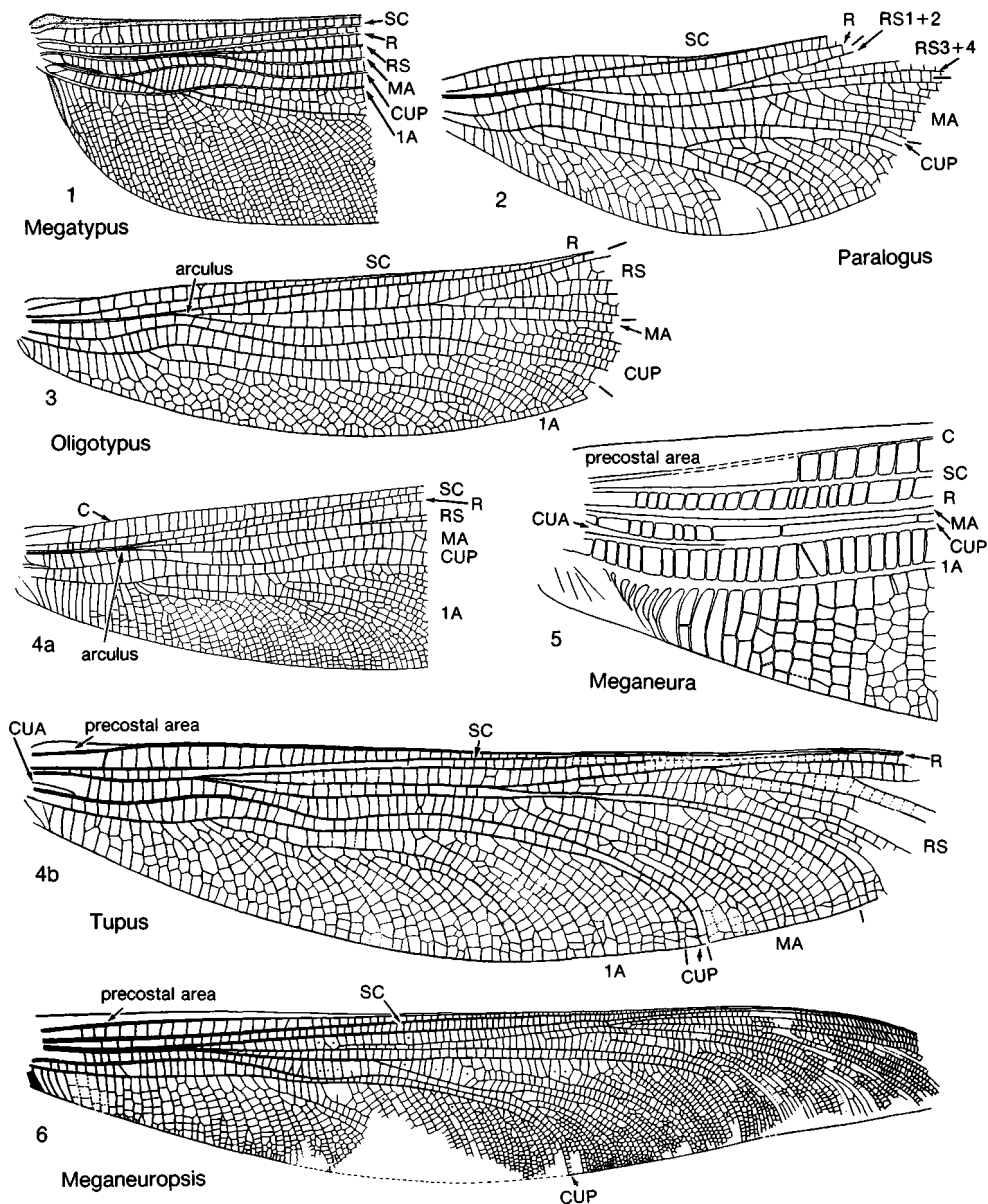


FIG. 38. Meganeuridae and Paralogidae (p. 60–62).

PENTER, 1931a, 1939, 1940b. *Perm.*, USA (Kansas).—FIG. 38, 1. **M. schucherti*; base of hind wing, $\times 0.9$ (Tillyard, 1925b).
Tupus SELLARDS, 1906, p. 249 [= *Typus* SELLARDS, 1909, p. 151, unjustified emendation, Opinion 1317, ICZN, 1984] [**Tupus permianus*; OD] [= *Meganeurula* HANDLIRSCH, 1906b, p. 309 (type, *Meganura selysii* BRONGNIART, 1893, p.

395); *Gilsonia* MEUNIER, 1908c, p. 243 (type, *G. titana*); *Meganeurina* HANDLIRSCH, 1919b, p. 570 (type, *M. confusa*); *Meganeurites* HANDLIRSCH, 1919b, p. 570 (type, *M. gracilipes*); *Arctorypus* MARTYNOV, 1932, p. 18 (type, *A. sinuatus*)]. Precostal area short, extending at most to one-fourth wing length from base; anal crossing not present in either fore or hind wing; 2A a distinct

branch of 1A. COCKERELL, 1913b; CARPENTER, 1931a, 1933a, 1939, 1947, 1960b; WHALLEY, 1980b. *U. Carb.*, Europe (France), England, USA (Georgia); *Perm.*, USSR (European and Asian RSFSR), USA (Kansas, Oklahoma, Arizona).—FIG. 38,4a. *T. gracilis* CARPENTER, *Perm.*, Oklahoma; base of fore wing, $\times 0.6$ (Carpenter, 1947).—FIG. 38,4b. **T. permianus* (SELLARDS), *Perm.*, Kansas; fore wing, $\times 1.3$ (Carpenter, 1931a).

Family PARALOGIDAE Handlirsch, 1906

[Paralogidae HANDLIRSCH, 1906b, p. 310]

Crossveins numerous; vein SC short, extending about to midwing; RS1+2 and RS3+4 widely divergent after origins. *U. Carb.*—*Perm.*

Paralogus SCUDDER, 1893b, p. 20 [**P. aeshnoides*; OD]. Wing nearly oval, with a strongly curved posterior margin. ROHDENDORF, 1940b; CARPENTER, 1960b. *U. Carb.*, USA (Rhode Island).—FIG. 38,2. **P. aeshnoides*; fore wing, $\times 1.3$ (Carpenter, 1960b).

Oligotypus CARPENTER, 1931a, p. 106 [**O. tillyardi*; OD]. Wing slender, hind margin only moderately curved. CARPENTER, 1947, 1960b; CARPENTER & RICHARDSON, 1971. *U. Carb.*, USA (Illinois); *Perm.*, USA (Kansas, Oklahoma).—FIG. 38,3. **O. tillyardi*, *Perm.*, Oklahoma; fore wing, $\times 2$ (Carpenter, 1947).

Family UNCERTAIN

The following genera, apparently belonging to the order Protodonata, are too poorly known to permit assignment to families.

Palaeotherates HANDLIRSCH, 1906a, p. 690 [**P. pennsylvanicus*; OD]. Little-known genus, based on wing fragment. HANDLIRSCH, 1906b; CARPENTER, 1980. *U. Carb.*, USA (Pennsylvania).

Paralogopsis HANDLIRSCH, 1911, p. 374 [**P. longipes*; OD]. Little-known genus, based on fragments of fore and hind wings. CARPENTER, 1960b. *U. Carb.*, USA (Pennsylvania, Illinois).

Petrotypus ZALESSKY, 1950, p. 100 [**P. multivenosus*; OD]. Little-known genus, based on basal part of wing. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).

Truemanina BOLTON, 1934, p. 183, *nom. subst. pro Tillyardia* BOLTON, 1922, p. 145, *non* CARTER, 1913 [**Tillyardia multiplicata* BOLTON; OD]. Little-known genus, based on distal fragment of wing. *U. Carb.*, England.

Typoides ZALESSKY, 1948a, p. 49 [**T. uralicus*; OD]. Little-known genus, based on wing fragment. *Perm.*, USSR (Asian RSFSR).

Order ODONATA Fabricius, 1793

[Odonata FABRICIUS, 1793, p. 373] [=Permononata G. M. ZALESSKY, 1931, p. 855]

Predaceous Palaeoptera, mostly large to very large; head unusually large, on a flexible cervix; compound eyes large, bulging; 3 ocelli present; antennae filiform, very short, with at most 7 segments; mandibles large, conspicuously dentate; maxillae spinose, palpi reduced; labial palpi forming a pair of large lobes, each with a prominent spine. Prothorax small, not fused to mesothorax; meso- and metathorax fused into a rigid, oblique pterothorax; legs homonomous, attached far forward on their thoracic segments and conspicuously spinose; tarsi with 3 segments. Wings homonomous or nearly so, with a very distinctive venation, a nodus at end of vein SC, and a conspicuous pterostigma on the anterior margin of the wings distally. Abdomen slender, elongate; second and third sterna of male with accessory reproductive structures; cerci short, consisting of a single segment; females with a short (rarely long) ovipositor. Eggs deposited in or near fresh water. Nymphs aquatic, with tracheal gills or filaments; labium of nymphs greatly modified, forming a long, dentate, grasping appendage. *Perm.*—*Holo.*

Other than the Ephemeroptera, this is the only order of the Palaeoptera that still exists. The internal structure of the odonates is that of a primitive pterygote, but the reduced cerci and antennae, the oblique position of the thoracic segments, and the complexity of their wing venation indicate a long evolutionary history of the order, especially since these specializations had been acquired before the end of the Jurassic Period. The geological record of the Odonata is, in fact, extensive and long. The aquatic nymphal stages and the tendency for the adults to remain near water have undoubtedly favored the preservation of specimens as fossils.

Until a few years ago, however, our knowledge of the Mesozoic odonates was based on a very few, poorly preserved specimens. The

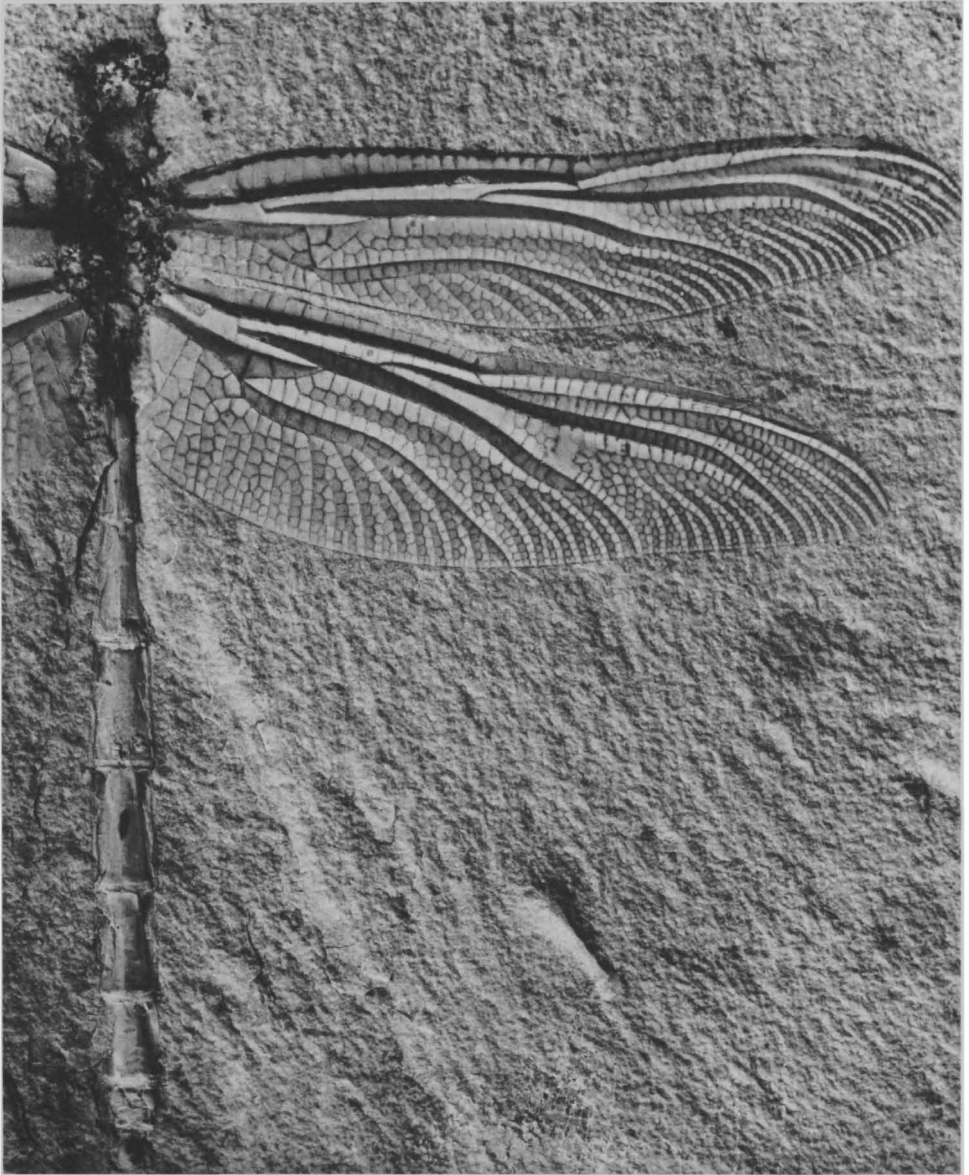


FIG. 39. Odonata; *Protolindenia wittei* (GIEBEL), Anisoptera, Gomphidae; $\times 2$ (Carpenter, new). This specimen shows the typical odonate body form and the convexity and concavity of the main wing veins as well as intercalary veins and triads.

recent investigations by Dr. L. N. PRITYKINA of the Paleontological Institute in Moscow of extensive collections from Mesozoic deposits in the Soviet Union have greatly improved our knowledge of the order during that important period in the history of these

insects. It is now apparent, as we could previously only assume, that the Odonata were at the peak of their diversity during the Jurassic and perhaps even the Triassic.

The existing Odonata and the extinct species from Tertiary, Cretaceous, and Jurassic

deposits show little diversity in general body structure (Fig. 39, *Protolindenia*). Unfortunately, we know virtually nothing of their body structure earlier than that.

The wing venation, on the other hand, shows great diversity from the beginning of the Jurassic, providing many diagnostic characters for genera and higher taxonomic categories. The venational pattern is complicated, and in the past there has been considerable controversy about the homologies of the veins with those of other insects. Subsequent studies, chiefly by LAMEERE (1922), MARTYNOV (1924a), CARPENTER (1931a), and TILLYARD and FRASER (1938–1940) have provided the interpretation of the venation now in general use. As previously noted, an important feature of the venational pattern that is shared with the Protodonata is the apparent absence of two main veins, the posterior media (MP, concave) and the anterior cubitus (CUA, convex). A presumed vestige of CUA is present at the base of the wings of at least some members of three extinct suborders, Protanisoptera (Fig. 40,1, *Ditaxineura*; see Fig. 42,1a), Archizygotera (see Fig. 43,1,5, *Kennedyia*, *Permolestes*), and Anisozygotera (Fig. 41, *Tarsophlebiopsis*). The longitudinal veins in the odonate wings are therefore the costa (C), the subcosta (SC), the radius (R), the radial sector (RS), the anterior media (MA), the posterior cubitus (CUP), and the anal vein (A). In addition, intercalary veins (indicated by an I prefix) are commonly present both between RS1 and RS2 and between RS2 and RS3 (or RS3+4), forming groups of three veins or triads (Fig. 41; see Fig. 42,1a, *Ditaxineura*). A precostal area, comparable to that of the Protodonata, occurs in several of the odonate suborders (Fig. 40,1).

In all odonates the junction of vein SC with the costal margin of both pairs of wings is marked by the presence of the nodus, a slight cuticular thickening associated with a bend in the wing margin and commonly with a definite break in the sclerotization of the margin. In some of the extinct suborders, such as the Archizygotera (see Fig. 43,6,

Progoneura), the nodus is incipient, with little sclerotization; in others the nodus is very distinct (Fig. 41, *Tarsophlebiopsis*; see Fig. 43,3, *Selenothemis*). Its position on the wings of course varies, depending on the length of SC. Two crossveins are commonly associated with the nodus: the nodal crossvein connects the nodus to R, and the subnodal crossvein joins R to RS1 (Fig. 41). In most odonates these crossveins are aligned (see Fig. 47,3, *Heterophlebia*), but in species with an incipient nodus they are not aligned or even near the nodus.

The odonate wing almost always has a series of crossveins along its front margin. Those in the costal area basal of the nodus are termed antenodals, and those distal of the nodus, between veins C and R, are termed the postnodals (Fig. 41). In some families two of the antenodals are consistently thicker than the others; these are the primary antenodals and the others are the secondaries.

In all odonate wings the basal parts of veins RS and MA are fused and are also coalesced with the stem of R, forming for a short distance a thick compound vein. The fused RS+MA then diverges from R, and after an even shorter distance RS and MA separate. The short segment of RS+MA, termed the arculus, is the center of the most diversified part of the wing (Fig. 40,1,2,4–6). In the Protanisoptera (see Fig. 42,1a, *Ditaxineura*) the arculus is almost parallel to the longitudinal axis of the wing, but in most odonate wings it is more oblique in position and directed toward the hind margin of the wing (see Fig. 43,6, *Progoneura*). In the fore wings of the more generalized members of the Anisozygotera, the arculus is connected to CUP by a discoidal vein (see Figs. 40,2 and 46,1, *Tarsophlebia eximia* and Fig. 41, *Tarsophlebiopsis*), which is often aligned with the base of MA and the arculus. This produces a small space, the open discoidal cell, just basal of the discoidal vein (Fig. 40,2). In most Anisozygotera the base of MA is also joined to CUP by another crossvein at the apex of the curve in CUP, forming a “closed” discoidal cell (Fig.

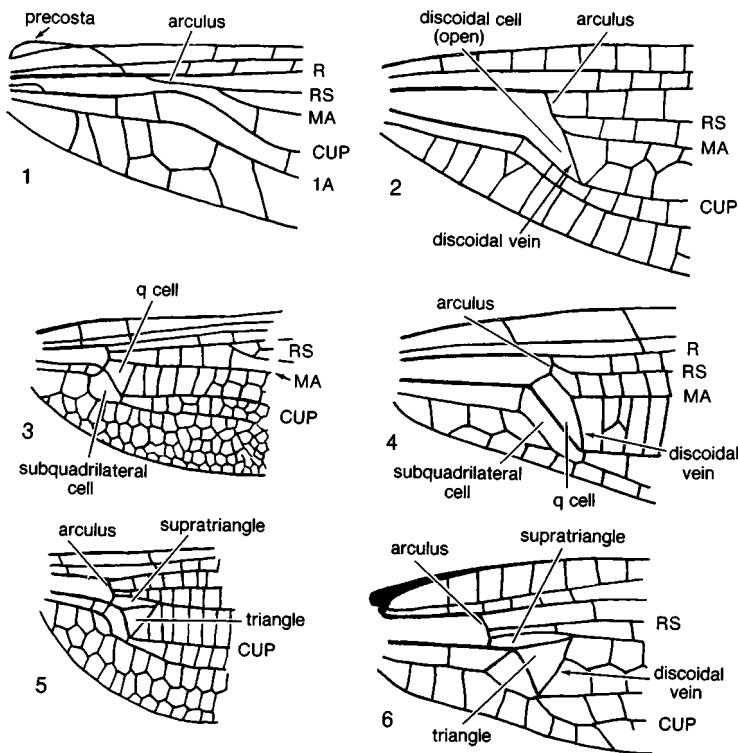


FIG. 40. Odonata; homology of wing structures in the region of the arculus in three suborders. Discoidal cell generally termed the q cell when closed.—1. Fore wing of *Ditaxineura anomalostigma*, Protanisoptera (Carpenter, new).—2. Fore wing of *Tarsophlebia eximia*, Anisozygotera (Carpenter, new).—3. Fore wing of *Turanothemis nodalis*, Anisozygotera (after Pritykina, 1968).—4,5. *Heterophlebia buckmani*, Anisozygotera; 4, fore and 5, hind wings (after Tillyard, 1925a).—6. Hind wing of *Gomphus exilis*, recent, Anisoptera (Carpenter, new).

40,3,4); since this cell is a quadrilateral, it is usually termed the q cell to distinguish it from the subquadrilateral (sq) cell below it. These cells occur in most fore wings and nearly all hind wings of the Anisozygotera as well as in all wings of the Zygotera. In the hind wings of some families of the Anisozygotera the q cell is divided by a crossvein that joins CUP to MA (Fig. 40,5,6), forming a triangle and a supratriangle. Homologous triangles occur in the fore and hind wings of all Anisoptera.

The positions, shapes, and sizes of these various structures in the wings provide the greater part of the basis for the classification of the fossil Odonata.

The order is here divided into six suborders: Protanisoptera, Archizygotera, Tri-

adophlebiomorpha, Anisozygotera, Anisoptera, and Zygotera. Only the last two are extant. The existing Odonata, estimated to be somewhat more than 5,000 species, are generally grouped into 16 families. The present geological record of the order comprises 42 families, of which 31 are extinct, mostly known only from the Mesozoic. The phylogenetic position of some of these families is uncertain. There has obviously been a great deal of convergence in the evolution of the wing venation. The closing of the discoidal cell and its division into two triangles, for example, have clearly occurred several times independently. The Triadophlebiomorpha are the most unusual of the known odonates. They possess a well-developed nodus, with nodal and subnodal crossveins, but com-

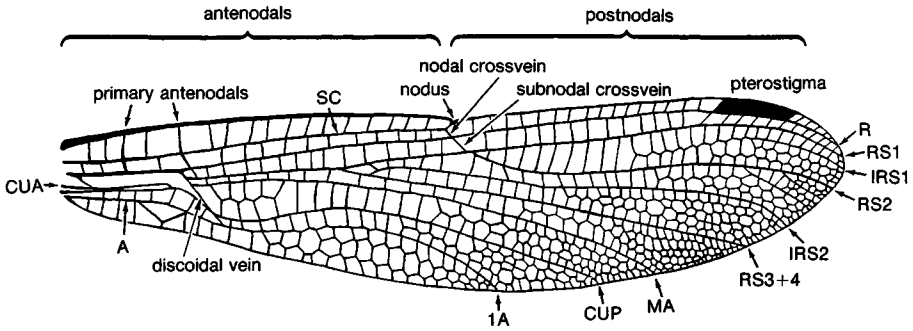


FIG. 41. Odonata; fore wing of *Tarsophlebiopsis mayi*, Anisozygoptera (after Fraser, 1955b).

pletely lack a pterostigma. In addition, when at rest, these odonates placed their wings over the abdomen with the dorsal surface inward like the Zygoptera (PRITYKINA, 1981). The general aspect of the wings of these triadophlebiomorphs resembles that of the Protodonata. However, the protodonate wing had no nodus, had a long subcosta, and could not be flexed over the abdomen.

The existing Odonata spend by far the greater part of their lives as nymphs. Only a few species reach the adult stage in one year; most species take two or three years and some require four or five. Fossil remains of nymphs are not uncommon in Tertiary deposits, but except for a few poorly preserved nymphs from the Jurassic, they appear to be absent from all pre-Cretaceous deposits.

Suborder PROTANISOPTERA Carpenter, 1931

[Protanisoptera CARPENTER, 1931a, p. 122] [=Permanisoptera MARTYNOV, 1931b, p. 146]

Wings moderately broad, nonpetiolate; hind wings much broader basally than fore wings; precostal area well developed; nodus weakly formed but wing margin at nodus with a distinct bend; at least 4 antennodals; arculus incipient, more longitudinal than oblique; pterostigma traversed by vein R; intercalary veins IRS1, IRS2, and IMA present; vestige of CUA at wing base; CUP with only a slightly sinuous curve; 1A long, extending to about midwing. Body and

immature stages unknown. FRASER, 1957; ROHDENDORF, 1962a; PRITYKINA, 1980b. *Perm.*

Family DITAXINEURIDAE Tillyard, 1926

[Ditaxineuridae TILLYARD, 1926b, p. 69]

Wings with 4 to 6 antennodals; crossveins few, regularly arranged, forming 2 graduate series in distal part of wing. *Perm.*

Ditaxineura TILLYARD, 1926b, p. 69 [**D. anomalostigma*; OD]. Nodal crossvein slightly distal of end of SC; postnodals absent. *Perm.*, USA (Kansas).—FIG. 42, 1. **D. anomalostigma*; a, fore wing, $\times 2.5$ (Carpenter, 1931a); b, hind wing, $\times 2.5$ (Carpenter, 1939).

Family PERMAESCHNIDAE Martynov, 1931

[Permaeschnidae MARTYNOV, 1931b, p. 141] [=Pholidoptilidae G. M. ZALESSKY, 1931, p. 855; Polytaxineuridae TILLYARD, 1935b, p. 375; Callimokaltaniidae ZALESSKY, 1955a, p. 630; Hemizygopteridae ZALESSKY, 1955a, p. 632]

Wings with numerous antennodals; crossveins irregularly arranged, forming an irregular network in some parts of wings. *Perm.*

Permaeschna MARTYNOV, 1931b, p. 141 [**P. dolloi*; OD] [=Pholidoptilon G. M. ZALESSKY, 1931, p. 855 (type, *P. camense*)]. Postnodals apparently absent; pterostigma remote from apex of wing; indentation of wing margin near end of RS3+4. *Perm.*, USSR (European RSFSR).—FIG. 42, 2a. **P. dolloi*; wing as preserved, $\times 1.2$ (Martynov, 1931b).—FIG. 42, 2b. *P. camense* (G. M. ZALESSKY); wing as preserved, $\times 1$ (G. M. Zalesky, 1931).

Callimokaltania ZALESSKY, 1955a, p. 630 [**C. martynovi*; OD]. Pterostigma very close to wing apex;

posterior margin of wing smoothly curved. ROHDENDORF, 1962a. *Perm.*, USSR (Asian RSFSR).—FIG. 42,3. **C. martynovi*; wing as preserved, $\times 1.8$ (Zalessky, 1955a).

Ditaxineurella MARTYNOV, 1940, p. 11 [**D. stigmatalis*; OD] [= *Hemizyopteron* ZALESSKY, 1955a, p. 632 (type, *H. uralensis*)]. Little-known genus, based on apical wing fragments. Several postnodals present; pterostigma nearer wing apex than in *Permaeschna*; no indentation of wing margin at end of RS3+4. ROHDENDORF, 1961a, 1962a. *Perm.*, USSR (Asian RSFSR).—FIG. 42,4. **D. stigmatalis*; wing as preserved, $\times 1.4$ (Martynov, 1940).

Polytaxineura TILLYARD, 1935b, p. 375 [**P. stanleyi*; OD]. Similar to *Permaeschna*, but hind margin of wing smoothly curved. *Perm.*, Australia (New South Wales).—FIG. 42,5. **P. stanleyi*; wing as preserved, $\times 1.4$ (Tillyard, 1935b).

Suborder ARCHIZYOPTERA Handlirsch, 1906

[Archizyoptera HANDLIRSCH, 1906b, p. 471] [=Protozyoptera TILLYARD, 1925b, p. 62]

Small species, with petiolate wings; petiole usually very slender; hind wings either similar to fore wings in form or somewhat broader; precostal area absent; nodus commonly incipient, much nearer to arculus than to pterostigma; arculus incipient or more nearly oblique; pterostigma between vein R and wing margin, well developed but slender; intercalary veins IRS1 and IRS2 usually present; MA without a concave, intercalary branch; vestige of CUA commonly present at wing base; CUP frequently abruptly curved near arculus; 1A commonly long but rarely very short or absent. Body and immature stages unknown. PRITYKINA, 1980a. *Perm.*—*Jur.*

Family KENNEDYIDAE Tillyard, 1925

[Kennedyidae TILLYARD, 1925b, p. 63]

Fore and hind wings long and slender; costal margin with or without a distinct bend at end of vein SC, but with no definite nodal crossvein; only 4 postnodals; a single row of cells between main veins; 1A short, extending at most only to slightly beyond level of nodus. *Perm.*—*Trias.*

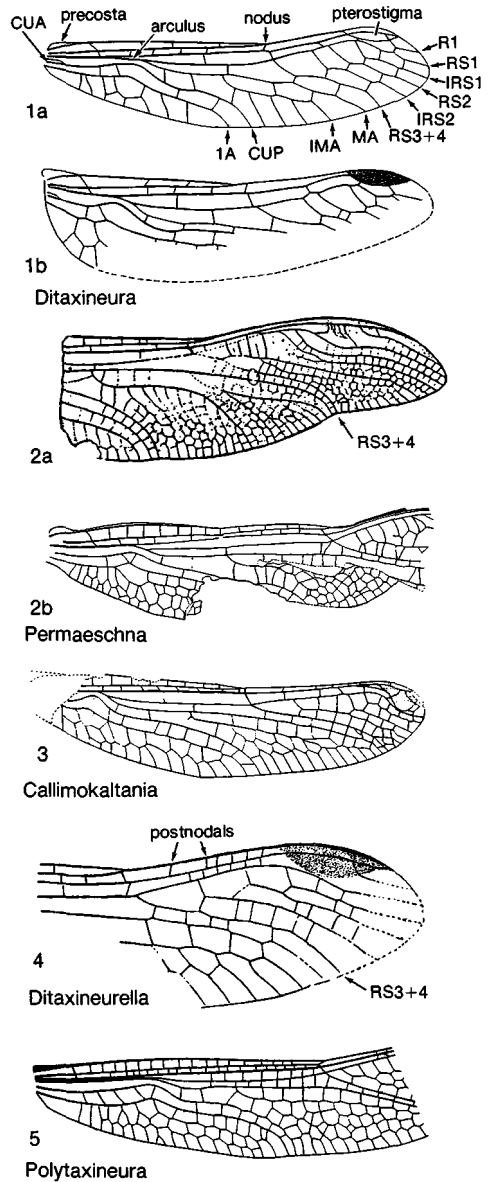


FIG. 42. Ditaxineuridae and Permaeschnidae (p. 66–67).

Kennedyia TILLYARD, 1925b, p. 63 [**K. mirabilis*; OD]. Costal margin of wing with a distinct break at end of SC; 1A terminating slightly beyond level of nodus; numerous crossveins between CUP and hind margin of wing. CARPENTER, 1931a, 1947; FRASER, 1957; PRITYKINA, 1980a, 1981. *Perm.*, USA (Kansas, Oklahoma); *Trias.*, USSR (Kirghiz).—FIG. 43,1. *K. fraseri* CARPENTER, *Perm.*, Oklahoma; wing, $\times 3$ (Carpenter, 1947).

Progoneura CARPENTER, 1931a, p. 119 [**P. minuta*; OD]. Anterior margin of fore wing without nodal break; few crossveins between CUP and wing margin; 1A much shorter than in *Kennedyia*. CARPENTER, 1947. *Perm.*, USA (Oklahoma).—FIG. 43,6. *P. nobilis* CARPENTER; wing, $\times 4$ (Carpenter, 1947).

Family PERMOLESTIDAE

Martynov, 1932

[Permolestidae MARTYNOV, 1932, p. 33] [=Solikamptilonidae ZALESSKY, 1948a, p. 49]

Wings similar to those of Kennedyidae but with definite nodal and subnodal crossveins, usually aligned or nearly so; crossveins more numerous over entire wing; vein 1A much longer than in Kennedyidae. *Perm.*

Permolestes MARTYNOV, 1932, p. 33 [**P. gracilis*; OD]. Arculus more nearly longitudinal than transverse; numerous cellules in distal and posterior parts of wings, including area between 1A and hind margin. ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 43,5. **P. gracilis*; wing, $\times 1$ (Martynov, 1932).

Epilestes MARTYNOV, 1937b, p. 16 [**E. kargalensis*; OD]. Wings with only a few small cellules, almost none between 1A and hind margin; pterostigma very long. ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 43,8. **E. kargalensis*; wing, $\times 1.7$ (Martynov, 1937b).

Scytolestes MARTYNOV, 1937b, p. 18 [**S. stigmalis*; OD]. Similar to *Permolestes*, but wings with arcules more nearly transverse than longitudinal; cellules numerous only in area between 1A and wing margin; pterostigma short. ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 43,7. **S. stigmalis*; wing, $\times 2$ (Martynov, 1937b).

Solikamptilon ZALESSKY, 1948a, p. 49 [**S. remuliforme*; OD]. Little-known genus, based on wing fragment; 1A very long, parallel to hind margin for most of its length. Pterostigma not preserved. *Perm.*, USSR (Asian RSFSR).—FIG. 43,9. **S. remuliforme*; wing, $\times 2$ (Zallessky, 1948a).

Sushkinia MARTYNOV, 1930a, p. 71 [**S. parvula*; OD]. Little-known genus, based on wing fragment; pterostigma unusually long. [Family assignment doubtful.] *Perm.*, USSR (European RSFSR).

Family PERMAGRIONIDAE

Tillyard, 1928

[Permagrionidae TILLYARD, 1928a, p. 56]

Similar to Kennedyidae, but nodus more pronounced; nodal and subnodal crossveins aligned; arculus more transverse than in Kennedyidae, and vein 1A longer. [The rela-

tionships of this family are uncertain. TILLYARD (1928a) and FRASER (1957) considered it to belong to the Zygoptera, FRASER placing it in the recent superfamily Coenagrionidae. PRITYKINA (1980a) has placed it in the suborder Archizygoptera, close to Kennedyidae and Permolestidae.] *Perm.*

Permagrion TILLYARD, 1928a, p. 56 [**P. falklandicum*; OD]. Wings with 8 postnodals, all aligned with crossveins below; pterostigma rhomboidal. PRITYKINA, 1980a. *Perm.*, South America (Falkland Islands).—FIG. 43,4. **P. falklandicum*; wing, $\times 1.5$ (Tillyard, 1928a).

Family PERMEPALLAGIDAE

Martynov, 1938

[Permepallagidae MARTYNOV, 1938b, p. 58]

Similar to Kennedyidae, but wings extremely slender; antenodals and postnodals numerous; several intercalary veins between branches of RS. *Perm.*

Permepallage MARTYNOV, 1938b, p. 50 [**P. angustissima*; OD]. Crossveins between 1A and hind margin of wing numerous and unbranched. ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).

Family PROTOMYRMELEONTIDAE

Handlirsch, 1906

[*nom. correct.* TILLYARD, 1925a, p. 36, ex Protomyrmeleontidae HANDLIRSCH, 1906b, p. 471, *nom. imperf.*] [=Triassagrionidae TILLYARD, 1922b, p. 454]

Fore and hind wings long and slender; costal margin without a distinct bend at end of vein SC and without a definite nodal crossvein; postnodals numerous; many crossveins between R and RS1; IRS2 weakly developed or absent; 1A extending well beyond level of nodus. *Trias.-Jur.*

Protomyrmeleon GEINITZ, 1887, p. 204 [**P. brunonis*; OD]. Wings with a single row of cells between RS1 and IRS1; IRS2 weakly developed. HANDLIRSCH, 1906b; MARTYNOV, 1927b; PRITYKINA, 1980b. *Jur.*, Europe (Germany), USSR (Kazakh).—FIG. 43,12a. **P. brunonis*, Germany; wing, $\times 2.5$ (Handlirsch, 1906b).—FIG. 43,12b. *P. handlirschi* MARTYNOV, USSR; wing, $\times 2$ (Martynov, 1927b).

Tillyardagrion MARTYNOV, 1927b, p. 762 [**Protomyrmeleon anglicanus* TILLYARD, 1925a, p. 37; OD]. Little-known genus, similar to *Triassagrion* but lacking small cellules between RS1 and

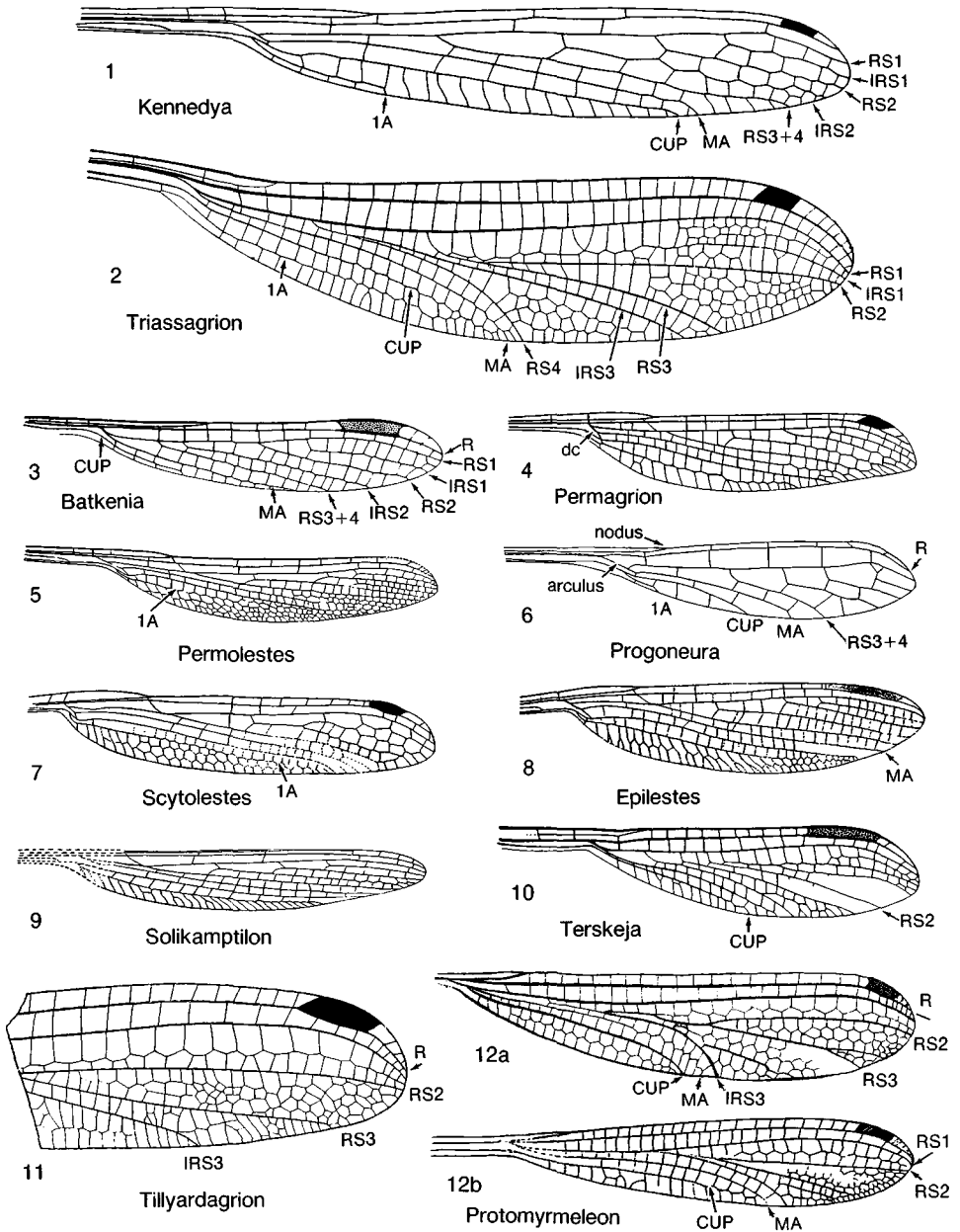


FIG. 43. Kennedyidae, Permolestidae, Permagrionidae, Protomyrmeleontidae, Batkeniidae, and Uncertain (p. 67–70).

IRS1 distally; RS2 and RS3 only slightly divergent; IRS3 and RS3 slightly divergent. *Jur.*, England. — FIG. 43,11. **T. anglicanus* (TILLYARD); wing, $\times 4$ (Tillyard, 1925a).

Triassagrion TILLYARD, 1922b, p. 455 [**T. australiense*; OD]. Wings with several rows of cells

between RS1 and IRS1 distally; IRS3 strongly developed, close to RS3 and nearly parallel to it; RS2 and RS3 widely divergent. MARTYNOV, 1927b. *Trias.*, Australia (Queensland). — FIG. 43,2. **T. australiense*; wing, $\times 4.5$ (Tillyard, 1922b).

Family BATKENIIDAE

Pritykina, 1981

[Batkeniidae PRITYKINA, 1981, p. 38]

Small species, with petiolate wings, hind pair much broader than fore pair; nodus incipient; pterostigma relatively broad; costal margin without a bend at end of vein SC; SC much longer than in Protomyrmeleontidae, extending well beyond level of origin of RS3+4; CUP very short, not as long as SC; 1A absent. *Trias*.

Barkenia PRITYKINA, 1981, p. 38 [**B. pusilla*; OD].

Fore wing with 3 antenodals and 4 postnodals; 2 cells below pterostigma. *Trias.*, USSR (Kirghiz).—FIG. 43,3. **B. pusilla*; fore wing, $\times 3.5$ (Pritykina, 1981).

Family UNCERTAIN

The following genera, apparently belonging to the order Odonata, suborder Archizygoptera, are too poorly known to permit assignment to families.

Terskeja PRITYKINA, 1981, p. 35 [**T. paula*; OD].

Wings as in Protomyrmeleontidae, but vein SC longer and distal branches of RS more evenly spaced and curving posteriorly more strongly; pterostigma slender and strongly developed; SC and R with a distinct bend before nodus, costal margin of wing with a slight bend at same level; IRS forming a triad complex of several branches, all curving posteriorly; RS2 ending on posterior margin of wing, remote from apex; RS3+4 unbranched. [This genus was placed in the Protomyrmeleontidae by its author. However, if *Terskeja* were included, the definition of that family would require drastic changes. It therefore seems advisable to separate *Terskeja* from the Protomyrmeleontidae, at least until additional genera connecting *Terskeja* to the Protomyrmeleontidae have been found.] *Trias.*, USSR (Kirghiz).—FIG. 43,10. **T. paula*; fore wing, $\times 4$ (Pritykina, 1981).

Suborder

TRIADOPHLEBIOMORPHA

Pritykina, 1981

[Triadophlebiomorpha PRITYKINA, 1981, p. 11]

Insects of moderate to large size. Wings petiolate; pterostigma absent; nodus and arculus well developed; bases of longitudinal veins very close together in petiole, almost

fused; triads present between veins RS1 and RS2, and between RS3 and RS4; crossveins forming a fine network in posterior areas of wings; vestige of CUA apparently absent. Hind wings apparently similar to fore wings. Wings held back over abdomen at rest. Immature stages unknown. *Trias*.

Family TRIADOPHLEBIIDAE

Pritykina, 1981

[Triadophlebiidae PRITYKINA, 1981, p. 11]

Postnodal margin of wing straight; hind margin smoothly curved; vein IRS1 arising very close to origin of RS2. *Trias*.

Triadophlebia PRITYKINA, 1981, p. 12 [**T. madygenica*; OD]. Antenodals and postnodals very numerous; large species. *Trias.*, USSR (Kirghiz).—FIG. 44,4. **T. madygenica*; wing, $\times 1.4$ (Pritykina, 1981).

Cladophlebia PRITYKINA, 1981, p. 20 [**C. parvula*; OD]. Similar to *Triadophlebia* but much smaller and with relatively fewer crossveins in anterior part of wings. *Trias.*, USSR (Kirghiz).—FIG. 44,5. **C. parvula*; wing, $\times 2.5$ (Pritykina, 1981).

Neritophlebia PRITYKINA, 1981, p. 16 [**N. elegans*; OD]. Wings much more slender than those of *Triadophlebia*; crossveins in anterior part of wing more widely spaced. *Trias.*, USSR (Kirghiz).—FIG. 44,1. *N. longa* PRITYKINA; wing, $\times 1.3$ (Pritykina, 1981).

Nonymophlebia PRITYKINA, 1981, p. 24 [**N. venosa*; OD]. Similar to *Triadophlebia*, but venation even more dense, with double rows of cells between veins forming triads. *Trias.*, USSR (Kirghiz).

Paurophlebia PRITYKINA, 1981, p. 21 [**P. lepida*; OD]. Wings similar to those of *Cladophlebia* but more slender; crossveins more dense; R curving anteriorly about one-fourth wing length from apex and touching or nearly touching costal margin. *Trias.*, USSR (Kirghiz).—FIG. 44,3. **P. lepida*; wing, $\times 2.5$ (Pritykina, 1981).

Family TRIADOTYPIDAE

Grauvogel & Laurentiaux, 1952

[Triadotypidae GRAUVOGEL & LAURENTIAUX, 1952, p. 124]

Large species; nodus distinct, with nodal and subnodal crossveins; antenodals and postnodals numerous; nodus about one-third wing length from base; vein RS3+4 forking near midwing, with 2 sets of triads; MA curving posteriorly toward wing margin, nearly touching end of CUP; anal area extensive. *Trias*.

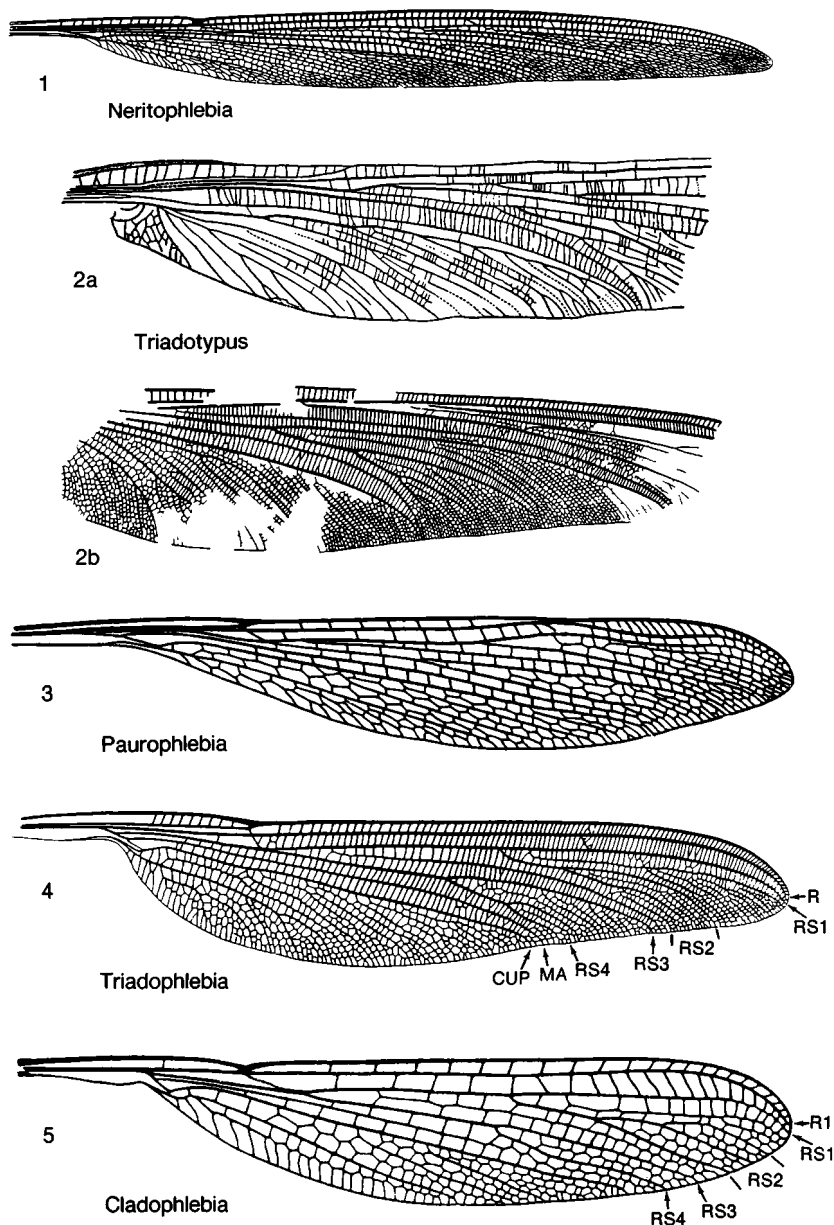


FIG. 44. Triadophlebiidae and Triadotypidae (p. 70–71).

Triadotypus GRAUVOGEL & LAURENTIAUX, 1952, p. 124 [**T. guillaumei*; OD]. RS2 arising at level of subnodal crossvein. PRITYKINA, 1981. *Trias.*, Europe (France), USSR (Kirghiz). —FIG. 44,2a. **T. guillaumei*, France; fore wing, $\times 0.75$ (Grauvogel & Laurentiaux, 1952). —FIG. 44,2b. *T. sogdianus* PRITYKINA, USSR; hind wing, $\times 1$ (Pritykina, 1981).

Family MITOPHLEBIIDAE
Pritykina, 1981

[Mitophlebiidae PRITYKINA, 1981, p. 24]

Wings with very thick veins; front margin of wings strongly convex in distal third, with a broad costal area; hind margin strongly lobed, widest at about midwing. *Trias.*

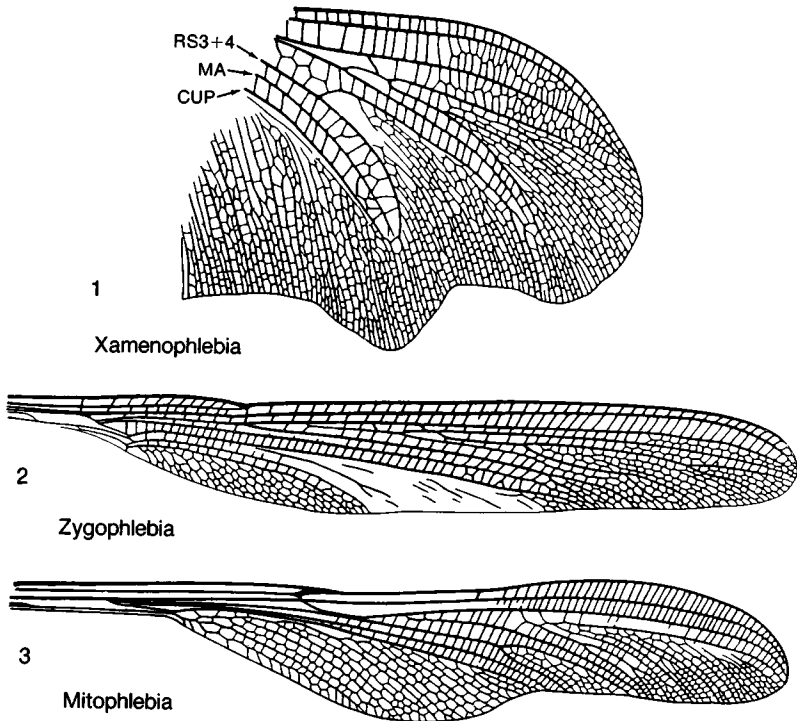


FIG. 45. Mitophlebiidae, Zygophlebiidae, and Xamenophlebiidae (p. 72).

Mitophlebia PRITYKINA, 1981, p. 25 [**P. enormis*; OD]. Wings with about 60 postnodals, none aligned with crossveins below. *Trias.*, USSR (Kirghiz).—FIG. 45,3. **M. enormis*; wing, $\times 2.3$ (Pritykina, 1981).

Family ZYGOPHLEBIIDAE Pritykina, 1981

[Zygophlebiidae PRITYKINA, 1981, p. 27]

Insects of moderate size; wings very long and slender; venation dense; distal two-thirds of wing of uniform width; nodus small. *Trias.*

Zygophlebia PRITYKINA, 1981, p. 27 [**Z. ramosa*; OD]. Nodal and subnodal crossveins aligned; RS3+4 arising from RS at level of nodus and continuing unbranched until near hind margin of wing. *Trias.*, USSR (Kirghiz).—FIG. 45,2. **Z. ramosa*; wing, $\times 2.5$ (Pritykina, 1981).

Cyrtophlebia PRITYKINA, 1981, p. 30 [**C. sinuosa*; OD]. Little-known genus. Wing much broader than in *Zygophlebia*; crossveins more dense, area between R and RS reticulate; IRS2 strongly curved. *Trias.*, USSR (Kirghiz).

Mixophlebia PRITYKINA, 1981, p. 29 [**M. mixta*; OD]. Wing similar to that of *Zygophlebia* but relatively broader; RS4+5 much longer. *Trias.*, USSR (Kirghiz).

Zygophlebiella PRITYKINA, 1981, p. 29 [**Z. curta*; OD]. Wings similar to those of *Zygophlebia*, but RS3 arising beyond nodus and 1A extending much farther distally. *Trias.*, USSR (Kirghiz).

Family XAMENOPHLEBIIDAE Pritykina, 1981

[Xamenophlebiidae PRITYKINA, 1981, p. 32]

Little-known family. Wings very broad, apex blunt, hind margin with broad undulations; base of wing unknown. *Trias.*

Xamenophlebia PRITYKINA, 1981, p. 32 [**X. ornata*; OD]. Crossveins very dense along hind margin and apical region of wing but relatively open in more anterior areas. *Trias.*, USSR (Kirghiz).—FIG. 45,1. **X. ornata*; distal part of wing, $\times 1.5$ (Pritykina, 1981).

Suborder ANISOZYGOPTERA Handlirsch, 1906

[Anisozygoptera HANDLIRSCH, 1906b, p. 463]

Wings moderately broad, narrowed basally but rarely petiolate; hind wings commonly much broader basally; nodus well formed,

usually distal of midwing; nodal and sub-nodal crossveins commonly aligned; arculus transverse or nearly so in most; discoidal cell usually closed in fore and hind wings, forming quadrilateral cell, but rarely open in fore wing and more rarely open in hind wing; quadrilateral cell of fore wing not divided; that of hind wing rarely divided by 1 or more crossveins; vestige of vein CUA rarely present; intercalary veins of RS well developed. Immature stages unknown. *Trias.—Cret.*

This is the most diverse of the suborders of the Odonata and was the dominant one during the Jurassic. Many years ago HANDLIRSCH (1906b) placed here the extant genus *Epiophlebia* of the family Epiophlebiidae (= *Palaeophlebia* SELYS), thus extending the range of the Anisozygoptera to the present. Since then the two species known in *Epiophlebia*, from Japan and India, have been studied in detail by ASAHINA (1954, 1958, 1963). As our knowledge of the Jurassic Anisozygoptera advanced, it became increasingly clear that *Epiophlebia* is not a member of that suborder (CARPENTER, 1931a). More recently, PRITYKINA (1980a) concluded that it is a derivative of an ancient aeshnoid line (Anisoptera) and placed it in a new superfamily, Epiophlebioidea.

Family TARSOPHLEBIIDAE Handlirsch, 1906

[Tarsophlebiidae HANDLIRSCH, 1906b, p. 467]

Discoidal cell open in fore and hind wings; arculus more oblique in fore wing than in hind wing. Body and legs slender. *Jur.*

Tarsophlebia HAGEN, 1866a, p. 58 [**Heterophlebia eximia* HAGEN, 1862, p. 106; OD]. Basal bend of CUP (near arculus) very abrupt and angular; 1A nearly parallel to CUP basally; fore wing very narrow at base. *Jur.*, Europe (Germany), USSR (Kazakh).—FIG. 46, 1a,b. **T. eximia* (HAGEN), Germany; *a*, hind wing, $\times 1.8$ (Hagen, 1866a); *b*, base of fore wing, $\times 5.3$ (Carpenter, 1932a).—FIG. 46, 1c. *T. neckini* MARTYNOV, USSR; fore wing base, $\times 2$ (Martynov, 1927b).

Sphenophlebia BODE, 1953, p. 41 [**S. interrupta*; OD]. Similar to *Tarsophlebiopsis*, but 1A shorter and CUP with definite branches. *Jur.*, Europe (Germany).—FIG. 46, 2. **S. interrupta*; fore wing, $\times 1.5$ (Bode, 1953).

Tarsophlebiopsis TILLYARD, 1923d, p. 149 [**T.*

mayi; OD]. Basal bend of CUP (near arculus) rounded; 1A only slightly curved basally. *Jur.*, England.—FIG. 41. **T. mayi*; fore wing, $\times 3.5$ (Fraser, 1955b).

Turanophlebia PRITYKINA, 1968, p. 42 [**T. martynovi*; OD]. Similar to *Tarsophlebia*, but pterostigma larger and wing more slender. PRITYKINA, 1977. *Jur.*, USSR (Kazakh).—FIG. 46, 4. **T. martynovi*; hind wing, $\times 1.6$ (Pritykina, 1968).

Family ISOPHLEBIIDAE Handlirsch, 1906

[Isophlebiidae HANDLIRSCH, 1906b, p. 582]

Discoidal cell closed in fore and hind wings, rectangular, without crossveins. Legs not so long as in Tarsophlebiidae. *Jur.*

Isophlebia HAGEN, 1866a, p. 68 [**I. aspasia* HAGEN, 1866a, p. 70; SD CARPENTER, herein]. Crossveins below distal side of discoidal cell aligned to form apparent continuation of that side, in both fore and hind wings; proximal and distal sides of cell nearly parallel in fore wing; 1A very short. *Jur.*, Europe (Germany).—FIG. 46, 3. **I. aspasia*; bases of *a*, fore and *b*, hind wings, $\times 1$ (Deichmüller, 1886).

Family LIASSOPHLEBIIDAE Tillyard, 1925

[Liassophlebiidae TILLYARD, 1925a, p. 111]

Discoidal cell open in fore wing, closed in hind wing; anterodistal angle of discoidal cell of hind wing slightly acute. *Jur.*

Liassophlebia TILLYARD, 1925a, p. 13 [**L. magnifica*; OD]. Two primary antenodals; MA separated from CUP by 4 to 7 rows of cells; CUA abruptly bent near arculus. ZEUNER, 1962a; PRITYKINA, 1970. *Jur.*, Europe (Germany), England.—FIG. 47, 2. **L. magnifica*; *a*, basal half of fore wing, $\times 0.7$; *b*, hind wing, $\times 0.7$ (both Tillyard, 1925a).

Bathmophlebia PRITYKINA, 1970, p. 111 [**B. unica*; OD]. Little-known genus, based on fragment of hind wing; CUP with an abrupt bend anteriorly, at about level of nodus; RS3+4 arising at level of distal antenodal. *Jur.*, USSR (Kirghiz).

Caraphlebia CARPENTER, 1969, p. 419 [**C. antarctica*; OD]. Hind wing similar to that of *Liassophlebia* but with several weak antenodals in addition to primary ones; IRS1 weakly developed; space between MA and CUP narrow. *Jur.*, Antarctica (South Victoria Land).

Ferganophlebia PRITYKINA, 1970, p. 116 [**F. insignis*; OD]. Little-known genus, based on fragment of fore wing; CUP smoothly curved; cells between CUP and M uncommonly large. *Jur.*, USSR (Kirghiz).

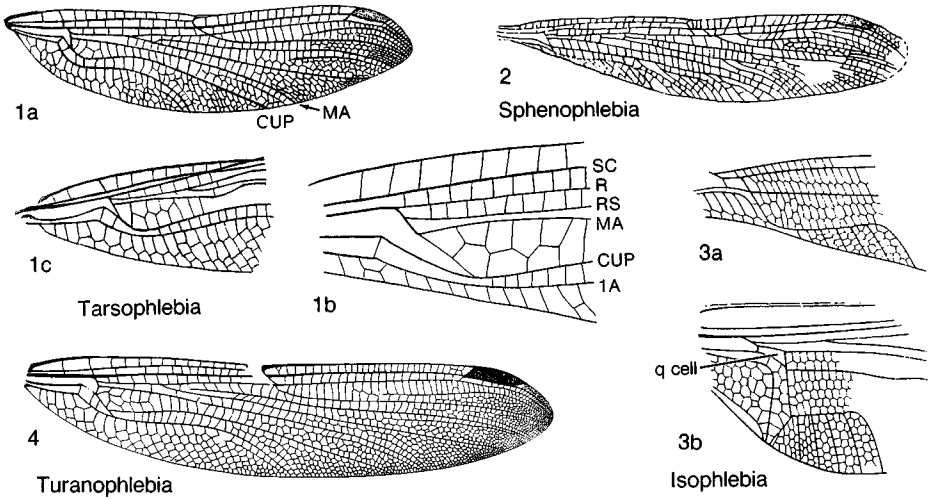


FIG. 46. Tarsophlebiidae and Isophlebiidae (p. 73).

Hypsophlebia PRITYKINA, 1970, p. 114 [**H. scalaris*; OD]. Little-known genus, similar to *Xanthohypsa*, but hind wing narrow basally and subquadrilateral cell extending close to hind margin of wing. *Jur.*, USSR (Kirghiz).

Oreophlebia PRITYKINA, 1970, p. 110 [**O. lata*; OD]. Venational pattern as in *Xanthohypsa*, but wing much broader; CUP and 1A extensively branched. *Jur.*, USSR (Kirghiz).—FIG. 47,7. **S. lata*; hind wing, $\times 1.2$ (Pritykina, 1970).

Petrophlebia TILLYARD, 1925a, p. 11 [**P. anglicana*; OD]. Similar to *Liassophlebia* but with 2 regular rows of cells between veins MA and CUP proximally; CUP only slightly bent near arculus. ZEUNER, 1962a; PRITYKINA, 1970. *Jur.*, England. —FIG. 47,1. **P. anglicana*; base of hind wing, $\times 1.5$ (Tillyard, 1925a).

Pternopteron PRITYKINA, 1970, p. 112 [**P. mirabile*; OD]. Wings long and narrow; 2 strong antennodals, aligned with subcostal crossveins; subquadrilateral cell abruptly geniculate; pterostigma long, narrow; posterior margin of hind wing in anal area with a prominent, recurved spur. *Jur.*, USSR (Kirghiz).

Sagulia PRITYKINA, 1970, p. 113 [**S. ansinervis*; OD]. Little-known genus, apparently related to *Xanthohypsa*, but with a semicircular loop formed by branches of 1A. *Jur.*, USSR (Kirghiz).

Sarytashia PRITYKINA, 1970, p. 115 [**S. gracilis*; OD]. Little-known genus, based on fore wing fragment; similar to *Xanthohypsa* but with shorter pterostigma and few costal veinlets distal of pterostigma. *Jur.*, USSR (Kirghiz).

Sogdophlebia PRITYKINA, 1970, p. 108 [**S. singularis*; OD]. Hind wing similar to that of *Xanthohypsa*, but subquadrilateral cell with a longitudinal vein; 1A with distinct branches. *Jur.*, USSR (Kirghiz).

Xanthohypsa PRITYKINA, 1970, p. 107 [**X. tillyardi*; OD]. Hind wing broad, with strongly curved hind margin; nodus slightly proximal of midwing; 2 antennodals, aligned with subcostal crossveins; 5 or 6 postnodals; pterostigma narrow and long; q cell narrow; subquadrilateral cell long, containing several crossveins, without a longitudinal vein; 1A with weakly defined branches. *Jur.*, USSR (Kirghiz).—FIG. 47,5. **X. tillyardi*; hind wing, $\times 1.2$ (Pritykina, 1970).

Family HETEROPHLEBIIDAE Handlirsch, 1906

[Heterophlebiidae HANDLIRSCH, 1906b, p. 466]

Discoidal cell of fore wing closed but not divided; discoidal cell of hind wing closed and divided, forming supratriangle and triangle. Two strong, primary antennodals present, and usually a few weak secondary ones. *Jur.*

Heterophlebia BRODIE, 1849, p. 35 [**Agrion buckmani* BRODIE, 1845, p. 102; SD TILLYARD, 1925a, p. 27]. MA in fore wing ending at level of middle of pterostigma; IRS1 about equidistant from RS1 and RS2. ZEISSIN, 1982. *Jur.*, England, Europe (Germany).—FIG. 47,3. **H. buckmani* (BRODIE), England; *a*, fore wing, $\times 1.6$; *b*, base of hind wing, $\times 4$ (both Tillyard, 1925a).

Clydonophlebia COWLEY, 1942, p. 70 [**Heterophlebia megapolitana* HANDLIRSCH, 1939, p. 26; OD]. Anterior side of triangle of hind wing ending at distal angle of supratriangle. *Jur.*, Europe (Germany).—FIG. 47,6. **C. megapolitana* (HANDLIRSCH); hind wing, $\times 1.4$ (Handlirsch, 1939).

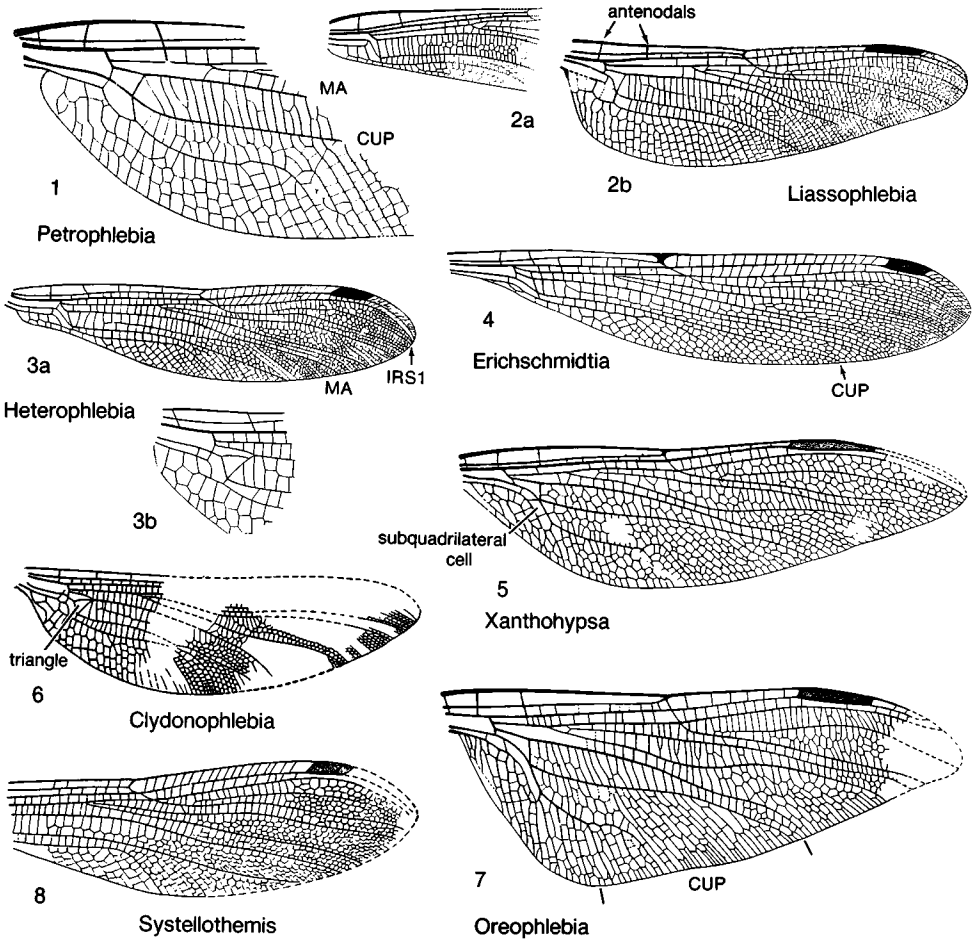


FIG. 47. Liassophlebiidae and Heterophlebiidae (p. 73–75).

Erichschmidtia PRITYKINA, 1968, p. 37 [**E. nigrimontana*; OD]. Fore wing as in *Heterophlebia*, but nodus only about one-third wing length from base; 6 to 8 subcostal crossveins in antenodal area; CUP with only a slight bend near discoidal cell. *Jur.*, USSR (Kazakh).—FIG. 47,4. **E. nigrimontana*; fore wing, $\times 1.7$ (Pritykina, 1968). *Systellothemis* HANDLIRSCH, 1939, p. 27 [**S. reticulata*; OD]. Little-known wing, probably synonymous with *Heterophlebia*. COWLEY, 1942. *Jur.*, Europe (Germany).—FIG. 47,8. **S. reticulata*; wing, $\times 2$ (Handlirsch, 1939).

Family PROGONOPHLEBIIDAE
Tillyard, 1925

[Progonophlebiidae TILLYARD, 1925a, p. 8]

Discoidal cell of hind wing closed and thus a q cell, undivided; 2 strong antennodals; at

most only a few weak secondary antennodals; subnodal crossvein not aligned with nodal crossvein. *Jur.*

Progonophlebia TILLYARD, 1925a, p. 9 [**T. woodwardi*; OD]. Hind wing: nodus at about level of midwing; q cell small, almost square. ZEUNER, 1959a. *Jur.*, England.—FIG. 48,1. **P. woodwardi*; hind wing, $\times 1.6$ (Tillyard, 1925a). *Cyclothemis* PRITYKINA, 1980a, p. 126 [**C. sagulica*; OD]. Based on incomplete wing; wings apparently similar to those of *Shurabiola*, but CUP less curved and subquadrilateral cell shorter. [Originally placed in Archithemistidae.] *Jur.*, USSR (Kirghiz).—FIG. 48,6. *C. sogjutensis* PRITYKINA; hind wing, $\times 4$ (Pritykina, 1980a). *Shurabiola* PRITYKINA, 1980a, p. 123 [**S. nana*; OD]. Small species, with broad wings and fewer crossveins than in *Progonophlebia*; q cell large, distal side twice as long as proximal side;

subquadrilateral cell long; CUP smoothly curved. [Originally placed in Archithemistidae.] *Jur.*, USSR (Kirghiz).—FIG. 48,7. **S. nana*; wing, $\times 6$ (Pritykina, 1980a).

Family ARCHITHEMISTIDAE

Tillyard, 1917

[*nom. transl.* HANDLIRSCH, 1920, p. 177, *et correct.* COWLEY, 1942, p. 65, *ex* Architheminae TILLYARD, 1917c, p. 307] [=Camptero-
phlebiidae HANDLIRSCH, 1920, p. 178; Selenothemistidae
HANDLIRSCH, 1939, p. 20]

Discoidal cell closed and undivided in fore and hind wings; primary antenodals absent; numerous weak secondary antenodals. *Jur.*

Archithemis HANDLIRSCH, 1906b, p. 466 [**Libellula brodiei* GEINITZ, 1884, p. 581; OD] [=*Dia-statommiter* TILLYARD, 1925a, p. 21 (type, *Aeschna liassina* STRICKLAND, 1840, p. 301)]. Numerous oblique, parallel veins between RS3+4 and hind margin distally; RS3+4 and CUP smoothly curved. *Jur.*, Europe (Germany), England.—FIG. 48,4a. **A. brodiei* (GEINITZ), Germany; fore wing, $\times 1.8$ (Handlirsch, 1906b).—FIG. 48,4b. *A. liassina* (STRICKLAND), England; hind wing, $\times 0.8$ (Tillyard, 1925a).

Camptero-phlebia BODE, 1905, p. 226 [**C. elegans*; OD]. RS3+4 and CUP strongly undulated distally. *Jur.*, Europe (Germany).

Selenothemis HANDLIRSCH, 1920, p. 178 [**S. liadis*; OD]. Area between RS3+4 and hind margin without series of long, oblique, parallel veinlets; RS3+4 and CUP smoothly curved. *Jur.*, Europe (Germany).—FIG. 48,3. **S. liadis*; hind wing, $\times 2$ (Handlirsch, 1920).

Family KARATAWIIDAE

Martynov, 1925

[Karatawiidae MARTYNOV, 1925b, p. 589]

Similar to Turanothemistidae, but wings commonly with 9 to 12 subcostal crossveins in antenodal area; discoidal cell incomplete (open) in fore wing but closed in hind wing, forming the q cell. *Jur.*—*Cret.*

Karatawia MARTYNOV, 1925b, p. 587 [**K. turanica*; OD]. Fore wing: 1A short and very close to hind margin; arculus about midway between wing base and origin of RS3+4. PRITYKINA, 1968, 1980a. *Jur.*, USSR (Kazakh, Kirghiz).

Adelophlebia PRITYKINA, 1980a, p. 130 [**A. obsoleta*; OD]. Little-known genus; area between M and CUP with 2 rows of cells. *Jur.*, USSR (Kirghiz).

Gampsophlebia PRITYKINA, 1980a, p. 131 [**G. modica*; OD]. Little-known genus, based on hind wing fragment; area between MA and CUP with only a single row of cells; posterior side of q cell strongly curved; 1A sigmoidally curved; at least

3 rows of cells between vein A and wing margin. *Jur.*, USSR (Kirghiz).

Hypsomelana PRITYKINA, 1968, p. 40 [**H. sepulta*; OD]. Hind wing similar to that of *Melanohypsa*, but distal angle of q cell nearly a right angle, posterior-distal angle slightly acute; only 1 row of cells between 1A and hind margin; hind margin of wing with a gently curved incision basally. *Jur.*, USSR (Kazakh).

Hypsothemis PRITYKINA, 1968, p. 41 [**H. jurasica*; OD]. Similar to *Hypsomelana* but hind margin of wing without an incision basally. *Jur.*, USSR (Kazakh).

Melanohypsa PRITYKINA, 1968, p. 39 [**M. angulata*; OD]. Hind wing with distal angle of q cell acute, posterior-distal angle slightly obtuse; 2 rows of cells between vein A and wing margin, 3 rows of cells between 1A and wing margin; hind margin of hind wing with a deep, abrupt incision basally. *Jur.*, USSR (Kazakh).—FIG. 48,2. **M. angulata*; a, fore and b, hind wings, $\times 3.3$ (Pritykina, 1968).

Nacholonda PRITYKINA, 1977, p. 83 [**N. crassicauda*; OD]. Hind wing: only 2 antenodals, aligned with subcostal crossveins; at least 6 postnodals; RS3+4 arising slightly beyond level of second antenodal; CUP sigmoidal; subquadrilateral cell long and wide, extending almost to hind margin of wing. [Family assignment doubtful.] *Cret.*, USSR (Asian RSFSR).—FIG. 48,5. **N. crassicauda*; hind wing as preserved, $\times 1$ (Pritykina, 1977).

Family OREOPTERIDAE

Pritykina, 1968

[Oreopteridae PRITYKINA, 1968, p. 29]

Fore and hind wings of similar width, hind wing more petiolate; 2 or 3 thickened antenodals, aligned with subcostal crossveins, basal one before level of arculus; commonly several subcostal crossveins, 9 to 12 postnodals, not aligned with subcostal crossveins; discoidal cell open in fore wing, closed in hind wing; vein RS2 arising distally of nodus; pterostigma short. PRITYKINA, 1980a. *Jur.*

Oreopteron PRITYKINA, 1968, p. 29 [**O. asiaticum*; OD]. Four subcostal crossveins in antenodal area; subquadrilateral cell of hind wing about same width as q cell. *Jur.*, USSR (Kazakh).—FIG. 49,2a. **O. asiaticum*; base of fore wing, $\times 4$ (Pritykina, 1968).—FIG. 49,2b. *O. simile* PRITYKINA; hind wing, $\times 4$ (Pritykina, 1980a).

Amblyopteron PRITYKINA, 1980a, p. 123 [**A. breve*; OD]. Apex of wing bluntly rounded; 3 crossveins below pterostigma; only 1 row of cells between RS1 and IRS1; cubitoanal area of wing narrow. *Jur.*, USSR (Kirghiz).

Oreopterella PRITYKINA, 1968, p. 33 [**O. paula*;

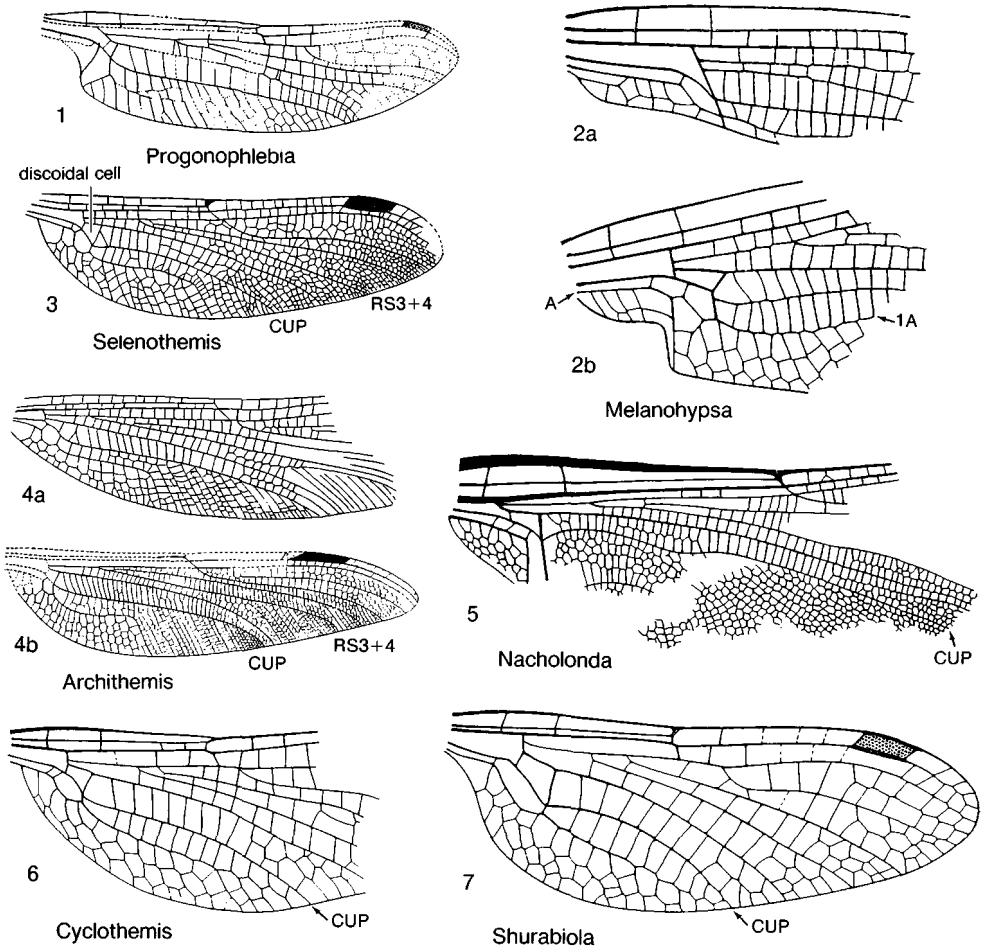


FIG. 48. Progonophlebiidae, Archithemistidae, and Karatawiidae (p. 75-76).

OD]. Little-known genus, based on fragments of fore and hind wings. Similar to *Oreopteron*, but pterostigma much longer; RS2 arising near nodal crossvein. *Jur.*, USSR (Kazakh).

Pauropteron PRITYKINA, 1980a, p. 124 [**P. miserum*; OD]. Similar to *Sogdopteron* but with only 1 row of cells between RS1 and IRS1; only 1 complete cell below pterostigma; vein A submarginal. *Jur.*, USSR (Kirghiz).

Sogdopteron PRITYKINA, 1980a, p. 121 [**S. leve*; OD]. Similar to *Oreopteron*, but petiole of wings more narrow; vein A marginal; 2 rows of cells between RS1 and IRS1. *Jur.*, USSR (Kirghiz). —FIG. 49,6. **S. leve*; wing, $\times 2.3$ (Pritykina, 1980a).

Sogjutella PRITYKINA, 1980a, p. 122 [**S. mollis*; OD]. Antenodal area of wings with only 2 subcostal crossveins; MA and CUP parallel but diverging distally; RS2 arising far distal of level of nodus. *Jur.*, USSR (Kirghiz).

Turanopteron PRITYKINA, 1968, p. 31 [**T. minor*;

OD]. Similar to *Oreopteron* but with only 2 antenodals and with a longer pterostigma. *Jur.*, USSR (Kazakh).

Family ASIOPTERIDAE
Pritykina, 1968

[Asiopteridae PRITYKINA, 1968, p. 34]

Hind wing slender, but petiole very short; 2 well-developed antenodals, aligned with crossveins below; 4 additional crossveins in antenodal area; 9 postnodals; q cell small; subquadrilateral cell with 6 sides; a single row of cells between veins M and CUP; anal area broad, with several rows of cells between 1A and wing margin. *Jur.*

Asiopteron PRITYKINA, 1968, p. 34 [**A. antiquum*; OD]. Hind wing: distal and proximal sides of q

cell parallel, former a little longer than latter; RS2 arising at second cell distal to nodus. *Jur.*, USSR (Kazakh).—FIG. 49,1. **A. antiquum*; hind wing, $\times 2$ (Pritykina, 1968).

Family EUTHEMISTIDAE Pritykina, 1968

[Euthemistidae PRITYKINA, 1968, p. 44]

Fore wing narrow but not petiolate; 2 primary antenodals and numerous other crossveins in antenodal area; discoidal cell open. *Jur.*

Euthemis PRITYKINA, 1968, p. 44 [**E. multivenosa*; OD]. Fore wing with about 20 crossveins in postnodal area; M and RS almost contiguous at arculus; arculus, 1A, and a hind marginal crossvein forming a straight line. *Jur.*, USSR (Kazakh).—FIG. 49,4. *E. cellulata* PRITYKINA; fore wing, $\times 1.6$ (Pritykina, 1968).

Family TURANOTHEMISTIDAE Pritykina, 1968

[Turanothemistidae PRITYKINA, 1968, p. 38]

Hind wing with 2 thick antenodals; subcostal area in antenodal region with 2 crossveins aligned with antenodals but no other crossveins; vein RS2 arising directly from subnodal crossvein; q cell without crossveins. *Jur.*

Turanothemis PRITYKINA, 1968, p. 38 [**T. nodalis*; OD]. RS3+4 arising slightly nearer to nodus than to arculus. *Jur.*, USSR (Kazakh).—FIG. 49,3. **T. nodalis*; hind wing, $\times 1.8$ (Pritykina, 1968).

Family TRIASSOLESTIDAE Tillyard, 1918

[*nom. transl.* PRITYKINA, 1981, p. 39, ex Triassolestinae TILLYARD, 1918c, p. 418]

Species of moderate size. Wings: fore wing slender, hind wing much broader; nodus slightly nearer to wing base than to pterostigma; discoidal cell open in fore wing, apparently closed in hind wing; anal veins much reduced. PRITYKINA, 1981. *Trias.*

Triassolestes TILLYARD, 1918c, p. 418 [**T. epio-phlebioides*; OD]. Little-known genus, based on small wing fragment. PRITYKINA, 1981. *Trias.*, Australia (Queensland).

Triassolestodes PRITYKINA, 1981, p. 40 [**T. asiaticus*; OD]. Fore wing: discoidal crossvein aligned with arculus; pterostigma much longer

than that of hind wing. RS3+4 in both wings arising at level of nodus. Hind wing more than twice as broad as fore wing. *Trias.*, USSR (Asian RSFSR).—FIG. 49,5. **T. asiaticus*; a, fore and b, hind wings, $\times 2.2$ (Pritykina, 1981).

Triassothemis CARPENTER, 1960c, p. 71 [**T. mendozensis*; OD]. Little-known genus, based on wing fragment; nodus incipient, remote from wing base. [Family assignment doubtful.] PRITYKINA, 1981. *Trias.*, South America (Argentina).

Family UNCERTAIN

The following genera, apparently belonging to the order Odonata, suborder Anisozygoptera, are too poorly known to permit assignment to families.

Acrophlebia COWLEY, 1942, p. 71 [**Heterophlebia geinitzi* HANDLIRSCH, 1906b, p. 467]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Anisophlebia HANDLIRSCH, 1906b, p. 584 [**Heterophlebia belle* HAGEN, 1862, p. 105; OD]. Little-known genus, based on poorly preserved fore wing; nodus weakly formed, nodal break absent; discoidal cell closed, containing a few crossveins; costal wing margin thick and spinous. *Jur.*, Europe (Germany).

Anomothemis HANDLIRSCH, 1906b, p. 470 [**A. brevistigma*; OD]. Little-known genus, based on apical wing fragment. *Jur.*, Europe (Germany).

Dialothemis COWLEY, 1942, p. 68 [**Liadothemis dubis* HANDLIRSCH, 1939, p. 22; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Ensphingophlebia BODE, 1953, p. 45 [**E. undulata*; OD]. Little-known genus, based on wing fragments; probably related to *Liassophlebia*. *Jur.*, Europe (Germany).

Hemerobioides BUCKLAND, 1838, p. 688 [**H. giganteus*; OD]. Little-known genus, based on wing fragment. *Jur.*, England.

Heterothemis HANDLIRSCH, 1906b, p. 468 [**H. germanica*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Isophlebiodes PRITYKINA, 1968, p. 46 [**I. obscurus*; OD]. Little-known genus, based on basal fragment of hind wing; q cell as in *Kazachophlebia* but less irregular. *Jur.*, USSR (Kazakh).

Kazachophlebia PRITYKINA, 1968, p. 47 [**K. curvata*; OD]. Little-known genus, based on basal fragment of fore(?) wing; q cell long and irregular, its anterodistal corner forming a right angle. *Jur.*, USSR (Kazakh).

Liadothemis HANDLIRSCH, 1906b, p. 469 [**L. hydrodictyon*; OD]. Little-known genus, based on wing fragment. ZESSIN, 1982. *Jur.*, Europe (Germany).

Oryctothemis HANDLIRSCH, 1906b, p. 469 [**O.*

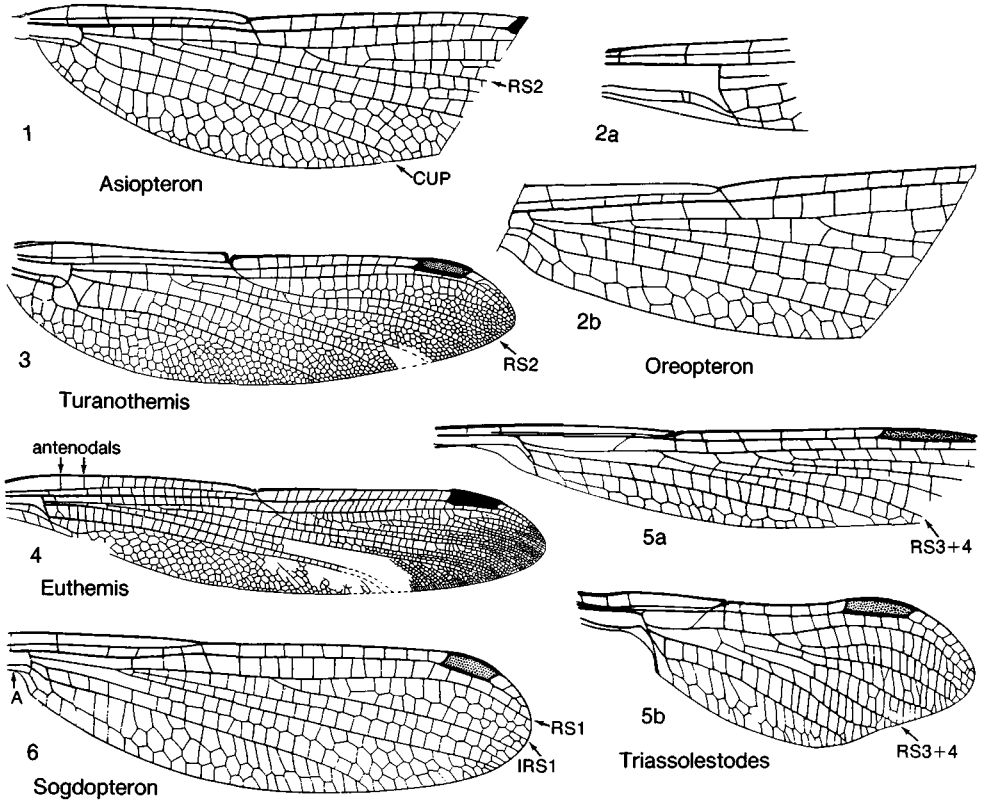


FIG. 49. Oreopteridae, Asiopteridae, Euthemistidae, Turanothemistidae, and Triassolestidae (p. 76–78).

- bageni*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).
- Parelthoemis** HANDLIRSCH, 1906b, p. 470 [**P. dobertinensis*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).
- Petrothemis** HANDLIRSCH, 1906b, p. 469 [**P. singularis*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).
- Plagiophlebia** BODE, 1953, p. 52 [**P. praecostarea*; OD]. Little-known genus, based on wing fragments. *Jur.*, Europe (Germany).
- Pycnothemis** HANDLIRSCH, 1939, p. 28 [**P. densa*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).
- Rhabdothemis** HANDLIRSCH, 1939, p. 28 [**R. strigivena*; OD]. Little-known genus, based on apical wing fragment. *Jur.*, Europe (Germany).
- Sogdothemis** MARTYNOV, 1937a, p. 116 [**S. moderata*; OD]. Little-known genus, based on wing fragment. *Jur.*, USSR (Tadzhik).
- Temnostigma** HANDLIRSCH, 1939, p. 28 [**T. singulare*; OD]. Little-known genus, based on wing fragments. *Jur.*, Europe (Germany).
- Triassoneura** RIEK, 1976b, p. 794 [**T. andersoni*; OD]. Little-known genus, based on basal frag-

ment of wing; discoidal cell open; vein A apparently coalesced with CUP basally. PRITYKINA, 1981. *Trias.*, South Africa, USSR (Asian RSFSR).

Triassophlebia TILLYARD, 1922b, p. 454 [**T. stigmatica*; OD]. Little-known genus, based on small wing fragment showing pterostigmal area. [Possibly related to *Triassolestes*.] PRITYKINA, 1981. *Trias.*, Australia (New South Wales).

Suborder ANISOPTERA Selys-Longchamps 1854

[Anisoptera SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1854, p. 1]

Wings broad basally, never petiolate; hind wings commonly markedly broadened; nodus very well developed, usually situated nearer to apex than to base of wing, occasionally near midwing; pterostigma well developed, commonly elongate; arculus specialized; discoidal cells of both wings closed and usually divided into a supratriangle (anterior) and a

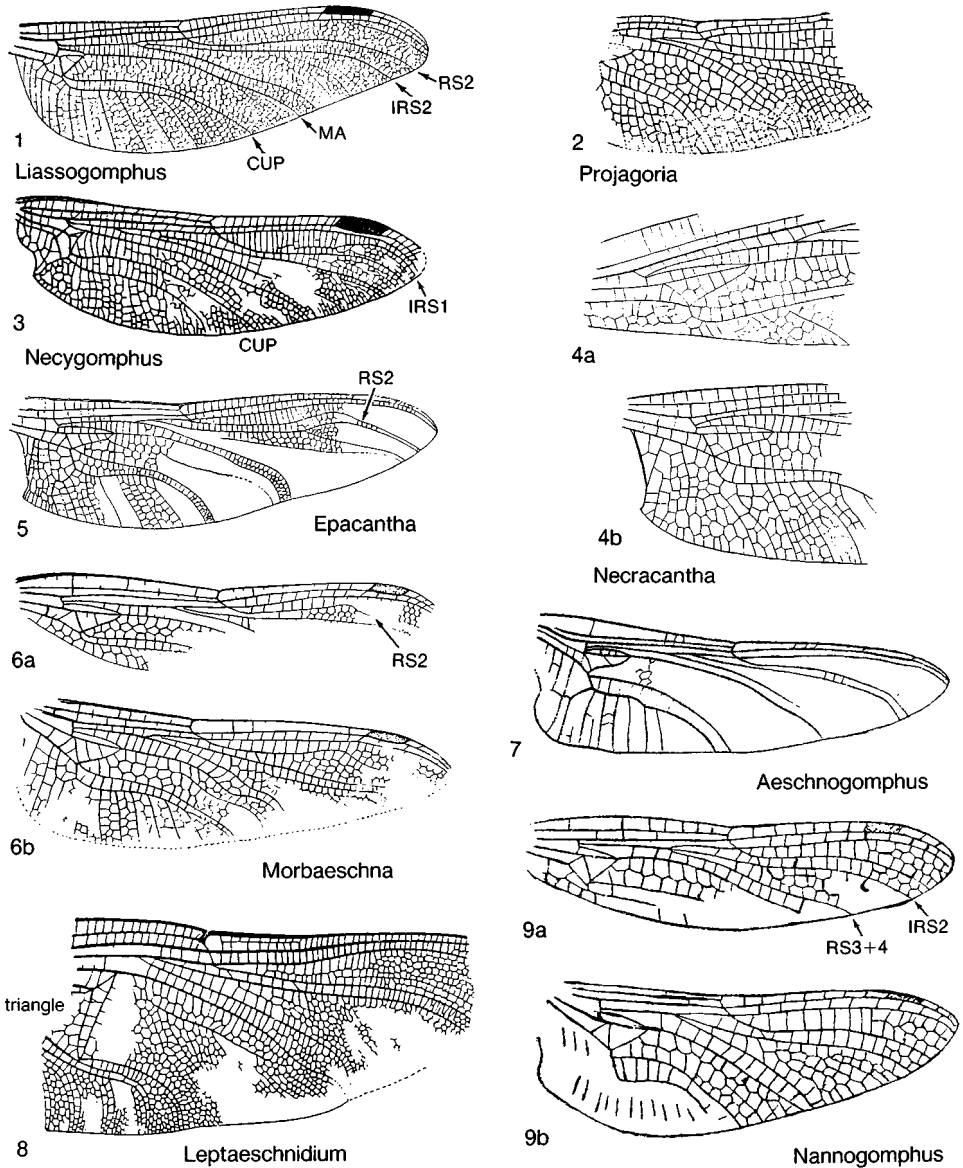


FIG. 50. Liassogomphidae, Gomphidae, and Aeshnidae (p. 81–82).

triangle (posterior), which is commonly divided by additional veins that may even form a reticulation; a third triangle, the sub-triangle, more rarely present just posterior to triangle; vein RS with 3 main branches; vestige of CUA absent; cells in hind wing commonly clustered in a loop resembling a boot. Nymphs with rectal gills. *Jur.*–*Holo.*

Family LIASSOGOMPHIDAE
Tillyard, 1935

[Liassogomphidae TILLYARD, 1935b, p. 381] [=Gomphitidae TILLYARD, 1925a, p. 33; Myopophlebiidae BODE, 1953, p. 63]

Wings apparently similar to those of Gomphidae, but hind wing with an extensive area behind vein 1A reaching to level of nodus; pterostigma slender. *Jur.*

- Liassogomphus** COWLEY, 1934c, p. 275, *nom. subst.* pro *Gomphites* TILLYARD, 1925a, p. 35, *non* CARTER, 1871 [*Aeschna brodiei* BUCKMAN, 1844, p. 82; OD]. Two rows of cells between RS2 and IRS2, beginning about halfway between nodus and pterostigma; 3 rows of cells between MA and CUP to level of origin of RS3+4. COWLEY, 1942. *Jur.*, England.—FIG. 50.1. **L. brodiei* (BUCKMAN); hind wing, $\times 1.5$ (Tillyard, 1925a).
- Necygomphus** COWLEY, 1942, p. 75, *nom. subst.* pro *Necrogomphus* HANDLIRSCH, 1939, p. 31, *non* CAMPION, 1923 [*Necrogomphus brunswigiae* HANDLIRSCH, 1939, p. 31; OD] [= *Myopophlebia* BODE, 1953, p. 63 (type, *M. libera*)]. Hind wing: intercalary vein IRS1 long, arising halfway between nodus and pterostigma. *Jur.*, Europe (Germany).—FIG. 50.3. *N. libera* (BODE); hind wing, $\times 1.5$ (Bode, 1953).
- Palaeogomphus** HANDLIRSCH, 1939, p. 31 [*Heterophlebia propingua* BODE, 1905, p. 233; OD]. Fore wing: MA and CUP subparallel for most of their lengths but converging abruptly distally; upper side of triangle ending below distal angle of supratriangle. *Jur.*, Europe (Germany).
- Phthitogomphus** COWLEY, 1942, p. 71, *nom. subst.* pro *Paragomphus* HANDLIRSCH, 1939, p. 31, *non* COWLEY, 1934 [*Paragomphus angulatus* HANDLIRSCH, 1939, p. 31; OD]. Two rows of cells between RS2 and IRS2 beginning just proximad of nodus between MA and CUP. *Jur.*, Europe (Germany).
- Proinogomphus** HANDLIRSCH, 1939, p. 31 [*P. bodei*; OD]. Hind wing: 2 rows of cells between MA and CUP from triangle to about 8 cells distal to it, then increasing to 3 or more rows. BODE, 1905; COWLEY, 1942. *Jur.*, Europe (Germany).

Family GOMPHIDAE Rambur, 1842

[Gomphidae RAMBUR, 1842, p. 152]

Eyes widely separated; antenodal system similar to that of Aeshnidae; triangles usually short, not elongate along longitudinal axis of wing and about equidistant from arculus in both pairs of wings; pterostigma with a distinct brace vein; anal loop, if present, very small. *Jur.*—*Holo.*

Gomphus LEACH, 1815, p. 37. [Generic assignment of fossil (nymph) doubtful.] HAGEN, 1848. *Oligo.*, Europe (Baltic)—*Holo.*

Aeschnogomphus HANDLIRSCH, 1906b, p. 590 [*Aeschna charpentieri* HAGEN, 1848, p. 11; SD COWLEY, 1934b, p. 249]. Little-known genus, based on fragments of fore and hind wings. Triangle of hind wing more slender than that of fore wing. TILLYARD, 1932b. *Jur.*, Europe (Ger-

many).—FIG. 50.7. **A. charpentieri* (HAGEN); hind wing, $\times 0.6$ (Hagen, 1861–1863).

Aeschnopsis HANDLIRSCH, 1939, p. 153 [*Aeschna perampla* BRODIE, 1845, p. 33; OD]. Little-known genus, based on hind wing. Apparently similar to *Protolindenia*; triangle greatly extended longitudinally and containing a crossvein. COWLEY, 1942. *Jur.*, England.

Gomphoides SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1850, p. 360. [Generic assignment of fossil doubtful.] PICTET & HAGEN, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

Nannogomphus HANDLIRSCH, 1906b, p. 586 [*N. bavaricus*; SD COWLEY, 1934b, p. 252]. Fore and hind wings with relatively few cells in most areas; only 2 rows of cells between MA and CUP proximally; in fore wing IRS2 and RS3+4 only slightly divergent distally, with only 3 or 4 rows of cells between them; RS2 smoothly curved; 1A close to posterior margin of wing. *Jur.*, Europe (Germany).—FIG. 50.9. **N. bavaricus*; *a*, fore and *b*, hind wings, $\times 2.5$ (Handlirsch, 1906b).

Protolindenia DEICHMÜLLER, 1886, p. 37 [*Aeschna wittei* GIEBEL, 1860, p. 127; OD]. Similar to *Nannogomphus*, but fore and hind wings with numerous small cells; 3 or more cells between MA and CUP proximally; in fore wing, IRS2 and RS2 strongly divergent, with many rows of cells between them distally; RS2 abruptly curved distally; 1A curving away from hind margin. FRASER, 1957; PRITYKINA, 1968. *Jur.*, Europe (Germany), USSR (Kazakh).—FIG. 39. **P. wittei* (GIEBEL), Germany; fore and hind wings and body, $\times 2$ (Carpenter, new).

Family AESHNIDAE Leach, 1815

[Aeshnidae LEACH, 1815, p. 126]

Head large, nearly hemispherical; eyes very large, meeting at middorsal region. Wings with 2 distinct primary antenodals; other antenodals usually not aligned with crossveins below; triangles of both pairs of wings similar in shape, elongate along longitudinal axis of wing; triangle of fore wing slightly longer than that of hind wing; triangles and supratrangles of both wings with several crossveins; vein RS2 arched forward near level of pterostigma; brace vein well developed at proximal end of pterostigma. *Jur.*—*Holo.*

Aeshna FABRICIUS, 1775, p. 424. COCKERELL, 1908q; PITON, 1935a; THÉOBALD, 1937a; TIMON-DAVID, 1946. *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Europe (France)—*Holo.*

Baissaeschna PRITYKINA, 1977, p. 85 [**B. prisca*; OD]. Similar to *Oligoaeschna* (recent), but net-

work of crossveins more dense; anal vein more extensive. *Cret.*, USSR (Asian RSFSR).

Basiaeschna SELYS-LONGCHAMPS, 1883, p. 735. MARTYNOV, 1929; FRASER, 1957. *Oligo.*, USSR (Kazakh)—*Holo.*

Epacantha MARTYNOV, 1929, p. 190 [**E. magnifica*; OD]. Hind wing unusually broad basally; apex subacute; RS2 with a prominent anterior curve just before level of pterostigma; IRS2 deeply forked; triangle with 5 cells. FRASER, 1957. *Oligo.*, USSR (Kazakh).—FIG. 50.5. **E. magnifica*; hind wing, $\times 1$ (Martynov, 1929).

Epiaeschna HAGEN, 1873, p. 271. MARTYNOV, 1927c. *Mio.*, USSR (European RSFSR)—*Holo.*

Gobiaeschna PRITYKINA, 1977, p. 85 [**G. occulta*; OD]. Fore wing as in *Hoplonaeschna* (recent) but with larger pterostigma; RS2 and IRS2 nearly parallel, with only 1 row of cells between them. *Cret.*, Asia (Mongolia).

Gomphaeschna SELYS-LONGCHAMPS, 1871, p. 413. PRITYKINA, 1977. *Cret.*, USSR (Asian RSFSR)—*Holo.*

Heliaeschna SELYS-LONGCHAMPS, 1882, p. 667. MARTYNOV, 1927c. [Generic assignment of fossil doubtful.] *Mio.*, USSR (European RSFSR)—*Holo.*

Leptaeschnidium PRITYKINA, 1977, p. 88 [**L. latum*; OD]. Hind wing: venation less dense than in other genera of family; only 1 row of cells in costal area; triangle very narrow. *Cret.*, USSR (Asian RSFSR).—FIG. 50.8. **L. latum*; hind wing as preserved, $\times 2$ (Pritykina, 1977).

Lithaeschna COCKERELL, 1907b, p. 133 [**L. needhami*; OD]. Similar to *Gomphaeschna* (recent), but anal loop with 5 cells; triangle with 3 cells. *Oligo.*, USA (Colorado).

Morbaeschna NEEDHAM, 1907, p. 141 [**Aeschna muensteri* GERMAR, 1839, p. 215; OD]. In fore and hind wings, RS2 strongly arched just proximad of pterostigma; triangle with a few cells. FRASER, 1957. *Jur.*, Europe (Germany).—FIG. 50.6. **M. muensteri* (Germar); *a*, fore and *b*, hind wings, $\times 0.8$ (Needham, 1907).

Necracantha MARTYNOV, 1929, p. 193 [**N. composita*; SD COWLEY, 1934d, p. 243]. Little-known genus, based on fragments of fore and hind wings; apparently similar to *Epacantha*, but triangle with 7 or 8 cells. FRASER, 1957. *Oligo.*, USSR (Kazakh).—FIG. 50.4. **N. composita*; *a*, fore and *b*, hind wings, $\times 1.5$ (Martynov, 1929).

Oligaeschna PITON & THÉOBALD, 1939, p. 6 [**O. jungi*; OD] [= *Neoligaeschna* CARPENTER, 1986, p. 576, obj.] Little-known genus, based on wing fragment. *Oligo.*, Europe (France).

Oligoaeschna SELYS-LONGCHAMPS, 1889, p. 470. ESAKI & ASAHINA, 1957; NEL & PAPAZIAN, 1983. *Oligo.*, Europe (France); *Plio.*, Japan—*Holo.*

Oplonaeschna SELYS-LONGCHAMPS, 1883, p. 375. COCKERELL, 1913c; HENRIKSEN, 1922a; PONGRÁČZ, 1928. *Oligo.*, USA (Colorado); *Mio.*, Europe (Denmark, Yugoslavia)—*Holo.*

Projagoria MARTYNOV, 1929, p. 186 [**P. con-*

juncta; OD]. Little-known genus, apparently similar to *Oligoaeschna* (recent) but with reticulation of crossveins more dense. *Oligo.*, USSR (Kazakh).—FIG. 50.2. **P. conjuncta*; hind wing, $\times 1.5$ (Martynov, 1929).

Triaeschna CAMPION, 1916, p. 230 [**T. gossi*; OD]. Fore wing: nodus almost exactly at midwing; RS2 arching anteriorly just before level of pterostigma, then curving posteriorly; IRS2 forking before proximal end of pterostigma, not arched anteriorly; triangle very long, curved. *Eoc.*, England.

Family AESCHNIDIIDAE Handlirsch, 1906

[Aeschnidiidae HANDLIRSCH, 1906b, p. 593]

Apparently related to the Cordulegastridae (recent). Wings very broad; nodus at about middle of wing; crossveins very numerous, forming a dense reticulation; triangles very narrow and elongate, with numerous cells; ovipositor very long. *Jur.*—*Cret.*

Aeschnidium WESTWOOD, 1854, p. 394 [**A. bubas*; OD] [= *Estemoa* GIEBEL, 1856, p. 286, obj.]. Triangles of both wings with a nearly straight distal side; arculus connected to CUP by a short crossvein. DEICHMÜLLER, 1886; TILLYARD, 1918a; RIEK, 1954b; FRASER, 1957. *Jur.*, England, Europe (Germany).—FIG. 51.7. *A. densum* HAGEN, Germany; fore and hind wings, $\times 1.5$ (Hagen, 1862).

Aeschnidiella ZALESSKY, 1953a, p. 165 [**A. abanovi*; OD]. Little-known genus, based on hind wing fragments. Similar to *Aeschnidiopsis*, but distal side of triangles only very slightly concave. *Cret.*, USSR (Kazakh).

Aeschnidiopsis TILLYARD, 1918a, p. 690 [**A. flindersiensis* WOODWARD, 1884, p. 337; OD]. Triangles with a strongly curved distal side; arculus not connected to CUP. FRASER, 1957. *Cret.*, Australia (Queensland).—FIG. 51.8. **A. flindersiensis*; base of hind wing, $\times 1.3$ (Tillyard, 1918a).

Family AKTASSIIDAE Pritykina, 1968

[Aktassiidae PRITYKINA, 1968, p. 48]

Large species; hind wing with nearly straight posterior margin except near wing base; pterostigma elongate, slender; intercalary vein IRS1 well developed, parallel to RS1; triangle almost equilateral; supra-triangle without crossveins. *Jur.*

Aktassia PRITYKINA, 1968, p. 48 [**A. magna*; OD]. Hind wing: distal and posterior areas with fine meshwork of crossveins; M terminating on hind margin slightly beyond level of midwing. *Jur.*,

USSR (Kazakh).—FIG. 51,5. **A. magna*; hind wing as preserved, $\times 0.9$ (Pritykina, 1968).

Family PETALURIDAE Needham, 1903

[Petaluridae NEEDHAM, 1903, p. 739]

Large to very large species, with long, reticulate, and slightly falcate wings; pterostigma long to very long, with a strong brace vein; 2 primary antenodals, with numerous secondary antenodals, as in Gomphidae; triangles of both wings usually similar; anal loop not well developed. Eyes separated, as in Gomphidae. *Jur.*—*Holo.*

Petalura LEACH, 1815, p. 95. *Holo.*

Cymatophlebiella PRITYKINA, 1968, p. 51 [**C. euryptera*; OD]. Similar to *Libellulum*, but triangle of hind wing equilateral, with 3 cells; 1A with 12 branches; 12 antenodals and 12 postnodals. *Jur.*, USSR (Kazakh).

Cymatophlebiopsis HANDLIRSCH, 1939, p. 153 [**C. pseudobubas*; OD]. Little-known genus, based on fragment of hind wing. Similar to *Libellulum*, but triangle more elongate along longitudinal axis of wing and divided by oblique crossvein; 1A with about 6 descending branches. [Family assignment doubtful; placed in Gomphidae by HANDLIRSCH (1939) and COWLEY (1942).] NEEDHAM, 1907; COWLEY, 1942. *Jur.*, England.

Libellulum WESTWOOD, 1854, p. 394 [**L. agrias*; OD] [= *Cymatophlebia* DEICHMÜLLER, 1886, p. 49 (type, *Libellula longialata* GERMAR, 1839, p. 216, *vide* FRASER, 1957)]. RS2 only slightly bent just basad of pterostigma; triangle with many cells. [Family assignment uncertain; placed in Gomphidae by HANDLIRSCH (1906b), in Aeschnidae by NEEDHAM (1907), and in Petaluridae by FRASER (1957).] *Jur.*, England, Europe (Germany).—FIG. 51,1. *L. longialata* (GERMAR); *a*, fore and *b*, hind wings, $\times 0.8$ (Needham, 1907).

Mesuropetala HANDLIRSCH, 1906b, p. 588 [**Gomphus koebleri* HAGEN, 1848, p. 8; SD COWLEY, 1934b, p. 252]. Little-known genus, apparently similar to *Petalura* (recent); RS2 smoothly curved, close and parallel to IRS1. DEICHMÜLLER, 1886; FRASER, 1957; PRITYKINA, 1968. *Jur.*, Europe (Germany), USSR (Kazakh).

Family CORDULIIDAE Selys-Longchamps, 1850

[Corduliidae SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1850, p. 66]

Antenodals aligned with subcostal crossveins below, not differentiated into primaries and secondaries; triangle of fore wing elon-

gate anteroposteriorly; that of hind wing slightly elongate along longitudinal axis of wing; anal loop of hind wing reduced or absent. *Eoc.*—*Holo.*

Cordulia LEACH, 1815, p. 136. *Holo.*

Croaticordulia KIAUTA, 1969, p. 86 [**Libellula platyptera* CHARPENTIER, 1843, p. 408; OD]. Similar to *Cordulia* (recent); 7 postnodals in both fore and hind wings; 5 antenodals in hind wing; pterostigma 4 times as long as wide; 2 cells in triangle of hind wing. *Mio.*, Europe (Yugoslavia).

Miocordulia KENNEDY, 1931, p. 314 [**M. latipennis*; OD]. Apparently related to *Somatochlora* and *Epicordulia* (both recent), but hind wing with 3 rows of cells extending outward from triangle. FRASER, 1957. *Mio.*, USA (Washington).—FIG. 51,3. **M. latipennis*; hind wing, $\times 1.5$ (Kennedy, 1931).

Stenogomphus SCUDDER, 1892, p. 13 [**S. carletoni*; OD]. Fore wing; triangle relatively remote from arculus; nodus slightly nearer to pterostigma than to arculus; MA sigmoidally curved. [Family position uncertain; considered by HAGEN and SELYS-LONGCHAMPS (SCUDDER, 1892) to be a gomphid but by RIS and MUTKOWSKI (RIS, 1910) to be a corduliid.] COCKERELL, 1921e. *Eoc.*, USA (Colorado, Wyoming).—FIG. 51,2. **S. carletoni*; fore wing, $\times 1.4$ (Scudder, 1892).

Family LIBELLULIDAE Leach, 1815

[Libellulidae LEACH, 1815, p. 136]

Adults similar to those of the Corduliidae, but with anal loop of hind wing well developed and boot-shaped. *Oligo.*—*Holo.*

Libellula LINNÉ, 1758, p. 543. [Generic assignment of fossils doubtful.] HANDLIRSCH, 1906b. *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Germany)—*Holo.*

Celithemis HAGEN, 1861, p. 147. STATZ, 1937. *Mio.*, Europe (Germany)—*Holo.*

Lithemis FRASER, 1951, p. 51 [**L. lejeunecarpentieri*; OD]. Related to *Neurothemis* (recent) but with only a single row of cells between RS2 and IRS2; arculus at level of first antenodal. *Mio.*, Europe (Germany).

Oligogaemia FRASER, 1951, p. 52 [**O. imperfecta*; OD]. Little-known genus, based on fragment of hind wing; apparently related to *Rhyothemis* (recent). Basal side of triangle at level of arculus; arculus between first and second antenodals. *Mio.*, Europe (Germany).—FIG. 51,4. **O. imperfecta*; hind wing, $\times 1$ (Fraser, 1951).

Trameobasileus ZEUNER, 1938, p. 109 [**T. moguntiacus*; OD]. Similar to *Hydrobasileus* (recent), but triangle of hind wing with 5 cells. *Mio.*, Europe (Germany).

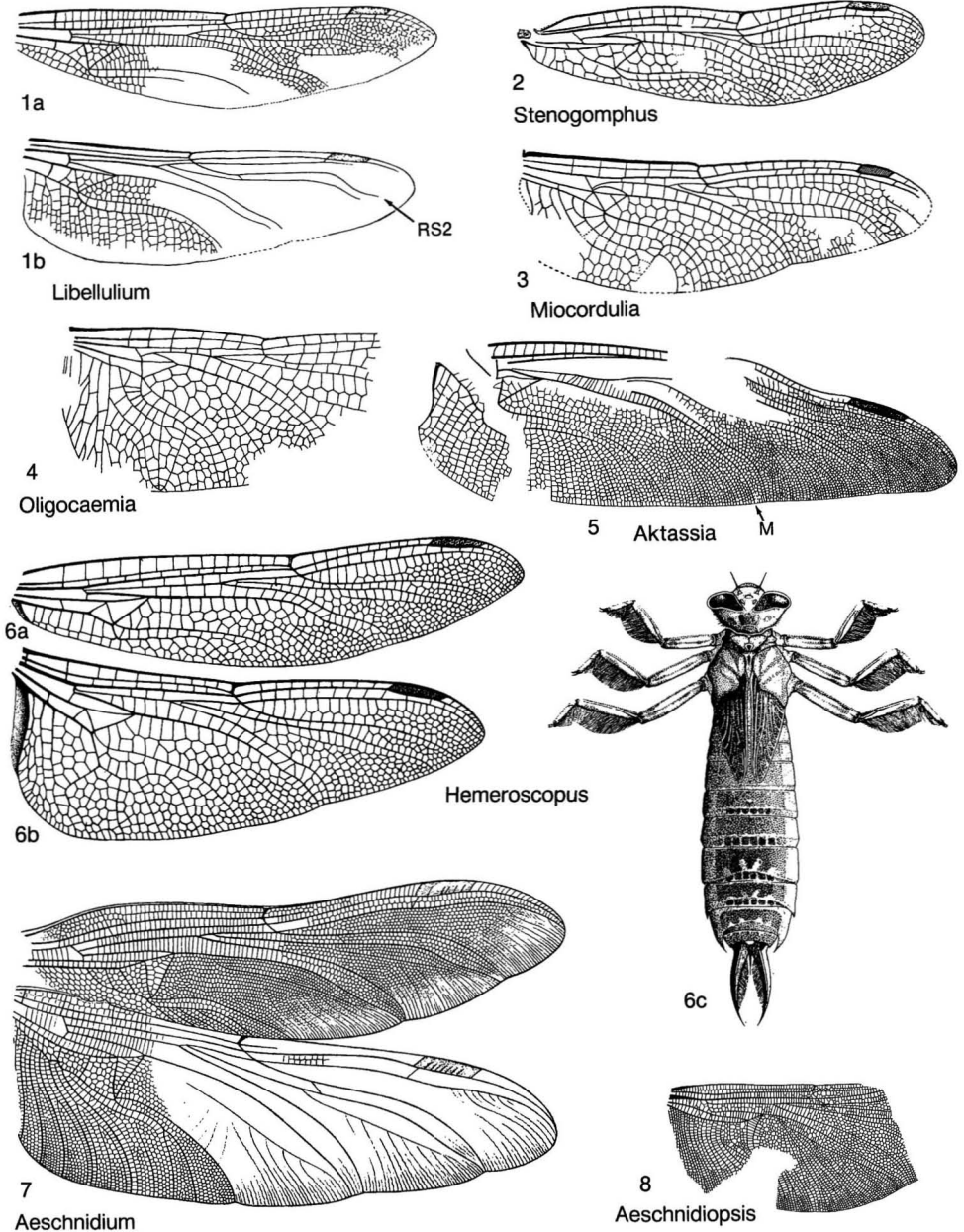


FIG. 51. Aeschniidae, Aktassiidae, Petaluridae, Corduliidae, Libellulidae, and Hemeroscopidae (p. 82-85).

Family HEMEROSCOPIDAE
Pritykina, 1977

[Hemeroscopidae PRITYKINA, 1977, p. 89]

Related to Cordulegastridae (recent).
Adults with triangles of fore and hind wings

similar in form and size in both sexes; hind wing much broader than fore wing; branches of vein 1A forming a large loop. Nymphs with streamlined body; eyes unusually large; tibiae with large brushes of long hairs. *Cret.*

Hemeroscopus PRITYKINA, 1977, p. 88 [**H. baisicus*; OD]. Wings: RS2 smoothly curved, slightly divergent from IRS2 distally; RS3+4 more sigmoidal in fore wing than in hind. *Cret.*, USSR (Asian RSFSR).—FIG. 51.6. **H. baisicus*; a, fore wing, b, hind wing, c, adult nymph, all $\times 1$ (Pritykina, 1977).

Family UNCERTAIN

The following genera, apparently belonging to the order Odonata, suborder Anisoptera, are too poorly known to permit assignment to families.

Elattogomphus BODE, 1953, p. 58 [**E. latus*; OD]. Little-known genus, based on incomplete, broad wing. *Jur.*, Europe (Germany).

Lithogomphus BEIER, 1952, p. 129 [**L. munzenbergianus*; OD]. Little-known genus, based on incomplete wing. *Mio.*, Europe (Germany).

Necrogomphus CAMPION, 1923, p. 669, *nom. subst. pro Mesogomphus* HANDLIRSCH, 1906b, p. 592, non FÖRSTER, 1906 [**Gomphus petrifactus* HAGEN in SELYS-LONGCHAMPS & HAGEN, 1850, p. 359; SD COWLEY, 1934a, p. 202]. Little-known genus, based on wing fragment. *Jur.*, England.

Paleoaeschna MEUNIER, 1914c, p. 180 [**P. vidal*; OD]. Little-known genus, based on nymph. *Jur.*, Europe (Spain).

Protopaltothemis PONGRÁČZ, 1928, p. 122 [**P. hageni*; OD]. Little-known genus, based on wing fragments. *Mio.*, Europe (Yugoslavia).

Sinaeschnidia HONG, 1965, p. 171 [**S. heishankowensis*; OD]. Little-known genus, based on wing fragment. ZHOU & WEI, 1980. *Jur.*, China (Zhejiang).

Strongylogomphus BODE, 1953, p. 62 [**S. graselianus*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Urogomphus HANDLIRSCH, 1906b, p. 594 [**Aeschna gigantea* GERMAR, 1839, p. 216; SD COWLEY, 1934b, p. 253]. Little-known genus, based on incomplete wings. *Jur.*, Europe (Germany).

Suborder ZYGOPTERA

Selys-Longchamps, 1854

[Zygoptera SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1854, p. 2]

Wings petiolate, subpetiolate, or nonpetiolate, but not greatly widened near base; fore and hind wings closely similar in size, shape, and venation; nodus well developed and situated at or slightly basad of middle of costal margin; arculus and pterostigma well developed; discoidal cell situated below arculus, either open or closed, formed by space between oblique basal part of vein MA above

and curving part of CUP below; discoidal cell not divided into triangle and supratringle; RS with 3 main branches and at least 2 intercalaries; no vestige of CUA present at wing base. Nymphs with 3 caudal gill plates. *Jur.—Holo.*

Family COENAGRIONIDAE

Kirby, 1890

[Coenagrionidae KIRBY, 1890, p. 119]

Wings petiolate and narrow; primary antenodals well developed and extending to vein R; rarely a few accessory antenodals present; discoidal cell complete but short; MA zigzagging for at least a considerable part of its length; veins IRS2 and RS3 arising closer to subnodal crossvein than to arculus. *Oligo.—Holo.*

Coenagrion KIRBY, 1890, p. 148. *Holo.*

Argia RAMBUR, 1842, p. 254. [Generic assignment of fossil doubtful.] SCUDDER, 1892. *Oligo.*, USA (Colorado)—*Holo.*

Enallagma CHARPENTIER, 1840, p. 21 [= *Sobobapteron* PIERCE, 1965, p. 160 (type, *S. kirbyae*)]. COCKERELL, 1925b; CARPENTER, 1968. *Oligo.*, USA (Colorado); *Pleist.*, USA (California)—*Holo.*

Hesperagrion CALVERT, 1902, p. 103. SCUDDER, 1892; COCKERELL, 1907b, 1908j; FRASER, 1957. *Oligo.*, USA (Colorado)—*Holo.*

Family LESTIDAE Calvert, 1901

[Lestidae CALVERT, 1901, p. 32]

Wings petiolate and slender; primary antenodals well developed; accessory nodals rarely present; postnodals aligned with crossveins below; pterostigma much longer than wide, not usually pointed distally; discoidal cell usually closed. *Oligo.—Holo.*

Lestes LEACH, 1815, p. 137. HEER, 1847, 1849, 1853a; HAGEN, 1858; THÉOBALD, 1937a; SCHMIDT, 1958. *Oligo.*, Europe (Germany, France)—*Holo.*

Oligolestes SCHMIDT, 1958, p. 3 [**Lestes grandis* STATZ, 1930, p. 11; OD]. Similar to *Lestes* but with more intercalary veins. *Oligo.*, Europe (Germany).—FIG. 52.4. **O. grandis* (STATZ); wings, $\times 1.4$ (Schmidt, 1958).

Family MEGAPODAGRIONIDAE

Tillyard, 1917

[Megapodagrionidae TILLYARD, 1917c, p. 278]

Wings petiolate; venation similar to that of *Lestes* (recent), but veins IRS2 and RS3

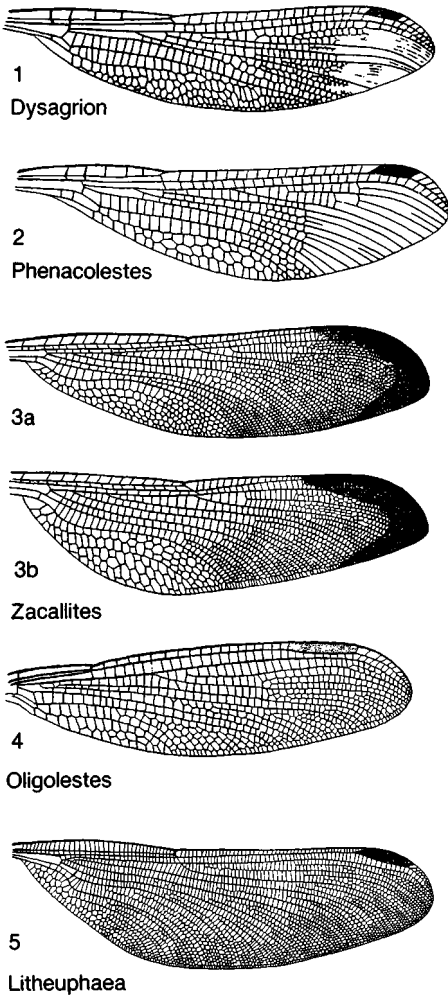


FIG. 52. Lestidae, Pseudolestidae, and Euphaeidae (p. 85–88).

arising nearer to nodus than to arculus; pterostigma usually pointed distally. *Eoc.*—*Holo.*

Megapodagrion SELYS-LONGCHAMPS, 1885, p. 29. *Holo.*

Eopodagrion COCKERELL, 1920c, p. 237 [**E. scuderi*; OD]. Little-known genus, based on wing fragment; related to *Megapodagrion* (recent) but with an oblique brace at proximal end of pterostigma. KENNEDY, 1925. *Eoc.*, USA (Wyoming).

Lithagrion SCUDDER, 1890, p. 134 [**L. byalinum*; SD COCKERELL, 1907b, p. 138]. Similar to *Melanagrion*, but pterostigma bounded by 3 or 4 cells below. COCKERELL, 1908j; MARTYNOV, 1929; FRASER, 1957. *Oligo.*, USA (Colorado), USSR (Kazakh).

Melanagrion COCKERELL, 1907b, p. 138 [**Lithagrion umbratum* SCUDDER, 1890, p. 136; OD]. Wings dark; pterostigma bounded by 5 cells below; cells of first 2 rows between nodus and pterostigma higher than long. FRASER, 1957. *Oligo.*, USA (Colorado).

Miopodagrion KENNEDY, 1925, p. 297 [**Lithagrion optimum* COCKERELL, 1916c, p. 101; OD]. Little-known genus, based on wing fragment; possibly close to *Argiolestes* (recent). FRASER, 1957. *Oligo.*, USA (Colorado).

Oligoargiolestes KENNEDY, 1925, p. 296 [**O. oligocenum*; OD]. Little-known genus, based on wing fragment; possibly close to *Megapodagrion*. FRASER, 1957. *Oligo.*, England.

Stenolestes SCUDDER, 1895a, p. 119 [**Agrion iris* HEER, 1865, p. 395; OD]. Little-known genus, based on wing fragment. *Mio.*, Europe (Germany).

Family PSEUDOLESTIDAE Fraser, 1957

[Pseudolestidae FRASER, 1957, p. 62]

Wings petiolate; primary antenodals well developed and commonly aligned with crossveins below; accessory antenodals few or absent; veins IRS2 and RS3 ordinarily arising nearer to arculus than to subnodal crossvein. *Eoc.*—*Holo.*

Pseudolestes KIRBY, 1900, p. 537. *Holo.*

Dysagrion SCUDDER, 1878a, p. 534 [**D. frederici*; OD]. Apparently related to *Thaumatonевра* (recent), but family assignment uncertain. Wings with 2 accessory antenodals; postnodals not aligned with crossveins below. CALVERT, 1913; FRASER, 1957. *Eoc.*, USA (Wyoming).—FIG. 52,1. **D. frederici*; wing, $\times 1.4$ (Fraser, 1957).

Phenacolestes COCKERELL, 1908p, p. 61 [**P. mirandus*; OD]. Similar to *Dysagrion* but with 3 accessory antenodals. CALVERT, 1913. *Oligo.*, USA (Colorado).—FIG. 52,2. **P. mirandus*; wing, $\times 2$ (Fraser, 1957).

Family AMPHIPTERYGIDAE Tillyard, 1926

[Amphipterygidae TILLYARD, 1926d, p. 79]

Wings petiolate; primaries distinct, extending to vein R; only a few accessory antenodals; postnodals not aligned with crossveins below; RS1 + 2 not arched toward R basally. *Eoc.*—*Holo.*

Amphipteryx SELYS-LONGCHAMPS, 1853, p. 66. *Holo.*

Petrolestes COCKERELL, 1927c, p. 81 [**P. bender-soni*; OD]. Little-known genus, based on wing

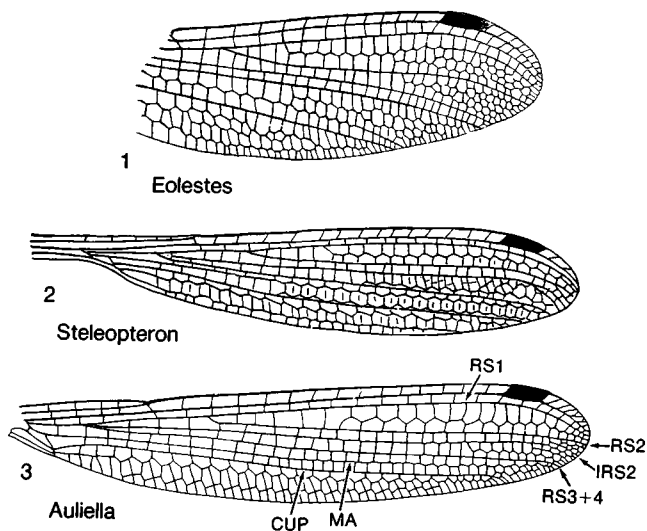


FIG. 53. Steleopteridae and Uncertain (p. 87-88).

fragment. [Family assignment doubtful.] FRASER, 1957. *Eoc.*, USA (Colorado).

Protamphipteryx COCKERELL, 1920c, p. 236 [**P. basalis*; OD]. Little-known genus, based on wing fragment; arculus midway between first and second antennodals. [Family assignment doubtful.] FRASER, 1957. *Eoc.*, USA (Wyoming).

Family STELEOPTERIDAE

Handlirsch, 1906

[Steleopteridae HANDLIRSCH, 1906b, p. 597]

Wings distinctly petiolate and slender; nodus only a short distance from level of arculus; several antennodals and numerous postnodals; only 2 rows of cells between veins RS1 and RS2; RS2, IRS2, RS3+4, MA, and CUP nearly parallel, with only a single row of cells between adjacent veins except at wing margin; CUP long, extending to level of proximal edge of prterostigma. *Jur.*

Steleopteron HANDLIRSCH, 1906b, p. 598 [**S. deichmulleri*; OD]. RS2, IRS2, RS3+4, MA, and CUP not equally spaced over wing. PRITYKINA, 1968. *Jur.*, Europe (Germany).—FIG. 53,2. **S. deichmulleri*; fore wing, $\times 2$ (Handlirsch, 1906b).

Auliella PRITYKINA, 1968, p. 35 [**A. crucigera*; OD]. Wings as in *Steleopteron*, but RS2, IRS2, R3+4, MA, and CUP equally spaced over wing. *Jur.*, USSR (Kazakh).—FIG. 53,3. **A. crucigera*; hind(?) wing, $\times 2$ (Pritykina, 1968).

Family CALOPTERYGIDAE

Selys-Longchamps, 1850

[Calopterygidae SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1850, p. 133]

Wings not petiolate; crossveins very numerous, forming a dense reticulation; antennodals numerous, extending to vein R, primaries not differentiated; RS1+2 arched toward R basally; pterostigma commonly obsolescent. *Eoc.*—*Holo.*

Calopteryx LEACH, 1815, p. 137. HEER, 1847, 1849, 1853a; HAGEN, 1848, 1861-1863; SCUDDER, 1890; ESAKI & ASAHINA, 1957. *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Europe (Germany, Yugoslavia); *Pleist.*, Japan—*Holo.*

Eocalopteryx COCKERELL, 1920c, p. 236 [**E. atavina*; OD]. Little-known genus, based on wing fragment. [Possibly a synonym of *Mnais* (recent).] FRASER, 1940. *Eoc.*, USA (Wyoming).

Eodichroma COCKERELL, 1923c, p. 397 [**E. mirifica*; OD]. Little-known genus, based on fragment of broad wing, with 13 antennodals. *Eoc.*, USA (Texas).

Family EUPHAEIDAE

Selys-Longchamps, 1853

[Euphaeidae SELYS-LONGCHAMPS, 1853, p. 47] [=Zacallitidae COCKERELL, 1928c, p. 297]

Wings subpetiolate or not petiolate; antennodals numerous and usually aligned with

crossveins below; primary antenodals not differentiated; nodus nearly at level of midwing; discoidal cell short, its base connected to vein R by arculus; pterostigma strongly developed. DAVIES, 1981. *Eoc.*—*Holo.*

Euphaea SELYS-LONGCHAMPS, 1840, p. 200. *Holo.*

Epallagites COCKERELL, 1924a, p. 9 [**E. avus*; OD]. Little-known genus; arculus at almost a third of distance from wing base to nodus. [Family assignment doubtful.] FRASER, 1957. *Eoc.*, USA (Colorado).

Indophaea FRASER, 1929, p. 293. THÉOBALD, 1937a; FRASER, 1957. *Oligo.*, Europe (France)—*Holo.*

Litheuphaea FRASER, 1955a, p. 43 [**L. carpenteri*; OD]. Similar to *Euphaea* (recent), but nodus situated more proximad, pterostigma much larger, and anal vein extending beyond level of nodus. *Oligo.*, USA (Oregon).—FIG. 52,5. **L. carpenteri*; wing, $\times 1.5$ (Fraser, 1955a).

Zacallites COCKERELL, 1928c, p. 298 [**Z. balli*; OD]. Wings subpetiolate; antenodals numerous, not aligned with crossveins below; pterostigma long; apical regions of both fore and hind wings conspicuously darkened. [Type of family Zacallitidae COCKERELL, 1928c.] FRASER, 1940, 1957. *Eoc.*, USA (Colorado).—FIG. 52,3. **Z. balli*; *a*, fore and *b*, hind wings, $\times 1.4$ (Fraser, 1940).

Family UNCERTAIN

The following genera, apparently belonging to the order Odonata, suborder Zygoptera, are too poorly known to permit assignment to families.

Austrolestidion TILLYARD in TILLYARD & DUNSTAN, 1916, p. 45 [**A. duaringae*; OD]. Little-known genus, based on nymph. *Paleoc.*—*Plio.*, Australia (Queensland).

Daemhippus NAVÁS, 1927, p. 91 [**Platynemius cineuneguli* COLLADO, 1926, p. 101; OD]. Little-known genus, based on wing fragment. *Oligo.*, Europe (Spain).

Eolestes COCKERELL, 1940a, p. 104 [**E. synthetica*; OD]. Little-known genus, based on wing fragment, with forking of 1A into 2 irregular branches. FRASER, 1945. *Eoc.*, USA (Colorado).—FIG. 53,1. **E. synthetica*; wing, $\times 2.5$ (Fraser, 1945).

Eosagrion HANDLIRSCH, 1920, p. 184 [**E. risi*; OD]. Little-known genus, based on wing fragment. [Type of family Eosagrionidae HANDLIRSCH, 1920.] *Jur.*, Europe (Germany).

Eothaumatoneura PONGRÁCZ, 1935, p. 527 [**E. ptychoptera*; OD]. Little-known genus, based on small wing fragments. *Eoc.*, Europe (Germany).

Euphaeopsis HANDLIRSCH, 1906b, p. 596 [**Euphaea multinervis* HAGEN, 1862, p. 119; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Megasemum MANEVAL, 1936, p. 28 [**M. ronzoneuse*; OD]. Little-known genus, based on wing fragment. *Oligo.*, Europe (France).

Protothore COCKERELL, 1930, p. 50 [**P. explicata*; OD]. Little-known genus, based on wing fragment, possibly related to Polythoridae (recent). *Eoc.*, USA (California).

Pseudoeuphaea HANDLIRSCH, 1906b, p. 596 [**Euphaea areolata* HAGEN, 1862, p. 106; SD COWLEY, 1934b, p. 252]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Suborder UNCERTAIN

The following genera, apparently belonging to the order Odonata, are too poorly known to permit assignment to suborders.

Family STENOPHLEBIIDAE

Handlirsch, 1906

[Stenophlebiidae HANDLIRSCH, 1906b, p. 581]

Fore and hind wings similar in form, narrowed basally but not petiolate; primary antenodals absent; numerous secondary antenodals; discoidal cell closed in both pairs of wings, irregular in shape, and divided by 1 or 2 crossveins; vein CUP strongly bent at arculus; 1A well developed. *Jur.*

Stenophlebia HAGEN, 1866a, p. 79 [**Heterophlebia amphitrite* HAGEN, 1862, p. 105; SD CARPENTER, herein]. Nodus at midwing; 1A with 3 distinct terminal branches. [This peculiar genus has been placed in the Anisoptera by HAGEN (1866a) and NEEDHAM (1903); in the Anisozygoptera by FRASER (1957); and in the Zygoptera by PRITYKINA (1980a), who designated a new superfamily, Stenophlebioidea, for it.] PRITYKINA, 1980a. *Jur.*, Europe (Germany).—FIG. 54,2. *S. latreillei* (GERMAR); *a*, fore and *b*, hind wings, $\times 0.7$ (Hagen, 1866a); *c*, fore wing, region of discoidal cell, $\times 5$ (Carpenter, 1932a).

Family UNCERTAIN

The following genera, apparently belonging to the order Odonata, are too poorly known to permit assignment to families.

Antitaxineura TILLYARD, 1935b, p. 382 [**A. anomala*; OD]. Small wing fragment showing nodal area. [Ordinal assignment doubtful.] RIEK, 1956. *Trias.*, Australia (New South Wales).

Camptotaxineura TILLYARD, 1937a, p. 88 [**C. ephialtes*; OD]. Apical wing fragment. [Type of family Camptotaxineuridae TILLYARD.] *Perm.*, USA (Kansas).

Kaltanoneura ROHDENDORF, 1961a, p. 86 [**K. bar-*

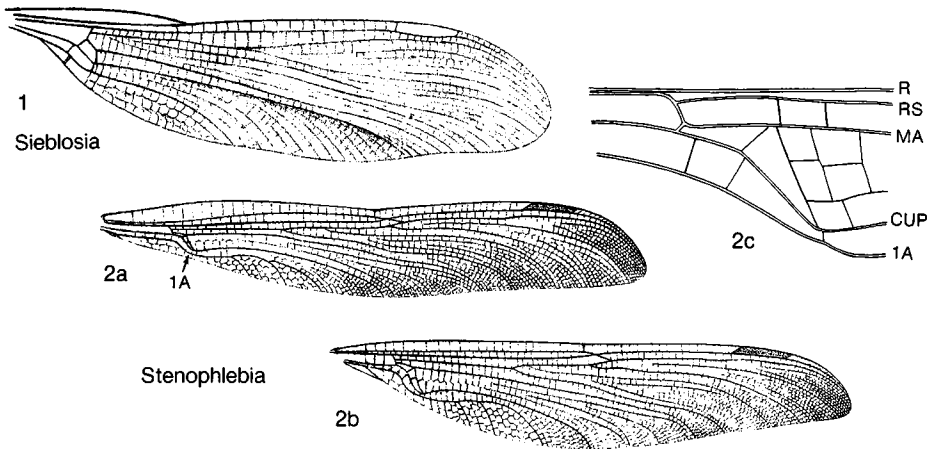


FIG. 54. Stenophlebiidae and Uncertain (p. 88–89).

tenevi; OD]. Wing fragment, with few crossveins and weak pterostigma. Probably protozygopterous. [Type of family Kaltanoneuridae ROHDENDORF.] *Perm.*, USSR (European RSFSR).

Kargalotypus ROHDENDORF, 1962a, p. 72 [**Megatytypus kargalensis* MARTYNOV, 1932, p. 19; OD]. Little-known genus, based on apical wing fragment. SC extending about two-thirds wing length from base; pterostigma absent. PRITYKINA, 1981. *Perm.*, USSR (Asian RSFSR).

Magnasupplephlebia ZESSIN, 1982, p. 105 [**M. kallweita*; OD]. Little-known genus, based on apical wing fragment. *Jur.*, Europe (Germany).

Mesonetopsis PING, 1935, p. 112 [**M. zeni*; OD]. Little-known nymph, probably anisopterous. *Jur.*, China (Xinjiang).

Mesophlebia TILLYARD in TILLYARD & DUNSTAN, 1916, p. 24 [**M. antinodalis*; OD]. Little-known genus, based on small wing fragment, including nodal area. [Type of family Mesophlebiidae TILLYARD, 1916; originally placed in Anisoptera.] PRITYKINA, 1981. *Trias.*, Australia (New South Wales).

Orthaschnites HAUPT, 1956, p. 31 [**O. primus*; OD]. Little-known genus, based on small wing fragment. *Eoc.*, Europe (Germany).

Palaeophlebia BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 6 [**P. synlestoides*; OD]. Little-known wing fragment. *Jur.*, USSR (Asian RSFSR).

Samarura BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 7 [**S. gigantea*; SD COWLEY, 1934b, p. 253]. Little-known nymphs. HANDLIRSCH, 1906b. *Jur.*, USSR (Asian RSFSR).

Sieblosia HANDLIRSCH, 1907, p. 896 [**Heterophlebia jucunda* HAGEN, 1858a, p. 121; OD]. Little-known genus, based on poorly preserved wing, with closed discoidal cell and weakly developed nodus much nearer to arculus than to pterostigma. [Type of family Sieblosiidae HANDLIRSCH,

1907; placed by HANDLIRSCH in the Anisozygoptera.] *Oligo.*, Europe (Germany).—FIG. 54, 1. **S. jucunda* (HAGEN); fore(?) wing, $\times 1.8$ (Hagen, 1858a).

Syrrhoë BODE, 1953, p. 69 [**S. comissa*; OD]. Wing fragment. *Jur.*, Europe (Germany).

INFRAClass PALAEOPTERA Order UNCERTAIN

The following genera, apparently belonging to the infraclass Palaeoptera, are too poorly known to permit assignment to orders.

Aedoeophasma SCUDDER, 1885g, p. 265 [**A. anglica*; OD]. Little-known genus, based on distal fragment of wing. [Placed by SCUDDER (1885g), HANDLIRSCH (1906b, 1919b), and BOLTON (1916, 1917b) in the Palaeodictyoptera, *incertae sedis*, but transferred to the Protodonata, *incertae sedis*, by HANDLIRSCH (1922).] *U. Carb.*, England.

Archaeoptilites HANDLIRSCH, 1919b, p. 534 [**Archaeoptilus lucasi* BRONGNIART, 1885a, p. 60; OD]. Little-known genus, based on very small fragment of wing. [Originally placed in the Palaeodictyoptera.] BRONGNIART, 1893; HANDLIRSCH, 1922. *U. Carb.*, Europe (France).

Archaeoptilus SCUDDER, 1881b, p. 295 [**A. ingens*; OD]. Little-known genus, based on small fragment of large wing. [Type of the family Archaeoptiliidae HANDLIRSCH, 1906b. Originally considered by SCUDDER to be "neuropterous," this genus was subsequently (1883b) placed by him in the orthopteroid complex. However, HANDLIRSCH (1906b) and BOLTON (1925) were of the opinion that it was more likely a member of the Palaeodictyoptera.] *U. Carb.*, England.

Bardapteris ZALESSKY, 1944a, p. 342 [**B. ovale*;

- OD]. Little-known genus, based on fragment of wing. [Type of the family Bardapteridae ZALESSKY, 1944a. Originally placed in a new order, Permodyctoptera, but transferred by ROHDENDORF (1962a) to the Palaeodictyoptera.] *Perm.*, USSR (European RSFSR).
- Breyeriodes** HANDLIRSCH, 1906b, p. 118 [**B. kliv-eri*; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] HANDLIRSCH, 1919b, 1922. *U. Carb.*, Europe, (Germany).
- Campteroneura** HANDLIRSCH, 1906a, p. 685 [**C. reticulata*; OD]. Little-known genus, based on small fragment of wing. HANDLIRSCH, 1906b, 1922. *U. Carb.*, USA (Alabama).
- Campyloptera** BRONGNIART, 1893, p. 406 [**C. eatoni*; OD]. Little-known genus, based on incomplete wing. [The generic name *Campyloptera* was first used in 1885 (BRONGNIART, 1885a), but no species was mentioned until 1893. Placed in the Megasecoptera by BRONGNIART (1885a), HANDLIRSCH (1906b), CARPENTER (1943b), and LAURENTIAUX (1953); in the Protodonata by BRONGNIART (1893) and TILLYARD (1928d); and in a new order, Campylopteroidea, by ROHDENDORF (1962a).] *U. Carb.*, Europe (France).
- Cryptovenia** BOLTON, 1912, p. 315 [**C. moyseyi*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Palaeodictyoptera. Type of the family Cryptoveniidae BOLTON, 1912.] LAMEERE, 1917b; HANDLIRSCH, 1919b, 1922. *U. Carb.*, England.
- Dictyoneurella** LAURENTIAUX, 1949b, p. 207 [**D. perfecta*; OD]. Little-known genus, based on incomplete wing. [Type of the family Dictyoneurellidae KUKALOVÁ-PECK, 1975. Placed in the Palaeodictyoptera by LAURENTIAUX (1949b); transferred to the Megasecoptera by KUKALOVÁ-PECK (1975).] *U. Carb.*, Europe (France).
- Dyadentomum** HANDLIRSCH, 1904b, p. 7 [**D. permense*; OD]. Little-known genus, based on a body fragment thought by HANDLIRSCH to be that of an ephemerid nymph. *Perm.*, USSR (European RSFSR).
- Eohymen** MARTYNOV, 1937b, p. 9 [**E. maculipennis*; OD]. Little-known genus, based on poorly preserved wing. [Type of the family Eohymenidae MARTYNOV, 1937b. Placed in the Megasecoptera (Protohymenoptera) by MARTYNOV (1937b), in the Palaeodictyoptera by ROHDENDORF (1962a), and in the Caloneuroidea by RASNITSYN (1980b).] *Perm.*, USSR (European RSFSR).
- Erasipterella** BRAUCKMANN, 1983, p. 9 [**E. piesbergensis*; OD]. Little-known genus, based on fragments of fore and hind wings. [Almost certainly a member of the odonate complex, but order doubtful.] *U. Carb.*, Europe (Germany).
- Erasipteron** PRUVOST, 1933a, p. 151 [**E. larischii*; OD]. Little-known genus, based on incomplete wings. [Type of the family Erasipteridae CARPENTER, 1939. Placed in the Odonata by PRUVOST (1933a) and KUKALOVÁ (1964b); transferred to the Protodonata by CARPENTER (1939), LAURENTIAUX (1953), WHALLEY (1979), and PRITYKINA (1980b).] *U. Carb.*, Europe (Czechoslovakia), England.
- Eurytaenia** HANDLIRSCH, 1906a, p. 674 [**E. virginica*; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the Palaeodictyoptera.] HANDLIRSCH, 1906b, 1922. *U. Carb.*, USA (West Virginia).
- Frankenholzia** GUTHÖRL, 1962c, p. 227 [**F. culmanni*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Palaeodictyoptera, but transferred to the Megasecoptera by KUKALOVÁ-PECK (1975).] *U. Carb.*, Europe (Germany).
- Gerephemera** SCUDDER, 1880, p. 12 [**G. simplex*; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the order Ephemeroptera by SCUDDER, but later (1890) transferred to the Orthoptera; assigned to the Odonata by HAGEN (1881a, 1881b, 1885) and to the Palaeodictyoptera by HANDLIRSCH (1906a, 1906b).] *U. Carb.*, Canada (Nova Scotia).
- Hypermegethes** HANDLIRSCH, 1906a, p. 672 [**H. schucherti*; OD]. Little-known genus, based on a small, proximal fragment of very large wing. [Type of the family Hypermegethidae HANDLIRSCH, 1906a. Placed in the Palaeodictyoptera by HANDLIRSCH (1906a, 1906b, 1922), but transferred to the Protohemiptera by LAMEERE (1917c).] *U. Carb.*, USA (Illinois).
- Kuloja** MARTYNOV, 1928b, p. 7 [**K. expansa*; OD]. Little-known genus, based on distal fragment of wing. [Type of the family Kulojidae MARTYNOV, 1928b. Originally placed in the Megasecoptera, but transferred to the Diaphanopteroidea by ROHDENDORF (1962a).] MARTYNOV, 1932. *Perm.*, USSR (European RSFSR).
- Leipsanon** HANDLIRSCH, 1906b, p. 120 [**L. reticulatum*; OD]. Little-known genus, based on minute wing fragment. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] HANDLIRSCH, 1919b. *U. Carb.*, Europe (Belgium).
- Lithentomum** SCUDDER, 1868c, p. 206 [**L. hartti*; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the Palaeodictyoptera.] SCUDDER, 1880; HANDLIRSCH, 1906a, 1922. *U. Carb.*, Canada (New Brunswick).
- Litoneura** SCUDDER, 1885a, p. 169 [**Dictyoneura anthracophila* GOLDENBERG, 1854, p. 35; SD HANDLIRSCH, 1906b, p. 77]. Little-known genus, based on fragment of small wing. [Originally placed in the Palaeodictyoptera.] *U. Carb.*, Europe (Germany).
- Litophlebia** HUBBARD & RIEK, 1978, p. 260, *nom. subst. pro Xenophlebia* RIEK, 1976, p. 150, *non*

- DEMOULIN, 1968 [**Xenophlebia optata* RIEK, 1976e, p. 150; OD]. Little-known genus, based on incomplete wing. [Type of the family Lito-phlebiidae HUBBARD & RIEK, 1978. Placed in the Ephemeroptera by RIEK (1976e) and HUBBARD & RIEK (1978) and in the Megasecoptera by HUBBARD & KUKALOVÁ-PECK (1980).] *Trias.*, South Africa.
- Megathentomum** SCUDDER, 1868b, p. 570 [**M. pustulatum*; OD]. Little-known genus, based on distal fragment of very large wing. SCUDDER, 1891; HANDLIRSCH, 1906a, 1906b, 1922. *U. Carb.*, USA (Illinois).
- Melanoblattula** COCKERELL, 1927g, p. 415 [**M. nigressens*; OD]. Little-known genus, based on fragment of small wing. [Originally placed in the Protorthoptera.] *U. Carb.*, USA (Maryland).
- Microblattina** SCUDDER, 1895c, p. 57 [**M. perdita*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Blattaria, but transferred by HANDLIRSCH (1906a, 1906b) to the Protoblattoidea.] *U. Carb.*, USA (Rhode Island).
- Orthogonophora** HANDLIRSCH, 1906a, p. 686 [**O. distincta*; OD]. Little-known genus, based on distal fragment of wing. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] HANDLIRSCH, 1906b, 1922. *U. Carb.*, USA (West Virginia).
- Palaeodictyopteron** HANDLIRSCH, 1906a, p. 688 [collective group]. Little-known nymphal forms. HANDLIRSCH, 1906b; CARPENTER, 1948a. *U. Carb.*, USA (Illinois, West Virginia), Europe (Germany).
- Palaeopalara** HANDLIRSCH, 1904a, p. 10 [**P. gracilis*; OD]. Little-known genus, based on small fragment of wing. [Placed in the Megasecoptera by HANDLIRSCH (1906b) and KUKALOVÁ-PECK (1975).] *U. Carb.*, Europe (Belgium).
- Parapaolia** HANDLIRSCH, 1906a, p. 687 [**Paolia superba* SCUDDER, 1885a, p. 173; OD]. Little-known genus. [Placed, with some doubt, by HANDLIRSCH (1906b) in the Palaeodictyoptera.] *U. Carb.*, USA (Illinois).
- Perissophlebia** TILLYARD, 1918c, p. 422 [**P. multiseriata*; OD]. Little-known genus, based on small wing fragment. [Placed in the Odonata by TILLYARD (1918c) and PRITYKINA (1981).] *Trias.*, Australia (Queensland).
- Permoneura** CARPENTER, 1931b, p. 124 [**P. lameerei*; OD]. Little-known genus, based on complete hind wing. [Type of the family Permoneuridae CARPENTER, 1931b. Placed in the order Palaeodictyoptera by CARPENTER (1931b) and TILLYARD (1937); transferred to a new order, Permoneurodea (allied to the Palaeodictyoptera), by LAURENTIAUX (1953); and included in a new order, Archodonata (along with several other genera formerly in the Palaeodictyoptera), by ROHDENDORF (1962a). The ordinal name Archodonata was changed by SINITSHENKOVA (1980a, 1980b) to Permothemistida. CARPENTER (1976) proposed that the genus *Permoneura* be assigned to the Palaeoptera, *incertae sedis*.] *Perm.*, USA (Kansas).
- Piroutetia** MEUNIER, 1907, p. 522 [**P. liassina*; OD]. Little-known genus, based on wing fragment and placed in the Odonata. MEUNIER, 1908b. *Jur.*, Europe (France).
- Progonopteryx** HANDLIRSCH, 1904a, p. 5 [**P. belgica*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Palaeodictyoptera (family Dictyoneuridae).] HANDLIRSCH, 1906b, 1919b. *U. Carb.*, Europe (Belgium).
- Protagrion** BRONGNIART, 1893, p. 403 [**P. audouini*; OD]. Little-known genus, based on incomplete wing. [Type of the family Protagrionidae HANDLIRSCH, 1906b. The generic name *Protagrion* was first used in 1885 (BRONGNIART, 1885a), but no species was mentioned until 1893. Placed in the Protodonata by BRONGNIART (1893), HANDLIRSCH (1906b), and MARTYNOV (1932); transferred to the Palaeodictyoptera by CARPENTER (1943b) and ROHDENDORF (1962a).] *U. Carb.*, Europe (France).
- Pseudohomothetus** HANDLIRSCH, 1906a, p. 685 [**Homothetus erutus* MATTHEW, 1895a, p. 95; OD]. Little-known genus, based on small wing fragment. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] HANDLIRSCH, 1906b, 1919b. *U. Carb.*, Canada (New Brunswick).
- Pseudopalingenia** HANDLIRSCH, 1906b, p. 124 [**Palingenia feistmanteli* FRITSCH, 1882, p. 1; OD]. Little-known genus, based on part of body, including cerci. [Originally placed, with some uncertainty, in the Palaeodictyoptera, *incertae sedis*.] HANDLIRSCH, 1922. *U. Carb.*, Europe (Czechoslovakia).
- Pseudopaolia** HANDLIRSCH, 1906a, p. 687 [**Paolia lacoana* SCUDDER, 1885a, p. 173; OD]. Little-known genus. [Placed by HANDLIRSCH (1906b), with uncertainty, in the order Palaeodictyoptera, *incertae sedis*.] *U. Carb.*, USA (Pennsylvania).
- Rectineura** BOLTON, 1934, p. 181 [**R. lineata*; OD]. Little-known genus, based on poorly preserved wing fragment. [Originally placed in the Palaeodictyoptera.] *U. Carb.*, England.
- Reisia** HANDLIRSCH, 1909c, p. 81, *nom. subst. pro Handlirschia* REIS, 1909, p. 693, *non* KOHL, 1896 [**Handlirschia gelasii* REIS, 1909; OD]. Little-known genus, based on small fragment of wing. [Placed by HANDLIRSCH (1909c, 1920) and REIS (1909) in the Protodonata.] *Trias.*, Europe (Germany).
- Severinula** PRUVOST, 1930, p. 151 [**S. leopoldi*; OD]. Little-known genus, based on wing fragment. [Placed in the Palaeodictyoptera by PRUVOST (1930) and ROHDENDORF (1962a).] *U. Carb.*, Europe (Belgium).
- Sherborniella** HANDLIRSCH, 1919b, p. 535

[**Palaeodictyopteron* (collective group) *bigginsi* HANDLIRSCH, 1906b, p. 125; OD]. Little-known genus, based on small basal fragment of wing. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] BOLTON, 1921, 1934. *U. Carb.*, England.

Sypharoptera HANDLIRSCH, 1911, p. 372 [**S. pneuma*; OD]. Little-known genus, based on incomplete wings. [Originally placed in the new order Sypharopteroidea by HANDLIRSCH (1911); transferred to order Diaphanopteroidea by ROHDENDORF (1962a).] HANDLIRSCH, 1919b, 1922. *U. Carb.*, USA (Illinois).

Titanoptera BRONGNIART, 1893, p. 379 [**T. maculata*; OD]. Little-known genus, based on small fragment of wing; probably a palaeodictyopteron. HANDLIRSCH, 1906b; LAMEERE, 1917b. *U. Carb.*, Europe (France).

Triadologus RIEK, 1976b, p. 793 [**T. biseriatatus*; OD]. Little-known genus, based on small fragment of wing. [Placed in the Protodonata by RIEK (1976b) and in the Odonata by PRITYKINA (1981).] *Trias.*, South Africa.

Wulasua T'AN, 1980, p. 159 [**W. maculata*; OD]. Little-known genus, based on a poorly preserved, small fragment of a wing. [Originally placed in the Diaphanopteroidea.] *Perm.*, China (Inner Mongolia).

Xenoneura SCUDDER, 1868c, p. 206 [**X. antiquorum*; OD]. Little-known genus, based on wing fragment. [Type of the family Xenoneuridae SCUDDER, 1885b. Originally placed in the Palaeodictyoptera.] SCUDDER, 1880; HANDLIRSCH, 1906b, 1922. *U. Carb.*, Canada (New Brunswick).

Infraclass NEOPTERA

Martynov, 1923

[Neoptera MARTYNOV, 1923, p. 89]

Wings articulated to thorax by sclerotized plates (axillaries), not fused or rigidly connected; third axillary Y-shaped and attached to second axillary and posterior notal process, and connected by flexor muscle to thorax; venation basically as in Palaeoptera, but vein MA flat or nearly so or absent; cerci commonly present but vestigial or absent in higher orders. Immature stages very diverse in structure and development. *U. Carb.—Holo.*

This infraclass has been the predominant one since the Permian. It includes 25 existing

orders and about 98 percent of the existing species of insects.

Division EXOPTERYGOTA

Sharp, 1899

[Exopterygota SHARP, 1899, p. 247]

Immature stages typically resembling the adults in general form, living in the same kind of environments, and having similar feeding habits; metamorphosis to adults gradual, wings developing within an externally visible cuticular sheath; pupal stage absent. *U. Carb.—Holo.*

Fifteen existing orders are generally recognized in this division, including about 11 percent of the existing species of insects. The orders are usually grouped into two categories, the orthopteroids and the hemipteroids, which have basic structural differences and which appear to represent two distinct lines of exopterygote evolution, although there is some doubt that either one is monophyletic (RICHARDS & DAVIES, 1977; I. M. MACKERRAS, 1970). The orthopteroids have mandibulate mouthparts; the fore wings are commonly tegminous or rarely elytrid; the hind wings commonly have a large fan-shaped anal area; cerci are present and are commonly well developed. These insects are known from the Upper Carboniferous to the present. Four very small, existing orders (Grylloblattodea, Zoraptera, Mallophaga, and Anoplura) belonging here are the only existing orders of insects absent from the geological record. They are discussed briefly below, within the Exopterygota.

The hemipteroids have haustellate mouthparts and feed on liquid food; the fore wings are diverse in structure, membranous or modified to hemelytra or elytra. The hind wings are broad, commonly with an anal fan in the more primitive families, but are small or very small in the more specialized families. Cerci are absent. These orders are known from the Permian to the present.

ORTHOPTEROID EXOPTERYGOTES

Order PERLARIA Latreille, 1802

[*nom. transl.* HANDLIRSCH, 1903, p. 733, ex *Perlariae* LATREILLE, 1802a, p. 292] [=Plecoptera BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 863] [Although the name Plecoptera is often used for this order, it has the distinct disadvantage of being easily confused with the ordinal name Plecoptera, occasionally used for mayflies. *Perlaria* is the older name.]

Fore wing membranous; costa marginal; vein SC usually extending to about midwing, rarely beyond, terminating on costa but connected distally to R; costal veinlets commonly few, even absent; R with several oblique veinlets leading to wing margin; RS arising at or before midwing, commonly near base, with 3 or 4 branches; M apparently dividing into MA and MP very near wing base; MA forked; MP obliquely or transversely directed toward CUA and anastomosed with it; MP+CUA with at least 2 terminal branches; CUA diverging from CUP near wing base; CUP, 1A, and 2A unbranched. Hind wing typically with expanded and folded anal area, reduced or absent in a few specialized genera; RS arising at or near wing base; M coalesced with base of RS; MA forked; MP diverging toward and anastomosing with CUA; MP+CUA and also CUP unbranched; anal veins varying in number and degree of development; crossveins usually few, highly variable, and in many genera restricted to certain areas of wing. Wings at rest held flat, not slanted, over abdomen. Mouthparts mandibulate, weak in recent species; antennae setaceous, long; body weakly sclerotized; cerci usually well developed, with numerous segments; ovipositor absent or vestigial. Nymphs similar to adults in general form but aquatic; tracheal gills on thorax, coxae, or other parts of body, including sides of abdominal segments (Eustheniidae). *Perm.—Holo.*

Difference of opinion exists about the homologies of some wing veins. The media (M) appears to be represented by a forked vein that has been generally interpreted as

MA (HANDLIRSCH, 1906b, 1907, 1908a; ROHDENDORF, 1962a). SHAROV (1961b) concluded that MP is actually present at the wing base, diverging from MA and coalescing with CUA, as in certain families of Protorthoptera. The free, diverging part of MP is apparently more distinct in the hind wing than in the fore. This interpretation of MA, MP, and CUA is followed here.

The existing *Perlaria* are usually divided into several suborders, but opinions differ about the number of these and the structural bases for the divisions (cf. ILLIES, 1965, and RASNITSYN, 1980d). However, since almost none of the fossil specimens shows the morphological features used in the subordinal classification, these groups are omitted from the following account.

The recognition of two Permian genera, *Stenoperlidium* and *Palaeotaeniopteryx*, as members of living families (Eustheniidae and Taeniopterygidae, respectively) is necessarily dubious. Only part of the fore wings and none of the hind wings are known for *Stenoperlidium*; the fore wings and part of the hind are known for *Palaeotaeniopteryx* but not the anal area of the hind wing. Nevertheless, the geological record as now known suggests that the stone flies were well established at the ordinal level before the end of the Paleozoic Era and that relatively few modifications, such as the reduction of the anal area of the hind wing and of crossveins, have taken place in the adults subsequently.

Family PALAEOPERLIDAE Sharov, 1961

[Palaeoperlidae SHAROV, 1961e, p. 227]

Costal area of fore wing with 4 or 5 veinlets; 3 or 4 veinlets from vein R to margin; free basal piece of MA slightly oblique; MP+CUA with 3 terminal branches; anal area narrow. Hind wing and body unknown. *Perm.*

Palaeoperla SHAROV, 1961e, p. 227 [**P. exacta*; OD]. RS with 3 or 4 branches; crossveins numer-

ous between MA and MP+CUA, few elsewhere. *Perm.*, USSR (Asian RSFSR).—FIG. 55,2a. **P. exacta*; fore wing, $\times 5.5$ (Sharov, 1961e). —FIG. 55,2b. *P.(?) prisca* SHAROV; nymph, $\times 9$ (Sharov, 1961e).

Family PERLOPSEIDAE

Martynov, 1940

[*nom. correct.* ROHDENDORF, 1957, p. 81, *pro* Perlopsididae MARTYNOV, 1940, p. 31]

Fore wing as in Palaeoperlidae but with only 1 veinlet from vein R to margin, 2 branches on MP+CUA. Hind wing unknown. Body slender, legs long, tarsi with 3 segments. *Perm.*

Perlopsis MARTYNOV, 1940, p. 31 [**P. flicornis*; OD]. Costal area very narrow; wing widest beyond middle. *Perm.*, USSR (Asian RSFSR).—FIG. 55,1. **P. flicornis*; a, fore wing, $\times 3.2$ (Rohdendorf, 1962a); b, body, $\times 4.0$ (Martynov, 1940).

Family SIBERIOPERLIDAE

Sinitshenkova, 1983

[Siberioperlidae SINITSHENKOVA, 1983, p. 96]

Antennae long, moniliform, shorter than body. Wings of females of normal size, with branches of RS directed posteriorly and MA and MP unbranched; hind wings with enlarged anal area; anal veins branched. Males micropterous; costal region of the fore wing enlarged; anal veins branched. Legs short, femora wide; cerci shorter than body. Nymphs with body densely covered with short hairs; antennae and cerci relatively short; tracheal gills absent. Apparently related to the existing family Gripopterygidae. *Jur.*

Siberioperla SINITSHENKOVA, 1983, p. 96 [**S. lacunosa*; OD]. Posterior margin of head convex; first antennal segment short. Female with fore wing about three times as long as wide; RS with 4 or 5 branches; CUA with 2 or 3 branches. *Jur.*, USSR (Asian RSFSR).

Family EUSTHENIIDAE Tillyard, 1921

[Eustheniidae TILLYARD, 1921d, p. 35]

Fore wing with few to many veinlets in costal area; vein RS with at least 3 branches; 3 anal veins; crossveins present over most of wing. Hind wing with prominent anal area

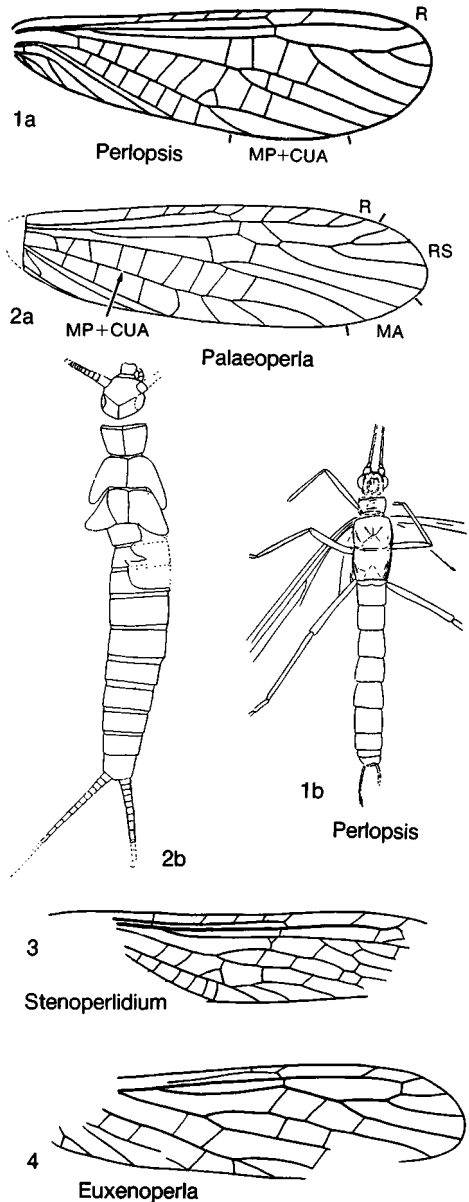


FIG. 55. Palaeoperlidae, Perlopseidae, Eustheniidae, and Uncertain (p. 94–97).

but without marginal indentation at end of CUP. Nymphs with 5 or 6 pairs of lateral abdominal gills. *Perm.*—*Holo.*

Eusthenia WESTWOOD, 1832, p. 348. *Holo.* **Stenoperlidium** TILLYARD, 1935c, p. 386 [**S. permianum*; OD]. Similar to *Stenoperla* (recent) but

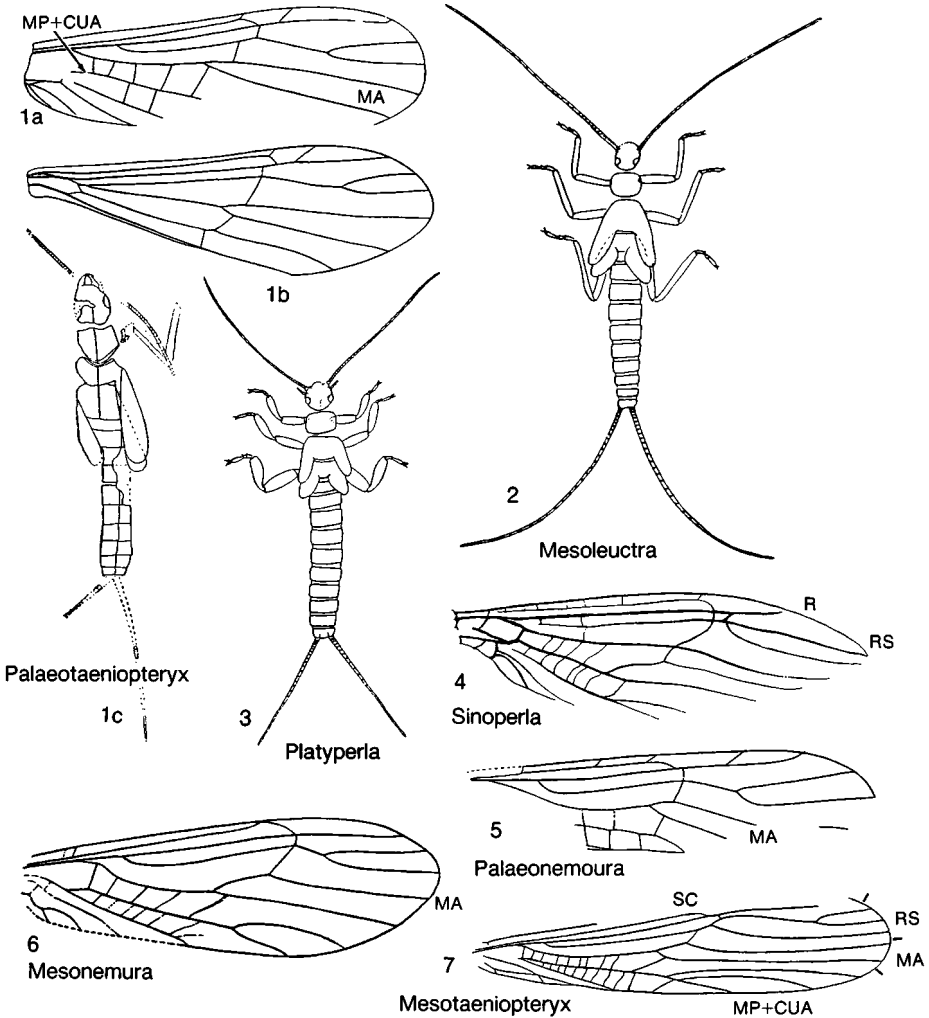


FIG. 56. Taeniopterygidae, Notonemouridae, Platyperlidae, and Perlidae (p. 95-97).

with fewer crossveins and with the broadest part of wing proximal to midwing. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).—FIG. 55,3. **S. permianum*; fore wing, $\times 2$ (Tillyard, 1935c).

Family TAENIOPTERYGIDAE
Klapálek, 1905

[Taeniopterygidae Klapálek, 1905, p. 30]

Costal area of fore wing with few veinlets; vein R with not more than single veinlet leading to margin; MA commonly with 2 branches; crossveins fewer than in Palaeopterlidae. *Perm.*—*Holo.*

Taeniopteryx PICTET, 1841, p. 343. Adults. HAGEN in PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Brachyptera NEWPORT, 1848, p. 388. ILLIES, 1967a. *Plio.*, Europe (Germany)—*Holo.*

Mesonemoura BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 11 [**M. maaki*; OD]. Crossveins from end of SC to MA forming continuously curved series. *Jur.*, USSR (Asian RSFSR).—FIG. 56,6. *M. turanica* MARTYNOV; fore wing, $\times 5.5$ (Martynov, 1937a).

Mesotaeniopteryx MARTYNOV, 1937a, p. 81 [**M. elongata*; OD]. RS forked to level of end of SC; MP+CUA with 3 terminal branches, first 2 close together, curved, and directed anteriorly; crossveins numerous between MA and MP+CUA,

more numerous between MP+CUA and CUP. *Jur.*, USSR (Tadzhik).—FIG. 56,7. *M. splendida* MARTYNOV; fore wing, $\times 2.5$ (Martynov, 1937a).

Palaeonemoura SHAROV, 1961e, p. 233 [**P. clara*; OD]. Fore wing as in *Palaeotaeniopteryx* but with MA more strongly curved and with fewer crossveins between MA and MP+CUA. *Perm.*, USSR (Asian RSFSR).—FIG. 56,5. **P. clara*; fore wing, $\times 6.5$ (Sharov, 1961e).

Palaeotaeniopteryx SHAROV, 1961e, p. 230 [**P. elegans*; OD]. MA forked before level of end of SC; several crossveins between MA and MP+CUA. *Perm.*, USSR (Asian RSFSR).—FIG. 56,1. **P. elegans*; *a*, fore and *b*, hind wings, $\times 8$; *c*, nymph, $\times 10$ (all Sharov, 1961e).

Perlariopsis PING, 1928, p. 31 [**P. peipiaoensis*; OD]. Little-known adult. [Family assignment doubtful.] ILLIES, 1965. *Cret.*, China.

Sinonemoura PING, 1928, p. 24 [**S. grabaui*; OD]. Little-known nymph. [Family position doubtful.] ILLIES, 1965. *Cret.*, China.

Family LEUCTRIDAE Klapálek, 1905

[Leuctridae Klapálek, 1905, p. 32]

Costal area with 1 or 2 veinlets; vein R with 1 veinlet to margin; RS forked to about half its length, branches parallel to those of MA; MP+CUA and CUP markedly divergent distally. *Eoc.*—*Holo.*

Leuctra STEPHENS, 1836, p. 144. Adults. PICTET & HAGEN, 1856; COCKERELL, 1922b; ILLIES, 1965; JARZEMBOWSKI, 1980. *Eoc./Oligo.*, England; *Oligo.*, Europe (Germany, Baltic), USA (Colorado)—*Holo.*

Megaleuctra NEAVE, 1934, p. 4. Adult female. RICKER, 1935; ILLIES, 1967b; ZWICK, 1973. *Oligo.*, Europe (Baltic)—*Holo.*

Family NOTONEMOURIDAE

Ricker, 1950

[Notonemouridae RICKER, 1950, p. 201]

Similar to Nemouridae (recent). Adults with vein SC arching toward C. Nymphs small, lacking external gills; cerci multisegmented, almost as long as antennae. ZWICK, 1973. *Jur.*—*Holo.*

Notonemoura TILLYARD, 1923, p. 215. *Holo.*

Mesoleuctra BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 9 [**M. gracilis*; OD]. Nymph: posterior margin of head rounded; basal antennal segment about as wide as long; mandibles slightly longer than wide, with many denticles; femora only slightly shorter and broader than tibiae; pronotum about as long as wide; posterior wing pads slightly broader than the fore pair; cerci

very thin distally; body without hair covering. PING, 1928; ILLIES, 1965; SINITSHENKOVA, 1982. *Jur.*, USSR (Asian RSFSR); *Cret.*, China (Inner Mongolia).—FIG. 56,2. **M. gracilis*; restoration, dorsal view, $\times 2$ (Sinitshenkova, 1982).

Family PERLODIDAE Klapálek, 1912

[Perlodidae Klapálek, 1912, p. 5]

Venation very diverse; costal space usually with several short veinlets; veinlets from vein R to margin commonly longer and more oblique than those of costal area; RS commonly with several branches; MP+CUA diverging anteriorly in distal region, appearing to coalesce with branches of MA. *Oligo.*—*Holo.*

Perlodes BANKS, 1903, p. 241. Adult. PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Isoperla BANKS, 1906, p. 175. Adult. PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Family PLATYPERLIDAE

Sinitshenkova, 1982

[Platyperlidae SINITSHENKOVA, 1982, p. 118]

Nymph: head about as long as wide; antennae long, basal segment large; labrum transverse; mandibles with only a few denticles apically; pronotum transverse; femora and tibiae relatively short and broad; 2 basal segments of tarsi short and broad, their combined lengths less than that of third segment; tarsal claws prominent; fore wing pads relatively long, hind pair much shorter and broader; body covered with hair; external gills apparently absent. *Jur.*

Platyperla BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 10 [**P. platypoda*; OD]. Posterior margin of head strongly convex; basal segment of antenna conical; pronotum with prominent posterior angles; posterior margin of terminal abdominal tergite with a short, broad median projection. PING, 1928; SINITSHENKOVA, 1982. *Jur.*, USSR (Asian RSFSR).—FIG. 56,3. **P. platypoda*; restoration of nymph, dorsal view, $\times 2$ (Sinitshenkova, 1982).

Family PERLIDAE Latreille, 1802

[Perlidae LATREILLE, 1802a, p. 292]

Costal area with numerous, short veinlets, those between vein R and margin continuing

series; RS usually with 3 or 4 branches; distal part of MP+CUA curving anteriorly. *Cret.—Holo.*

Perla GEOFFROY, 1762, p. 229. Adult. PICTET & HAGEN, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

Sinoperla PING, 1928, p. 28 [**S. abdominalis*; OD]. Little-known wings, with 2 crossveins between R and RS near end of SC. ILLIES, 1965. *Cret.*, China. —FIG. 56,4. **S. abdominalis*; fore wing, $\times 5.3$ (Ping, 1928).

Family UNCERTAIN

The following genera, apparently belonging to the order Perlaria, are too poorly known to permit assignment to families.

Euxenoperla RIEK, 1973, p. 531 [**E. simplex*; OD]. Little-known genus, possibly related to the Gripopterygidae. Vein RS of fore wing arched anteriorly at level of end of SC; RS with 3 or 4 branches; M deeply forked, branching before midwing; few crossveins. *Perm.*, South Africa; *Trias.*, Australia (Queensland). —FIG. 55,4. **E. simplex*, South Africa; fore wing, $\times 2.8$ (Riek, 1973).

Euxenoperlella RIEK, 1976a, p. 770 [**E. jacquesi*; OD]. Similar to *Euxenoperla*, but RS with only 2 branches and M forking more distally. *Perm.*, South Africa.

Gondwanoperlidium PINTO & PURPER, 1978, p. 79 [**G. argentinorum*; OD]. Little-known genus, similar to *Euxenoperla*, but fore wings with many more crossveins. *Trias.*, South America (Argentina).

Mesonotoperla RIEK, 1954c, p. 167 [**M. sinuata*; OD]. Fore wing fragment, possibly of an eustheniid. *Trias.*, Australia (New South Wales).

Permoleuctropsis MARTYNOV, 1937b, p. 34 [**P. gracilis*; OD]. Little-known nymph. *Perm.*, USSR (European RSFSR).

Uralonympha ZALESSKY, 1939, p. 64 [**U. varica*; OD]. Little-known nymph. CARPENTER, 1969. [Ordinal assignment uncertain.] *Perm.*, USSR (Asian RSFSR); *Jur.*, Antarctica (Ohio Range).

Order PROTORTHOPTERA Handlirsch, 1906

[Protorthoptera HANDLIRSCH, 1906a, p. 695] [=Hadentomoidea HANDLIRSCH, 1906a, p. 692; Hapalopteroidea HANDLIRSCH, 1906a, p. 694; Protoblattoidea HANDLIRSCH, 1906a, p. 704; Reculoidea HANDLIRSCH, 1906b, p. 127; Protoperlaria TULLYARD, 1928b, p. 187; Cnemidolestoidea HANDLIRSCH, 1937, p. 63; Paraplecoptera MARTYNOV, 1938b, p. 98; Strephocladodea MARTYNOV, 1938b, p. 100; Protocicadida HAUPT (in part), 1941, p. 75; Protofulgorida HAUPT (in part), 1941, p. 75] [The ordinal name Protoblattoidea HANDLIRSCH (1906a) was changed to Protoblattoidea by SHAROV (1962a) and has generally been accepted.]

Wings typically containing all main veins, including MA and MP, but without com-

plete alternation of convexities and concavities; MA apparently absent in some families (see below). Main veins usually independent; in some families CUA anastomosed with part of M or MP and CUP; in a few families MA tending to coalesce with branches of RS. Fore and hind wings commonly similar in form and venation, anal area of hind wing rarely expanded to form prominent lobe. Fore wing membranous in more primitive groups, but slightly coriaceous or distinctly coriaceous in others; hair covering usually well developed on membranous wings, reduced or absent on coriaceous wings; prominent setae may be present on certain parts of wings; wing area between veins with archedictyon, resembling that of Palaeodictyoptera, or with coarse network of crossveins or more commonly with regular system of nearly straight crossveins; anal area in many families set off from remigium by strongly concave CUP. Hind wing membranous, venation of remigium usually slightly different from that of fore wing; RS arising nearer wing base, and stems of CUA and M coalesced; CUA much less developed; CUP setting off anal area, which includes several anal veins. Fore wings (and more rarely hind wings) may have conspicuous maculations or prominent cuticular thickenings.

Body structure: antennae prominent, usually long (e.g., Liomopteridae), with numerous segments; head (known in very few families) small, almost always hypognathous; prothorax commonly bearing pronotal disc (e.g., Liomopteridae) or slender, without such disc; some families (e.g., Geraridae) with elongate prothorax, which may bear prominent spines; prothorax very rarely (e.g., Lemmatophoridae) with pair of membranous paranotal lobes (Fig. 57, *Lemmatophora*), resembling those of certain Palaeodictyoptera; pterothorax with usual form; legs usually cursorial, but forelegs in some families apparently raptorial; in none, as the order is treated here, were hind legs modified for jumping (saltatorial); five tarsomeres (little known). Abdomen of moderate length; cerci usually prominent, long in some forms (e.g., Liomopteridae), but commonly small (e.g.,



FIG. 57. *Lemmatophora typha* SELLARDS, Lemmatophoridae, Permian of Kansas. Dorsal view of head and anterior portion of thorax, showing the reticulate, pronotal lobes and hair covering. Specimen MCZ 3539, $\times 40$ (Carpenter, new).

Protrembiidae) or modified (e.g., males, Chelopteridae).

Nymphal forms little known; antennae and cerci well developed; most nymphs clearly terrestrial (e.g., *Liomopterites*, *Kaltanympha*), others apparently modified for aquatic life, with tracheal gills along sides of abdomen (see Fig. 61,1b, *Lemmatophora*). U. Carb.—Trias.

The extinct order Protorthoptera was named by HANDLIRSCH (1906a, 1906b) for a diverse assemblage of Paleozoic species with presumed orthopteroid affinities. He also named another extinct order, Protoblattodea, for other species that he considered to be intermediate between the Palaeodictyoptera and the Blattodea, Manteodea, and Phasmatoidea; at the same time he named a

third order, "Protorthoptera vel Protoblattodea," for species that were apparently intermediate between the Protorthoptera and the Protoblattodea. As more Paleozoic insects became known, a gradual diminution of the distinctions between the Protorthoptera and the Protoblattodea became apparent, the number of genera placed in the "Protorthoptera vel Protoblattodea" complex being nearly double that in the Protoblattodea (HANDLIRSCH, 1922). This classification proved unsatisfactory, and MARTYNOV subsequently (1937b, 1938b) proposed that the order Protorthoptera be restricted to species having saltatorial hind legs, like the true Orthoptera, and that the remaining species in that order be placed in another new, extinct order, Paraplecoptera. In the same year ZEUNER transferred the saltatorial species cited by MARTYNOV to the order Orthoptera, where they clearly belonged (Zeuner, 1937). The cursorial species were then distributed among the other three orders, the Protorthoptera, Protoblattodea, and Paraplecoptera. This arrangement was followed for many years. However, SHAROV (1961a, 1966a) was convinced that one family, Sthenaropodidae, which had slender, cursorial hind legs and which was previously included in the Protorthoptera, represented the actual stock from which the true Orthoptera were derived. Accordingly, he proposed that the order Protorthoptera be limited to that family. He placed the other families in the Protoblattodea and Paraplecoptera. CARPENTER (1966), objecting to SHAROV's concept of the Sthenaropodidae, proposed that the Protoblattodea and Paraplecoptera be merged with the Protorthoptera to form a single order until more is known of the morphology of the families involved. SHAROV (1968) agreed with CARPENTER that the Protoblattodea and Paraplecoptera were inseparable and should be combined into one order, the Protoblattodea, but insisted that the order Protorthoptera, with its single family, Sthenaropodidae, should be retained. Since then, there has been little consistency in the use of these ordinal names.

In a general review of the orthopteroids, RASNITSYN (1980c) transferred the Sthenaropodidae to the order Orthoptera, completely dropping the names Protorthoptera, Protoblattodea, and Paraplecoptera, and assigned most of the families previously included in those orders to the small existing order of flightless insects, the Grylloblattodea. The family Geraridae, formerly included in the Paraplecoptera, was placed in a new order, Gerarida. More recently, BURNHAM (1983), following her study of the types of orthopteroids in the Museum d'Histoire Naturelle in Paris, including those of *Sthenaropoda*, the type genus of Sthenaropodidae, placed *Sthenaropoda* in synonymy with *Gerarus*, the type genus of the Geraridae. It is clear that we need to know much more about the morphology of these extinct families before we can reach an acceptable conclusion about their relationships.

In the present work the order Protorthoptera is retained and includes the families formerly in the Protoblattodea and Paraplecoptera, as well as in the Protorthoptera itself. However, a substantial number of genera, based on fragments of wings, have been placed in the category of order Uncertain.

The division of the Protorthoptera into suborders seems virtually meaningless at present. Although a few groups of families can be recognized, most of the families remain isolated, mainly as a result of the lack of detailed knowledge of both fore and hind wings and the body. The lines of evolution within this Paleozoic complex have not yet been satisfactorily untangled. The assumption of most workers that these lines must lead to existing orders (e.g., Blattodea, Orthoptera, Perlaria) appears incorrect; more likely they radiated in diverse directions, only a very few leading to existing ordinal groups.

The homologies of the protorthopterous venation present no special difficulties, except for the media. In palaeopterous orders the anterior and posterior median veins (MA, MP) are readily recognizable as convex and concave, respectively. That both MA and MP exist in any of the orthopteroids (or in any

of the Neoptera) is not certain; the loss of the convex vein in the median complex of the Neoptera has convinced some entomologists that the only element remaining is MP. On the other hand, even this vein is not always clearly concave, the coriaceous nature of the tegmen altering the thickness and general nature of the wing surface and membrane. Evidence for the presence of both MA and MP in the primitive Neoptera is indicated by the similarity between the fore wing venation of primitive Palaeodictyoptera (e.g., Dictyoneuridae) and that of the existing Orthoptera of the family Pneumoridae (RAGGE, 1955a).

In the following account of the Protorthoptera, the branches of the media are designated MA and MP only if the media divides before or near the middle line of the wing, and then only if there is no specific evidence against this interpretation, such as the presence of a media that is strongly concave entirely. In view of the uncertainties noted above, as well as the lack of knowledge of hind wings and body structures of most Protorthoptera, it is not possible to identify with confidence the most primitive families in the order. However, the Homoeodictyidae, Thoronysididae, and Paoliidae, which have an archedictyon as well as a concave MP in the fore wing, might well occupy that position. The venational specializations that have developed in the order have apparently involved the loss of the archedictyon and its replacement by a reticulation of crossveins and eventually by more regular crossveins; this has apparently taken place independently of the development of the fore wing as a tegmen. In contrast to most other orders of insects, only rarely has MA tended to anastomose with R and RS. On the other hand, in many families, MP and CUA show various degrees of anastomosis (Cacurgidae, Aenigmatodidae, Protokollariidae); in some of these, the stem of CUA is apparently anastomosed with the stem of M (or MP), CUP arising independently from the wing base. Also, in some of these genera, CUA, after diverging from MP, coalesces for a short dis-

tance with a branch of CUP. In all probability, these specializations of MP, CUA, and CUP, have been developed independently several times within the order. The fore wings commonly bear maculations (see Fig. 61,3, *Lisca*) or more elaborate markings (see Figs. 75 and 76, *Protodiamphipnoa*).

The hind wing is known in so few families of Protorthoptera that little can be said about its evolution. A well-developed anal area was present in many families (Lemmatophoridae, Liomopteridae), and this probably indicates a specialized condition of the hind wing. In others (Geraridae), the hind wing apparently had a very small anal area.

The general body structure is known in a very few families of Protorthoptera, and details of structure are known in even fewer (Lemmatophoridae, Chelopteridae, Probnidae, Liomopteridae, and Eucaenidae). The prothorax seems to show the greatest diversity of structure. In some families (e.g., Liomopteridae) the prothorax consists of a discrete pronotal plate surrounded by an oval or nearly oval disc, which in some genera may be covered with fine hairs. In the Lemmatophoridae the prothorax bears a pair of distinct paranotal lobes, which are membranous and covered with microtrichia, like those on the wings. In other families the prothorax is more slender, and in the Geraridae it is long and bears numerous long spines. The legs of the Protorthoptera also show various structural trends. In most families the three pairs of legs are similar, the third pair being slightly longer than the others. In a few families the forelegs are apparently adapted for raptorial purposes.

There are several basic features characteristic of the Protorthoptera in addition to the cursorial legs. The wings at rest, as far as is known, were folded flat over the abdomen, not slanted, as in the Orthoptera. The costal vein of the fore wing was usually marginal basally, but if it were submarginal the subcostal area was small and included only a few veinlets at most, in contrast to the Orthoptera, in which the precostal area tended to be long and replete with veinlets.

As treated here, the order Protorthoptera was almost exclusively Permo-Carboniferous, with most of the genera from the Permian. Two genera, not well known, are from the Triassic: *Tomia* MARTYNOV (family Tomiidae) and *Mesorthopteron* TILLYARD (family uncertain). Both of these are poorly known and may turn out to belong elsewhere.

Family HOMOEODICTYIDAE Martynov, 1937

[Homoeodictyidae MARTYNOV, 1937b, p. 26]

Fore wing slender, with fine archedictyon; vein SC terminating on costa; MA without definite convexity; MP concave; CUP branched. *Perm.*

Homoeodictyon MARTYNOV, 1937b, p. 26 [**H. elongatum*; OD]. Fore wing with broad costal area, traversed by several distinct veinlets, and with archedictyon. *Perm.*, USSR (European RSFSR).—FIG. 58,5. **H. elongatum*; fore wing, $\times 1$ (Martynov, 1937b).

Family THORONYSIDIDAE Handlirsch, 1919

[Thoronyssididae HANDLIRSCH, 1919b, p. 544]

Fore wing slender, crossveins forming irregular coarse network over entire wing, no anastomosis of main veins. Vein CUA extensively developed, its most distal branch terminating well beyond midwing. Hind wing unknown. *U. Carb.*

Thoronysis HANDLIRSCH, 1906b, p. 139 [**Oedischbia ingbertensis* VON AMMON, 1903, p. 282; OD]. Fore wing with SC terminating on R near wing apex; M forking before midwing and after origin of RS. GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 58,11. **T. ingbertensis* (VON AMMON); fore wing, $\times 0.9$ (Guthörl, 1934).

Family PAOLIIDAE Handlirsch, 1906

[Paoliidae HANDLIRSCH, 1906a, p. 682]

Fore wing oval, slender, with broad costal area; fine network, resembling archedictyon, over entire wing; veinlets also present in costal area and some other parts of wing; vein SC terminating (usually on R) in distal fourth of wing; RS arising proximally of midwing; MA apparently absent; MP (concave) well developed; CU dividing very close to wing

base; CUA branched; anal area weakly set off by marginal indentation at end of CUP. Hind wing triangular, with anal-posterior extension but no anal fan; venation basically as in fore wing. KUKALOVÁ, 1958a. *U. Carb.*

Paolia SMITH, 1871, p. 44 [**P. vetusta*; OD]. Hind wing with MP dividing before midwing but distally of origin of RS; proximal part of wing only slightly broader than distal half. LAURENTIAUX, 1950; KUKALOVÁ, 1958a. *U. Carb.*, USA (Indiana), Europe (The Netherlands).—FIG. 58,3. **P. vetusta*, Indiana; hind wing, $\times 8$ (Smith, 1871).

Holascia KUKALOVÁ, 1958a, p. 942 [**H. vetula*; OD]. Fore wing slender; MP forked at midwing; costal margin straight. *U. Carb.*, Europe (Czechoslovakia).—FIG. 58,1. **H. vetula*; fore wing, $\times 1.4$ (Kukalová, 1958a).

Olinka KUKALOVÁ, 1958a, p. 944 [**O. modica*; OD]. Little-known genus; similar to *Holascia*, but fore wing with convex costal margin and MP forking distally of midwing. *U. Carb.*, Europe (Czechoslovakia).—FIG. 58,9. **O. modica*; fore wing, $\times 1.5$ (Kukalová, 1958a).

Paoliola HANDLIRSCH, 1919b, p. 533 [**P. gurleyi*; OD]. Hind wing similar to that of *Paolia* but with MP forked more deeply. MELANDER, 1903. *U. Carb.*, USA (Indiana).—FIG. 58,10. **P. gurleyi*; hind wing, $\times 1.4$ (Melander, 1903).

Pseudofouquea HANDLIRSCH, 1906b, p. 125 [**Fouquea cambrensis* ALLEN, 1901, p. 68; OD]. Fore wing similar to *Olinka*, but costal space narrower and MP dividing before midwing. LAURENTIAUX, 1950. *U. Carb.*, Wales.—FIG. 58,12. **P. cambrensis* (ALLEN); fore wing, $\times 1$ (Laurentiaux, 1950).

Sustaia KUKALOVÁ, 1958a, p. 946 [**S. impar*; OD]. Little-known fore wing, similar to *Olinka* but much larger; hind wing with branch of MP terminating on apical end of hind margin. *U. Carb.*, Europe (Czechoslovakia).—FIG. 58,7. **S. impar*; *a*, fore and *b*, hind wings, $\times 0.4$ (Kukalová, 1958a).

Zdenekia KUKALOVÁ, 1958a, p. 937 [**Z. grandis*; OD]. Fore wing broader than in *Holascia*; costal margin convex; MP forked at midwing. Hind wing much broader proximally than in distal half; branches of MP terminating along middle part of hind margin. *U. Carb.*, Europe (Czechoslovakia).—FIG. 58,8. **Z. grandis*; *a*, fore wing, $\times 1$; *b*, hind wing, $\times 0.8$ (both Kukalová, 1958a).

Family STYGNIDAE Handlirsch, 1906

[Stygnidae HANDLIRSCH, 1906b, p. 115]

Related to Paoliidae, but crossveins distinct, though irregular, and vein MP less developed. *U. Carb.*

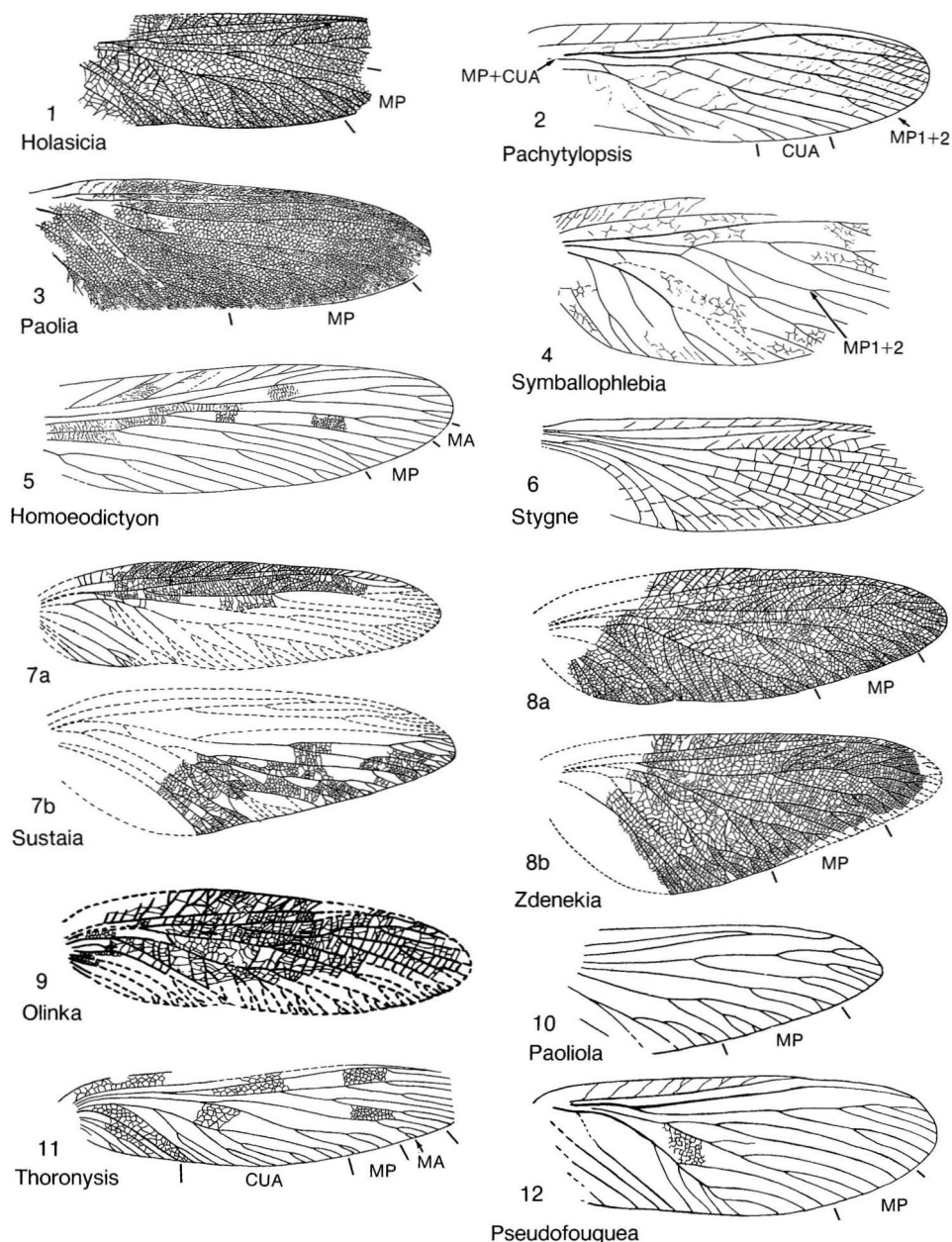


FIG. 58. Homoeodictyidae, Thoronyssididae, Paoliidae, Stygnidae, and Pachytylopsidae (p. 101–103).

Stygne HANDLIRSCH, 1906b, p. 115 [**S. roemeri*; ODJ]. Fore wing with narrow costal area; RS arising very close to base of wing, its first branch at about midwing. SCHWARZBACH, 1939. *U. Carb.*, Poland (Upper Silesia).—FIG. 58,6. **S. roemeri*; fore wing, $\times 2.2$ (Handlirsch, 1906b).

Family HAPALOPTERIDAE Handlirsch, 1906

[Hapalopteridae HANDLIRSCH, 1906b, p. 304]

Fore wing similar to that of *Cacurgidae* but with fewer branches of main veins; vein

CUP forking further from wing base; cuticular spots absent from wings. *U. Carb.*

Haploptera HANDLIRSCH, 1906a, p. 694 [**H. gracilis*; OD]. Fore wing with SC extending nearly to wing apex; costal veinlets unbranched; RS with 4 branches; MP forked to about midwing; CUA with terminal fork only; crossveins numerous, weakly formed. CARPENTER, 1965. *U. Carb.*, USA (Pennsylvania).—FIG. 59,1. **H. gracilis*; fore wing, $\times 4$ (Carpenter, 1965).

Family PACHYTYLOPSIDAE

Handlirsch, 1906

[Pachytylopsiidae HANDLIRSCH, 1906b, p. 138] [=Anthraconeuridae LAURENTIAUX & LAURENTIAUX-VIEIRA, 1980, p. 407]

Fore wing with vein SC terminating on costal margin well before wing apex; MA apparently absent; CUA anastomosed with MP for a short interval basally; crossveins weak, apparently forming an irregular network over most of wing. Probably related to Paoliidae. *U. Carb.*

Pachytylopsi BORRE, 1875a, p. xl [**P. persenairei*; SD BORRE, 1875b, p. lvi] [=Palorthopteron HANDLIRSCH, 1904a, p. 3 (type, *P. melas*)]. Costal area of moderate width; MP1+2 directed anteriorly shortly after its separation from CUA1 and connected to RS by a short but stout crossvein; R with several terminal branches. HANDLIRSCH, 1906b; PRUVOST, 1930, 1933b; LAURENTIAUX & LAURENTIAUX-VIEIRA, 1981. *U. Carb.*, Europe (Belgium).—FIG. 58,2. **P. persenairei*; fore wing, $\times 1.4$ (Handlirsch, 1904a).

Anthraconeura LAURENTIAUX & LAURENTIAUX-VIEIRA, 1980, p. 407 [**A. silvatica*; OD]. Similar to *Protopachytylopsi*, but costal area much narrower, especially basally; R without terminal branches; CUA with 2 long branches. [Type of family Anthraconeuridae LAURENTIAUX & LAURENTIAUX-VIEIRA.] *U. Carb.*, Europe (Belgium).

Protopachytylopsi LAURENTIAUX & LAURENTIAUX-VIEIRA, 1981, p. 83 [**P. leckwycki*; OD]. Similar to *Pachytylopsi*, but costal area broader basally; R without terminal branches; CUA with several short marginal branches. *U. Carb.*, Europe (Belgium).

Symbalophlebia HANDLIRSCH, 1904a, p. 3 [**S. latipennis*; OD]. Similar to *Pachytylopsi*, but fore wing much broader; MP1+2 in short contact with RS. [Family assignment doubtful.] PRUVOST, 1930. *U. Carb.*, Europe (Belgium).—FIG. 58,4. **S. latipennis*; fore wing, $\times 1.2$ (Pruvost, 1930).

Family BLATTINOPSIDAE

Bolton, 1925

[Blattinopsidae BOLTON, 1925, p. 23] [=Oryctoblattinidae HANDLIRSCH, 1906b, p. 155]

Fore wing with vein SC terminating on costal margin well before apex; R usually sigmoidally curved, numerous oblique veinlets between R and costal margin beyond SC; RS with numerous branches; MA apparently absent; MP often with one or more branches anastomosed with R or RS; CUA anastomosed with basal portion of M, diverging away, and then fusing with CUA2; strong indentation at end of CUP; anal veins straight; crossveins numerous, commonly forming meshwork of cells. Hind wing unknown. *U. Carb.—Perm.*

The venation is highly variable within genera and species of this family. In addition, some specimens show a more or less distinct curving line near the middle of the wing and extending from R to the hind margin. This has led some workers to consider the Blattinopsidae to be Homoptera, related to the Fulgoridae. However, a similar line, present on the wings of some species of roaches, is apparently due to a pressure mark on the tegmina, resulting from the flexed position of the wings. It is commonly better developed on one tegmen than on the other and may be missing from one of them. Such an origin of the cross lines could explain why they are present in some blattinopsisid fore wings but lacking in others. KUKALOVÁ, 1959b; CARPENTER, 1966.

Blattinopsis GIEBEL, 1867, p. 417 [**Blattina reticulata* GERMAR, 1851 in GERMAR, 1844–1853, p. 87; OD] [=Oryctoblattina SCUDDER, 1879b, p. 122, obj.; *Protociccus* BRONGNIART, 1885a, p. 67, nom. nud.; *Prisca* K. W. FRITSCH, 1900, p. 45 (type, *P. wittinensis*); *Oryctomylabris* HANDLIRSCH, 1906b, p. 346 (type, *Oryctoblattina oblonga* DEICHMÜLLER, 1882, p. 41); *Pseudofulgora* HANDLIRSCH, 1906b, p. 357 (type, *Fulgora ebersi* DOHRN, 1867, p. 131); *Blattinopsiella* MEUNIER, 1907, p. 523 (type, *B. pygmaea*); *Anadymenella* STRAND, 1929, p. 19, nom. subst. pro *Anadymene* K. W. FRITSCH, 1900, p. 45, non GISTEL, 1848 (type, *A. huyseni*); *Palaeorincanites* HAUPT, 1941, p. 90 (type, *Blattinopsis anthracina* HANDLIRSCH,

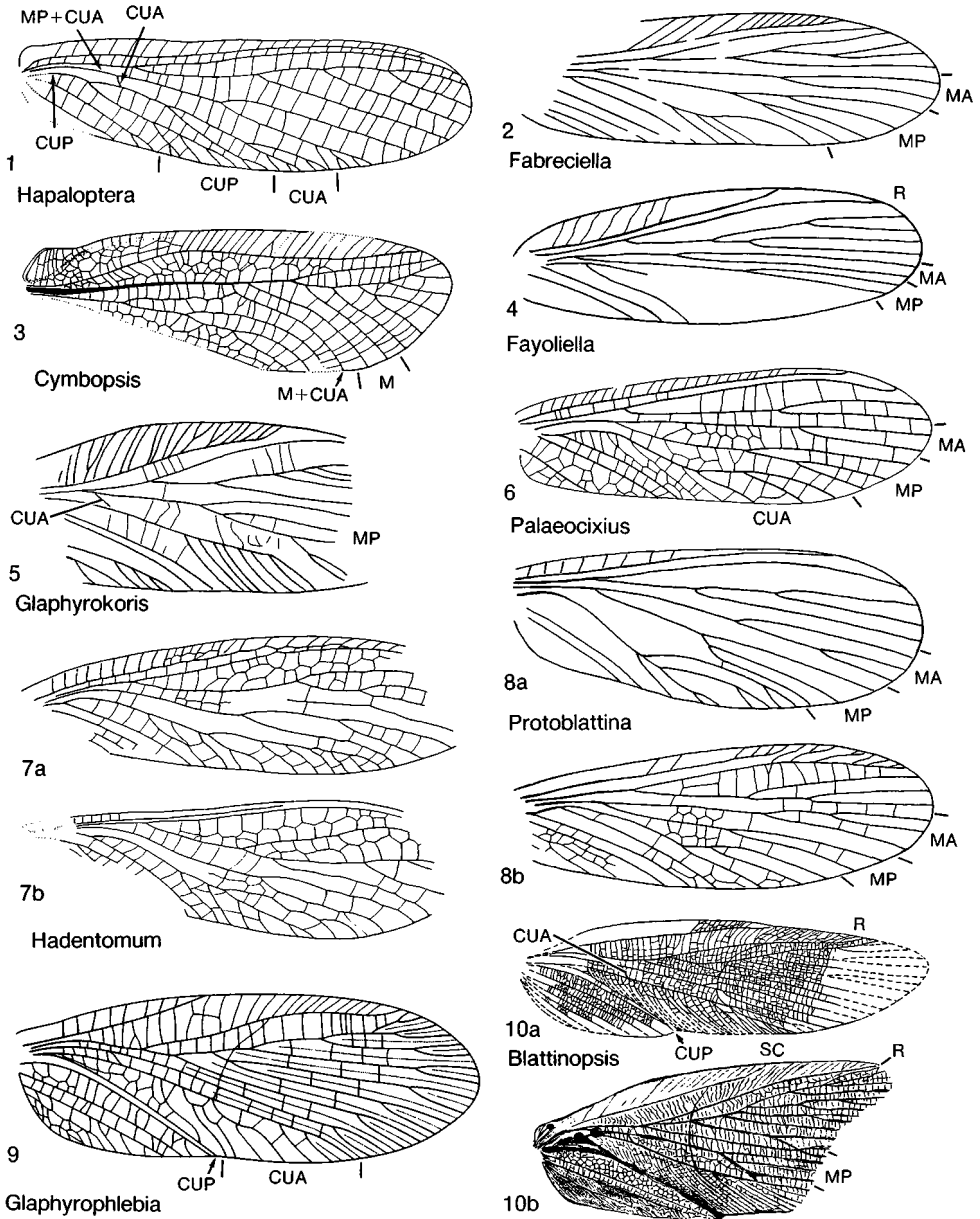


FIG. 59. Haplopteridae, Blattinopsidae, Cymbopsidae, and Hadentomidae (p. 103–106).

1906a, p. 706)]. Fore wing with SC extending to midwing; crossveins very close together over most of wing; numerous oblique veinlets between CUA and CUP. KUKALOVÁ, 1959b; CARPENTER, 1966; MÜLLER, 1977. *U. Carb.*, Europe (Germany, France), USA (Ohio); *Perm.*, Europe (Germany, Czechoslovakia).—FIG. 59,10a. *B. angustai* KUKALOVÁ, *Perm.*, Czechoslovakia; fore

wing, $\times 2$ (Kukalová, 1959b).—FIG. 59,10b. **B. reticulata* (GERMAR), *U. Carb.*, Germany; fore wing, $\times 2$ (Schlectendal, 1913). Glaphyrokoris RICHARDSON, 1956, p. 38 [**G. mirandus*; OD]. Similar to *Glaphyrophlebia* but with SC and R longer. *U. Carb.*, USA (Illinois).—FIG. 59,5. **G. mirandus*; fore wing as preserved; $\times 2.6$ (Richardson, 1956).

Glaphyrophlebia HANDLIRSCH, 1906a, p. 707 [**G. pusilla*; OD] [= *Pursa* SELLARDS, 1909, p. 153 (type, *P. ovata*); *Sindon* SELLARDS, 1909, p. 154 (type, *S. speciosa*)]. Similar to Blattinopsis but with 2 rows of cells proximally between CUA and CUP. BOLTON, 1934; KUKALOVÁ, 1965; CARPENTER, 1966. *U. Carb.*, USA (Pennsylvania), Wales; *Perm.*, USA (Kansas), Europe (Czechoslovakia).—FIG. 59,9. *G. speciosa*, (SELLARDS), *Perm.*, Kansas; fore wing, $\times 7$ (Carpenter, 1966).

Protoblattiniella MEUNIER, 1912d, p. 1194 [**P. minutissima*; OD]. Little-known genus, based on fragment of nymph. [Family assignment doubtful.] LAURENTIAUX, 1959b. *U. Carb.*, Europe (France).

Family CYMBOPSIDAE Kukalová, 1965

[Cymbopsidae KUKALOVÁ, 1965, p. 86]

Little-known family of uncertain affinities. Fore wing tegminous; vein SC extending very nearly to wing apex; RS arising in distal third of wing, with several branches; M apparently coalesced with stem R to about midwing; crossveins numerous. [Placed in Protorthoptera by KUKALOVÁ, but ordinal assignment doubtful.] *Perm.*

Cymbopsis KUKALOVÁ, 1965, p. 86 [**C. excelsa*; OD]. SC sigmoidally curved; crossveins reticulate only in basal costal area and in area between SC and R + M. *Perm.*, Europe (Czechoslovakia).—FIG. 59,3. **C. excelsa*; fore wing, $\times 5.7$ (Kukalová, 1965).

Family EUCAENIDAE Handlirsch, 1906

[Eucenidae HANDLIRSCH, 1906a, p. 709] [= *Teneopteridae* RICHARDSON, 1956, p. 46]

Fore wing coriaceous, oval; costal space broad, with numerous veinlets; vein R with few distal branches; RS arising near wing base, with many branches; M well developed, with several branches leading to posterior border; CUP curved, well developed. Hind wing little known; costal area narrow; R with few terminal branches; anal area unknown. Head slender, long; antennae long, setaceous; mandibles dentate; maxillary palpi very long; prothorax long, broad posteriorly, narrowed anteriorly, with a constricted area adjoining the head; legs alike, all femora stout; tarsi with 5 segments; abdominal seg-

ments with posteriorly directed lateral lobes; cerci very short. Females with a short ovipositor. CARPENTER & RICHARDSON, 1976. *U. Carb.*

Eucaenus SCUDDER, 1885d, p. 325 [**E. ovalis*; OD] [= *Teneopteron* CARPENTER, 1944, p. 17 (type, *T. mirabile*)]. Fore wing: veinlets of costal area unbranched; RS with branches directed toward wing apex. MELANDER, 1903; HANDLIRSCH, 1922; CARPENTER & RICHARDSON, 1976. *U. Carb.*, USA (Illinois).—FIG. 60. **E. ovalis*; whole insect, $\times 2.8$ (Carpenter & Richardson, 1976).

Family HADENTOMIDAE Handlirsch, 1906

[Hadentomidae HANDLIRSCH, 1906b, p. 303] [= *Fayoliellidae* HANDLIRSCH, 1919b, p. 558; *Palaecixiidae* HANDLIRSCH, 1919b, p. 539]

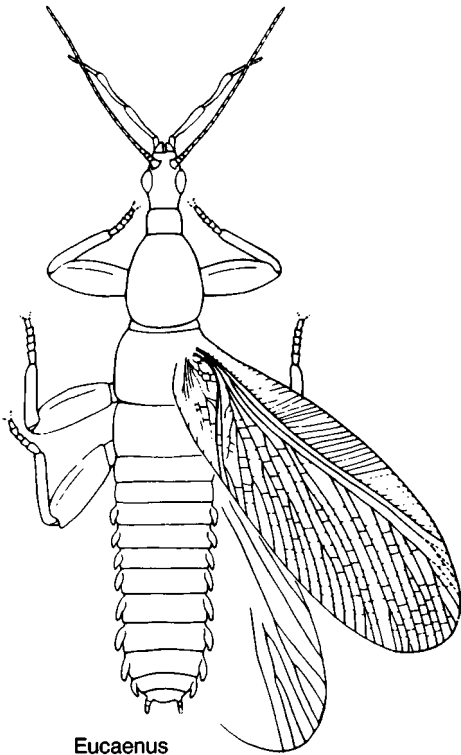
Fore wing with vein SC ending on costal margin well beyond level of midwing; costal area with a series of veinlets, mostly straight; RS arising well before midwing, with 2 to 4 long branches; M forking near or before midwing; CUA with several terminal branches. Hind wing with venation essentially as in fore wing, but costal area much narrower; anal area unknown. [Placed by HANDLIRSCH (1906a) in order Hadentomidea.] CARPENTER, 1965. *U. Carb.*

Hadentomum HANDLIRSCH, 1906a, p. 693 [**H. americanum*; OD]. M forking at about midwing; RS with at least 3 branches in both wings. CARPENTER, 1965. *U. Carb.*, USA (Illinois).—FIG. 59,7. **H. americanum*; a, fore and b, hind wings, $\times 2.4$ (Carpenter, 1965).

Fabreciella CARPENTER, 1934, p. 327 [**F. pennsylvanica*; OD]. Fore wing as in *Palaecixius*, but costal area broader; M with 6 branches, RS with 4. [Family assignment doubtful.] *U. Carb.*, USA (Pennsylvania).—FIG. 59,2. **F. pennsylvanica*; fore wing, $\times 4.2$ (Carpenter, 1934).

Fayoliella MEUNIER, 1908j, p. 247 [**F. elongata*; OD]. Costal area of fore wing broad, with irregular veinlets; RS and M with 4 branches. [Family assignment doubtful.] *U. Carb.*, Europe (France).—FIG. 59,4. **F. elongata*; fore wing, $\times 2.5$ (Carpenter, new).

Palaecixius HANDLIRSCH, 1906b, p. 326 [**P. antiquus*; SD HANDLIRSCH, 1922, p. 74] [= *Palaecixius* BRONGNIART, 1885a, p. 67, *nom. nud.*; *Fabrecia* MEUNIER, 1911a, p. 123 (type, *F. pygmaea*)]. Fore wing with fork of M at about level of origin of RS; RS and MA forking at about same level; RS with 2 branches, M with 5; a few large cells formed in region of M and



Eucanenus

FIG. 60. Eucanidae (p. 105).

in anal area. *U. Carb.*, Europe (France).—FIG. 59,6. **P. antiquus*; fore wing, $\times 4$ (Carpenter, new).

Protoblattina MEUNIER, 1909d, p. 48 [**P. bouvieri*; OD]. Fore wing as in *Palaeocixius*, but RS with 3 branches, M with 6. *U. Carb.*, Europe (France).—FIG. 59,8a. **P. bouvieri*; fore wing, $\times 2.8$ (Carpenter, new).—FIG. 59,8b. *P. giardi* MEUNIER, 1912d; fore wing, $\times 2$ (Carpenter, new).

Family LEMMATOPHORIDAE

Sellards, 1909

[Lemmatophoridae SELLARDS, 1909, p. 162] [=Ortoidae SELLARDS, 1909, p. 167; Lecortidae HANDLIRSCH, 1919b, p. 556]

Fore wing with costal area moderately broad; vein SC terminating on costa at least slightly beyond midwing; R unbranched; MA and MP present, but neither convex nor concave; proximal half of MP obsolete; CUA very strongly developed, usually with 3 branches; CUP obsolete, forming a straight vena divdians; 2 anals present. Hind wing shorter than fore wing but with expanded

anal area, and with at least slight incision of wing margin at end of CUP; R unbranched; MA unbranched and coalesced to variable extent with RS; CUA well developed, CUP obsolete; anal fan with four main veins. Venation highly variable among species. Antennae long, multisegmented; head small, hypognathous; eyes small; prothorax bearing pair of membranous paranota, with reticulated venation and covered with microtrichia; mesonotum and metanotum broad and flat; five tarsomeres; abdomen unspecialized but bearing on the first nine segments small lateral processes resembling vestigial gills; cerci about as long as abdomen; female with very short ovipositor. Nymphs apparently aquatic, with lateral gills on first nine abdominal segments. CARPENTER, 1935a, 1939. *Perm.*

Lemmatophora SELLARDS, 1909, p. 162 [**L. typa*; SD TILLYARD, 1928b, p. 189]. SC terminating just beyond midwing; RS unbranched; hind wing with deep incision at end of CUP. *Perm.*, USA (Kansas).—FIG. 57. **L. typa*; head, prothorax, prothoracic lobes, neotype, $\times 40$ (Carpenter, new).—FIG. 61,1a. **L. typa*; restoration of adult, $\times 2.4$ (Carpenter, 1935a).—FIG. 61,1b. *Lemmatophora* sp. (probably *typa*); nymph, $\times 2.4$ (Carpenter, 1935a).

Artinska SELLARDS, 1909, p. 165 [**A. clara*; SD TILLYARD, 1928e, p. 321] [=Estadia SELLARDS, 1909, p. 166 (type, *E. elongata*); *Lectrum* SELLARDS, 1909, p. 167 (type, *L. anomalum*); *Orta* SELLARDS, 1909, p. 168 (type, *O. ovata*)]. SC extending well beyond midwing; RS with at least one fork. *Perm.*, USA (Kansas).—FIG. 62,1. **A. clara*; a, fore wing, $\times 6$ (Carpenter, 1935a); b, hind wing, $\times 6$ (Tillyard, 1928e).

Blania KUKALOVÁ, 1964c, p. 101 [**B. rotunda*; OD]. Fore wing as in *Artinska* but broader and more nearly oval; costal area relatively broad. *Perm.*, Europe (Czechoslovakia).—FIG. 62,4. **B. rotunda*; fore wing, $\times 7.5$ (Kukalová, 1964c).

Lecorium SELLARDS, 1909, p. 167 [**L. elongatum*; OD] [=Stemta SELLARDS, 1909, p. 168 (type, *S. elegans*); *Sellardsia* TILLYARD, 1928e, p. 343 (type, *S. kansensis*); *Metalecorium* HANDLIRSCH, 1937, p. 96, *nom. nud.*; *Paralecorium* HANDLIRSCH, 1937, p. 96 (type, *Lecorium parvum*)]. Fore wing with costal area narrow, as in *Paraprisca*; CUA coalesced with M basally but diverging just before origin of MA. CARPENTER, 1935a, 1939. *Perm.*, USA (Kansas).—FIG. 61,2. **L. elongatum*; adult, $\times 6$ (Carpenter, 1935a).

Lisca SELLARDS, 1909, p. 163 [**L. minuta*; OD].

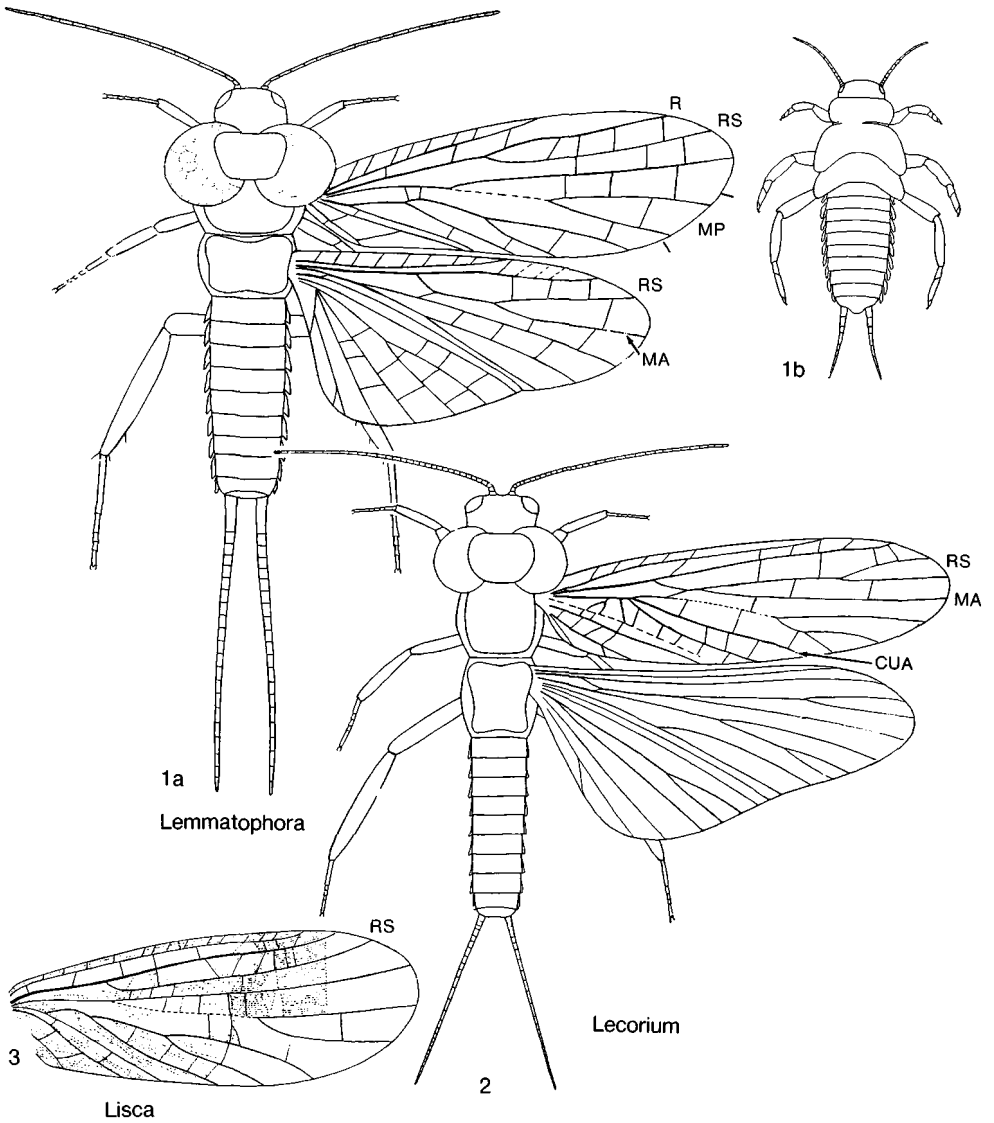


FIG. 61. Lemmatophoridae (p. 106–107).

Fore wing with costal area much narrower than in *Lemmatophora*; RS unbranched; RS arising much nearer wing base than in *Lemmatophora*. Perm., USA (Kansas).—FIG. 61,3. **L. minuta*; fore wing, $\times 8$ (Tillyard, 1928e).

Maculopterum KUKALOVÁ, 1964c, p. 107 [**M. maculatum*; OD]. Little-known genus. Fore wing as in *Torrentopterus* but with numerous maculations. [Probably a synonym of *Torrentopterus*.] Perm., Europe (Czechoslovakia).

Oborella KUKALOVÁ, 1964c, p. 93 [**O. matura*;

OD]. Fore wing as in *Artinska*, but costal area much broader; CU usually anastomosed with M before separating into CUA and CUP. Central disc of pronotum oval. Perm., Europe (Czechoslovakia).

Paraprisca HANDLIRSCH, 1919b, p. 555, *nom. subst. pro Prisca* SELLARDS, 1909, p. 167, *non* K. W. FRITSCH, 1900 [**Prisca fragilis* SELLARDS, 1909, p. 167]. Fore wing more slender than in *Lemmatophora*; R straight; CUA not anastomosed with M; hind wing with only slight incision at

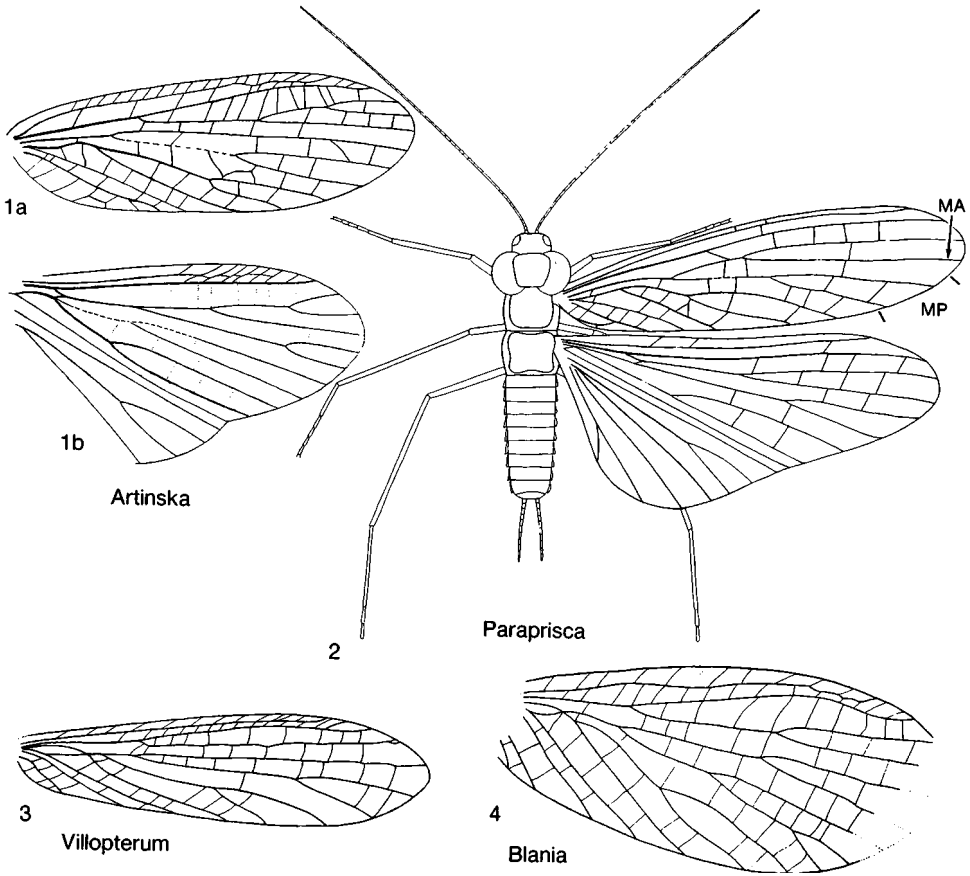


FIG. 62. Lemmatophoridae (p. 106–108).

CUP. Antennae longer and legs much longer than in *Lemmatophora*. ZALESSKY, 1952. *Perm.*, USA (Kansas), USSR (Asian RSFSR).—FIG. 62,2. **P. fragilis* (SELLARDS), Kansas; adult, $\times 6$ (Carpenter, 1935a).

Quecopterum KUKALOVÁ, 1964c, p. 98 [**Q. decusatum*; OD]. Little-known genus. Fore wing as in *Oborella*, but central disc of pronotum irregular in shape. *Perm.*, Europe (Czechoslovakia).

Sharovipterum KUKALOVÁ, 1964c, p. 100 [**S. alatum*; OD]. Little-known genus. Fore wing apparently broadly oval; costal area narrow; RS and MA apparently unbranched. Pronotum subtriangular. *Perm.*, Europe (Czechoslovakia).

Torrentopterum KUKALOVÁ, 1964c, p. 105 [**T. pallidum*; OD]. Fore wing as in *Lecorium*, but crossveins apparently more numerous. [Probably a synonym of *Lecorium*.] *Perm.*, Europe (Czechoslovakia).

Villopterum KUKALOVÁ, 1964c, p. 108 [**V. villosum*; OD]. Fore wing as in *Lecorium* but more elongate and slightly broader distally; RS appar-

ently unbranched; CUA1 with a deep fork. *Perm.*, Europe (Czechoslovakia).—FIG. 62,3. **V. villosum*; fore wing, $\times 8$ (Kukalová, 1964c).

Family LIOMOPTERIDAE Sellards, 1909

[Liomopteridae SELLARDS, 1909, p. 157] [=Khosaridae MARTYNOV, 1937b, p. 29]

Fore wing membranous, usually with microtrichia well developed on at least part of wing; vein SC terminating on costa beyond midwing; costal area with numerous, slanted veinlets, not forming regular cells; R extending nearly to wing apex; RS with at least two branches; M forked at about level of origin of RS or slightly toward base; MA and MP not anastomosed with other veins; CUA typically diverging anteriorly shortly after its origin and forking into CUA1 and CUA2;

CUP and 1A unbranched. Hind wing with costal area narrow; R extending nearly to apex; RS arising much nearer base than in fore wing; M and CU fused at base; CUA strong and deeply forked; 1A close to CUP; anal area forming lobe containing numerous anal veins. Antennae long, multisegmented; head hypognathous; eyes prominent; prothorax usually with paranotal expansions continuing anteriorly and posteriorly around pronotum itself; reticulation not visible, but paranotals commonly membranous and covered with microtrichia; legs slender, hind legs longer than others, not modified for jumping; 5 tarsomeres; cerci long. CARPENTER, 1950. *Perm.*

Liomopterum SELLARDS, 1909, p. 157 [**L. ornatum*; SD CARPENTER, 1950, p. 189] [=*Horates* SELLARDS, 1909, p. 158 (type, *H. elongatus*)]. Costal space moderately broad; fork of M proximal to origin of RS; cells (when present) almost exclusively confined to area of CUA and CUP. *Perm.*, USA (Kansas).—FIG. 63,7. **L. ornatum*; adult, $\times 3.5$ (Carpenter, 1950).

Abashevnia SHAROV, 1961d, p. 194 [**A. suchovi*; OD]. Similar to *Parapermula*, but costal area narrower and branches of MA arising pectinately. *Perm.*, USSR (Asian RSFSR).—FIG. 63,3. **A. suchovi*; fore wing, $\times 1.8$ (Sharov, 1961d).

Alicula SCHLECHTENDAL, 1913, pl. 2 [**A. lebachensis*; OD] [=*Permula* HANDLIRSCH, 1919b, p. 542, obj.]. Little-known genus, with fore wing apparently similar to that of *Liomopterum*, but crossveins numerous and forming a fine reticulation; CUA with several additional branches. [HANDLIRSCH (1919b) considered the names *Alicula lebachensis* to be *nomina nuda*, but under article 12, section 7, of the ICZN (p. 35, 1985 ed.) both names are available.] KUKALOVÁ, 1964c. *Perm.*, Europe (Germany, Czechoslovakia).—FIG. 64,1. *A. acra* (KUKALOVÁ); fore wing as preserved, $\times 3$ (after KUKALOVÁ, 1964c).

Cerasopterum KUKALOVÁ, 1964c, p. 60 [**C. gracile*; OD]. Fore wing as in *Tapopterum*, but RS with only 3 branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,4. **C. gracile*; fore wing, $\times 6$ (KUKALOVÁ, 1964c).

Climaconeurites SHAROV, 1961d, p. 195 [**C. asiaticus*; OD]. MA branching dichotomously; anterior branch of MA anastomosed for short distance with RS. *Perm.*, USSR (Asian RSFSR).—FIG. 63,1. **C. asiaticus*; a, fore wing; b, hind wing, $\times 2.6$ (Sharov, 1961d).

Depressopterum KUKALOVÁ, 1964c, p. 48 [**D. senior*; OD]. Little-known genus. Fore wing as in *Parapermula* but more elongate and with less

convex anterior margin. *Perm.*, Europe (Czechoslovakia).—FIG. 64,2. **D. senior*; fore wing as preserved, $\times 4$ (KUKALOVÁ, 1964c).

Donopterum KUKALOVÁ, 1964c, p. 54 [**D. carpenteri*; OD]. Fore wing as in *Turbopterum* but broader; costal area narrower; RS and MA with more branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,5. **D. carpenteri*; fore wing, $\times 2$ (KUKALOVÁ, 1964c).

Drahania KUKALOVÁ, 1964c, p. 51 [**D. avia*; OD]. Similar to *Depressopterum*, but fore wing more slender; CUA with only 2 main branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,3. **D. avia*; fore wing, $\times 5$ (KUKALOVÁ, 1964c).

Fumopterum KUKALOVÁ, 1964c, p. 59 [**F. largum*; OD]. Little-known genus, based on distal half of wing. Venation as in *Donopterum*, but wing much more slender. *Perm.*, Europe (Czechoslovakia).

Ideliopsis CARPENTER, 1948b, p. 101 [**I. ovalis*; OD]. Costal margin only slightly curved; MP coalesced proximally with CUA1. Crossveins numerous, regular; no reticulation in apical part of wing. [Family assignment doubtful.] *Perm.*, USA (Texas).—FIG. 63,4. **I. ovalis*; fore wing, $\times 1.8$ (Carpenter, 1948b).

Kaltanella SHAROV, 1961d, p. 206 [**K. lata*; OD]. Fore wing broadly oval, with almost no cells; MA with 2 main stems arising before level of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 63,8. **K. lata*; a, fore and b, hind wings, $\times 2.6$ (Sharov, 1961d).

Kaltanympha SHAROV, 1961d, p. 220 [**K. thysanuriformis*; OD]. Nymph with long, slender cerci; apparently terrestrial. *Perm.*, USSR (Asian RSFSR).—FIG. 63,2. **K. thysanuriformis*; nymph, $\times 4$ (Sharov, 1961d).

Kazanella MARTYNOV, 1930d, p. 1116 [**K. rotundipennis*; OD]. Little-known fore wing, with broad costal margin. *Perm.*, USSR (European RSFSR).—FIG. 63,6. **K. rotundipennis*; fore wing, $\times 4$ (Sharov, 1962b).

Khosara MARTYNOV, 1937b, p. 30 [**K. permiakovae*; OD]. Apex of fore wing rounded but markedly asymmetrical; no cells; MA with long branches. *Perm.*, USSR (European RSFSR).—FIG. 63,5. **K. permiakovae*; fore wing, $\times 2.2$ (Sharov, 1962c).

Lioma KUKALOVÁ, 1964c, p. 56 [**L. moravica*; OD]. Fore wing as in *Donopterum* but more slender and with a longer SC. *Perm.*, Europe (Czechoslovakia).

Liomopterella SHAROV, 1961d, p. 202 [**L. vulgaris*; OD]. Similar to *Abashevnia*, but M forking well before origin of RS and MA dichotomously branched. *Perm.*, USSR (Asian RSFSR).—FIG. 65,1. **L. vulgaris*; a, fore and b, hind wings, $\times 2.6$ (Sharov, 1961d).

Liomopterina RIEK, 1973, p. 518 [**L. clara*; OD]. Little-known genus, based on proximal fragment

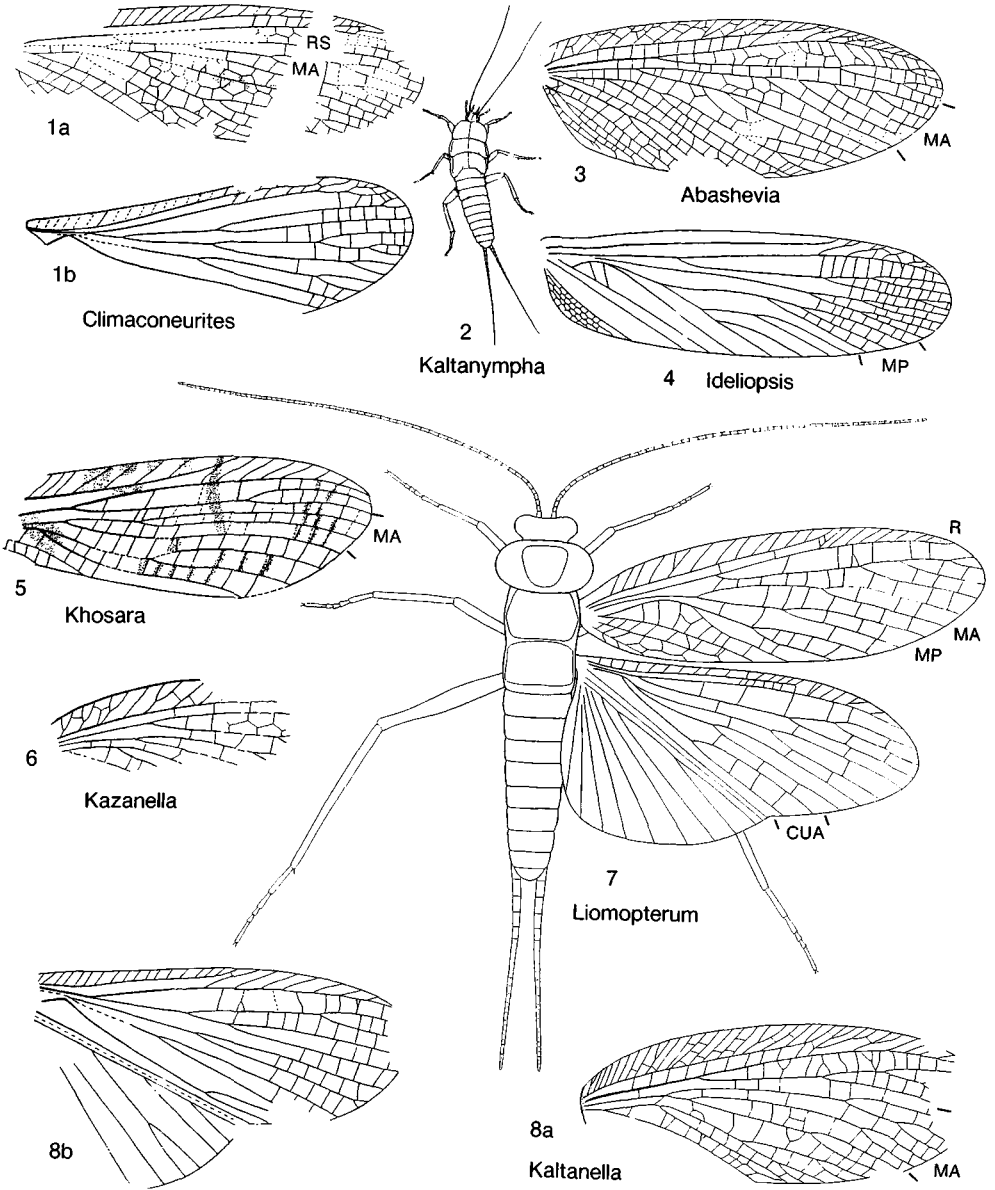


FIG. 63. Liomopteridae (p. 109).

of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).
Liomopterites SHAROV, 1961d, p. 207 [**L. expletus*; OD]. Fore wing similar to that of *Liomopterum* but with curvature of CUA less pronounced and with fewer crossveins; in hind wing, MA anastomosed with RS. Nymph slender, apparently terrestrial. *Perm.*, USSR (Asian RSFSR). — FIG. 65,2a. **L. expletus*; fore

wing, $\times 4.5$ (Sharov, 1961e). — FIG. 65,2b. *L. comans* SHAROV; hind wing, $\times 4.5$ (Sharov, 1961e). — FIG. 65,2c. *L. (?) gracilis* SHAROV; nymph, $\times 6$ (Sharov, 1961d).
Liomoptoides RIEK, 1973, p. 515 [**L. similis*; OD]. Little-known genus, based on small, apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).
Mioloptera RIEK, 1973, p. 515 [**M. stuckenbergi*;

OD]. Little-known genus, apparently similar to *Parapermula*. RIEK, 1976a. *Perm.*, South Africa (Natal).

Miolopterina RIEK, 1976a, p. 762 [**M. tenuipennis*; OD]. Little-known genus, based on small fragment of wing. *Perm.*, South Africa (Natal).

Mioloptoides RIEK, 1976a, p. 761 [**M. andrei*; OD]. Little-known genus, based on wing fragment; similar to *Mioloptera*. *Perm.*, South Africa (Natal).

Neoliomopterum RIEK, 1976a, p. 762 [**N. picturatum*; OD]. Little-known genus, based on apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).

Ornaticosta SHAROV, 1961d, p. 197 [**O. magna*; OD]. Apex of fore wing acute; costal area with dark pigmentation extending nearly to apex of wing. *Perm.*, USSR (Asian RSFSR).—FIG. 65,3. **O. magna*; fore wing, $\times 1$ (Sharov, 1961d).

Paraliomopterum SHAROV, 1961d, p. 218 [**P. paulum*; OD]. Similar to *Liomopterum*, but SC extending much further towards apex. *Perm.*, USSR (Asian RSFSR).—FIG. 65,4. **P. paulum*; fore wing, $\times 2.4$ (Sharov, 1961d).

Parapermula SHAROV, 1961d, p. 191 [**P. sibirica*; OD]. Fore wing oval, with very broad costal space; RS with numerous terminal branches; MA dichotomously branched; at least a few cells between most main veins. *Perm.*, USSR (Asian RSFSR).—FIG. 65,5. **P. sibirica*; a, fore and b, hind wings, $\times 2.5$ (Sharov, 1961d).

Sarbalopterum SHAROV, 1961d, p. 217 [**S. ignorabile*; OD]. Little-known fore wing, with broad costal area and no cells. *Perm.*, USSR (Asian RSFSR).—FIG. 65,6. **S. ignorabile*; fore wing, $\times 6.6$ (Sharov, 1961d).

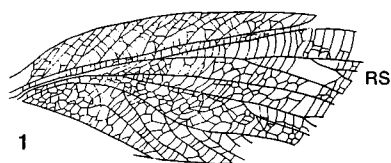
Semopterum CARPENTER, 1950, p. 197 [**S. venosum*; OD]. Fore wing similar to that of *Liomopterum* but with more numerous crossveins and with several additional anal veins. *Perm.*, USA (Kansas).—FIG. 65,7. **S. venosum*; fore wing, $\times 1.8$ (Carpenter, 1950).

Sibirella SHAROV, 1961d, p. 215 [**S. paucinervis*; OD]. Subcostal area nearly as wide as costal area; few crossveins and branches of main veins. *Perm.*, USSR (Asian RSFSR).—FIG. 65,8. **S. paucinervis*; fore wing, $\times 3.4$ (Sharov, 1961d).

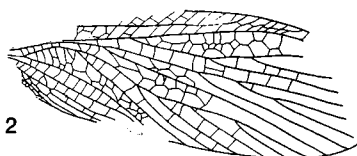
Tapopterum CARPENTER, 1950, p. 195 [**T. celsum*; OD]. Costal space narrower than in *Liomopterum*; crossveins more numerous, with at least a few cells between most main veins. *Perm.*, USA (Kansas).—FIG. 65,9. **T. celsum*; fore wing, $\times 2.5$ (Carpenter, 1950).

Turbopterum KUKALOVÁ, 1964c, p. 52 [**T. finum*; OD]. Fore wing as in *Drahania*, but costal area broader, SC much shorter, and MA with a short fork. *Perm.*, Europe (Czechoslovakia).

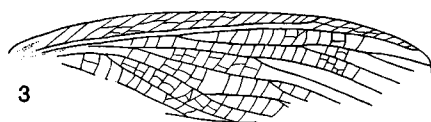
Tyrannopterum KUKALOVÁ, 1964c, p. 70 [**T. minimum*; OD]. Similar to *Cerasopterum* but much smaller; fore wing with branches of RS directed



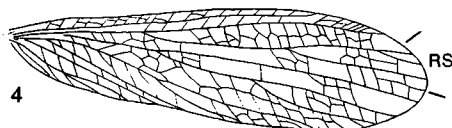
Alicula



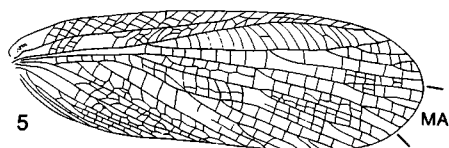
Depressopterum



Drahania



Cerasopterum



Donopterum

FIG. 64. Liomopteridae (p. 109).

anteriorly, away from M. *Perm.*, Europe (Czechoslovakia).

Family PHENOPTERIDAE Carpenter, 1950

[Phenopteridae CARPENTER, 1950, p. 204]

Related to Liomopteridae. Fore wing membranous, delicate; vein SC terminating on margin well beyond midwing; costal area with numerous, oblique veinlets; RS arising before midwing, with a few branches; M forked at about level of origin of RS, rarely with three branches; CUA with a basal branch (CUA2) and a distal branch dividing near wing margin; crossveins numerous, irregular,

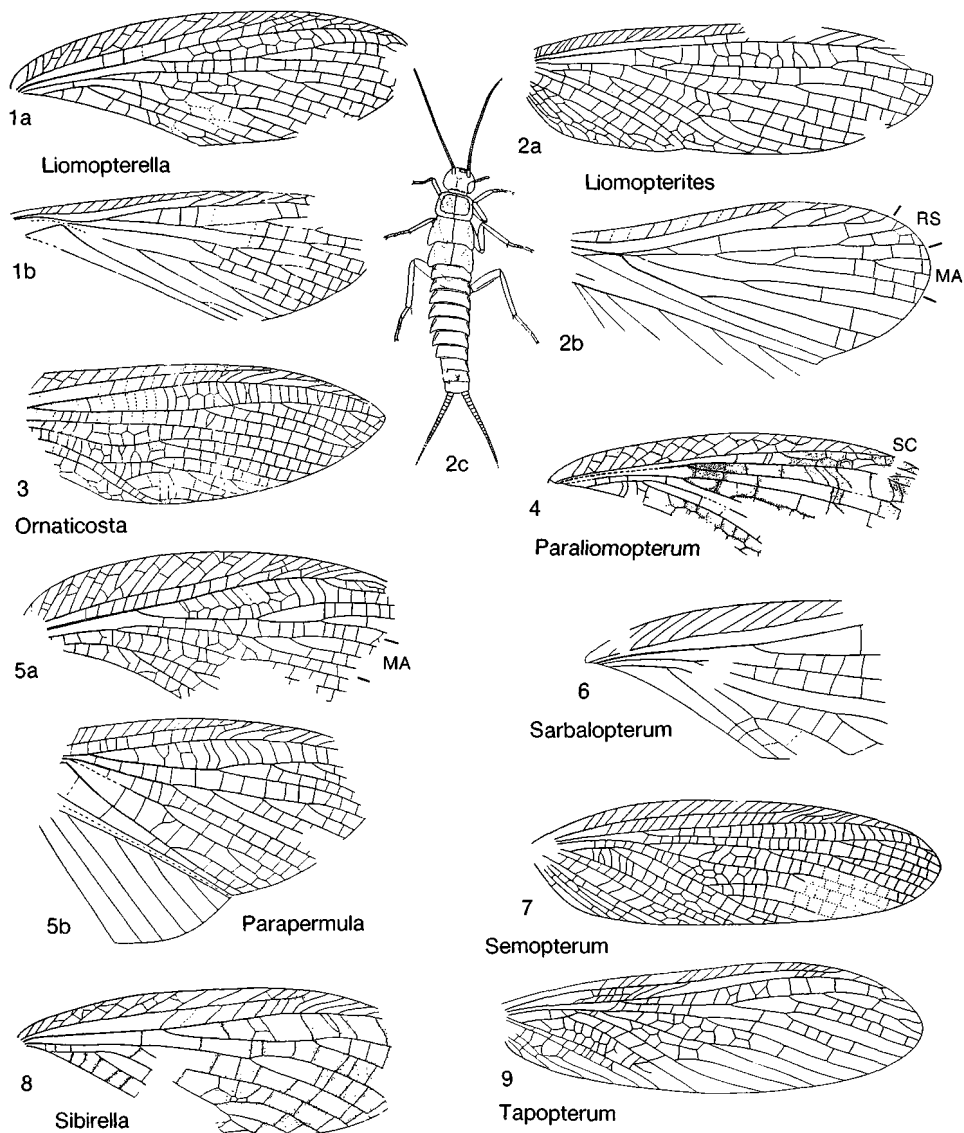


FIG. 65. Liomopteridae (p. 109–111).

forming irregular reticulation over most of wing. Hind wing with RS, M, and CUA arising from single stem near wing base; CUA branched; anal area well developed. Body structure unknown. *Perm.*

Phenopterum CARPENTER, 1950, p. 205, *nom. subst. pro Lepium* SELLARDS, 1909, p. 156, *non* ENDERLEIN, 1906 [*Lepium elongatum* SELLARDS, 1909, p. 156; OD]. RS with 3 branches; fork of M slightly basal of origin of RS. *Perm.*, USA (Kan-

sas).—FIG. 66,3. **P. elongatum* (SELLARDS); *a*, fore and *b*, hind wings, $\times 4$ (Carpenter, 1950). **Brunia** KUKALOVÁ, 1964c, p. 72 [**B. raketa*; OD]. Similar to *Phenopterum*, but wings more slender and RS with only 2 branches; costal area very narrow. *Perm.*, Europe (Czechoslovakia).—FIG. 66,2. **B. raketa*; fore wing, $\times 4$ (Kukalová, 1964c).

Chlumia KUKALOVÁ, 1964c, p. 77 [**C. parva*; OD]. Fore wing as in *Brunia* but much broader. *Perm.*, Europe (Czechoslovakia).

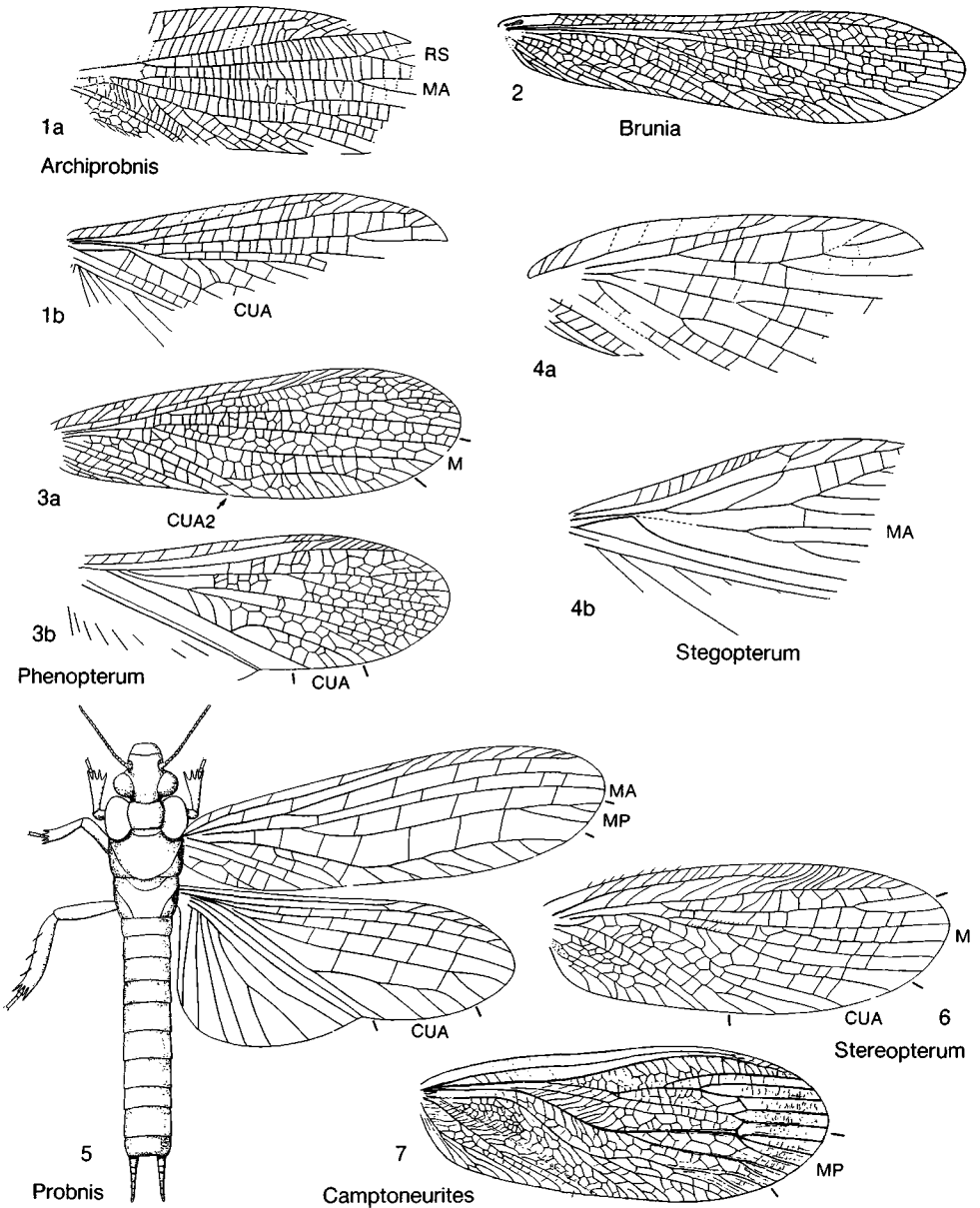


FIG. 66. Phenopteridae, Probnidae, Stegopteridae, Stereopteridae, Camptoneuritidae, and Archiprobnidae (p. 112–115).

Family HAVLATIIDAE
Kukalová, 1964

[Havlatiidae KUKALOVÁ, 1964c, p. 83]

Similar to Liomopteridae, but fore wing markedly broader distally and crossveins less numerous. *Perm.*

Havlatia KUKALOVÁ, 1964c, p. 84 [**H. annae*; OD]. Costal and subcostal areas very narrow; SC extending nearly to wing apex. *Perm.*, Europe (Czechoslovakia). — FIG. 67,3. **H. annae*; fore wing, ×8 (Kukalová, 1964c).

Ventopterum KUKALOVÁ, 1964c, p. 87 [**V. rapidum*; OD]. Little-known genus. Fore wing as in *Zephyropterum*, but subcostal area broader; cross-

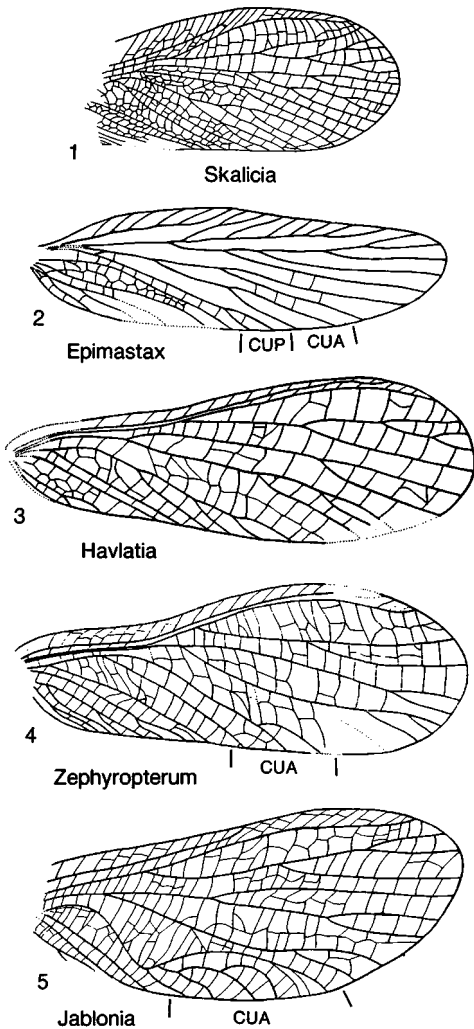


FIG. 67. Havlatiidae, Jabloniidae, Skaliciidae, and Epimastacidae (p. 113–115).

veins more irregular. *Perm.*, Europe (Czechoslovakia).

Zephyropterum KUKALOVÁ, 1964c, p. 85 [**Z. lentum*; OD]. Fore wing as in *Havlatia*, but costal margin more concave before midwing; CUA with 2 long branches. *Perm.*, Europe (Czechoslovakia).—FIG. 67,4. **Z. lentum*; fore wing, $\times 6.5$ (Kukalová, 1964c).

Family JABLONIIDAE Kukalová, 1964

[Jabloniidae KUKALOVÁ, 1964c, p. 81]

Small species, related to the Phenopteridae, but fore wing very broad, with strongly convex hind margin; vein CUA markedly

sigmoidal, its terminal branches almost semi-circular. *Perm.*

Jablonia KUKALOVÁ, 1964c, p. 82 [**J. aestiva*; OD]. Anterior wing margin almost straight; both RS and MA with 3 branches. *Perm.*, Europe (Czechoslovakia).—FIG. 67,5. **J. aestiva*; fore wing, $\times 10$ (Kukalová, 1964c).

Family SKALICIIDAE Kukalová, 1964

[Skaliciidae KUKALOVÁ, 1964c, p. 88]

Fore wing slightly coriaceous, with covering of fine hairs and with prominent setae distally; vein SC terminating well before apex; RS arising near midwing, with several terminal branches; MA and MP terminating near wing apex; CUA2 with long fork; cross-veins reticulate in distal part of wing only. *Perm.*

Skalicia KUKALOVÁ, 1964c, p. 89 [**S. rara*; OD]. Fore wing very broad distally; apex rounded. *Perm.*, Europe (Czechoslovakia).—FIG. 67,1. **S. rara*; fore wing, $\times 3.5$ (Kukalová, 1964c).

Doubravia KUKALOVÁ, 1964c, p. 90 [**D. annosa*; OD]. Little-known genus. Fore wing apparently long and slender. [Family assignment doubtful.] *Perm.*, Europe (Czechoslovakia).

Family PROBNIDAE Sellards, 1909

[*nom. correct.* CARPENTER, herein, *pro* Probnisidae SELLARDS, 1909, p. 159]

Related to Lemmatophoridae. Fore wing coriaceous, granular in texture; costal area narrow; vein R extending nearly to wing apex; RS unbranched; MA and MP separating at about level of origin of RS, their branching very variable; CUA1 producing variable number of arched branches along posterior margin of wing; CUA2 usually unbranched; 1A unbranched. Hind wing membranous but with wrinkles; costal space narrower than in fore wing; RS arising almost at base of wing, unbranched; CUA1 as in fore wing but with longer branches; deep indentation of hind margin at end of CUP; anal fan well developed, with 6 anal veins. Head small, eyes prominent; antennae rather short and robust; prothorax with small lateral lobes, without venation; legs of moderate length; tarsi three-segmented; abdomen robust; cerci short; ovipositor apparently small. CARPENTER, 1943a. *Perm.*

Probnis SELLARDS, 1909, p. 159 [**P. speciosa*; SD TILLYARD, 1937c, p. 415] [= *Espira* SELLARDS, 1909, p. 160 (type, *E. obscura*); *Stoichus* SELLARDS, 1909, p. 160 (type, *S. elegans*); *Stinus* SELLARDS, 1909, p. 161 (type, *S. breve-cubitalis*)]. Fore wing: SC terminating at midwing; R with several veinlets from R to costal margin beyond SC; crossveins straight, widely separated over most of wing; CUA1 extending nearly to wing apex. *Perm.*, USA (Kansas).—FIG. 66,5. **P. speciosa*; whole insect, $\times 4$ (Carpenter, 1943a).

Family STEGOPTERIDAE Sharov, 1961

[Stegopteridae SHAROV, 1961d, p. 220]

Similar to Liomopteridae, but fore wing more coriaceous and rough. *Perm.*

Stegopterum SHAROV, 1961d, p. 221 [**S. hirtum*; OD]. Fore wing with few crossveins; no cells. Hind wing with MA free from RS. *Perm.*, USSR (Asian RSFSR).—FIG. 66,4. **S. hirtum*; *a*, fore and *b*, hind wings, $\times 4.4$ (Sharov, 1961d).

Family STEREOPTERIDAE Carpenter, 1950

[Stereopteridae CARPENTER, 1950, p. 201]

Related to Liomopteridae. Fore wing slightly coriaceous, with few patches of conspicuous setae but without covering of microtrichia; vein SC terminating on margin beyond midwing; costal area narrow, with numerous oblique veinlets; RS arising before midwing; CUA anastomosed with stem of M for short distance; crossveins numerous, irregular. Hind wing and body structure little known. CARPENTER, 1966. *Perm.*

Stereopterum CARPENTER, 1950, p. 202 [**S. rotundum*; OD]. M forking at level of origin of RS; row of stout setae along basal third of costal margin; smaller setae or branches of M near midwing. CARPENTER, 1966. *Perm.*, USA (Kansas).—FIG. 66,6. **S. rotundum*; fore wing, $\times 4$ (Carpenter, 1950).

Family EPIMASTACIDAE Martynov, 1928

[Epimastacidae MARTYNOV, 1928b, p. 63]

Fore wing narrowed beyond midwing; vein SC remote from wing margin and terminating on costal margin near midwing; RS arising before midwing and with several long branches; CUA anastomosed for a short interval with M basally before forking. *Perm.*

Epimastax MARTYNOV, 1928b, p. 63 [**E. parvulus*; OD]. Fore wing: R with several branches to the costal margin of wing; RS with 5 terminal branches. *Perm.*, USSR (European RSFSR), Europe (Czechoslovakia).—FIG. 67,2. *E. celer* KUKALOVÁ, 1965; fore wing, $\times 8$ (Kukalová, 1965).

Family CAMPTONEURITIDAE Martynov, 1931

[Camptoneuritidae MARTYNOV, 1931a, p. 98, *nom. subst. pro* Camptoneuridae MARTYNOV, 1928b, p. 53]

Related to Phenopteridae. Fore wing with narrow costal area; vein RS arising before midwing; crossveins forming strong, irregular network; distal branches of RS, MA, and MP straight and parallel, without crossveins. Hind wing unknown. *Perm.*

Camptoneurites MARTYNOV, 1931a, p. 98, *nom. subst. pro* *Camptoneura* MARTYNOV, 1928b, p. 53, *non* AGASSIZ, 1846 [**Camptoneura reticulata* MARTYNOV, 1928b, p. 35; OD]. Fore wing with costal margin slightly concave; 2 rows of irregular cells between MP and CUA. *Perm.*, USSR (European RSFSR).—FIG. 66,7. **C. reticulata* (MARTYNOV); fore wing, $\times 3.5$ (Martynov, 1928b).

Family ARCHIPROBNIDAE Sharov, 1961

[*nom. correct.* CARPENTER, herein, *pro* Archiprobnisidae SHAROV, 1961d, p. 185]

Fore wing with main veins more widely spaced than in Idelliidae; crossveins irregular but not forming distinct reticulation except in and near anal areas; veins RS and MA arising at same level close to base of wing. Hind wing little known; CUA sharply bent near base, as in some Liomopteridae. *Perm.*

Archiprobnis SHAROV, 1961d, p. 186 [**A. repens*; OD]. Fore wing broadly oval with rounded apex. *Perm.*, USSR (Asian RSFSR).—FIG. 66,1. **A. repens*; *a*, fore and *b*, hind wings, $\times 2.5$ (Sharov, 1961d).

Family PROTEMBIIDAE Tillyard, 1937

[Protembiidae TILLYARD, 1937b, p. 243] [= *Telactinopterygidae* CARPENTER, 1943a, p. 78]

Related to Phenopteridae. Fore wing slightly coriaceous; distal parts of veins RS, MA, MP bordered by delicate lines on each side; SC terminating on costal margin; costal space very narrow; RS arising at midwing.

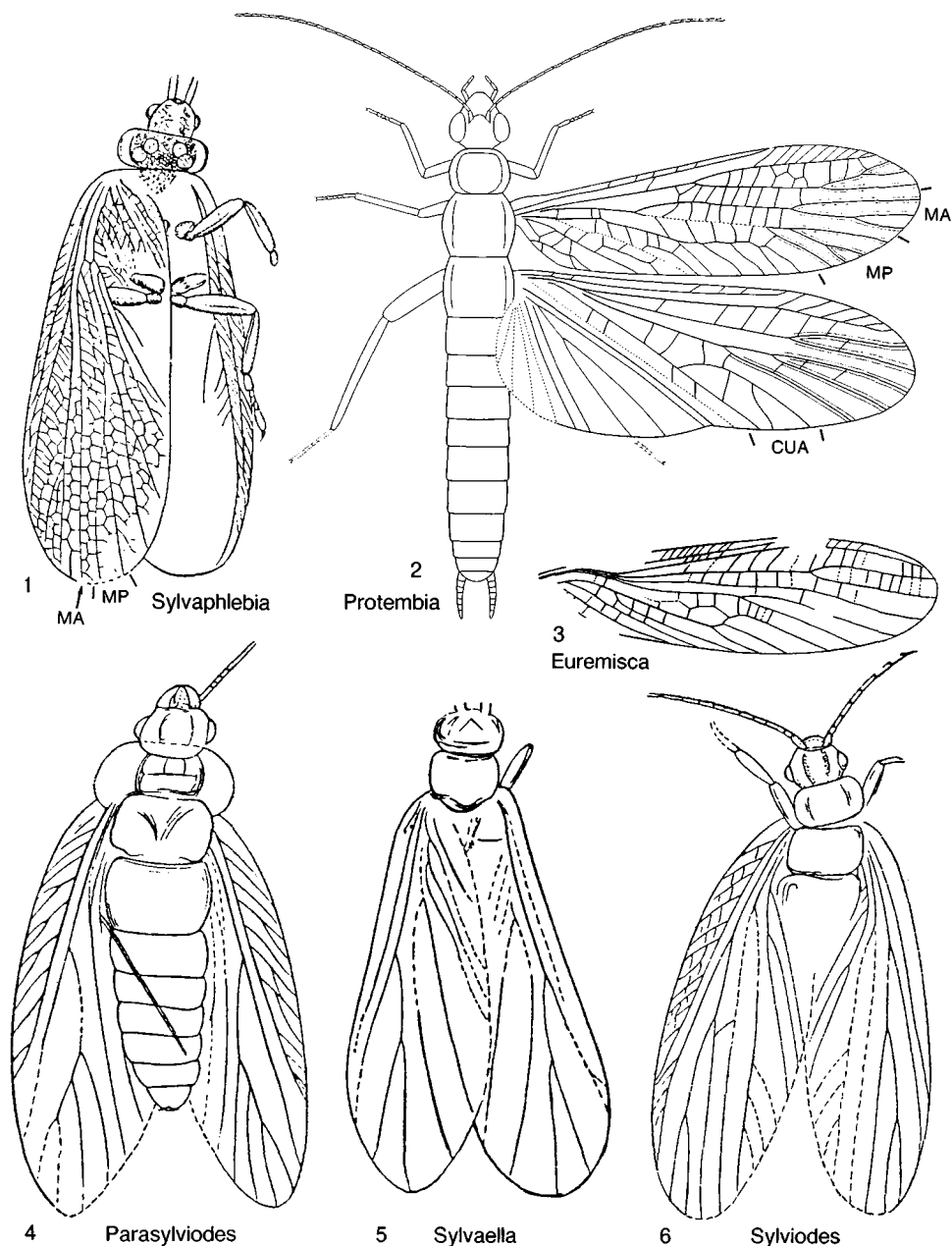


FIG. 68. Protombiidae, Euremisciidae, and Sylvaphlebiidae (p. 117).

branched; M forked before origin of RS; CUA without definite CUA2, having several distal branches; crossveins few, unequally distributed. Hind wing with RS arising near wing

base; M forking slightly beyond midwing; CUA forked distally; anal lobe well developed. Antennae long; head small, with large eyes; prothorax with small disc; hind legs

longer than others, all with five tarsomeres; cerci short but distinct. CARPENTER, 1950. *Perm.*

Protombia TILLYARD, 1937b, p. 245 [**P. permiana*; OD] [= *Telactinopteryx* TILLYARD, 1937c, p. 422 (type, *T. striatipennis*)]. Fore wing: RS with 3 terminal branches; several veinlets between R and margin beyond end of SC; a few cells formed between R and RS. *Perm.*, USA (Kansas).—FIG. 68,2. **P. permiana*; whole insect, $\times 6.5$ (Carpenter, 1950).

Family EUREMISCIDAE Zalessky, 1951

[Euremiscidae ZALESSKY, 1951b, p. 81]

Related to Phenopteridae, but fore wing without network of crossveins. *Perm.*

Euremisca ZALESSKY, 1951b, p. 82 [**E. splendens*; OD]. Slender fore wing, with very narrow costal space. *Perm.*, USSR (Asian RSFSR).—FIG. 68,3. **E. splendens*; fore wing, $\times 3.5$ (Sharov, 1962c).

Family SYLVAPHLEBIIDAE Martynov, 1940

[Sylvaphlebiidae MARTYNOV, 1940, p. 18] [= *Sylvaelidae* MARTYNOV, 1940, p. 26; *Sylvioididae* MARTYNOV, 1940, p. 23]

Related to Phenopteridae; fore wing coriaceous, without hairs; veins MA and MP long, with few branches; prothorax short and broad, with small or large membranous lobes. *Perm.*

Sylvaphlebia MARTYNOV, 1940, p. 18 [**S. tuberculata*; OD] [= *Biarmopteron* ZALESSKY, 1953c, p. 42 (type, *B. protoblattoides*)]. Fore wing little known; 2 rows of cells between MA and MP. *Perm.*, USSR (Asian RSFSR).—FIG. 68,1. **S. tuberculata*; fore wing and part of body, $\times 3.2$ (Sharov, 1962c).

Parasyliodes MARTYNOV, 1940, p. 23 [**P. tetracladus*; OD]. Fore wing with very broad costal area; RS arising near midwing; large lobes on prothorax. *Perm.*, USSR (Asian RSFSR).—FIG. 68,4. **P. tetracladus*; fore wings and part of body, $\times 3.4$ (Sharov, 1962c).

Sylvaella MARTYNOV, 1940, p. 55 [**S. paurovenosa*; OD]. Fore wing little known; RS arising at midwing but with fewer branches than in *Parasyliodes*; costal area narrow. *Perm.*, USSR (Asian RSFSR).—FIG. 68,5. **S. paurovenosa*; fore wings and part of body, $\times 6$ (Sharov, 1962c).

Sylviodes MARTYNOV, 1940, p. 23 [**S. perloides*;

OD] [= *Biarmopterites* ZALESSKY, 1953c, p. 45 (type, *B. reticulatus*)]. Fore wing little known; costal space much broader than in *Sylvaphlebia*. *Perm.*, USSR (Asian RSFSR).—FIG. 68,6. **S. perloides*; fore wing and part of body, $\times 1.6$ (Sharov, 1962c).

Family CHELOPTERIDAE Carpenter, 1950

[Chelopteridae CARPENTER, 1950, p. 198]

Related to the Liomopteridae. Fore wing membranous or only slightly coriaceous; hairs absent; costal area broad; subcostal area very narrow in proximal region; crossveins numerous, forming coarse reticulation between veins CUA1 and CUA2 and in anal area; crossveins between R and RS very slanted and parallel. Hind wing with RS arising nearer base than in Liomopteridae; CUA unbranched; crossveins forming coarse network in distal and cubital areas of wing. Antennae long, but with fewer segments than in Liomopteridae; head broad; pronotum with flat, membranous marginal area, lacking hairs; tarsi five-segmented; cerci of male modified to form forceps; female with prominent ovipositor. *Perm.*

Chelopteron CARPENTER, 1950, p. 199 [**C. peregrinum*; OD]. Fore wing with SC approaching costal margin at about midwing; main fork of M just proximal to origin of RS; MA and MP about equally developed. *Perm.*, USA (Kansas).—FIG. 69,4. **C. peregrinum*; complete insect, male, $\times 3.4$ (Carpenter, 1950).

Family DEMOPTERIDAE Carpenter, 1950

[Demopteridae CARPENTER, 1950, p. 203]

Related to Liomopteridae. Fore wing with membrane strongly coriaceous; costal margin slightly concave; costal area narrow, about as wide as subcostal; CUA branched only in its distal half. Hind wing unknown. *Perm.*

Demopteron CARPENTER, 1950, p. 203 [**D. gracile*; OD]. Fore wing slender; SC with series of stout spines along its proximal part; MP much more extensively developed than MA. *Perm.*, USA (Kansas).—FIG. 69,5. **D. gracile*; fore wing, $\times 2.7$ (Carpenter, 1950).

Family ATACTOPHLEBIIDAE

Martynov, 1930

[Atactophlebiidae MARTYNOV, 1930c, p. 952]

Fore wing with costal area slightly broader than subcostal; crossveins tending to be irregularly shaped; two rows of irregular cells between veins R and anterior branch of RS. Hind wing little known, with broad costal area and very narrow subcostal. Branching of veins of both wings highly variable. Ovipositor small but distinct. *Perm.*

Atactophlebia MARTYNOV, 1928b, p. 51 [**A. termitoides*; OD]. Fore wing with area of RS narrow; RS with few branches. *Perm.*, USSR (Asian RSFSR).—FIG. 69,3. **A. termitoides*; *a*, fore and *b*, hind wings, $\times 1.4$ (Martynov, 1930c).

Family MEGAKHOSARIDAE

Sharov, 1961

[Megakhosaridae SHAROV, 1961d, p. 178]

Fore wing long, slender; costal area very narrow; both veins MA and MP apparently present; series of strong crossveins between CUP and most posterior branch of CUA, more basal ones being abruptly curved at junction with CUP; crossveins over rest of wing numerous and irregular. Hind wing with MA anastomosed for short distance with RS. *Perm.*

Megakhosara MARTYNOV, 1937b, p. 31 [**M. fasciipennis*; OD] [= *Syndesmothora* MARTYNOV, 1937b, p. 41 (type, *S. composita*)]. Fore wing with RS dichotomously branched; no anastomosis between main veins; both fore and hind wings with irregular crossveins. *Perm.*, USSR (Asian RSFSR).—FIG. 69,1a. *M. dilucida* SHAROV; fore wing, $\times 1.8$ (Sharov, 1961e).—FIG. 69,1b. **M. fasciipennis*; hind wing, $\times 1.5$ (Martynov, 1937b).

Megakhosarella SHAROV, 1961d, p. 182 [**M. regressa*; OD]. Little-known fore wing; MA and RS anastomosed for very short distance. *Perm.*, USSR (Asian RSFSR).—FIG. 69,2. **M. regressa*; fore wing, $\times 3$ (Sharov, 1961d).

Family IDELIIDAE Zalesky, 1929

[Ideliidae M. D. ZALESSKY, 1929, p. 21] [= *Rachimentomidae* G. M. ZALESSKY, 1939, p. 55]

Fore wing with broad costal area having numerous slanting veinlets, usually forming reticulation; no anastomosis of veins MA and RS; RS usually with more than three branches;

stem CU formed as in Liomopteridae but CUA more elaborately branched; CUP not so strongly developed as in Liomopteridae; crossveins numerous, usually forming reticulation. Hind wing little known, apparently similar to that of Liomopteridae. Antennae prominent; pronotum with broad, coriaceous expansions; cerci probably well developed; long ovipositor present. *U. Carb.*—*Perm.*

Stenaropodites MARTYNOV, 1928b, p. 47 [**S. reticulata*; OD] [= *Idelia* ZALESSKY, 1929, p. 4 (type, *I. permiakovi*)]. Fore wing with fine network of cells, resembling archidictyon; costal margin weakly curved; CUA2 strongly sigmoidal. *Perm.*, USSR (Asian RSFSR).—FIG. 70,6. *S. permiakovi* (ZALESSKY); fore wing, $\times 1.2$ (Zalesky, 1929).

Aenigmidelia SHAROV, 1961d, p. 175 [**A. incredibilis*; OD]. Fore wing oval, with strongly curved costal margin; SC with basal branch, resembling submarginal costa; main branch of SC coalesced with R basally; crossveins as in *Archidelia*; M forking at level of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 70,8. **A. incredibilis*; fore wing, $\times 1$ (Sharov, 1961d).

Archidelia SHAROV, 1961d, p. 172 [**A. elongata*; OD]. Fore wing with strongly convex costal margin; crossveins forming irregular reticulation, much finer than that in *Kortshakolia*, but no archidictyon; costal veinlets branched; M forking before origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 70,2. **A. elongata*; *a*, fore and *b*, hind wings, $\times 1$ (Sharov, 1961d).

Kortshakolia SHAROV, 1961d, p. 171 [**K. ideliformis*; OD]. Little-known genus, based on fragment of fore wing, with costal margin shaped as in *Stenaropodites*; RS with at least 4 branches; MA directed anteriorly at its origin toward R before curving distally. *U. Carb.*, USSR (Asian RSFSR).—FIG. 70,1. **K. ideliformis*; fore wing, $\times 1.6$ (Sharov, 1961d).

Metidelia MARTYNOV, 1937b, p. 23 [**M. kargalensis*; OD]. Fore wing with costal area narrower than in *Stenaropodites*; crossveins forming nearly regular network, not so fine as archidictyon. *Perm.*, USSR (Asian RSFSR).—FIG. 70,3. **M. kargalensis*; fore wing, $\times 1.8$ (Martynov, 1937b).

Paridelia SHAROV, 1961d, p. 175 [**P. pusilla*; OD]. Fore wing with costal margin as in *Stenaropodites*; RS arising near midwing, with 2 branches; MA with 2 branches, MP with 3. SHAROV, 1962c. *Perm.*, USSR (Asian RSFSR).—FIG. 70,9. **P. pusilla*; fore wing, $\times 1.8$ (Sharov, 1961d).

Rachimentomon ZALESSKY, 1939, p. 56 [**R. reticulatum*; OD]. Little-known genus. Costal margin of fore wing nearly straight; fine archidictyon present; venation little known; pronotal disc large; ovipositor well developed, nearly half as long as

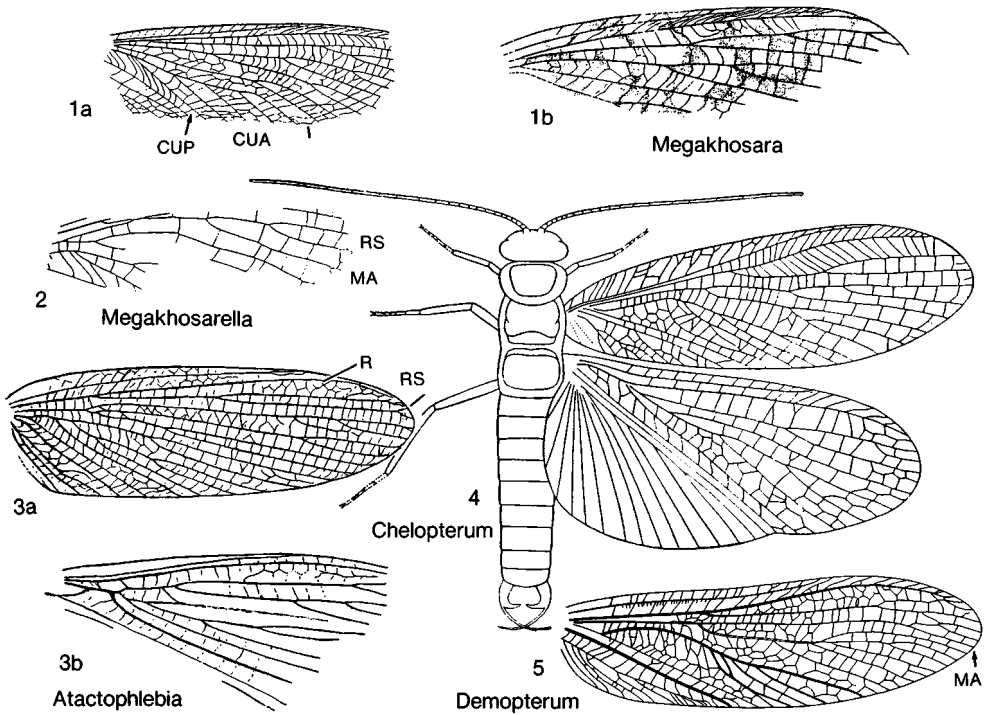


FIG. 69. Chelopteridae, Demopteridae, Atactophlebiidae, and Megakhosaridae (p. 117-118).

abdomen. *Perm.*, USSR (Asian RSFSR).—FIG. 70,5. **R. reticulatum*; whole specimen, $\times 2$ (Zalessky, 1939).
Sylvidelia MARTYNOV, 1940, p. 19 [**S. latipennis*; OD]. Fore wing with archedictyon as in *Stenaropodites* but with more strongly curved costal margin, more branches to RS, and without sigmoidal CUA2. *Perm.*, USSR (Asian RSFSR).—FIG. 70,7. **S. latipennis*; fore wing, $\times 1.4$ (Martynov, 1940).

Family EURYPTILONIDAE
Martynov, 1940

[Euryptilonidae MARTYNOV, 1940, p. 16]

Fore wing oval, with narrow costal area; vein RS arising near midwing; CUA arising from stem of CU at base of wing and coalescing with M for short distance; CUA with several long, parallel branches. Pronotal disc well developed; legs adapted for running, spinous. *Perm.*

Euryptilon MARTYNOV, 1940, p. 16 [**E. blattoides*; OD]. Fore wing with subcostal space much broader than costal; M sigmoidally curved. *Perm.*,

USSR (Asian RSFSR).—FIG. 70,10. **E. blattoides*; fore wing, $\times 5.5$ (Martynov, 1940).

Family NARKEMIDAE
Handlirsch, 1911

[Narkemidae HANDLIRSCH, 1911, p. 321]

Little-known family. Vein SC of fore wing terminating on R at level of midwing; RS with numerous parallel branches ending on wing apex; M apparently with a single distal fork; CUA apparently extensively branched; anal area unknown. *U. Carb.*

Narkema HANDLIRSCH, 1911, p. 322 [**N. taeniatum*; OD]. Little-known genus, based on incomplete fore wing. RS with at least 5 terminal branches. Wing with 7 narrow, dark transverse bands. SHAROV, 1961e; PINTO & ORNELLAS, 1978c. *U. Carb.*

Family HERBSTIALIDAE
Schmidt, 1953

[Herbstialidae SCHMIDT, 1953, p. 165]

Related to Cacurgidae (probably synonymous). Fore wing with reticulation of cross-

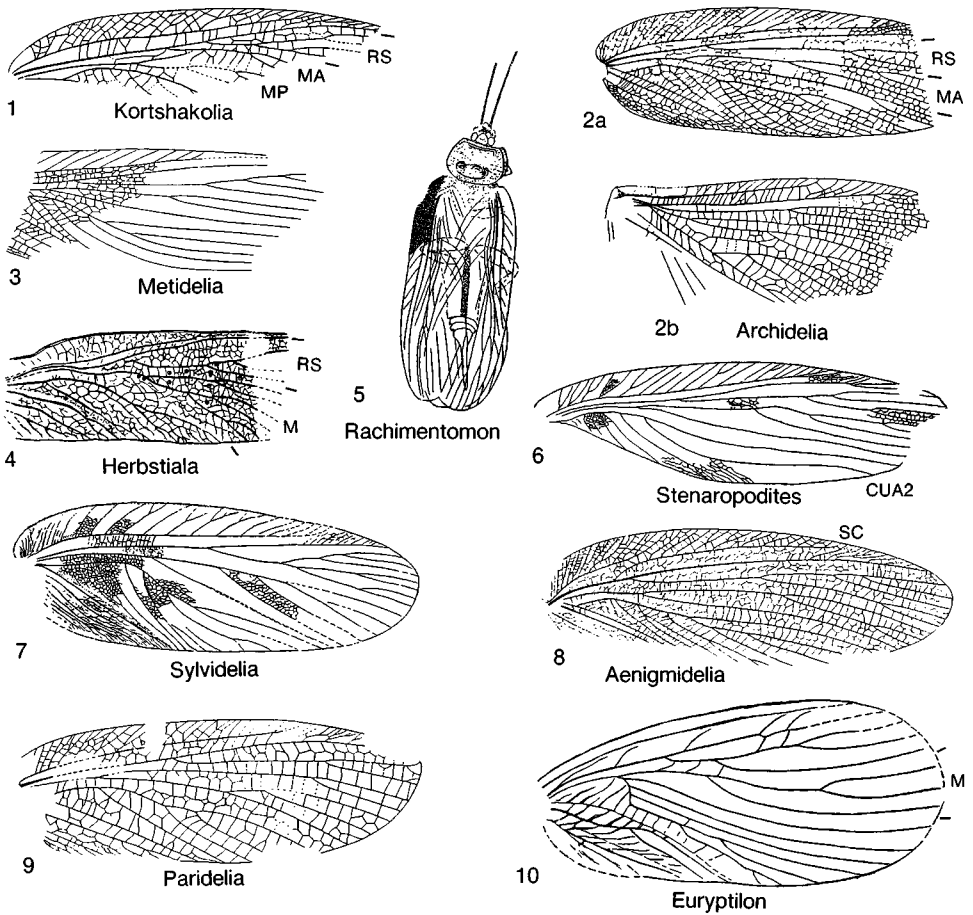


FIG. 70. Ideliidae, Euryptilonidae, and Herbstialidae (p. 118–120).

veins over entire wing surface; cuticular spots as in *Cacurgidae*. *U. Carb.*

Herbstiala SCHMIDT, 1953, p. 153 [**H. herbsti*; OD]. Origin of RS at about same level as first fork of M. [Placed in order Protocicadida.] *U. Carb.*, Europe (Germany).—FIG. 70,4. **H. herbsti*; fore wing, $\times 1.5$ (Schmidt, 1953).

Family CACURGIDAE
Handlirsch, 1911

[Cacurgidae HANDLIRSCH, 1911, p. 324]

Apparently related to *Omalidae*. Fore wing oval, apex broadly rounded; vein SC nearly straight, terminating on wing margin beyond midwing; RS arising well before midwing; MA apparently absent; CUA anastomosed with MP basally, diverging before level of origin of RS, then anastomosed with CUP1;

crossveins numerous. Hind wing unknown. *U. Carb.*

Cacurgus HANDLIRSCH, 1911, p. 324 [**C. spilopterus*; OD]. Little-known genus. Fore wing broadest at level of midwing; R with several oblique veinlets leading to fore margin of wing; crossveins forming a coarse network over most of wing except costal area; wing membrane with many circular thickenings. *U. Carb.*, USA (Illinois).—FIG. 71,6. **C. spilopterus*; fore wing, $\times 1$ (Handlirsch, 1911).

Heterologus CARPENTER, 1944, p. 14 [**H. langfordorum*; OD]. Fore wing as in *Cacurgus*, but costal area narrower and more tapering and no network of crossveins. *U. Carb.*, USA (Illinois).—FIG. 71,8. **H. langfordorum*; fore wing, $\times 3.5$ (Carpenter, 1944).

Protodictyon MELANDER, 1903, p. 196 [**P. pulchripenne*; OD]. Similar to *Heterologus*, but crossveins of fore wing forming a coarse reticulation in several areas of the wing; RS remote from M.

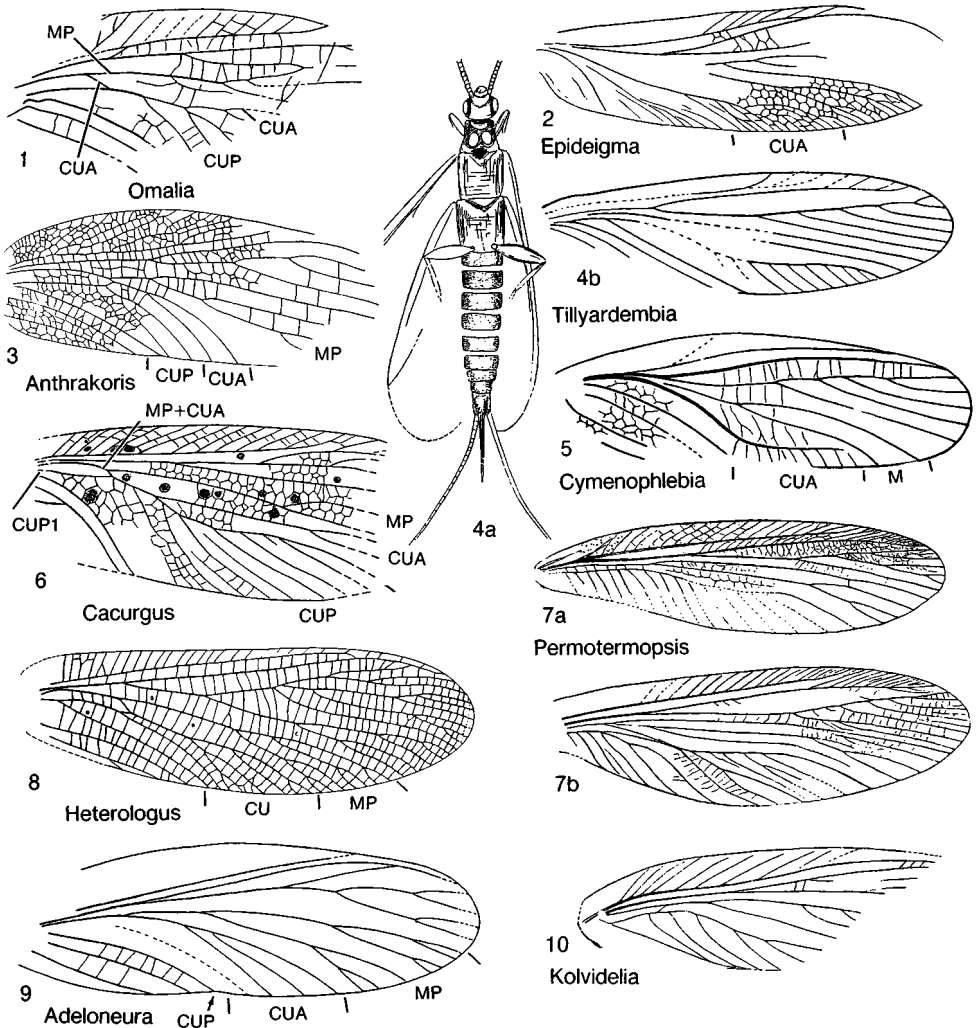


FIG. 71. Cacurgidae, Omaliidae, Tillyardembiidae, Epideigmatidae, Permotermopsidae, and Adelonuridae (p. 120-124).

basally. [Placed by MELANDER in Hemeristina group of Palaeodictyoptera.] *U. Carb.*, USA (Illinois).

Spilomastax HANDLIIRSCH, 1911, p. 326 [**S. oligoneurus*; OD]. Apparently similar to *Cacurgus*, but M forked before level of origin of RS. *U. Carb.*, USA (Illinois).

Family OMALIIDAE Handlirsch, 1906

[Omaliidae HANDLIIRSCH, 1906b, p. 145]

Related to Cacurgidae, but fore wing without circular thickenings and with vein RS less developed than MP; CUA coalesced

with MP at base. Hind wing unknown. *U. Carb.*

Omalia VAN BENEDEN & COEMANS, 1867, p. 384 [**O. macroptera*; OD] [= *Palaeomastax* HANDLIIRSCH, 1904a, p. 16 (type, *P. carbonis*)]. Little-known fore wing; costal margin strongly curved and costal area broad; first fork of CUP beyond anastomosis with CUA. *U. Carb.*, Europe (Belgium). — FIG. 71, 1. **O. macroptera*; fore wing, $\times 1$ (Pruvost, 1930).

Anthrakoris RICHARDSON, 1956, p. 36 [**A. aethereus*; OD]. Related to *Omalia*, but costal margin of fore wing more strongly curved and CUA with only 2 branches. *U. Carb.*, USA (Illinois). —

FIG. 71,3. **A. aetherius*; fore wing, $\times 5$ (Carpenter, new).

Coselia BOLTON, 1922, p. 81 [**C. palmiformis*; OD]. Little-known genus, based on small fragment of wing. [Type of family Coseliidae BOLTON.] PRUVOST, 1930. *U. Carb.*, England.

Family GERARIDAE Scudder, 1885

[*nom. correct.* HANDLIRSCH, 1906a, p. 701, *pro* Gerarina SCUDDER, 1885b, p. 762] [=Schenaropodidae HANDLIRSCH, 1906b, p. 141; Genopterygidae RICHARDSON, 1956, p. 41]

Fore wing membranous; costal area of uniform width for most of its length, with many crossveins, mostly unbranched; vein SC terminating on C; R without branches; RS commonly anastomosed with M for a short distance or connected to it by a short crossvein; CUA strongly developed, arising from the combined bases of R and M; CUP forked. Hind wing with the costal area more narrow than in the fore wing; RS arising very near the wing base; anal area little known but apparently not enlarged. Head relatively small, with long, filamentous antennae; prothorax long, slender anteriorly but broad posteriorly, bearing prominent spines; legs cursorial, slender, with five tarsal segments. Abdomen very little known. BURNHAM, 1983. *U. Carb.*

Gerarus SCUDDER, 1885d, p. 344 [**G. vetus*; OD] [=Genopteryx SCUDDER, 1885d, p. 327 (type, *G. constricta*); *Sthenaropoda* BRONGNIART, 1885a, p. 59 (type, *S. fischeri*); *Archaeacridites* MEUNIER, 1909c, p. 39 (type, *A. bruesi*); *Rossites* RICHARDSON, 1956, p. 44 (type, *R. inopinus*)]. Moderately large species. Fore wing with RS branched 2 or 3 times; M with 4 or 5 branches and either anastomosed for a short interval with RS or connected to it by a strong crossvein. BURNHAM, 1983. *U. Carb.*, USA (Illinois), Europe (France).—FIG. 72,3a. *G. bruesi* (MEUNIER); fore wing, $\times 1$ (Burnham, 1983).—FIG. 72,3b. *G. danielisi*; reconstruction, based on many specimens, $\times 0.7$ (Burnham, 1983).

Anepitidius HANDLIRSCH, 1911, p. 318 [**A. giraffa*; OD]. Little-known genus, based on wing and body fragments. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

Genentomum SCUDDER, 1885d, p. 329 [**G. validum*; OD]. Similar to *Gerarus*, but branches of M straight and parallel in fore wing; first fork of CUP very close to wing base. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

Gerarulus HANDLIRSCH, 1911, p. 316 [**G. radialis*; OD]. Little-known genus, based on wing frag-

ments; RS with not more than 4 branches. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

Nacekoma RICHARDSON, 1956, p. 33 [**N. rossae*; OD]. Fore wing similar to that of *Gerarus* but more slender; M not connected to RS by a thickened crossvein. BURNHAM, 1983. *U. Carb.*, USA (Illinois).—FIG. 72,2. **N. rossae*; fore wing, $\times 1.4$ (Carpenter, new).

Progenentomum HANDLIRSCH, 1906a, p. 701 [**P. carbonis*; OD]. Fore wings as in *Gerarus* but more pointed; SC shorter; RS with 4 main branches; branches of CUA nearly parallel. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

Family SPANIODERIDAE Handlirsch, 1906

[Spanioderidae HANDLIRSCH, 1906a, p. 695]

Fore wing coriaceous, with granular surface resembling that of Probnidae; costal margin only slightly curved; costal area narrow, with regular series of oblique, simple crossveins; vein SC terminating on R beyond midwing; RS arising near base; M flat or slightly concave, with several terminal branches; stem of CUA apparently anastomosed with base of M, diverging from M at about level of origin of RS, commonly with a series of long branches; CUP nearly straight; anal area with several veins; crossveins numerous, unbranched. Hind wing little known; remigium as in fore wing, but CUA strongly diverging away from M, its branches shorter than in fore wing; anal area unknown. Head small; prothorax elongate, without spines; legs slender, cursorial; abdomen little known; cerci unknown; ovipositor long. *U. Carb.*

Propteticus SCUDDER, 1885d, p. 334 [**P. infernus*; OD] [=Petromartus MELANDER, 1903, p. 191 (type, *P. indistinctus*); *Spaniodera* HANDLIRSCH, 1906a, p. 696 (type, *S. ambulans*); *Camptophlebia* HANDLIRSCH, 1906a, p. 698 (type, *Dictyoneura clarinervis* MELANDER, 1903); *Paracheliphlebia* HANDLIRSCH, 1906a, p. 699 (type, *Cheliphlebia extensa* MELANDER, 1903); *Metryia* HANDLIRSCH, 1906a, p. 700 (type, *M. analis*)]. Fore wing with vein R terminating just before wing apex; M with basal fork at about level of origin of RS, anterior branch with at least one fork; CUA with at least 4 to 7 branches. Hind wing narrower than fore wing. BURNHAM, 1986. *U. Carb.*, USA (Illinois).—FIG. 72,1. **P. infernus*; reconstruction, based on type and sev-

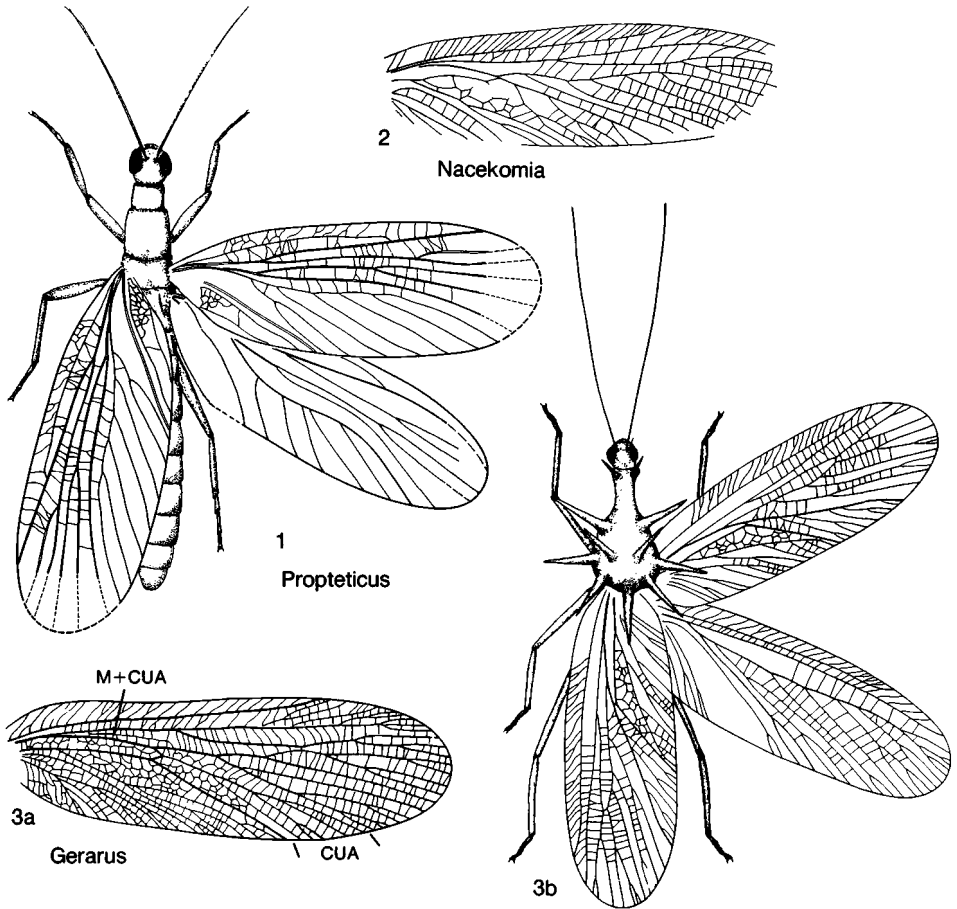


FIG. 72. Geraridae and Spanioderidae (p. 000).

eral additional specimens, $\times 1.3$ (Burnham, 1986).

Dieconeura SCUDDER, 1885d, p. 336 [**D. arcuata*; SD HANDLIRSCH, 1906a, p. 699]. Little-known genus, with fore wing more slender than in *Propteticus*; M with only one fork, anterior branch briefly anastomosed with branch of RS. [Family assignment doubtful.] *U. Carb.*, USA (Illinois).

Family APITHANIDAE

Handlirsch, 1911

[Apithanidae HANDLIRSCH, 1911, p. 320]

Related to Spanioderidae. Fore wing with vein R1 extending nearly to apex, a series of oblique veinlets between R1 and the costal margin beyond SC; RS arising in distal third of wing; prothorax shorter than in Spanioderidae. *U. Carb.*

Apithanus HANDLIRSCH, 1911, p. 320 [**A. jocularis*; OD]. Fore wing little known; M apparently forking at about midwing. *U. Carb.*, USA (Illinois).

Family TILLYARDEMBIIDAE

Zalessky, 1938

[Tillyardembiidae ZALESSKY, 1938, p. 64] [=Permocapniidae MARTYNOV, 1940, p. 52]

Fore wing little known; vein SC terminating on costa; RS pectinately branched; CUA with at least 4 parallel branches to apical and hind margins. Body slender, with prominent cerci and ovipositor. SHAROV, 1962c. *Perm.*

Tillyardemia ZALESSKY, 1937d, p. 847 [**T. biarmica*; OD] [=Permocapnia MARTYNOV, 1940, p.

52 (type, *P. brevipes*). RS with about 6 branches; M with deep fork. *Perm.*, USSR (Asian RSFSR). —FIG. 71,4. *T. brevipes* (MARTYNOV); *a*, complete specimen, $\times 4.5$ (Martynov, 1940); *b*, fore wing, $\times 4$ (Sharov, 1962c).

Family EPIDEIGMATIDAE Handlirsch, 1911

[Epeideigmatidae HANDLIRSCH, 1911, p. 356 [=Cymenophlebiidae PRUVOST, 1919, p. 128]

Fore wing coriaceous; costal area of moderate width; vein RS arising in basal third of wing, with several parallel branches; M apparently independent of RS; CUA branching only distally, forming many terminal branches along posterior border; anal area sharply marked by curved suture and very small; irregular reticulation over most of wing. Hind wing unknown. Pronotum elongate, oval. *U. Carb.*

Epeideigma HANDLIRSCH, 1911, p. 357 [**E. elegans*; OD]. Fore wing slender, length almost 4 times width; SC terminating on R. *U. Carb.*, USA (Illinois). —FIG. 71,2. **E. elegans*; fore wing, $\times 2$ (Handlirsch, 1911).

Cymenophlebia PRUVOST, 1919, p. 128 [**C. carpentieri*; OD]. Fore wing as in *Epeideigma*, but costal area wider; SC terminating on costa. *U. Carb.*, Europe (France). —FIG. 71,5. **C. carpentieri*; fore wing, $\times 3$ (Pruvost, 1919).

Family PERMOTERMOPSIDAE Martynov, 1937

[Permotermopsidae MARTYNOV, 1937b, p. 84]

Fore wing similar to that of Ideliidae, but basal part narrowed and vein CUA more remote distally from wing margin. Hind wing unknown. *Perm.*

Permotermopsis MARTYNOV, 1937b, p. 84 [**P. roseni*; OD]. Costal veinlets simple; crossveins forming delicate, irregular network. *Perm.*, USSR (European RSFSR). —FIG. 71,7a. **P. roseni*; fore wing, $\times 1.0$ (Martynov, 1937b). —FIG. 71,7b. *P. pectinata* MARTYNOV; fore wing, $\times 1.2$ (Martynov, 1937b).

Kolvidelia ZALESSKY, 1956a, p. 282 [**K. curta*; OD]. Little-known fore wing, with costal area broader than in *Permotermopsis*. [Family assignment doubtful.] *Perm.*, USSR (Asian RSFSR). —FIG. 71,10. **K. curta*; fore wing, $\times 2$ (Zalesky, 1956a).

Family ADELONEURIDAE Carpenter, 1938

[Adeloneuridae CARPENTER, 1938, p. 450]

Fore wing with very broad costal area having long, oblique veinlets; vein MA apparently absent; CUA anastomosed with MP proximally; distinct marginal indentation at end of CUP. *U. Carb.*

Adeloneura CARPENTER, 1938, p. 450 [**A. thompsoni*; OD]. Little-known fore wing, with very narrow subcostal space; CUA and MP separating at about level of origin of RS. *U. Carb.*, USA (Illinois). —FIG. 71,9. **A. thompsoni*; fore wing, $\times 1.6$ (Carpenter, 1938).

Family AENIGMATODIDAE Handlirsch, 1906

[Aenigmatodidae HANDLIRSCH, 1906a, p. 683]

Crossveins forming reticulated network over most of fore wing; vein MA apparently absent; CUA anastomosed with stem of MP, unbranched. *U. Carb.*

Aenigmatodes HANDLIRSCH, 1906a, p. 683 [**A. danielisi*; OD]. Little-known genus, based on fragment of fore wing; RS and MP with 3 distinct branches. *U. Carb.*, USA (Illinois).

Family STREPHOCLADIDAE Martynov, 1938

[Strephocladidae MARTYNOV, 1938b, p. 100]

Fore wing coriaceous; precostal area absent; vein SC well developed, extending to midwing or beyond, with several branches; RS arising before midwing; R ending well before apex, with several oblique branches to wing margin; RS with several long branches; M forked before origin of RS, anterior branch commonly touching RS or connected to it by a crossvein; CUA longitudinal, with several long branches; branches of RS, M, and CUA parallel and slightly sigmoidal; distinct furrow posterior to CUA; 1A close and parallel to CUP. Crossveins numerous and regularly arranged, an irregular network in costal area and between CUA and CUP and anal veins. Wing membrane with fine microtrichia between veins; prominent setae on most veins. Hind wing and body unknown. [The relationships of this family within the Protor-

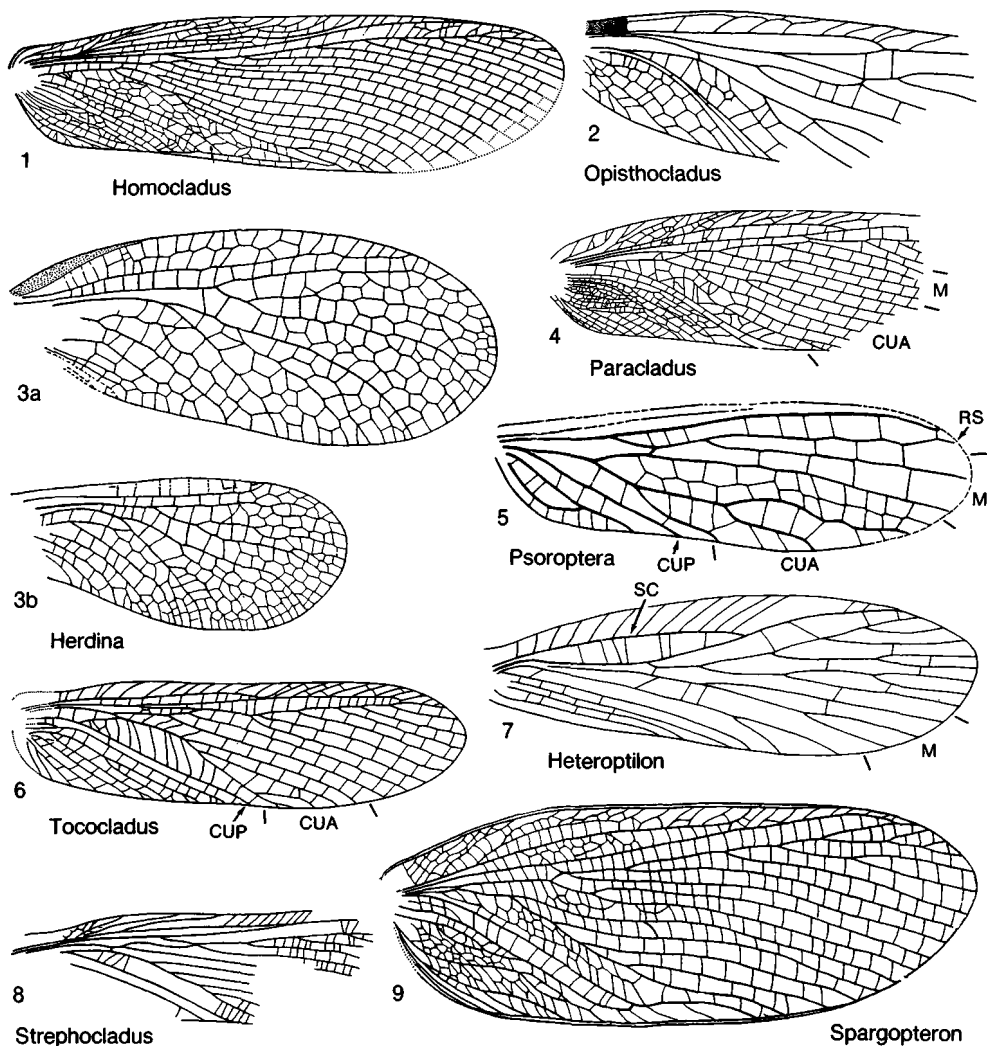


FIG. 73. Strephocladidae, Tococladidae, Heteroptilidae, Herdinidae, and Psoropteridae (p. 125–126).

thoptera are uncertain; MARTYNOV (1938a) placed it in a new order, Strephocladodea.] CARPENTER, 1966. *U. Carb.*—*Perm.*

Strephocladus SCUDDER, 1885d, p. 337 [*Petrablattina subtilis* KLIVER, 1883, p. 251; OD]. Little-known genus. Costal area with straight, oblique veinlets near level of midwing; branches of CUA and RS dichotomously formed. KUKALOVÁ, 1965; CARPENTER, 1966. *U. Carb.*, Europe (Germany).—FIG. 73,8. **S. subtilis*; fore wing as preserved (holotype), $\times 2$ (Carpenter, 1966).

Homocladus CARPENTER, 1966, p. 60 [**H. grandis*; OD]. Fore wing slender; costal area much as in

Spargopteron; branches of RS arising pectinately, those of CUA dichotomously. *Perm.*, USA (Kansas).—FIG. 73,1. **H. grandis*; fore wing, $\times 1.3$ (Carpenter, 1966).

Paracladus CARPENTER, 1966, p. 62 [**P. retardatus*; OD]. Fore wing as in *Homocladus*, but branches of RS, M, and CUA nearly straight. *Perm.*, USA (Kansas).—FIG. 73,4. **P. retardatus*; fore wing, $\times 3$ (Carpenter, 1966).

Spargopteron KUKALOVÁ, 1965, p. 89 [**S. latericius*; OD]. Fore wing much broader than in *Strephocladus*; all veinlets in costal area branched or irregular; branches of RS dichotomous, those of CUA pectinate. CARPENTER, 1966. *Perm.*, Europe (Czechoslovakia).—FIG. 73,9. **S. latericius*; fore wing, $\times 1.8$ (Kukalová, 1965).

Family TOCOCLADIDAE

Carpenter, 1966

[Tococladidae CARPENTER, 1966, p. 77]

Similar to Protokollaridae, but fore wing with anterior branch of vein M anastomosed for short interval with stem of RS; SC ending on R, just beyond midwing; crossveins not reticulate. Body little known (*Opisthocladus*); head relatively large; pronota of thoracic segments large and nearly circular. *Perm.*

Tococladus CARPENTER, 1966, p. 77 [**T. rallus*; OD]. Area between CUA and CUP very broad, traversed by long crossveins, not reticulate. *Perm.*, USA (Kansas).—FIG. 73,6. **T. rallus*; fore wing, $\times 2.3$ (Carpenter, 1966).

Opisthocladus CARPENTER, 1976, p. 342 [**O. arcuatus*; OD]. Fore wing as in *Tococladus*, but costal veinlets looped and RS arising more distally; basal part of costal area thick and strongly sclerotized. *Perm.*, USA (Kansas).—FIG. 73,2. **O. arcuatus*; fore wing as preserved, $\times 4$ (Carpenter, 1976).

Family HETEROPTILIDAE

Carpenter, 1976

[Heteroptilidae CARPENTER, 1976, p. 346]

Insects of moderate size; affinities uncertain within the Protorthoptera. Fore wing oval, anterior margin strongly curved; vein SC unusually remote from wing margin, ending on R near midwing; SC curving posteriorly near midwing; RS with several branches, M with few; CUA nearly straight and ending on hind margin about three-fourths wing length from base; CUP and anal veins close together and straight. *Perm.*

Heteroptilon CARPENTER, 1976, p. 346 [**H. costale*; OD]. Fore wing broadest beyond midwing; RS with 8 terminal branches; CUA with a short, distal fork. *Perm.*, USA (Kansas).—FIG. 73,7. **H. costale*; fore wing, $\times 3.7$ (Carpenter, 1976).

Family HERDINIDAE

Carpenter & Richardson, 1971

[Herdinidae CARPENTER & RICHARDSON, 1971, p. 287]

Apparently related to Cacurgidae. Wings very short; venation strongly developed; small tubercles on all main veins and crossveins of fore and hind wings. Fore wing with base of costal area strongly sclerotized; vein SC ending on costal margin well before apex of wing;

RS arising at level of midwing, with 3 main branches; M independent of R basally and with two main branches. Crossveins numerous, forming a coarse network over the wing. Hind wing much smaller than fore wing; costal area narrow; venation apparently as in fore wing. Body little known; pronotum large. *U. Carb.*

Herdina CARPENTER & RICHARDSON, 1971, p. 291 [**H. mirificus*; OD]. CUA apparently unbranched; CUP forked, one branch directed toward hind margin of wing and very irregular. [It has been suggested by some workers that the specimen on which this genus is based is in fact a nymph, not an adult. However, the wings are well sclerotized, have thick veins, and are covered with tubercles. Two additional specimens, with similarly reduced wings, have more recently been found in the same deposit.] *U. Carb.*, USA (Illinois).—FIG. 73,3. **H. mirificus*; *a*, fore and *b*, hind wings, $\times 7$ (Carpenter & Richardson, 1971).

Family PSOROPTERIDAE

Carpenter, 1976

[Psoropteridae CARPENTER, 1976, p. 345]

Small insects of uncertain affinities. Fore wing membrane coriaceous and rugose, with hair covering; veins M and CU coalesced near base of wing; M with 2 branches, CUA with 3; longitudinal veins thick; crossveins weak. Hind wing and body unknown. *Perm.*

Psoroptera CARPENTER, 1976, p. 345 [**P. cubitalia*; OD]. Fore wing with R extending almost to wing apex; RS arising at about level of fork of CUA; 2 rows of cells between M3+4 and CUA. *Perm.*, USA (Kansas).—FIG. 73,5. **P. cubitalia*; fore wing, $\times 9$ (Carpenter, 1976).

Family STREPHONEURIDAE

Martynov, 1940

[Strephoneuridae MARTYNOV, 1940, p. 14]

Fore wing with costal area of moderate width; vein SC with branched veinlets and terminating on costa; crossveins numerous, without reticulation; R with series of close veinlets to costal margin distally. *Perm.*

Strephoneura MARTYNOV, 1940, p. 14 [**S. robusta*; OD]. Subcostal area very narrow; MP anastomosed with CUA proximally. *Perm.*, USSR (Asian RSFSR).—FIG. 74,1. **S. robusta*; fore wing, $\times 1$ (Sharov, 1962c).

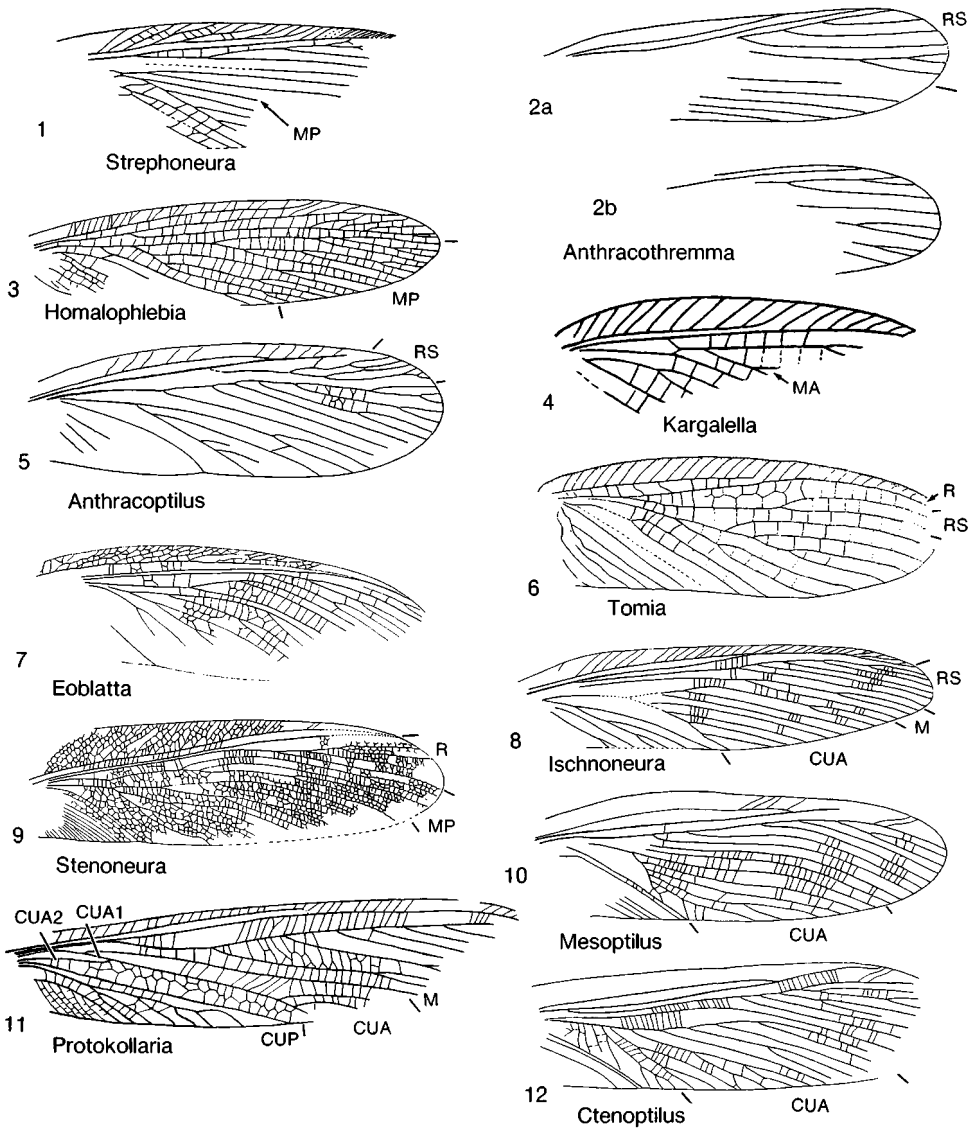


FIG. 74. Strephoneuridae, Anthracothremmidae, Tomiidae, Anthracoptilidae, Stenoneuridae, Homalophlebiidae, Ischnoneuridae, and Protokollariidae (p. 126–130).

Family ANTHRACOTHREMMIDAE
Handlirsch, 1906

[Anthracothremmidae HANDLIRSCH, 1906a, p. 712]

Little-known insects. Fore wing with branches of vein RS forming series of nearly parallel veins leading to apical area of wing. Hind wing with remigium shaped as in fore wing and venation similar; anal area unknown. *U. Carb.*

Anthracothremma SCUDDER, 1885d, p. 327 [**A. robusta*; OD]. Wings with rounded apex; RS of fore wing with at least 6 straight, main branches, some forked. *U. Carb.*, USA (Illinois).—FIG. 74,2. **A. robusta*; a, fore and b, hind wings, X2.5 (Carpenter, new).

Melinophlebia HANDLIRSCH, 1911, p. 364 [**M. analis*; OD]. Little-known genus, based on fragment of fore wing. RS with only 3 or 4 main branches. *U. Carb.*, USA (Illinois).

Pericalyphe HANDLIRSCH, 1911, p. 363 [**P. longa*; OD]. Similar to *Anthracothremma* but larger; RS

with simple branches. [Probably a synonym of *Anthracothebma*.] *U. Carb.*, USA (Illinois).

Silphion HANDLIRSCH, 1911, p. 365 [**S. latipenne*; OD]. Fore wing as in *Pericalypbe* but broader. *U. Carb.*, USA (Illinois).

Family TOMIIDAE Martynov, 1936

[Tomiidae MARTYNOV, 1936, p. 1254]

Costal area wider than in *Atactophlebiidae*, with series of evenly spaced veinlets; vein SC terminating slightly beyond midwing; R with series of costal veinlets continuing series of veinlets from SC; crossveins of wing more regular than in *Atactophlebiidae*. [Ordinal assignment uncertain.] *Perm.—Trias*.

Tomia MARTYNOV, 1936, p. 1255 [**T. costalis*; OD]. Double row of cells between RS and R proximally; other crossveins simple; MA with 4 branches. *Trias.*, USSR (Asian RSFSR).—FIG. 74,6. **T. costalis*; fore wing, $\times 3.5$ (Martynov, 1936).

Kargalella MARTYNOV, 1937b, p. 32 [**K. subcostilis*; OD]. Little-known genus, based on fragment of fore wing. Costal area broader than in *Tomia*; single row of cells between all veins. RS anastomosed with MA basally. [Family position doubtful.] *Perm.*, USSR (European RSFSR).

—FIG. 74,4. **K. subcostilis*; fore wing, $\times 3.5$ (Martynov, 1937b).

Family ANTHRACOPTILIDAE Handlirsch, 1922

[Anthracoptilidae HANDLIRSCH, 1922, p. 98]

Related to *Ischnoneuridae*. Fore wing with vein SC terminating on R well before apex; RS apparently originating about midwing; CUA extensively developed with dichotomous branching; wing membrane granular, as in *Probnidae*; crossveins numerous, irregular, and weak. *U. Carb.*

Anthracoptilus LAMEERE, 1917b, p. 180 [**Homalophlebia perrieri* MEUNIER, 1909d, p. 46; OD] [= *Prostenoneura* HANDLIRSCH, 1919b, p. 559, obj.]. All branches of RS directed anteriorly; RS with fewer branches than *M. U. Carb.*, Europe (France).—FIG. 74,5. **A. perrieri* (MEUNIER); fore wing, $\times 1.5$ (Carpenter, new).

Family CNEMIDOLESTIDAE Handlirsch, 1906

[Cnemidolestidae HANDLIRSCH, 1906b, p. 135]

Fore wing similar to that of *Ischnoneuridae*, but RS arising near midwing and cross-

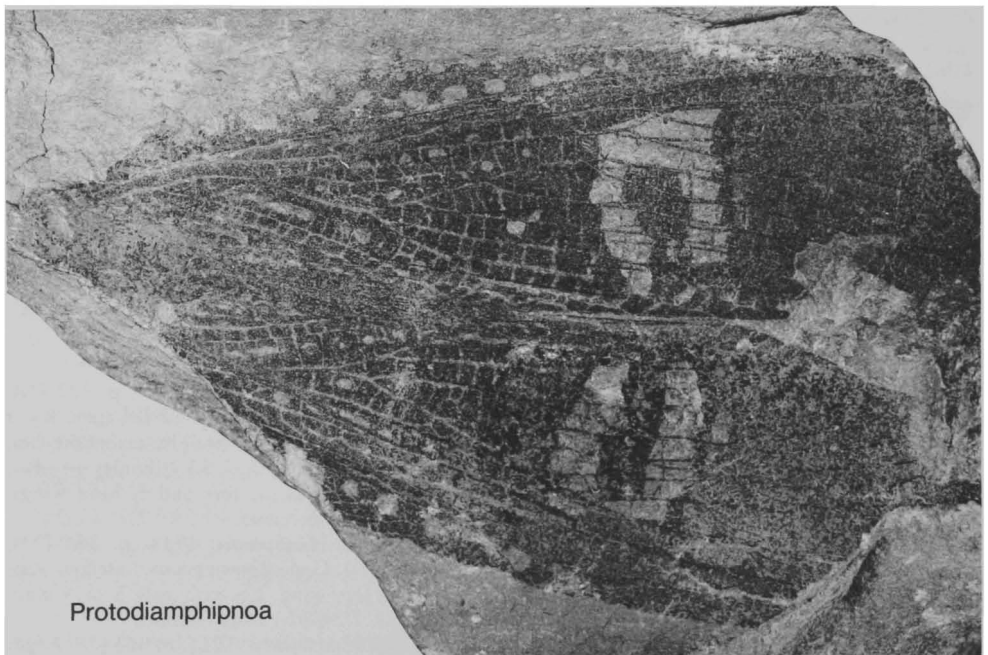


FIG. 75. *Cnemidolestidae* (p. 129).

veins fewer, more widely separated. Hind wing unknown. Prothorax small, about as long as wide; head small, slenderly oval; antennae long and filamentous; forelegs long and apparently raptorial. *U. Carb.*

Protodiamphipnoa BRONGNIART, 1893, p. 410 [**P. tertrini*; OD] [= *Cnemidolestes* HANDLIRSCH, 1906b, p. 135 (type, *Protophasma woodwardi* BRONGNIART, 1893, p. 427)]. Fore wing with M and CUA dividing at level of origin of RS; wings with conspicuous "eye spot." HANDLIRSCH, 1937. *U. Carb.*, Europe (France).—FIG. 75. **P. tertrini*; fore wings, $\times 1.5$ (Carpenter, new).—FIG. 76. *P. gaudryi* (BRONGNIART); fore wings and part of body, holotype, $\times 1.7$ (Carpenter, new).

Family STENONEURITIDAE

Lameere, 1917

[Stenoneuritidae LAMEERE, 1917b, p. 197]

Fore wing similar to that of Stenoneuridae, but RS arising near midwing and MP much less developed, branching only in its distal half near posterior margin. *U. Carb.*

Stenoneurites HANDLIRSCH, 1906b, p. 153 [**Stenoneura maximi* BRONGNIART, 1893, p. 430; OD]. MP forking before the origin of RS. *U. Carb.*, Europe (France).

Family STENONEURIDAE

Handlirsch, 1906

[Stenoneuridae HANDLIRSCH, 1906b, p. 152] [= Eoblattidae HANDLIRSCH, 1906b, p. 155]

Fore wing slightly coriaceous; vein SC extending nearly to wing apex, terminating on R; RS arising at wing base, parallel and close to R up to at least midwing; RS with several branches; MA apparently absent; MP dividing at about midwing, the most anterior branch directed anteriorly towards RS; CUA forking well before midwing; each main branch subdividing; CUP marking off the anal area, which contains numerous anal veins, very close together and nearly parallel. Hind wing little known, apparently similar to fore wing except that M is reduced and the anal area is expanded. Prothorax broad, distinctly broader than long; prothoracic legs robust, moderately long. *U. Carb.*

Stenoneura BRONGNIART, 1893, p. 429 [**S. fayoli*; OD]. Fore wing with numerous crossveins forming very irregular, fine reticulation over most of wing, except anal area. *U. Carb.*, Europe (France).



Protodiamphipnoa

FIG. 76. Cnemidolestidae (p. 129).

—FIG. 74,9. **S. fayoli*; fore wing, $\times 1.2$ (Carpenter, new).

Eoblatta HANDLIRSCH, 1906b, p. 155 [**Stenoneura robusta* BRONGNIART, 1893, p. 429; OD]. Fore wing with fewer crossveins than in *Stenoneura*, forming coarse reticulation only in costal area and a few small regions of wing. *U. Carb.*, Europe (France).—FIG. 74,7. **E. robusta* (BRONGNIART); fore wing, $\times 0.9$ (Carpenter, new).

Family HOMALOPHLEBIIDAE

Handlirsch, 1906

[Homalophlebiidae HANDLIRSCH, 1906b, p. 136]

Related to Stygnidae, but fore wing with very extensive vein MP; MA apparently absent; CUA forked at margin. Hind wing unknown. *U. Carb.*

Homalophlebia BRONGNIART, 1893, p. 437 [**H. finoti*; SD HANDLIRSCH, 1906b, p. 136]. Fore wing with RS arising about one-third of wing length from base, with several branches; first fork of MP at same level. *U. Carb.*, Europe (France).—FIG. 74,3. **H. finoti*; fore wing, $\times 0.8$ (Carpenter, new).

Parahomalophlebia HANDLIRSCH, 1906b, p. 137 [**Homalophlebia courtini* BRONGNIART, 1893, p. 438; OD]. Similar to *Homalophlebia*, but RS with single fork. *U. Carb.*, Europe (France).

Family ISCHNONEURIDAE

Handlirsch, 1906

[Ischnoneuridae HANDLIRSCH, 1906b, p. 133] [=Stenoneurellidae HANDLIRSCH, 1919b, p. 560]

Related to Stenoneuridae. Fore wing with vein SC terminating on R well before apex; RS arising close to wing base with several long branches; CUA very extensively developed; crossveins numerous, mostly straight, not forming reticulation. Hind wing unknown. Prothorax and legs long. *U. Carb.*

Ischnoneura BRONGNIART, 1893, p. 433, *nom. subst. pro Leptoneura* BRONGNIART, 1885a, p. 62, *non* WALLENGREN, 1857 [**Leptoneura oustaleti* BRONGNIART, 1885a, p. 62; SD HANDLIRSCH, 1922, p. 76] [=*Ischnoneurilla* HANDLIRSCH, 1919b, p. 556 (type, *Ischnoneura elongata* BRONGNIART, 1893, p. 433); *Ischnoneurona* HANDLIRSCH, 1919b, p. 557 (type, *Ischnoneura delicatula* BRONGNIART, 1893, p. 433)]. Branches of CUA close together and parallel. *U. Carb.*, Europe (France).—FIG. 74,8. **I. oustaleti* (BRONGNIART); fore wing, $\times 0.6$ (Carpenter, new).

Ctenoptilus LAMEERE, 1917b, p. 180 [**Homalophlebia trouessarti* MEUNIER, 1911a, p. 127; OD]. Similar to *Ischnoneura*, but branches of CUA more widely separated and divergent. *U. Carb.*, Europe (France).—FIG. 74,12. **C. trouessarti* (MEUNIER); fore wing, $\times 1.4$ (Carpenter, new).

Mesoptilus LAMEERE, 1917b, p. 174 [**M. dolloi*; OD] [=*Pseudoedischia* HANDLIRSCH, 1919b, p. 557 (type, *P. berthaudi*); *Stenoneurella* HANDLIRSCH, 1919b, p. 559 (type, *S. fayoliana*)]. Similar to *Ischnoneura*, but first branch of RS arising well before midwing; posterior branch of CUA more oblique than in *Ischnoneura*. *U. Carb.*, Europe (France).—FIG. 74,10. **M. dolloi*; fore wing, $\times 1.2$ (Carpenter, new).

Family PROTOKOLLARIIDAE

Handlirsch, 1906

[Protokollariidae HANDLIRSCH, 1906b, p. 137] [=Sthenaroceridae HANDLIRSCH, 1906b, p. 149; Laspeyresiellidae SCHLECHTENDAL, 1913, p. 96]

Fore wing very long, slender; vein SC terminating not far beyond midwing; RS arising near wing base, with several long branches. M and CUA1 anastomosed at wing base, separating before level of origin of RS; M apparently unbranched; CUA2 arising inde-

pendently of CUA1 but anastomosed with it shortly after separation of CUA1 from M; crossveins numerous. Hind wing unknown. Head small; antennae thick at base; prothorax narrow; front legs long. *U. Carb.*

Protokollaria BRONGNIART, 1893, p. 409 [**P. ingens*; OD]. CUA with 2 branches arising distally and curved; crossveins between CUA and CUP forming a coarse reticulation. *U. Carb.*, Europe (France).—FIG. 74,11. **P. ingens*; fore wing, $\times 1.5$ (Carpenter, new).

Laspeyresiella SCHLECHTENDAL, 1913, p. 96, *nom. subst. pro Laspeyresia* HANDLIRSCH, 1906b, p. 140, *non* HÜBNER, 1825 [**Laspeyresia wettinensis* HANDLIRSCH, 1906b, p. 140; OD] [=*Laspeyresiella* KRAUSSE, 1922, p. 132, obj. synonym & homonym]. Little-known genus, with wings and body shaped as in *Protokollaria*. *U. Carb.*, Europe (Germany).

Sthenarocera BRONGNIART, 1885a, p. 59 [**S. pachytyloides*; OD]. Similar to *Protokollaria*, but fore wing more slender; crossveins not forming a reticulation. *U. Carb.*, Europe (France).

Family PROTOPHASMATIDAE

Brongniart, 1885

[*nom. correct.* CARPENTER, herein, *pro* Protophasmida BRONGNIART, 1885a, p. 59]

Little-known family, apparently related to Geraridae. Fore wing with small but distinct precostal area; several veinlets arising from costa; crossveins forming network; costal space much broader than subcostal; vein RS arising nearer wing base than in Geraridae, with several branches. *U. Carb.*

Protophasma BRONGNIART, 1878, p. 57 [**P. dumasi*; OD]. Fore and hind wings with several transverse rows of maculations. *U. Carb.*, Europe (France).

Family UNCERTAIN

The following genera, apparently belonging to the order Protorthoptera, are too poorly known to permit assignment to families.

Acridites GERMAR, 1842, p. 93 [**A. carbonarius*; OD]. Little-known genus, based on poorly preserved fore wing with narrow costal area. [Probably related to Geraridae.] *U. Carb.*, Europe (Germany).

Adiphlebia SCUDDER, 1885d, p. 345 [**A. lacoana*; OD]. Based on little-known insect, with short oval wings and robust body. [Type of Adiphlebiidae HANDLIRSCH, 1906a.] *U. Carb.*, USA (Illinois).

Aenigmarella SHAROV, 1961c, p. 159 [**A. com-*

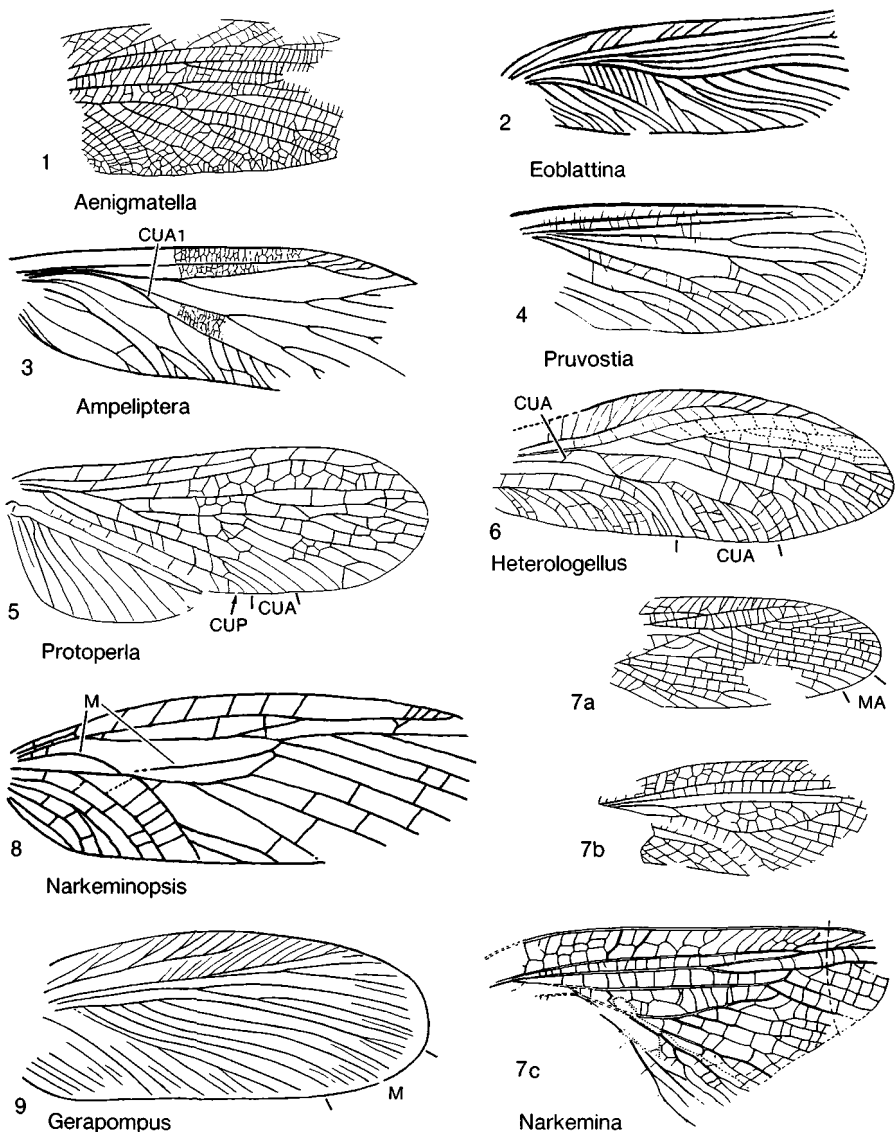


FIG. 77. Uncertain (p. 130–134).

parabilis; OD]. Costal area broad, with numerous veinlets; RS and M dividing at about same level; CUA very extensively developed. *U. Carb.*, USSR (Asian RSFSR).—FIG. 77.1. **A. comparabilis*; fore wing, $\times 1.4$ (Sharov, 1961c).

Aetophlebia SCUDDER, 1885d, p. 338 [**A. singularis*; OD]. Based on fragments of wing. [Type of Aetophlebiidae HANDLIRSCH, 1906a, p. 708.] *U. Carb.*, USA (Illinois).

Aetophlebiopsis ZALESSKY, 1955b, p. 347 [**A. fusca*; OD]. Based on fragments of wings. *Perm.*, USSR (Asian RSFSR).

Agogoblattina HANDLIRSCH, 1906a, p. 714 [**Oryctoblattina occidua* SCUDDER, 1885e, p. 37; OD]. Based on fragments of wings and body. *U. Carb.*, USA (Illinois).

Ampeliptera PRUVOST, 1927, p. 76 [**A. limburgica*; OD]. Little-known genus, based on incomplete fore wing with fine archidictyon; CUA1 apparently anastomosed with M near wing base and diverging away before the level of the origin of RS, as in some Permian Orthoptera. [Placed in Hapalopteridae (order Hapaloptera) by PRUVOST (1927); in Palaeocixiidae (order Protor-

- thoptera) by HANDLIRSCH (1937); in family uncertain (order Paraplecoptera) by MARTYNOV (1938b); in new family Ampelipteridae (order Protocicadida) by HAUPT (1941); and in Paoliidae (order Protorthoptera) by KUKALOVÁ (1958b).] *U. Carb.*, Europe (Holland).—FIG. 77,3. **A. limburgica*; fore wing, holotype, $\times 5$ (Kukalová, 1958b).
- Anergertus** HANDLIRSCH, 1911, p. 353 [**A. cubitalis*; OD]. Based on wing fragments. *U. Carb.*, USA (Illinois).
- Anthracomastax** HANDLIRSCH, 1904a, p. 17 [**A. furcifer*; OD]. Based on wing fragment. *U. Carb.*, Europe (Belgium).
- Archaeologus** HANDLIRSCH, 1906a, p. 807 [**A. falcatus*; OD]. Based on fore and hind wing fragments. *U. Carb.*, USA (Illinois).
- Archimastax** HANDLIRSCH, 1906a, p. 806 [**A. americanus*; OD]. Based on wing fragment. *U. Carb.*, USA (Arkansas).
- Asiopompus** SHAROV, 1961c, p. 160 [**A. tomicus*; OD]. Based on fragment of fore wing. [Type of Asiopompidae SHAROV, 1961d.] *U. Carb.*, USSR (Asian RSFSR).
- Atava** SELLARDS, 1909, p. 157 [**A. ovata*; OD]. Based on fragment of hind wing. *Perm.*, USA (Kansas).
- Axiologus** HANDLIRSCH, 1906a, p. 805 [**A. thoracicus*; OD]. Based on fragments of body and wings. *U. Carb.*, USA (Illinois).
- Balduriella** MEUNIER, 1925, p. 105 [**B. latissima*; OD]. Based on wing fragment. *U. Carb.*, Europe (Germany).
- Boutakovia** PRUVOST, 1934, p. 1 [**B. saleei*; OD]. Based on wing fragment. [Placed in Homalophlebiidae by PRUVOST.] *U. Carb./Perm.*, Africa (Zaire).
- Cacurgellus** PRUVOST, 1919, p. 125 [**C. barryi*; OD]. Based on wing fragment. *U. Carb.* Europe (France).
- Cheliphlebia** SCUDDER, 1885d, p. 328 [**C. carbonaria*; OD]. Little-known genus, based on fragments of fore wings. [Type of Cheliphlebiidae HANDLIRSCH, 1906a, p. 709.] *U. Carb.*, USA (Illinois).
- Chrestotes** SCUDDER, 1868b, p. 567 [**C. lapidea*; OD]. Based on fragments of wings. *U. Carb.*, USA (Illinois).
- Commentrya** LAMEERE, 1917b, p. 176 [**Oedischia maximae* BRONGNIART, 1893, p. 437; OD]. Little-known genus, based on body fragment. *U. Carb.*, Europe (France).
- Danielsiella** COCKERELL, 1916c, p. 100 [**D. priscula*; OD]. Based on fragments of wings and body. *U. Carb.*, USA (Illinois).
- Didymophleps** SCUDDER, 1885d, p. 330 [**Termes contusa* SCUDDER, 1878c, p. 300; OD]. Based on small fragment of wing. *U. Carb.*, USA (Illinois).
- Dieconeurites** HANDLIRSCH, 1906a, p. 699 [**Dieconeurina rigida* SCUDDER, 1885d, p. 336; OD]. Based on wing fragment. *U. Carb.*, USA (Pennsylvania).
- Distasis** HANDLIRSCH, 1904a, p. 17 [**D. rhipophora*; OD]. Based on distal fragment of hind wing. *U. Carb.*, Europe (Belgium).
- Endoiasmus** HANDLIRSCH, 1906a, p. 805 [**E. reticulatus*; OD]. Based on wing fragment. *U. Carb.*, USA (Illinois).
- Eoblattina** BOLTON, 1925, p. 19 [**E. complexa*; OD]. Little-known genus, based on fragments of wings and body; fore wing with extensive, sigmoidal CUA having several short, straight branches leading to CUP. *U. Carb.*, Europe (France). — FIG. 77,2. **E. complexa*; fore wing, $\times 1.3$ (Bolton, 1925).
- Gerapompus** SCUDDER, 1885d, p. 326 [**G. blattinoides*; SD HANDLIRSCH, 1906a, p. 711]. Little-known genus, based on poorly preserved fore wing; R and RS apparently with several long branches distally; M extensively branched. [Type of Gerapompidae HANDLIRSCH, 1906a, p. 711.] *U. Carb.*, USA (Illinois).—FIG. 77,9. *G. schucherti* HANDLIRSCH; fore wing, $\times 2$ (Handlirsch, 1906a).
- Gerarianus** HANDLIRSCH, 1919b, p. 551 [**G. commentryanus*; OD]. Based on wing fragments. *U. Carb.*, Europe (France).
- Gerarites** HANDLIRSCH, 1919b, p. 551 [**Gerarus commentryi* BRONGNIART, 1893, pl. 24, fig. 10; OD]. Based on wing fragment. *U. Carb.*, Europe (France).
- Geraroides** HANDLIRSCH, 1906a, p. 704 [**Dieconeurina maxima* MELANDER, 1903, p. 193; OD]. Little-known genus, based on fragments of wings and body. HANDLIRSCH, 1922. *U. Carb.*, USA (Illinois).
- Germanoprisca** ZEUNER, 1936a, p. 267 [**F. zimmermanni*; OD]. Little-known insect with prominent, slender cerci; fore wing fragment. [Type of Germanopriscidae ZEUNER, 1936a.] MÜLLER, 1978b. *Perm.*, Europe (Germany).
- Gyrophlebia** HANDLIRSCH, 1906a, p. 697 [**G. longicollis*; OD]. Little-known genus, based on poorly preserved fore wing and body. *U. Carb.*, USA (Illinois).
- Hadentomoides** RIEK, 1974a, p. 15 [**H. duykenensis*; OD]. Little-known genus, based on apical fragment of wing. [Originally placed in family Hadentomidae.] *Perm.*, South Africa (Natal).
- Haplopterum** MARTYNOV, 1928b, p. 84 [**H. majus*; OD]. Based on hind wing fragment. *Perm.*, USSR (European RSFSR).
- Hemeristia** DANA, 1864, p. 35 [**H. occidentalis*; OD] [= *Hemeristica* GOLDENBERG, 1877, p. 15, obj.]. Based on wing fragments. *U. Carb.*, USA (Illinois).
- Heterologellus** SCHMIDT, 1962, p. 843 [**H. teichmuelleriae*; OD]. Apparently similar to *Omalia*, but fore wing with SC terminating on R well before wing apex; MP dividing distally, near

- wing margin; CUA only just touching CUP, not coalesced with it; MP not as extensively branched as CUA. [Placed in Omaliidae by SCHMIDT.] *U. Carb.*, Europe (Germany).—FIG. 77,6. **H. teichmuelleriae*; fore wing, $\times 3$ (Schmidt, 1962).
- Heterologopsis** BRAUCKMANN & KOCH, 1982, p. 18 [**H. rubrensis*; OD]. Little-known genus, apparently related to the Cacurgidae, but SC much shorter and terminating on R. *U. Carb.*, Europe (Germany).
- Kaltanopterodes** SHAROV, 1961d, p. 223 [**K. vanus*; OD]. Based on hind wing of nymph. *Perm.*, USSR (Asian RSFSR).
- Kargalodes** MARTYNOV, 1937b, p. 33 [**K. incerta*; OD]. Based on wing fragment. *Perm.*, USSR (European RSFSR).
- Kelleropteron** BRAUCKMANN & HAHN, 1980, p. 308 [**K. kaelberbesense*; OD]. Little-known genus, based on small fragment of wing. *U. Carb.*, Europe (Germany).
- Khosarophlebia** MARTYNOV, 1940, p. 24 [**K. sylvaensis*; OD]. Based on hind wing fragment. *Perm.*, USSR (Asian RSFSR).
- Klebsiella** MEUNIER, 1908c, p. 242 [**K. exstincta*; OD]. Based on fragments of fore and hind wings. [Type of Klebsiellidae HANDLIRSCH, 1919b, p. 552.] *U. Carb.*, Europe (France).
- Lecopterum** SELLARDS, 1909, p. 161 [**L. delicosum*; OD]. Based on wing fragment. *Perm.*, USA (Kansas).
- Limburgina** LAURENTIAUX, 1950, p. 14 [**L. antiqua*; OD]. Based on wing fragment, with suggestions of convex MA. [Ordinal position doubtful.] *U. Carb.*, Europe (Netherlands).
- Macrophlebiom** GOLDENBERG, 1869, p. 164 [**M. hollebeni*; OD]. Based on wing fragment. *U. Carb.*, Europe (Germany).
- Megalometer** HANDLIRSCH, 1906a, p. 713 [**M. lata*; OD]. Based on fragments of wings. *U. Carb.*, USA (Illinois).
- Mesorthopteron** TILLYARD in TILLYARD & DUNSTAN, 1916, p. 14 [**M. locustoides*; OD]. Little-known genus, based on fragments of fore wing. Fore wing elongate-oval, with fine archidictyon; costal area broad, with numerous, parallel veinlets; SC straight and close to R and RS, with several distal branches; M weakly formed; CUA with numerous long, pectinate branches; anal area small. [Type of family Mesorthopteridae TILLYARD, 1922b.] RIEK, 1956. *Trias.*, Australia (New South Wales).
- Metacheliphlebia** HANDLIRSCH, 1906a, p. 698 [**Cheliphlebia elongata* SCUDDER, 1885d, p. 328; OD]. Little-known genus, based on small fragments of wings. HANDLIRSCH, 1906b. *U. Carb.*, USA (Illinois).
- Miamia** DANA, 1864, p. 34 [**M. bronsoni*; OD]. Little-known genus, based on wing fragments. [Possibly belonging to the Spanioderidae.] *U. Carb.*, USA (Illinois).
- Mitinovia** SHAROV, 1961d, p. 223 [**M. dubia*; OD]. Based on hind wing with extensive veinlets from R to costa beyond SC. *Perm.*, USSR (Asian RSFSR).
- Narkemina** MARTYNOV, 1931a, p. 81 [**N. angustata*; OD]. Fore wing elongate-oval; venation with some resemblance to that of the Narkemidae. RS forking near midwing; M dividing near base, MA continuing in a straight line and branching beyond origin of RS; MP diverging posteriorly and coalescing with CUA for a considerable interval before diverging anteriorly, its terminal branches joining some of those of MA; CUA with a few short, terminal branches; CUP unbranched. Hind wing very broad, with an enlarged anal area, but with the venation of the remigium much as in the fore wing. [PINTO & ORNELLAS (1978c) correctly recognized that the genus *Narkemina*, formerly placed in the Narkemidae, required a separate family, but they proposed the invalid family name, Narkemiparacurgidae, for the type genus *Narkemina*.] SHAROV, 1961e; PINTO & ORNELLAS, 1978c; LEWIS, 1979; RASNITSYN, 1980c. *U. Carb.*, USSR (Asian RSFSR), Brazil (Parana Basin), USA (Missouri).—FIG. 77,7a. **N. angustata*; fore wing, $\times 2.6$ (Sharov, 1961e).—FIG. 77,7b. *N. angustiformis* SHAROV; fore wing, $\times 2$ (Sharov, 1961e).—FIG. 77,7c. *N. rodendorfi* PINTO & ORNELLAS; hind wing, $\times 1.2$ (Pinto & Ornellas, 1978c).
- Narkeminopsis** WHALLEY, 1979, p. 87 [**N. eddi*; OD]. Little-known genus. Apparently similar to *Narkemina*, but fore wing with M diverging posteriorly near wing base, then anastomosing briefly with CUA before diverging anteriorly and joining RS at level of end of SC; few costal veinlets; archidictyon present in costal and CUA areas. *U. Carb.*, England.—FIG. 77,8. **N. eddi*; fore wing, $\times 2.5$ (Whalley, 1979).
- Ochetopteron** COCKERELL, 1927g, p. 414 [**O. cancellulatum*; OD]. Little-known genus, based on wing fragment. *U. Carb.*, USA (Maryland).
- Orthoneurites** MARTYNOV, 1928b, p. 49 [**O. regularis*; OD]. Based on distal wing fragment. *Perm.*, USSR (European RSFSR).
- Palaeocarrina** COCKERELL, 1917e, p. 80 [**P. ornata*; OD]. Based on fragment of wing. *U. Carb.*, USA (Illinois).
- Palaeoedischia** MEUNIER, 1914d, p. 364 [**P. boulei*; OD]. Based on fragment of fore wing. *U. Carb.*, Europe (France).
- Palaeomantopsis** MARTYNOV, 1928b, p. 83 [**P. furcatella*; OD]. Based on distal wing fragment. *Perm.*, USSR (European RSFSR).
- Paolekia** RIEK, 1976a, p. 764 [**P. perditae*; OD]. Little-known genus, based on small apical fragment of wing. [Placed originally in Paoliidae.] *Perm.*, South Africa (Natal).
- Paranarkemina** PINTO & ORNELLAS, 1980a, p. 288

- [**P. kurtzi*; OD]. Little-known genus, based on incomplete wing. SC ending on R beyond level of midwing; RS arising basally and forking at about level of end of SC, with numerous branches; M forking before origin of RS; MA with 2 distal branches; CUA anastomosed briefly with MP before terminating in many branches. *U. Carb.*, Argentina (San Luis).
- Polyernus** SCUDDER, 1885d, p. 343 [**D. complanatus*; OD]. Based on fragments of wings and body. *U. Carb.*, USA (Illinois).
- Polyetes** HANDLIRSCH, 1906a, p. 715 [**P. furcifer*; OD]. Based on small wing fragment. *U. Carb.*, USA (Illinois).
- Protoperla** BRONGNIART, 1893, p. 407 [**P. westwoodi*; OD]. Little-known genus, based on hind wing. SC ending on costal margin near midwing; M apparently coalesced with R and RS basally; RS with 2 main branches; M with numerous irregular branches; CUA with 3 very short terminal branches; CUP unbranched. Anal area enlarged, with a series of long pectinate branches from 2A. [Placed in the family Protoperlidae by BRONGNIART.] LAMEERE, 1917b. *U. Carb.*, Europe (France).—FIG. 77,5. **P. westwoodi*; hind wing, $\times 4$ (Carpenter, new).
- Prototettix** GIEBEL, 1856, p. 306 [**Gryllacris lithantraca* GOLDENBERG, 1854, p. 24; OD]. Based on fore wing fragment. [Type of Prototettigidae HANDLIRSCH, 1906b, p. 135.] *U. Carb.*, Europe (Germany).
- Pruvostia** BOLTON, 1921, p. 48 [**P. spectabilis*; OD]. Little-known wing (probably hind) with basal origin of RS. *U. Carb.*, Europe (England).—FIG. 77,4. **P. spectabilis*; wing, $\times 0.9$ (Bolton, 1921).
- Pseudetoblattina** HANDLIRSCH, 1906a, p. 714 [**Etoblattina reliqua* SCUDDER, 1893b, p. 18; OD]. Based on wing fragment. *U. Carb.*, USA (Rhode Island).
- Pseudogerarus** HANDLIRSCH, 1906a, p. 804 [**P. scudderi*; OD]. Based on small fragments of wings. *U. Carb.*, USA (Illinois).
- Pseudopolyernus** HANDLIRSCH, 1906a, p. 803 [**Polyernus laminarum* SCUDDER, 1885d, p. 343; OD]. Little-known genus, based on wing fragments. *U. Carb.*, USA (Pennsylvania).
- Ptenodera** BOLTON, 1922, p. 90 [**P. dubius*; OD]. Based on distal wing fragment. *U. Carb.*, England.
- Rhipidoptera** BRONGNIART, 1893, p. 447 [**R. elegans*; OD]. Little-known genus, based on small fragment of wing. *U. Carb.*, Europe (France).
- Roomeria** MEUNIER, 1914e, p. 388 [**R. carbonaria*; OD]. Based on little-known fore wing. [Type of Roomeriidae HANDLIRSCH, 1919.] *U. Carb.*, Europe (France).
- Schuchertiella** HANDLIRSCH, 1911, p. 311 [**S. gracilis*; OD]. Little-known genus, based on small wing fragment. [Type of Schuchertiellidae HANDLIRSCH, 1911.] *U. Carb.*, USA (Illinois).
- Sellardsiopsis** ZALESKY, 1939, p. 51 [**S. conspicua*; OD]. Little-known fore wing. *Perm.*, USSR (Asian RSFSR).
- Sharovia** PINTO & ORNELLAS, 1978b, p. 100, *junior homonym*, *Sharovia* SINITSHENKOVA, 1977 [**S. permiafricana*; OD]. Little-known genus, based on wing fragment. [Originally placed in Lemmatophoridae.] *Perm.*, South Africa (Cape of Good Hope).
- Sindonopsis** MARTYNOV, 1928b, p. 61 [**S. subcostalis*; SD SHAROV, 1962c, p. 117]. Little-known wing with short SC. *Perm.*, USSR (European RSFSR).
- Thaumatophora** RIEK, 1976d, p. 147 [**T. pronotalis*; OD]. Little-known genus, based on nymph with lateral abdominal gills. *Perm.*, South Africa (Natal).

Order BLATTARIA

Latreille, 1810

[Blattaria LATREILLE, 1810, p. 246] [=Blattodea BRUNNER, 1882, p. 26; Protolulitoria HAUPT (in part), 1941, p. 75]

Oxopterygotes with dorsoventrally compressed bodies; head free, commonly hypognathous or opisthognathous, rarely prognathous; antennae filiform, multisegmented; compound eyes of moderate size; mandibles well developed; pronotum large, commonly covering head and extending laterally (Fig. 78); legs cursorial, spinous, with 5 tarsal segments; wings typically well developed, aptery not uncommon; fore wings tegminous, broadly oval, commonly as broad basally as at midwing; hind wings membranous, with an expanded anal fan, at least as large as remigium and containing radiating veins; abdomen with tenth tergite enlarged, forming a conspicuous supra-anal plate; cerci typically multisegmented, commonly of moderate length; external ovipositors absent in existing species but well developed in Paleozoic and many Mesozoic species. Most existing Blattaria nocturnal, omnivorous, commonly occurring in warm, moist environments. *U. Carb.*—*Holo.*

These are primitive orthopteroids, probably most closely related to the Isoptera among existing orders (McKITTRICK, 1965). The order is now a relatively small one, containing less than 4,000 species (M. J. MAC-

KERRAS, 1970), but the geological record indicates that it was one of the largest orders of insects during the late Paleozoic.

The venational pattern of the cockroaches is typically orthopteroïd (Fig. 78,1,2,). In the fore wing, however, the costa is completely marginal, there being no precostal area. Veins RS, M, and CUA are well developed, and CUP is strongly concave and curved. Crossveins are numerous but weak in existing species; in most Paleozoic species they are much stronger or commonly form a fine network (archedictyon). The venational pattern of the remigium of the hind wing is like that of the fore wing except that RS, M, and CUA have fewer branches.

The basic venational pattern of the fore wing is unusually constant throughout the order, with very few exceptions. On the other hand, the detailed branching of the veins is extremely variable within all taxonomic levels. Early attempts at family classification, in which wing venation was used (REHN, 1951), were very controversial, but the one proposed by MCKITTRICK (1964) has been generally accepted. This classification bases the families on the genitalic structures of both sexes, the nature of the proventriculus, egg-laying behavior, and the structure of certain appendages. MCKITTRICK recognized five existing families: Blattidae, Cryptoceridae, Polyphagidae, Blattellidae, and Blaberidae. The existing genera are usually based on the more detailed structure of the genitalia, hind wings, legs, and male tergal glands.

Unfortunately, such details of structure are rarely preserved in fossil roaches, with the exception of those in amber. The vast majority of fossil Blattaria, close to 90 percent, consist of isolated wings or wing fragments. Furthermore, most of the specimens with bodies preserved have the two pairs of wings folded back over the body in the usual resting position, obscuring most of the body structures that are preserved (Fig. 78). Study of extensive series of Paleozoic roaches has shown that their venational variability was at least as great as that of existing species (SCHNEIDER, 1977, 1978a, 1978b). The tendency in

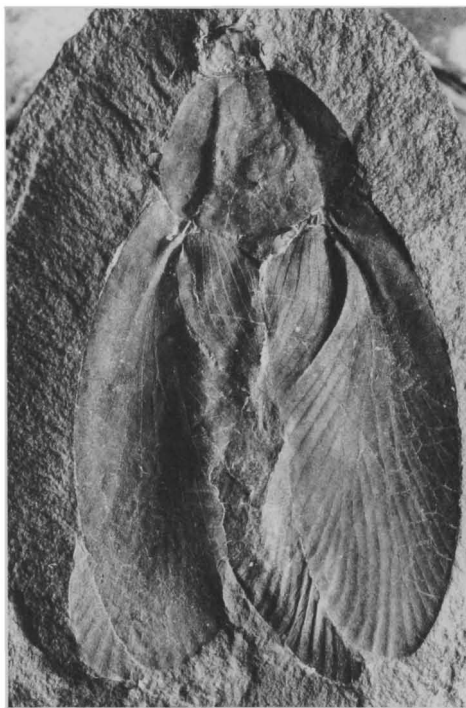


FIG. 78. Blattaria; dorsal view of an archimylacrid roach from the Upper Carboniferous of Illinois in its normal resting posture, $\times 3.4$ (Carpenter, new).

publications on these fossils has been to place emphasis on slight differences in venation, resulting in many families and genera. At least 25 extinct families and 370 extinct genera have been named from Paleozoic and early Mesozoic deposits, and fully half of these are based on single specimens.

The fossil record shows only a few obvious trends in the evolution of the fore wings of the Blattaria. In the most primitive and largest extinct family of the order, the Archimylacridae, the subcosta arises as a separate vein, isolated from R and giving rise to a series of branches toward the costa (Fig. 79,1,). Also, R arises as a distinct branch of stem R and has several branches. In most specialized species, as in the existing family Blattidae (Fig. 79,2), SC, R, and RS arise from a single stem.

Quite apart from the wings, the geological record has provided some interesting data bearing on the reproduction of the Blattaria.

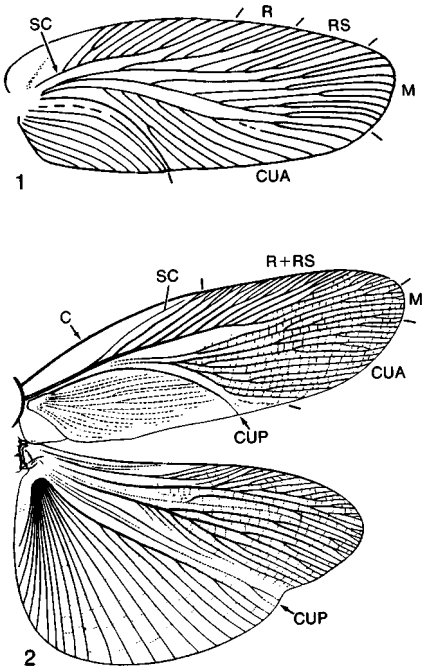


FIG. 79. Blattaria; typical venation.—1. Tegmen of *Phyloblatta manebachensis* GOLDENBERG, Upper Carboniferous of Germany, Archimylicridae, $\times 2.2$ (Schneider, 1978b).—2. Tegmen and hind wing of *Periplaneta brunnea*, Holocene of Australia, Blattidae, $\times 2.3$ (CSIRO, 1970).

The females of existing roaches lack a true ovipositor but commonly possess short internal valves that serve only to guide the fertilized eggs (several to many) into the genital atrium, where the ootheca is formed. In some species the oothecae are deposited within a few days, the embryos developing outside the body of the female. In others, the oothecae are first extruded, then retracted, and finally deposited in the brood sac, where the embryos continue their development. When they are mature, the ootheca is extruded again and the nymphs emerge from it (ROTH, 1967; M. J. MACKERRAS, 1970). Several small and obscure fossils, presumed to be oothecae, have been reported from Paleozoic deposits, but these are not very convincing as oothecae, and all are now considered to be fragments

of other organisms (BROWN, 1957; VISHNIAKOVA, 1968). Furthermore, numerous specimens of female Blattaria with long, external ovipositors are known from Upper Carboniferous and Permian deposits of Europe, Asia, and North America (BRONGNIART, 1889; SELLARDS, 1904; ZALESSKY, 1939, 1940, 1953b). In more recent years Dr. V. N. VISHNIAKOVA of the Paleontological Institute in Moscow has described similar ovipositors on specimens from Triassic and Jurassic deposits of the USSR (VISHNIAKOVA, 1965, 1968, 1973) (Fig. 80, 1–3). From her detailed study of these remarkable fossils, Dr. VISHNIAKOVA concluded that these ovipositors were derived from the eighth and ninth abdominal sternites and that they were therefore homologous with the ovipositors of the Orthoptera but not with the short internal valves of the existing Blattaria, which are derived from the seventh sternite (NEL, 1929; SHAROV, 1966b). It is noteworthy that in some of the Jurassic species the ovipositor is very short (Fig. 80, 1). The gradual shortening and ultimate loss of the long external ovipositors apparently took place toward the end of the Mesozoic.

The systematics of the fossil Blattaria has been in need of a thorough revision for many years, especially considering the additional information acquired during the past twenty years. Recognizing the unsatisfactory state of the classification of the extinct species, in 1977, Dr. Jörg SCHNEIDER, of the Department of Geological Sciences, Bergakademie Freiberg, Germany, began a long-range study of type specimens, as well as new material, from the Paleozoic and Mesozoic, with full recognition of the variability of the wing venation. Up to the present time seven papers in this series have been published (SCHNEIDER, 1977, 1978a, 1978b, 1980, 1982, 1983, 1984), and others are in preparation. Since Dr. SCHNEIDER's studies are continuing, it would be presumptuous and futile for me to attempt to present here a systematic treatment of the extinct genera of the order.

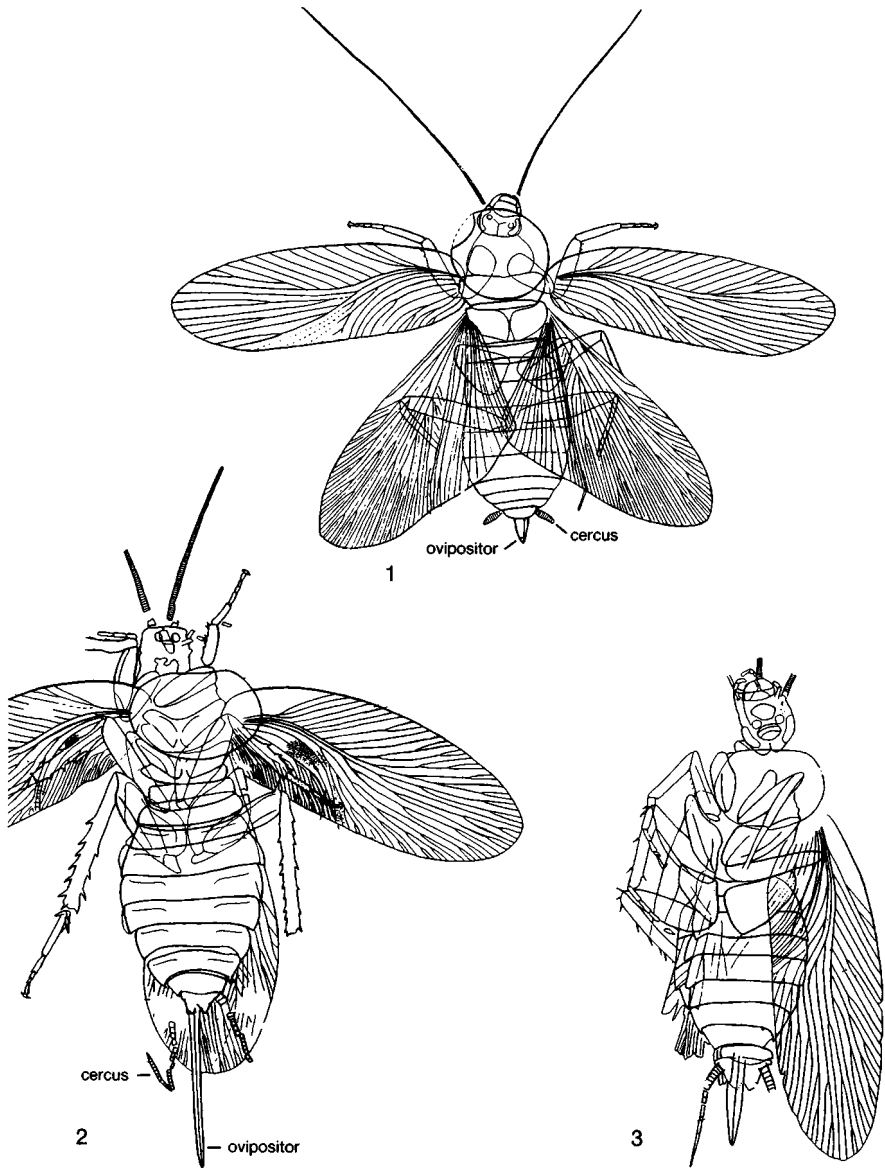


FIG. 80. Blattaria; wings and body of several female specimens from the family Mesoblattinidae.—1. *Artitocoblatta asiatica* VISHNIAKOVA, Jurassic of the USSR, $\times 3.5$.—2. *Karatavoblatta longicaudata* VISHNIAKOVA, Jurassic of the USSR, $\times 1$.—3. *Rhipidoblatta brevisvalvata* VISHNIAKOVA, Jurassic of the USSR, $\times 2$ (all Vishniakova, 1968).

Order ISOPTERA Brullé, 1832

[Isoptera BRULLÉ, 1832, p. 66]

Wings membranous, usually very similar, held flat over abdomen at rest, and possessing a transverse humeral or basal suture; veins

in anterior part of wings more strongly sclerotized than in remainder; crossveins very weakly developed, commonly forming delicate reticulation covering all or greater part of wing surface; vein C marginal; SC simple or branched, in some species very short or



FIG. 81. Isoptera; holotype specimen of *Cretatermes carpenteri*, Hodotermitidae, Cretaceous of Labrador, $\times 16.5$ (Carpenter, new).

completely absent as distinct vein; radial system usually consisting of distinct R of variable length, equally distinct RS1+2 arising from R very near base of wing, and more highly developed RS3+4 arising about at origin of RS1+2 and forming a series of branches extending to apical or subapical region of wing (with much variation in degree of development of these radial veins); M weak but often extensively branched, no indication of division into MA and MP; CUA also weak, tending to be extensively branched along posterior margin; CUP usually weak and commonly short; anal fold formed along CUP in some; 1A usually short and reduced. Mouthparts mandibulate; antennae moniliform; cerci distinct in all castes. All species social and polymorphic, their communities composed of reproductive forms and numerous workers and soldiers. *Cret.—Holo.*

The Isoptera, commonly known as termites, are clearly related to the orthopteroids and show closest affinities with the Blattodea (McKITTICK, 1964, 1965). The known range of the existing family Mastotermitidae, universally regarded as the most primitive family, is only from the late Oligocene or early Miocene. The earliest records of the order, however, consist of two genera from the Cretaceous (EMERSON, 1967; JARZEMBOWSKI, 1981). Both belong to the existing

family Hodotermitidae, which, although less specialized than the Termitidae, is distinctly more advanced than the Mastotermitidae with respect to both morphology and social behavior. It seems almost certain, therefore, that some species closely related to the Mastotermitidae will eventually be found in Jurassic or even Triassic deposits.

The brief geological record of the Mastotermitidae is, in fact, of much significance. The family includes only one living species, *Mastotermes darwiniensis*, restricted to tropical Australia. The Tertiary record of the family, however, contains representatives from all other continents except Africa, suggesting a wide dispersal during the Mesozoic (EMERSON, 1965). Also, the presence of specimens of all castes in mid-Tertiary amber from Mexico shows that by that time the family had achieved as complicated a social structure as now exists in *M. darwiniensis* (KRISHNA & EMERSON, 1983).

That some degree of social behavior was present among the Isoptera as far back as the Cretaceous is also apparent. In all existing termites the main part of the wing is separated from its base by a line of fracture, the humeral or basal suture (Fig. 81, *Cretatermes*; see also Fig. 82, 2a, *Mastotermes*, and Fig. 83, 7a, *Proelectrotermes*); shortly after the adult's flight from the parent colony, the

wings break off at the suture, leaving a stub or scale. The dropping of the wings after nuptial flight is obviously related to the founding of a new colony, the wings no longer being useful. The presence of humeral sutures in the Cretaceous specimens is therefore convincing evidence that colony founding had already been developed in the family Hodotermitidae by the Early Cretaceous.

Five of the six families of Isoptera generally recognized (EMERSON & KRISHNA, 1975) have records extending at least into the Tertiary: the Mastotermitidae and Kalotermitidae from the Eocene, the Hodotermitidae from the Cretaceous, the Rhinotermitidae from the Oligocene, and the Termitidae from the Miocene. The family Serritermitidae, which is based on a single genus, has no known geological record.

In the course of their evolution the Isoptera have tended toward a secondarily homonomous condition of the wings. The primitive hind wing of the Mastotermitidae has a small but distinct anal lobe, which does not occur in any other family. In general, also, the tendency has been for reduction of the wing veins, with R and SC losing their identity as the anterior veins become compressed toward the anterior margin. These are relatively minor changes, however, in comparison with the differentiation of castes and the development of social behavior, which reach extraordinary levels of complexity in the Termitidae.

The Isoptera is one of the very few orders of insects of which the extinct forms have received careful study by specialists on recent species. SNYDER's catalogue of the Isoptera of the world, including the extinct species (1949); EMERSON's review of the Termopsinae (1933), his account of the geographic origins of termite genera (1955), and his reviews of the Mastotermitidae (1965), Kalotermitidae (1969), and Rhinotermitidae (1971); and KRISHNA's earlier revisional study of the Kalotermitidae (1961) and his joint paper with EMERSON on *Mastotermes* (1983) cover almost completely the record of the fossil Isoptera.

Family MASTOTERMITIDAE

Desneux, 1904

[Mastotermitidae DESNEUX, 1904a, p. 284]

Hind wing with distinct anal lobe; tarsi clearly with 5 segments; left mandible with 2 marginal teeth. EMERSON, 1965. *Eoc.*—*Holo.*

Mastotermes FROGGATT, 1896, p. 517 [= *Pliotermes* PONGRÁ CZ, 1926, p. 26 (type, *P. hungaricus*)]. EMERSON, 1965; JARZEMBOWSKI, 1980; KRISHNA & EMERSON, 1983. *Eoc.*, England; *Oligo.*, Europe (Germany), England; *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*—FIG. 82.2. *M. darwiniensis* FROGGATT, recent; *a*, fore and *b*, hind wings (humeral suture absent), $\times 2$ (CSIRO, 1970).

Blattotermes RIEK, 1952b, p. 17 [**B. neoxenus*; OD]. Similar to *Mastotermes* but with less consolidation of RS. COLLINS, 1925; EMERSON, 1965. ?*Eoc.*, Australia (Queensland); *Eoc.*, USA (Tennessee).—FIG. 82.3a. **B. neoxenus*, ?*Eoc.*, Australia; fore wing, $\times 2.4$ (Riek, 1952a).—FIG. 82.3b. *B. wheeleri* (COLLINS), *Eoc.*, Tennessee; wing, $\times 2.0$ (Collins, 1925).

Miotermes VON ROSEN, 1913, p. 325 [**M. procerus* HEER; OD]. Wing venation as in *Mastotermes* but with more extensively developed M. [Family assignment doubtful.] *Mio.*, Europe (Germany, Yugoslavia).—FIG. 82.1. **M. procerus* (HEER); hind wing, $\times 1.8$ (Pongrácz, 1926).

Spargotermes EMERSON, 1965, p. 19 [**S. costalimai*; OD]. Hind wings: RS diffuse, with several main branches forking to form additional branches reaching to wing tip. *Mio./Plio.*, Brazil.—FIG. 82.4. **S. costalimai*; hind wing with anal area folded under rest of wing, $\times 3.4$ (Emerson, 1965).

Family KALOTERMITIDAE

Froggatt, 1896

[Kalotermitidae FROGGATT, 1896, p. 516]

Wing membrane reticulate; vein R short and almost always unbranched; pronotum as wide as head or nearly so; 4 tarsal segments. KRISHNA, 1961; EMERSON, 1969. *Eoc.*—*Holo.*

Kalotermes HAGEN, 1853, p. 479. HAGEN, 1861–1863; HANDLIRSCH, 1907; COCKERELL, 1917a; SNYDER, 1949; KRISHNA, 1961; EMERSON, 1969; JARZEMBOWSKI, 1980. *Eoc.*, Europe (France); *Oligo.*, England, Europe (Baltic, Germany); *Mio.*, Europe (Germany, Italy), Asia (Burma)—*Holo.*

Calcaritermes SNYDER, 1925, p. 155. EMERSON, 1969. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Cryptotermes BANKS, 1906, p. 336. [Generic position of fossil uncertain.] PIERCE, 1958. *Mio.*, USA (California)—*Holo.*

Electrotermes VON ROSEN, 1913, p. 331 [**Termes*

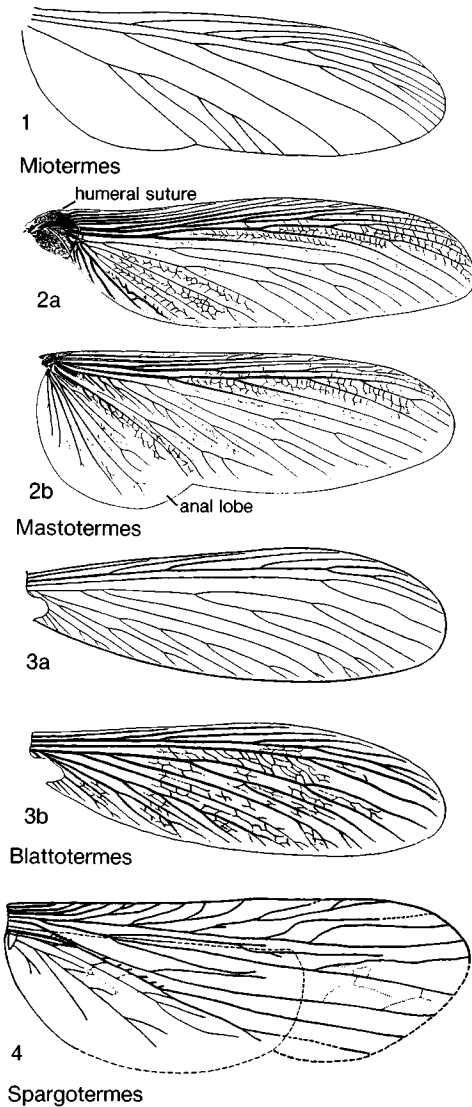


FIG. 82. Mastotermitidae (p. 139).

affinis HAGEN in PICTET & HAGEN, 1856, p. 49; OD]. Similar to *Kalotermes*, but middle tibiae with 2 outer spines distally. KRISHNA, 1961; EMERSON, 1969. *Oligo.*, Europe (Baltic).—FIG. 83,6. *E. affinis* (HAGEN); a, fore wing, $\times 7.0$; b, right middle leg, $\times 1.2$ (both Krishna, 1961).

Eotermes STATZ, 1939–1940, p. 13 [**E. grandaeva*; OD]. Similar to *Proelectrotermes* but much larger; lateral spines on middle tibiae relatively shorter; M weak, its main stem close and parallel to RS. EMERSON, 1969. *Oligo.*, Europe (Germany).—FIG. 83,8. **E. grandaeva*; fore wing, $\times 1.5$ (Emerson, 1969).

Incisitermes KRISHNA, 1961, p. 353. EMERSON, 1969. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Neotermes HOLMGREN, 1911, p. 53. PITON, 1940a; EMERSON, 1969. *Eoc.*, Europe (France)—*Holo.*

Proelectrotermes VON ROSEN, 1913, p. 331 [**Kalotermes berendtii* PICTET in PICTET & HAGEN, 1856, p. 49; OD]. Similar to *Kalotermes*, but middle tibiae with a single inner-lateral spine and 2 outer-lateral spines; fore wing with a very short SC; branches of RS directed anteriorly and terminating on anterior margin; M slightly nearer to RS than to CU at midwing. SCUDDER, 1883a; KRISHNA, 1961; EMERSON, 1969. *Oligo.*, Europe (Baltic).—FIG. 83,7. **P. berendtii* (PICTET); a, fore wing as preserved, $\times 5.5$; b, right middle leg, $\times 6.0$ (both Krishna, 1961).

Prokalotermes EMERSON, 1933, p. 189 [**Parotermes hageni* SCUDDER, 1883a, p. 139; OD]. Similar to *Proelectrotermes* but with 24 to 26 antennal segments. EMERSON, 1969; LEWIS, 1977a. *Oligo.*, USA (Colorado, Montana).

Family HODOTERMITIDAE

Desneux, 1904

[Hodotermitidae DESNEUX, 1904b, p. 14]

Wings with vein CU well developed; short anal vein present in hind wing; ocelli absent; left mandible with 3 marginal teeth; pronotum usually much narrower than head; tarsi with 4 segments. *Cret.*—*Holo.*

Hodotermes HAGEN, 1853, p. 480. *Holo.*

Archotermopsis DESNEUX, 1904b, p. 13. VON ROSEN, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Cretatermes EMERSON, 1967, p. 284 [**C. carpenteri*; OD]. Fore wing small, humeral suture evenly curved; RS area gradually widened from base to apical quarter of wing; M about midway between RS and CU; CU short, not reaching beyond basal half of posterior margin of wing. *Cret.*, Canada (Labrador).—FIG. 81. **C. carpenteri*; holotype, $\times 16.5$ (Carpenter, new).—FIG. 83,5. **C. carpenteri*; venation of fore wing, $\times 8.0$ (Emerson, 1967).

Parotermes SCUDDER, 1883a, p. 135 [**P. insignis*; OD]. Second marginal tooth of left mandible slightly shorter than first marginal tooth; posterior edge of second marginal tooth and anterior edge of third marginal tooth not symmetrical. *Oligo.*, USA (Colorado).—FIG. 83,4. **P. insignis*; outline of left mandible, $\times 26$ (Emerson, 1933).

Termopsis HEER, 1849, p. 23 [**T. breinii*; SD HAGEN, 1858c, p. 74] [= *Xestotermopsis* VON ROSEN, 1913, p. 330, obj.]. Similar to *Zootermopsis* but having 5 hind tarsal segments visible above and below; humeral suture in fore wing only slightly curved. EMERSON, 1933. *Oligo.*,

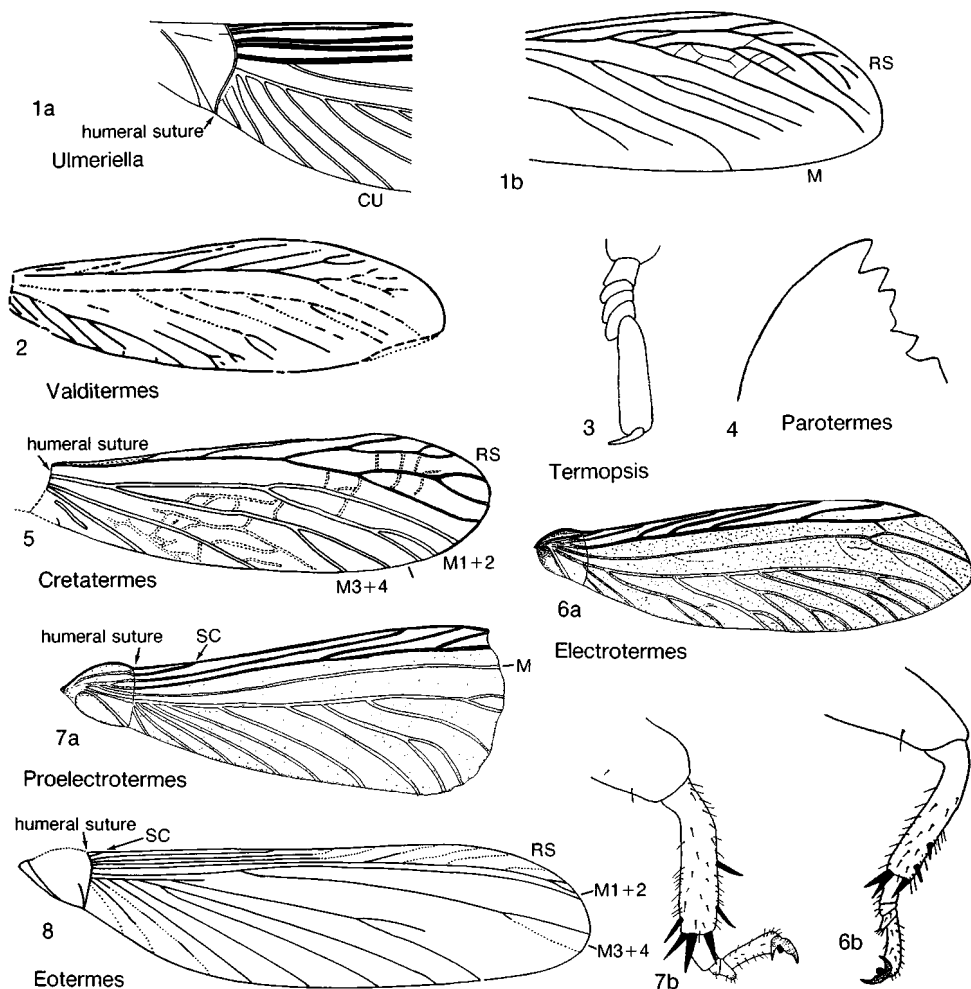


FIG. 83. Kalotermitidae and Hodotermitidae (p. 139-141).

Europe (Baltic).—FIG. 83,3. **T. breinii*; hind tarsus, $\times 7$ (Emerson, 1933).
Ulmeriella MEUNIER, 1920a, p. 728 [**U. bauckborni*; OD] [= *Diatermes* MARTYNOV, 1929, p. 178 (type, *D. cockerelli*)]. Vein RS with several branches directed posteriorly and terminating on hind margin. MARTYNOV, 1929; ZEUNER, 1938; STATZ, 1939-1940; SNYDER, 1949; WEIDNER, 1967, 1968b, 1971; EMERSON, 1968. *Oligo.*, Europe (Germany), USSR (Kazakh); *Mio.*, Europe (Germany), USA (Washington); *Plio.*, Europe (Germany).—FIG. 83,1. **U. bauckborni*; a, base of fore wing, $\times 8$; b, distal half of fore wing, $\times 6$ (both Emerson, 1968).
Valditermes JARZEMBOWSKI, 1981, p. 92 [**V. brenanae*; OD]. Similar to *Cretatermes* but larger; fore wing more elongate; branching of RS and CU more complex. *Cret.*, England.—FIG. 83,2.

**V. brenanae*; fore wing, $\times 5.5$ (Jarzembowski, 1981).
Zootermopsis EMERSON, 1933, p. 182. [Generic assignment doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Family RHINOTERMITIDAE
Froggatt, 1896

[*Rhinotermitidae* FROGGATT, 1896, p. 518]

Wings commonly reticulate; vein R much reduced; RS unbranched; M usually approaching very close to CU or coalesced with it; frontal gland always present; left mandible with 3 marginal teeth; ocelli present; tarsi with 4 segments, cerci with 2. *Oligo.*—*Holo.*

- Rhinotermes** HAGEN, 1858, p. 233. *Holo.*
Coptotermes WASMANN, 1896, p. 629. SNYDER, 1960; EMERSON, 1971. *Oligo./Mio.*, Dominican Republic, Mexico (Chiapas)—*Holo.*
Heterotermes FROGGATT, 1896, p. 518. Adult. SNYDER, 1960. *Mio.*, Mexico (Chiapas)—*Holo.*
Parastylotermes SNYDER & EMERSON in SNYDER, 1949, p. 378 [**Stylotermes washingtonensis* SNYDER, 1931, p. 317; OD]. Similar to *Reticulitermes*, but wing membrane and veins almost without hairs; eyes relatively larger than in *Reticulitermes*; ocelli distinct; stump of fore wing (basal scale) proportionately large. SNYDER, 1950, 1955; PIERCE, 1958. *Oligo.*, Europe (Baltic); *Mio.*, USA (Washington, California).
Reticulitermes HOLMGREN, 1913, p. 60. ARMBRUSTER, 1941; WEIDNER, 1955, 1971; PIERCE, 1958; EMERSON, 1971. *Oligo.*, Europe (Baltic, Germany), USA (Colorado); *Mio.*, USA (California), Europe (Germany); *Plio.*, Europe (Germany)—*Holo.*
Rhinotermes ARMBRUSTER, 1941, p. 21 [**R. dzierzoni*; OD]. Little-known genus, based on wing and body fragments. EMERSON, 1971. *Mio.*, Europe (Germany).

Family TERMITIDAE

Westwood, 1840

[Termitidae WESTWOOD, 1840, p. 11]

Wings not conspicuously reticulate; vein R greatly reduced or absent; left mandible usually with 2 marginal teeth; frontal gland well developed; basal scale of fore wing always proportionately small. *Mio.*—*Holo.*

- Termes** LINNÉ, 1758, p. 609. *Holo.*
Gnathamitermes LIGHT, 1932, p. 390. PIERCE, 1958. *Mio.*, USA (California)—*Holo.*
Macrotermes HOLMGREN, 1909, p. 193. [Generic assignment of fossil doubtful.] CHARPENTIER, 1843; SNYDER, 1949. *Mio.*, Europe (Yugoslavia)—*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the order Isoptera, are too poorly known to permit family assignment.

- Architermes** HAUPT, 1956, p. 28 [**A. simplex*; OD]. Little-known wing. *Eoc.*, Europe (Germany).
Mastotermes ARMBRUSTER, 1941, p. 13 [**M. stuttgartensis*; OD]. Little-known genus, possibly a synonym of *Miotermes*. EMERSON, 1971. *Plio.*, Europe (Germany).
Metatermes ARMBRUSTER, 1941, p. 26 [**M. statzi*; OD]. Little-known genus. EMERSON, 1971. *Mio.*, Europe (Germany).

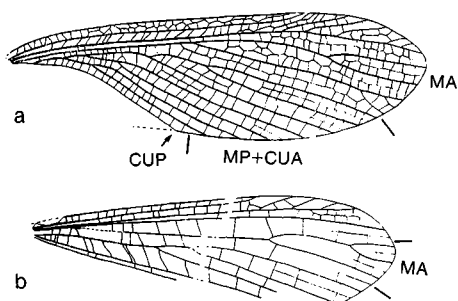
Order MANTEODEA

Burmeister, 1838

[Manteodea BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 517, as Mantodea]

Fore wings usually tegminous, strongly so in most, more rarely membranous; costa marginal, no precostal space; vein SC distinct, long, extending well beyond midwing; R strongly developed, terminating nearly at wing apex; RS arising distally, consisting of 1 or several distal branches, or commonly absent as distinct vein; M well developed, typically dividing near base into 2 main branches, which may represent MA and MP (SHAROV, 1962a); CUA apparently anastomosed with stem of posterior branch of M; CUP separating from CUA at wing base, nearly straight, unbranched; anal veins at least slightly sigmoidal; posterior part of anal area commonly expanded to form small, prominent lobe containing distal parts of several anal veins. Hind wings with slender remigium, anal area greatly expanded; RS unbranched, arising near wing base; M fused basally with stem of R; MP apparently diverging from R and anastomosing with CUA; MA continuing nearly straight, unbranched; CUA extensively developed, with several branches; CUP and 1A unbranched, nearly straight; several radiating anal veins. Antennae of moderate length, multisegmented; mouthparts mandibulate; forelegs raptorial, others cursorial; tarsi typically with 5 segments; pronotum not usually extending over head; prothorax commonly (but not invariably) elongate, forelegs attached near anterior end; ovipositor not usually developed externally but rarely protruding slightly; cerci usually conspicuous, multisegmented. *Oligo.*—*Holo.*

The Manteodea, although clearly related to the Orthoptera, are less specialized in some respects (e.g., five-segmented tarsi, segmented cerci). In all probability they are even more closely related to the Blattaria (McKITTRICK, 1964, 1965) but appear to have been derived independently from a protorthopterous stock and to have evolved



Lithophotina

FIG. 84. Chaeteessidae (p. 143).

entirely as predators; the raptorial forelegs, present in all known species, show several types of modification. Although the oldest known Manteodea are from the Baltic amber (Oligocene), the group probably existed in the Mesozoic and even in the Permian. Some of the Late Carboniferous Protorthoptera are known to have possessed raptorial forelegs, but they do not appear to be related closely to the Manteodea.

The venation of the Manteodea is clearly orthopteroid but is characterized by such distinct features as the differences in RS in the fore and hind wings and the apparent anastomosis of MP and CUA in both wings. Convexities and concavities, as in the Orthoptera, are not distinct for all veins. Veins SC and CUP are markedly concave and R and CUA similarly convex; RS and M show no definite topography. That both MA and MP are present in the hind wing is suggested by the basal separation of veins that appear to be main branches of M, although other interpretations of these branches are possible. The evidence for the presence of MP in the fore wing is virtually nonexistent in the Manteodea and rests upon the similarity of that part of the fore wing to the corresponding part of the hind wing.

Family CHAETEESSIDAE
Handlirsch, 1920

[Chaeteessidae HANDLIRSCH, 1920, p. 497]

Fore wing having vein R with several distinct, anteriorly pectinate branches distally;

fore tarsus attached to distal end of tibia; tibia lacking terminal projecting hook. *Oligo.*—*Holo.*

Chaeteessa BURMEISTER, 1838, p. 527. [Generic assignment very dubious.] GIEBEL, 1862. *Oligo.*, Europe (Baltic)—*Holo.*

Lithophotina COCKERELL, 1908s, p. 343 [**L. floccosa*; OD]. Similar to *Chaeteessa* (recent) but with more pectinate branches on R in fore wing. SHAROV, 1962a. *Oligo.*, USA (Colorado).—FIG. 84. **L. floccosa*; a, fore wing and b, remigium of hind wing, $\times 2.5$ (Cockerell, 1908s).

Family MANTEIDAE Saussure, 1859

[*nom. correct.* ROBERTS, 1941, p. 15, *pro* Mantidae SAUSSURE, 1859, p. 59]

Fore wing having R with 2 or fewer anteriorly pectinate branches distally; fore tibia extending beyond point of tarsal attachment, forming curved, projecting hook. *Oligo.*—*Holo.*

Mantis LINNÉ, 1758, p. 425. ZEUNER, 1931. *Mio.*, Europe (Germany)—*Holo.*

Eobruneria COCKERELL, 1913b, p. 343 [**E. tessellata*; OD]. Little-known genus, based on fragment of fore wing with broad costal area. [Possibly related to *Stagmomantis* (recent).] *Oligo.*, USA (Colorado).

Order PROTELYTROPTERA

Tillyard, 1931

[Protelytroptera TILLYARD, 1931, p. 234] [=Protocoleoptera TILLYARD, 1924b, p. 434]

Small to medium-sized insects, related to the orthopteroids. Head small, eyes conspicuous; antennae prominent, moderately long, stout, multisegmented; pronotum broad, flattened, commonly with microtrichia laterally; legs robust, spiny, with 5 tarsal segments. Fore wings typically forming convex elytra (only rarely flat) with distinct venation in primitive forms and weak venation in specialized species; costal area expanded at base of wing, forming prominent, flattened lobe (costal expansion); veins SC, R, RS, M, CUA, CUP, and 3 anal veins present in more generalized forms; in more specialized species only basal parts of SC, RS, and CUP discernible; most species with submarginal thickening (sutural margin) parallel to pos-

terior margin of elytron; cluster of small setae commonly present near subcosta and another along basal part of sutural margin; in Megelytridae microtrichia covering entire elytron. Hind wings typically longer and much broader than elytra; anal area expanded, with longitudinal and, in some families, transverse folding. Abdomen broad, terminating in short but prominent cerci about as long as last 3 abdominal segments. Females with short external ovipositor. Immature stages unknown. CARPENTER & KUKALOVÁ, 1964. *Perm.—Cret.*

The fore wings in this extinct order of elytriphorous insects resemble those of the Coleoptera, but the general nature of the venation of both fore and hind wings and the presence of prominent cerci indicate relationship with the orthopteroids, especially the Blattaria and Dermaptera. Although few species of Protelytroptera are known at present, their diversity suggests that the order was a large and varied group, at least during the Permian. The relatively recent discovery of the family Umenocoleidae in a Cretaceous deposit (see below) indicates that the order may have continued to diversify throughout the Mesozoic.

In the more primitive species the fore wings tended to be tegminous and almost flat, with the costal expansion small, the sutural margin absent or weakly developed, and the crossveins numerous (e.g., Archelytridae, Apachelytridae). In the more specialized forms, in which the fore wings were convex and heavily sclerotized, the main veins were reduced or obsolescent distally, crossveins were virtually absent, and the surfaces of the elytra were granulate or rugose (e.g., Protelytridae, Permelytridae, Planelytridae, Umenocoleidae).

The hind wings, which are known in four families (Archelytridae, Protelytridae, Permelytridae, Apachelytridae), had a narrow remigium and a well-developed anal fan. However, there were substantial differences in the structure of the wings in these families. Those of the Protelytridae could fold at rest transversely as well as longitudinally

(TILLYARD, 1931; CARPENTER, 1933a), but those of the Permelytridae and Apachelytridae could apparently fold only longitudinally (CARPENTER & KUKALOVÁ, 1964).

The body structure is known, very incompletely, in the families Protelytridae, Permelytridae, and Apachelytridae.

Family ELYTRONEURIDAE Carpenter, 1933

[Elytroneuridae CARPENTER, 1933a, p. 478]

Elytron nearly flat, not convex; sutural margin apparently absent; vein SC branched; M and CUA fused for considerable distance beyond wing base. *Perm.*

Elytroneura CARPENTER, 1933a, p. 478 [*E. permiana*; OD]. Costal margin convex, costal expansion very prominent; SC remote from anterior wing margin. *Perm.*, USA (Kansas).—FIG. 85.4. *E. permiana*; elytron, $\times 4$ (Carpenter, 1933a).

Family ARCHELYTRIDAE Carpenter, 1933

[Archelytridae CARPENTER, 1933a, p. 477]

Elytron slightly convex; costal expansion weakly developed; stems of main veins independent; vein SC long, terminating about two-thirds of wing length from base; SC, R, M, CUP, and 1A unbranched; CUP strongly concave; sutural margin well developed, terminating before apex; weak crossveins over entire wing. *Perm.*

Archelytron CARPENTER, 1933a, p. 477 [*A. superbium*; OD]. Costal margin strongly arched. Vein SC weakly developed at base but strong distally; RS arising at level of termination of SC; CUA and CUP diverging about one-fifth wing length from base; CUA with 3 terminal branches; most crossveins unbranched. [The generic name *Archelytron* was subsequently proposed by HAUPT (1952, p. 248) for a Permian species, *priscus*, that he assigned to the Coleoptera. However, Dr. Jörg SCHNEIDER of the Bergakademie Freiberg, Germany, who recently examined the unique specimen for me, found that it is a plant fragment, not an insect. No homonymy is, therefore, involved.] CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).—FIG. 85.2. *A. superbium*; fore wing, $\times 8$ (Carpenter & Kukalová, 1964).

Ortelytron KUKALOVÁ, 1965, p. 66 [*O. europaeum*; OD]. Similar to *Archelytron*, but fore wing with much shorter sutural margin and with crossveins

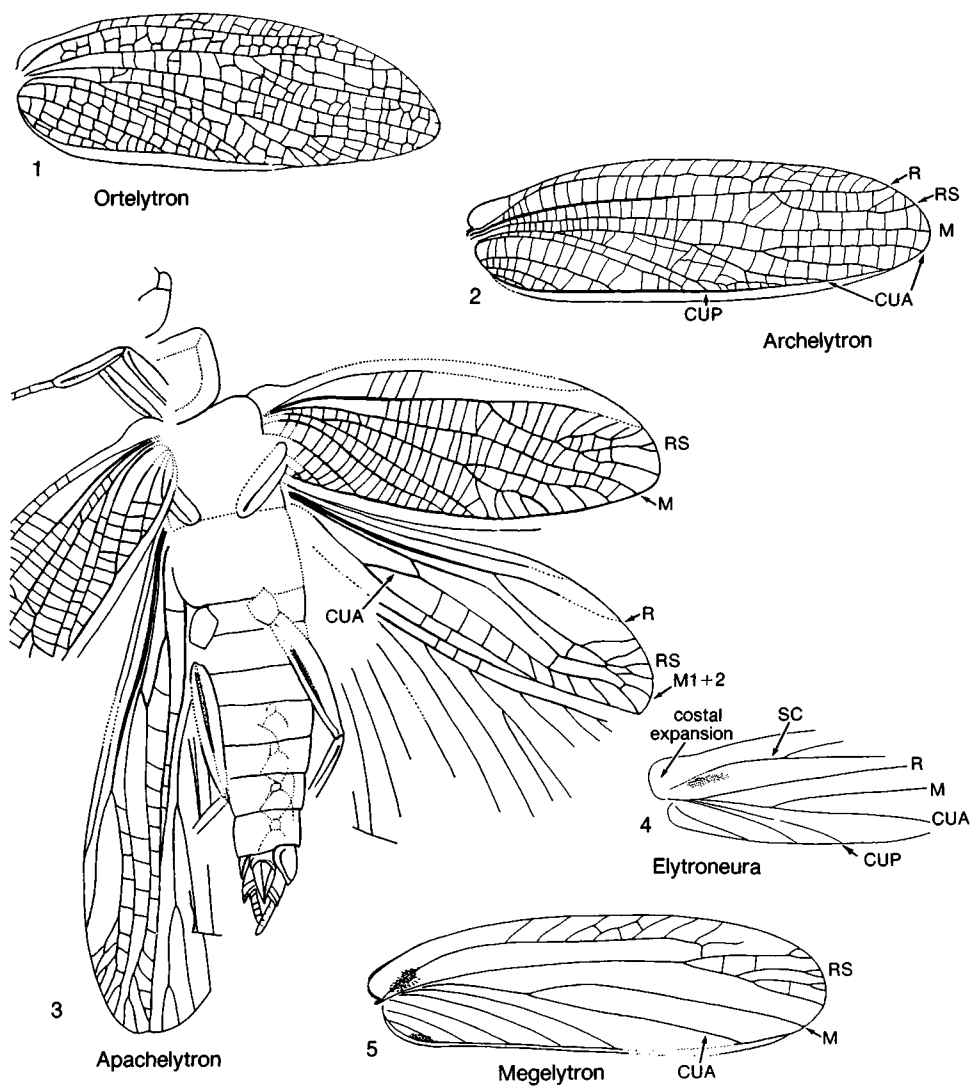


FIG. 85. Elytroneuridae, Archelytridae, Apachelytridae, and Megelytridae (p. 144–147).

more irregular. Hind wing with CUP and 1A close together and parallel from wing base to distal margin. *Perm.*, Europe (Czechoslovakia). —FIG. 85, 1. **O. europaeum*; fore wing, ×14 (Kukalová, 1965).

Family APACHELYTRIDAE
Carpenter & Kukalová, 1964

[Apachelytridae CARPENTER & KUKALOVÁ, 1964, p. 185]

Related to Archelytridae. Fore wing weakly tegminous, similar to that of Archelytridae, but costal expansion larger and crossveins

more numerous and virtually all unbranched. Hind wing with expanded anal area as in Protelytridae; stem of vein M independent of R; M forked near midwing; CUP coalesced with 1A. Body little known; eyes relatively small; pronotum rectangular; forelegs short, hind legs much longer, with well-developed femora; tarsi short, segmented. *Perm.*

Apachelytron CARPENTER & KUKALOVÁ, 1964, p. 187 [**A. transversum*; OD]. Costal margin of fore wing arched; RS arising slightly beyond

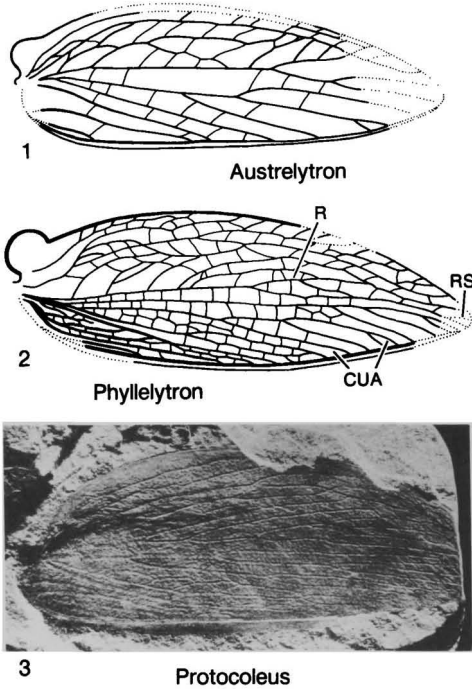


FIG. 86. Protocoleidae (p. 146).

midwing. *Perm.*, Europe (Moravia).—FIG. 85,3. **A. transversum*; holotype as preserved, $\times 9$ (Carpenter & Kukalová, 1964).

Family PROTOCOLEIDAE Tillyard, 1924

[Protocoleidae TILLYARD, 1924b, p. 434]

Fore wing tegminous, only slightly convex; anterior margin strongly arched; sutural margin nearly straight and bordering entire posterior margin; wing surface granulate and with tubercles at least in some areas; setae commonly present in subcostal area; costal expansion large; vein SC long with several to many branches; RS arising near midwing; M and CUA with several branches, variable in form. Hind wing and body unknown. *Perm.*

Protocoleus TILLYARD, 1924b, p. 434 [**P. mitcheli*; OD]. Fore wing uniformly covered with flat tubercles; main veins and their branches parallel with longitudinal axis of wing; RS arising near midwing. KUKALOVÁ, 1966. *Perm.*, Australia (New South Wales).—FIG. 86,3. **P. mitcheli*; fore wing, holotype, $\times 3.2$ (Tillyard, 1924b).

Austrelytron KUKALOVÁ, 1966, p. 96 [**A. tillyardi*; OD]. Similar to *Protocoleus* but with fewer branches of main veins and crossveins; tubercles few and pointed. *Perm.*, Australia (New South Wales).—FIG. 86,1. **A. tillyardi*; fore wing, $\times 5$ (Kukalová, 1966).

Phyllelytron KUKALOVÁ, 1966, p. 94 [**P. folium*; OD]. Similar to *Protocoleus*, but main veins and their branches very irregular, not aligned or parallel with longitudinal axis of wing; granulation of wing surface coarse. *Perm.*, Australia (New South Wales).—FIG. 86,2. **P. folium*; fore wing, $\times 2.3$ (Kukalová, 1966).

Family PROTELYTRIDAE Tillyard, 1931

[Proteilytridae TILLYARD, 1931, p. 235]

Elytron convex, anterior margin strongly arched; vein SC short, not extending beyond midwing; venation and sutural margin well developed; RS and CUP unbranched; M free from CUA or coalesced with it basally for a short interval; 3 or 4 anal veins. Hind wing: anal area with about 10 anal veins; stem of M coalesced with R. Body apparently flattened; antenna well developed, with short, thick segments. *Perm.*

Proteilytron TILLYARD, 1931, p. 239 [**P. permianum*; OD]. Vein CUA unbranched; patches of setae along SC and basal part of sutural margin. *Perm.*, USA (Kansas).—FIG. 87,3a. *P. furcatum* CARPENTER; elytron, $\times 8.8$ (Carpenter, 1933a).—FIG. 87,3b. **P. permianum*; reconstruction, $\times 5.4$ (Carpenter, 1933a).

Permelytropis CARPENTER, 1933a, p. 474 [**P. cubitalis*; OD]. CU unbranched. *Perm.*, USA (Kansas).—FIG. 87,1. **P. cubitalis*; elytron, $\times 10$ (Carpenter, 1933a).

Uraleytron ROHDENDORF, 1939, p. 506 [**U. martynovi*; OD]. Little-known elytron and body fragments. [Family assignment uncertain.] *Perm.*, USSR (Asian RSFSR).—FIG. 87,2. **U. martynovi*; elytron, $\times 8$ (Rohdendorf, 1939).

Family MEGELYTRIDAE Carpenter, 1933

[Megelytridae CARPENTER, 1933a, p. 476]

Fore wing flat except for basal part of costal area; costal expansion very small; vein R very strong; RS arising in distal part of wing, branched; CUA and M coalesced basally, both unbranched; sutural margin complete; several oblique crossveins in costal area; entire

wing with a dense covering of fine hair. Hind wing unknown. *Perm.*

Megelytron TILLYARD, 1931, p. 247 [**M. robustum*; OD]. Vein RS with 4 terminal branches and several twigs; one cluster of setae at base of subcosta and another near inner margin of anal area. CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).—FIG. 85,5. **M. robustum*; fore wing, $\times 5$ (Carpenter & Kukalová, 1964).

Family PLANELYTRIDAE
Kukalová, 1965

[Planelytridae KUKALOVÁ, 1965, p. 75]

Fore wing almost flat; anterior margin strongly arched; costal expansion well developed; vein SC extending about two-thirds of wing length from base; veins M and CUA coalesced for about one-third wing length from base; sutural margin well developed. *Perm.*

Planelytron KUKALOVÁ, 1965, p. 75 [**P. planum*; OD]. SC strongly arched in costal area; weak crossveins in subcostal area. *Perm.*, Europe (Czechoslovakia).—FIG. 88,2. **P. planum*; fore wing, $\times 8$ (Kukalová, 1965).

Family PERMELYTRIDAE
Tillyard, 1931

[Permelytridae TILLYARD, 1931, p. 246] [=Blattelytridae TILLYARD, 1931, p. 249; Acosmelytridae TILLYARD, 1931, p. 252]

Fore wing convex; costal margin arched; veins weakly developed, commonly obsolescent distally; vein RS absent; MA commonly free from CU, rarely coalesced with it; sutural margin normally developed. Hind wing apparently like that of *Protelytron*, but SC much longer and terminating on RS. Body little known; head smaller than in Protelytridae and Apachelytridae; antenna, as preserved, about as long as abdomen; cerci short, segmented. *Perm.*

Permelytron TILLYARD, 1931, p. 246 [**P. schucherti*; OD]. Vein M of fore wing not coalesced with CUA. CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).—FIG. 88,4. **P. schucherti*; elytron, $\times 6.7$ (Carpenter, 1939).

Blattelytron TILLYARD, 1931, p. 250 [**B. permianum*; OD]. Little-known genus, based on fragment of elytron. *Perm.*, USA (Kansas).—FIG. 88,5. **B. permianum*; elytron, $\times 5$ (Tillyard, 1931).

Parablattelytron TILLYARD, 1931, p. 251 [**P. sub-*

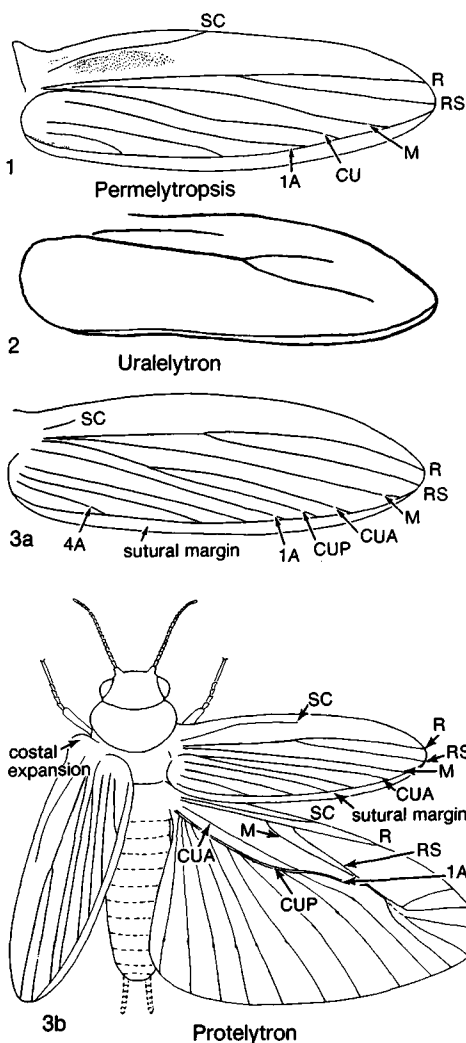


FIG. 87. Protelytridae (p. 146).

incisum; OD] [=Acosmelytron TILLYARD, 1931, p. 253 (type, *A. elongatum*)]. Vein CUA coalesced with M basally; main veins commonly obsolescent in distal half of wing. *Perm.*, USA (Kansas).—FIG. 88,6. **P. subincisum*; dorsal view as preserved, $\times 7$ (Carpenter & Kukalová, 1964).

Family PERMOPHILIDAE
Tillyard, 1924

[Permophilidae TILLYARD, 1924b, p. 430]

Fore wing tegminous, slightly convex; sutural margin distinct but narrow; wing surface with granulation and tubercles; costal

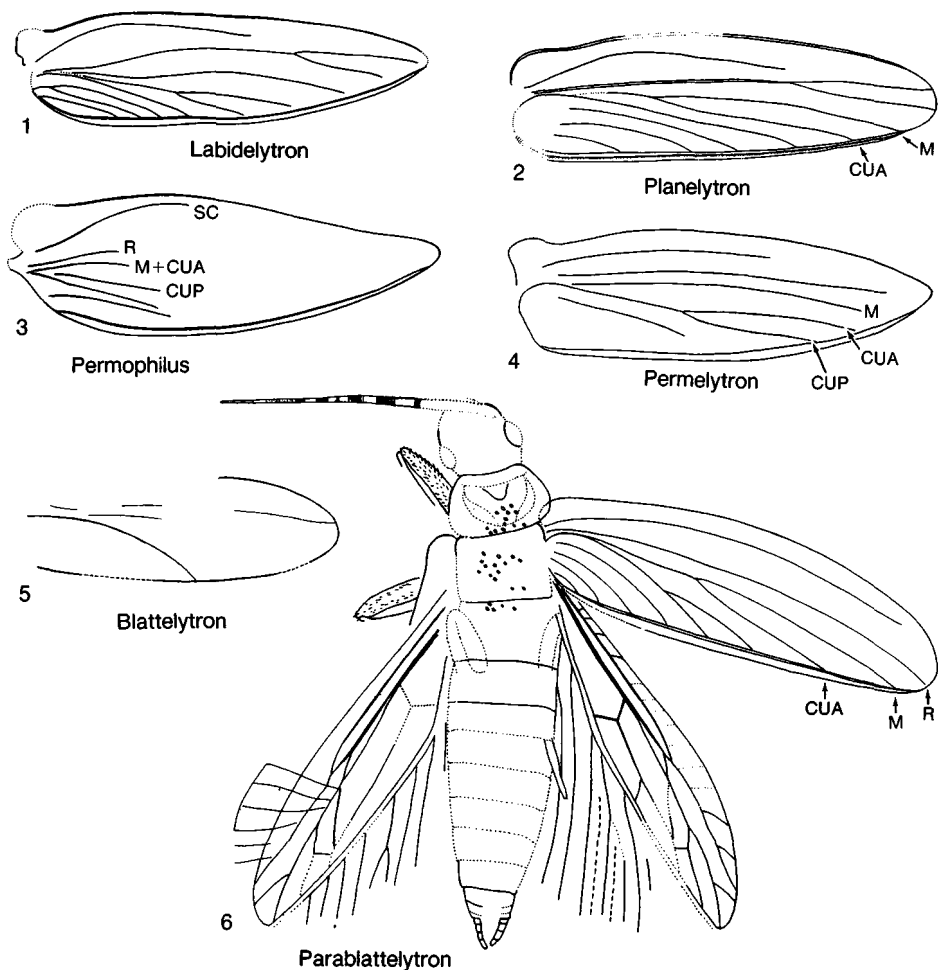


FIG. 88. Planelytridae, Permelytridae, Permophilidae, and Labidelytridae (p. 147–148).

expansion prominent; costal margin arched but asymmetrical; apex acute; main veins present in basal half of wing only. [Originally placed in Coleoptera.] *Perm.*

Permophilus TILLYARD, 1924b, p. 430 [**P. pincombei*; OD]. Fore wing with very narrow sutural margin; wing surface with dense granulation and indistinct tubercles; wing strongly narrowed in distal half. KUKALOVÁ, 1966. *Perm.*, Australia (New South Wales).—FIG. 88,3. *P. hirtus* KUKALOVÁ; fore wing, $\times 8$ (Kukalová, 1966).

Elytrathrix KUKALOVÁ, 1966, p. 102 [**E. hirsuta*; OD]. Similar to *Permophilus* but with conspicuous tubercles and setae in basal half of wing, including costal expansion. *Perm.*, Australia (New South Wales).

Family LABIDELYTRIDAE Kukalová-Peck, 1988

[Labidelytridae KUKALOVÁ-PECK, 1988, p. 339, *nom. subst. pro* Stenelytridae KUKALOVÁ, 1966, p. 102]

Fore wing tegminous, nearly flat, long and slender; apex pointed; surface finely granulate; costal expansion large; venation as in Protelytridae. *Perm.*

Labidelytron KUKALOVÁ-PECK, 1988, p. 339, *nom subst. pro Stenelytron* KUKALOVÁ, 1966, p. 102, *non* HANDLIRSCH, 1906 [**Stenelytron enervatum* KUKALOVÁ, 1966; OD]. Vein M of fore wing unbranched, not coalesced with CU basally. *Perm.*, Australia (New South Wales).—FIG. 88,1. **L. enervatum*; fore wing, $\times 4$ (Kukalová, 1966).

Xenelytron KUKALOVÁ, 1966, p. 105 [**X. ligula*; OD]. Similar to *Stenelytron*, but M coalesced with CU in basal half of wing. *Perm.*, Australia (New South Wales).

Family DERMELYTRIDAE

Kukalová, 1966

[Dermelytridae KUKALOVÁ, 1966, p. 105]

Fore wing convex, apparently weakly sclerotized; anterior margin convex; sutural margin well developed; venation much reduced, at most with only basal parts of veins R, CU, and A present. *Perm.*

Dermelytron KUKALOVÁ, 1966, p. 106 [**D. conservativum*; OD]. Fore wing oval, apex directed posteriorly; costal expansion small. *Perm.*, Australia (New South Wales).

Chanoselytron KUKALOVÁ, 1966, p. 108 [**C. gingiva*; OD]. Similar to *Dermelytron*, but costal expansion much larger. *Perm.*, Australia (New South Wales).

Psychelytron KUKALOVÁ, 1966, p. 108 [**P. progressivum*; OD]. Fore wing as in *Dermelytron*, but apex directed anterolaterally. *Perm.*, Australia (New South Wales).

Family UMENOCOLEIDAE

Chen & T'an, 1973

[Umenocoleidae CHEN & T'AN, 1973, p. 174]

Elytron apparently only slightly convex, elongate, with well-developed longitudinal veins; vein SC very close to and paralleling anterior margin of wing; R nearly parallel to SC; RS arising about one-fifth of wing length from base; M and CU coalesced; M diverging from common stem just before level of origin of RS, parallel to RS; CUA diverging posteriorly as far as midwing, then continuing parallel to posterior margin of wing; CUP apparently forked, with an anterior branch directed toward posterior margin of wing, then continuing parallel to CUA; 4 short anal veins; crossveins apparently absent, but surface of wing finely granulate. Hind wing little known, extending a short distance beyond end of fore wing. Body little known; antennae filiform, with at least 16 segments; pronotum broader than long, coarsely granulate. *Cret.*

The remarkable fossil on which this genus

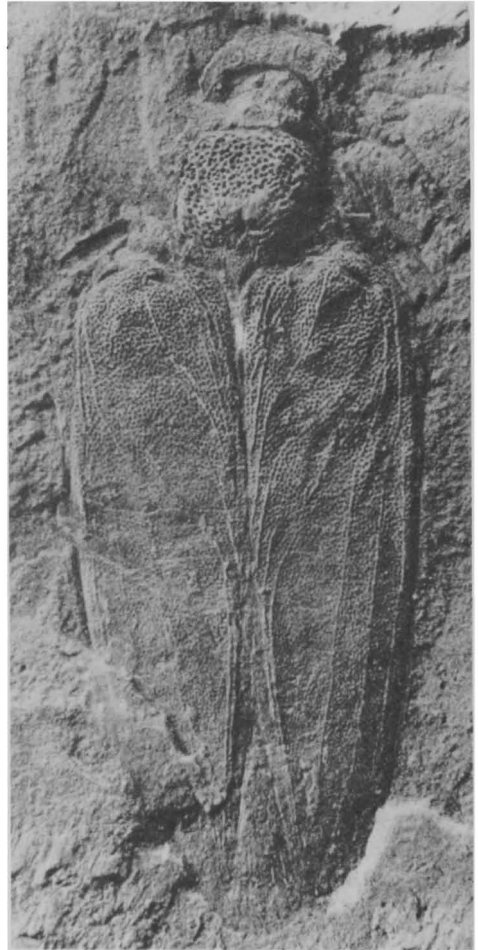
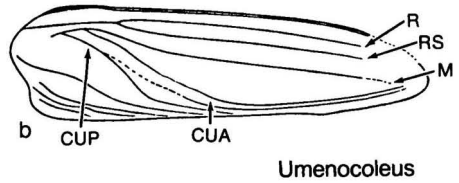


FIG. 89. Umenocoleidae (p. 150).

and family is based was placed by its authors in the order Coleoptera. However, the general structure of the elytra and of their venation in particular is so much like that of the Protelytroptera that I transferred the insect to that order. The filiform and segmented nature of the antennae and the peculiar vena-

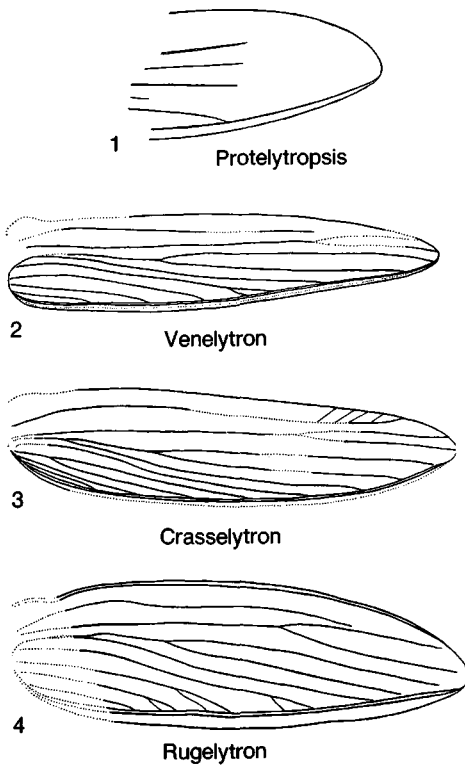


FIG. 90. Uncertain (p. 150).

tional pattern are not at all like those of the Coleoptera, as noted by the authors. Of course, since no Protelytroptera have been reported from deposits later than the Permian, this Cretaceous fossil extends the range of the order at least a hundred million years. It also suggests the possibility that some of the isolated and poorly preserved elytra found in Triassic or Jurassic deposits and identified as Coleoptera may actually be Protelytroptera.

Umenocoleus CHEN & T'AN, 1973, p. 169 [**U. sinuatus*; OD]. RS and CUA unbranched. *Cret.*, China (Kansu).—FIG. 89. **U. sinuatus*; a, dorsal view of holotype, $\times 7.0$ (Chen & T'an, 1973); b, elytron, $\times 4.5$ (after Chen & T'an, 1973).

Family UNCERTAIN

The following genera, apparently belonging to the order Protelytroptera, are too poorly known to permit assignment to families.

Artocoleus MARTYNOV, 1933b, p. 78 [**A. ivensis*; OD]. Little-known elytron. [Ordinal assignment doubtful.] *Perm.*, USSR (European RSFSR).

Crasselytron KUKALOVÁ, 1965, p. 70 [**C. convexum*; OD]. Fore wing very convex, slender and long; anterior margin nearly straight; SC extending nearly to wing apex; M coalesced with CUA for about one-third of wing length from base; wing surface granulate; sutural margin very narrow. *Perm.*, Europe (Czechoslovakia).—FIG. 90,3. **C. convexum*; fore wing, $\times 7$ (Kukalová, 1965).

Glablytron KUKALOVÁ, 1965, p. 77 [**G. lativenosum*; OD]. Fore wing flat; anterior margin arched; SC sigmoidal, unbranched, extending about two-thirds of wing length. *Perm.*, Europe (Czechoslovakia).

Protelytroptis TILLYARD, 1931, p. 245 [**P. grandis*; OD]. Distal fragment of large elytron. *Perm.*, USA (Kansas).—FIG. 90,1. **P. grandis*; elytron, $\times 7$ (Tillyard, 1931).

Rugelytron KUKALOVÁ, 1965, p. 72 [**R. fuscum*; OD]. Fore wing convex, relatively long; anterior margin arched; sutural margin well developed, extending to wing apex; M coalesced with CUA for about one-third of wing length from base; wing surface granulate. *Perm.*, Europe (Czechoslovakia).—FIG. 90,4. **R. fuscum*; fore wing, $\times 7$ (Kukalová, 1965).

Venelytron KUKALOVÁ, 1965, p. 73 [**V. tuberculatum*; OD]. Fore wing long and narrow; anterior margin nearly straight; SC long, extending nearly to apex; M and CUA coalesced for about one-third wing length from base; posterior margin of wing slightly concave distally; wing surface granulate. *Perm.*, Europe (Czechoslovakia).—FIG. 90,2. **V. tuberculatum*; fore wing, $\times 4.5$ (Kukalová, 1965).

Order DERMAPTERA de Geer, 1773

[Dermaptera DE GEER, 1773, p. 399]

Head broad, with mandibulate mouthparts and conspicuous antennae, consisting of at least 10 segments, usually many more; compound eyes commonly very large; ocelli absent in recent species; fore wings forming short, convex tegmina or elytra, typically lacking veins; hind wings semicircular, with greatly expanded anal area; remigium much reduced, with at most vestiges of veins SC, R, M, and CU; at rest, hind wings folded radially and also transversely beneath tegmina; hind wings commonly absent; abdomen usually broad, first tergum fused with

metathorax; in typical species (suborder Forficulina) cerci forming pair of heavily sclerotized, unsegmented forceps; ovipositor present in primitive species, absent in others. Immature stages similar to adults in general characteristics; cerci usually styliform. Subsocial habits in several genera. Most species omnivorous. *Jur.—Holo.*

The Dermaptera share many features of the Orthoptera and Blattaria, and they almost certainly arose from related stock. However, their peculiarly modified wings and thorax indicate that they belong to a widely divergent line.

The most distinctive characteristics of the Dermaptera are found in the modifications of their wings and cerci. Although the tegmina of existing species lack veins, those of most Jurassic species (suborder Archidermaptera) have veins that are apparently homologous with R, RS, M, CUA, and CUP of other insects (VISHNIAKOVA, 1980a). Also, two Jurassic genera belonging to the existing family Pygidicranidae, considered to be the most primitive of existing families, have several simple veins in the tegmina. The hind wings are membranous and when expanded are large and semicircular. The anterior half of the remigium is at least slightly sclerotized, forming a leathery scale; several of the main veins seem to have been lost in the sclerotization, only their basal parts persisting (Fig. 91). The rest of the hind wing is supported by a series of radiating veins, which appear to arise from a fulcrum at the distal end of the scale (Fig. 91). The complicated folding of these hind wings has been described in detail by MARTYNOV (1938b) and VERHOEFF (1917).

The heavily sclerotized forceps, which are modified cerci, show much diversity of form and size in recent Dermaptera. Segmentation of the forceps is not visible in adults of recent Dermaptera but is clearly indicated in the nymphs of some of the Pygidicranidae. The cerci of the adults of the Archidermaptera, all Jurassic, are very diverse in form, some being long and setaceous, with as many as 40 segments (VISHNIAKOVA, 1980a). In oth-

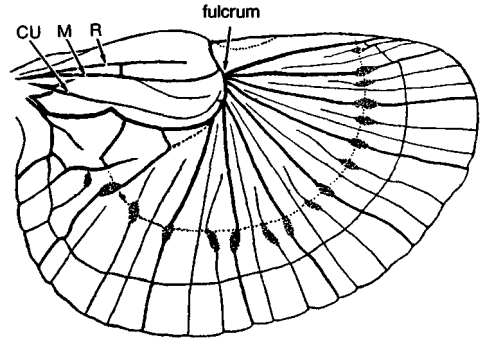


FIG. 91. Dermaptera; expanded hind wing of *Forficula auricularia* LINNÉ, Holocene (Bey-Bienko, 1936).

ers they are shorter, with a tendency for the basal segments to be more sclerotized and coalesced, forming incipient forceps (see Fig. 92,3).

The order Dermaptera is generally considered to consist of four suborders: Archidermaptera, Forficulina, Arixeniina, and Diploglossata. The last two, which include only a very few species, have no geological record; they are apterous, with short, styliform, unsegmented cerci, and are associated with bats (Arixeniina) or are ectoparasites of rodents (Diploglossata). The Archidermaptera include the most generalized members of the order and are known at present only from the Jurassic. The Forficulina, consisting of several families of typical earwigs, extend back to the Jurassic.

Suborder ARCHIDERMAPTERA Bey-Bienko, 1936

[Archidermaptera BEY-BIENKO, 1936, p. 215]

Tarsi with 4 or 5 segments; tegmina with distinct but much reduced venation; cerci commonly long, slender, multisegmented, rarely short. Hind wings unknown. *Jur.*

Family PROTODIPLATYIDAE Martynov, 1925

[Protodiplatyidae MARTYNOV, 1925b, p. 573] [=Protodiplatidae ROHDENDORF, 1957, p. 78, unjustified emendation]

Antenna filiform, with 17 to 23 segments, the first segment enlarged and second at least

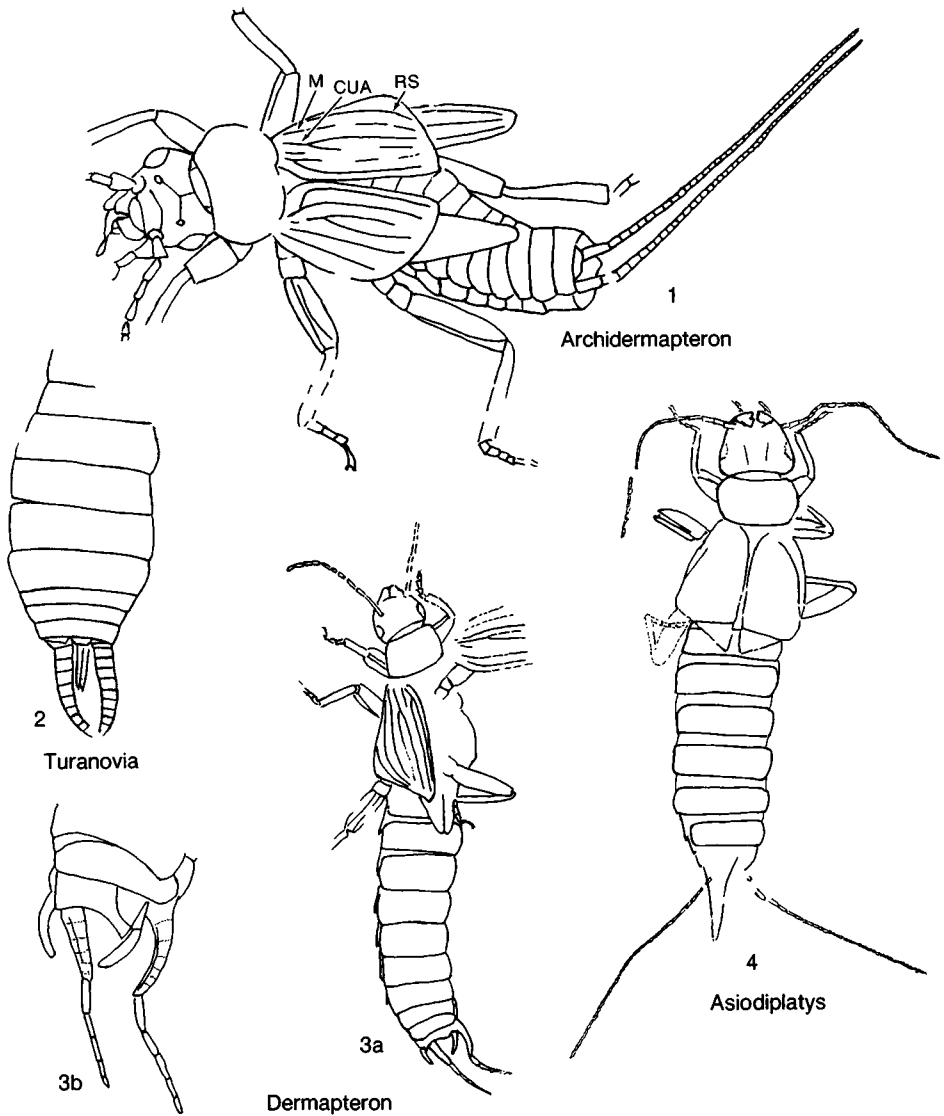


FIG. 92. Protodiplatyidae (p. 152–153).

as long as third; ocelli present; pronotum transverse; tegmina relatively long, apically dilated, and with veins RS and M unbranched, CUA and A forked, and CUP reduced; tarsi long; fore and middle tarsi with 4 segments, hind tarsi with 5; pretarsi with 2 claws and arolium; abdomen with 10 visible segments. Females with prominent, external ovipositor. *Jur.*

Protodiplatys MARTYNOV, 1925b, p. 573 [**P. fortis*; OD]. Head small; antenna with 17 to 19

segments; tegmina broad, not extending beyond second abdominal segment; cerci about half as long as body, with no more than 40 segments. VISHNIAKOVA, 1980a. *Jur.*, USSR (Kazakh).

Archidermapteron VISHNIAKOVA, 1980a, p. 82 [**A. martynovi*; OD]. Similar to *Protodiplatys* but with much larger and longer tegmina; cerci nearly as long as body, with more than 40 segments. *Jur.*, USSR (Kazakh).—FIG. 92, 1. **A. martynovi*; lateral view of holotype as preserved, $\times 2.5$ (after Vishniakova, 1980a).

Asiodiplatys VISHNIAKOVA, 1980a, p. 85 [**P. speciosus*; OD]. Similar to *Protodiplatys*, but head larger; antenna with 22 segments; tegmina api-

cally truncate in straight line; cerci about half length of body. *Jur.*, USSR (Kazakh).—FIG. 92,4. **A. speciosus*; dorsal view of holotype as preserved, $\times 5.5$ (after Vishniakova, 1980a).

Dermapteron MARTYNOV, 1925b, p. 575 [**D. incerta*; OD]. Similar to *Protodiplatys*; anterior margin of pronotum concave, posterior margin slightly convex; femora without spines; cerci short, with only 6 segments and only about one-fifth length of body; basal segment of cerci enlarged and falciform, with vestigial segmentation; ovipositor short. VISHNIAKOVA, 1980a. *Jur.*, USSR (Kazakh).—FIG. 92,3. **D. incerta*; a, paratype as preserved, $\times 3$; b, apex of abdomen, $\times 6$ (both after Vishniakova, 1980a).

Microdiplatys VISHNIAKOVA, 1980a, p. 85 [**V. campodeiformis*; OD]. Similar to *Protodiplatys* but smaller; antenna with 19 segments; pronotum with lateral margins almost parallel; cerci as long as body. *Jur.*, USSR (Kazakh).

Turanovia VISHNIAKOVA, 1980a, p. 88 [**T. incompleta*; OD]. Similar to *Dermapteron*, but anterior and posterior margins of pronotum nearly parallel; cerci short, about one-sixth length of body, weakly curved and converging, consisting of 9 more or less coalesced segments. *Jur.*, USSR (Kazakh).—FIG. 92,2. **T. incompleta*; distal part of abdomen and cerci, $\times 7$ (after Vishniakova, 1980a).

Suborder FORFICULINA

Newman, 1835

[Forficulina NEWMAN, 1835, p. 424]

Tarsi with 3 segments; cerci forming heavy forceps, without segmentation in adults; eyes well developed. *Jur.—Holo.*

Family PYGIDICRANIDAE

Verhoeff, 1902

[Pygidicranidae VERHOEFF, 1902, p. 188]

Head depressed, truncate, concave, not emarginate posteriorly; femora commonly compressed and carinulate; body typically pubescent; tarsi commonly simple. Cerci of nymphs of two subfamilies segmented. [A diverse family generally considered to be the most primitive of the existing families of the order.] *Jur.—Holo.*

Pygidicrana SERVILE, 1831, p. 30. *Holo.*

Semenoviola MARTYNOV, 1925c, p. 74 [**S. obliquotruncata*; OD]. Head large, transverse, posterior margin concave; antenna with 11 moniliform segments, first 2 segments of nearly identical length; ocelli present; tegmina with unbranched veins RS, M, and CUA; vein A forked; cerci

short, strongly curved; ovipositor short, external. VISHNIAKOVA, 1980a. *Jur.*, USSR (Kazakh).

Semenovioloidea VISHNIAKOVA, 1980a, p. 92 [**S. capitatus*; OD]. Similar to *Semenoviola* but larger; anterior margin of pronotum concave. *Jur.*, USSR (Kazakh).

Turanoderma VISHNIAKOVA, 1980a, p. 92 [**T. sepultum*; OD]. Similar to *Semenoviola*, but tegmina widened distally and truncate apically in a straight line; antenna with 12 segments; cerci short, strongly falciform. *Jur.*, USSR (Kazakh).—FIG. 93,2. **T. sepultum*; dorsal view of holotype as preserved, $\times 3.7$ (after Vishniakova, 1980a).

Family LABIDURIDAE

Verhoeff, 1902

[Labiduridae VERHOEFF, 1902, p. 189]

Body usually convex; femora not flattened or carinulate; cerci of nymphs not segmented. *Paleoc.—Holo.*

Labidura LEACH, 1815, p. 118. COCKERELL, 1920e; ZEUNER, 1962b. *Mio.*, Asia (Burma); *Pleist.*, St. Helena—*Holo.*

Carcinophora SCUDDER, 1876b, p. 291. COCKERELL, 1925e; BOGACHEV, 1940. *Paleoc.—Plio.*, Argentina; *Mio.*, Europe (Germany)—*Holo.*

Labiduromma SCUDDER, 1890, p. 203 [**L. avia*; SD TOWNES, 1945, p. 350]. First segment of anterior tarsus stout and swollen; forceps very broad. [Family assignment doubtful.] COCKERELL, 1924a; BROWN, 1984. *Oligo.*, USA (Colorado).—FIG. 93,1 **L. avia*; whole insect, $\times 2$ (Scudder, 1890).

Family FORFICULIDAE

Verhoeff, 1902

[Forficulidae VERHOEFF, 1902, p. 190]

Body usually moderately flattened; antenna with 12 to 15 cylindrical or subcylindrical segments; elytra commonly present; legs short, flattened; second tarsal segment dilated on each side; abdomen with parallel sides, rarely tapering or dilated; forceps flattened or cylindrical. *Eoc.—Holo.*

Forficula LINNÉ, 1758, p. 423. BOGACHEV, 1940. *Eoc.*, Europe (Italy); *Mio.*, Europe (Germany)—*Holo.*

Suborder UNCERTAIN

The following genera, apparently belonging to the order Dermaptera, are too poorly known to permit assignment to suborders.

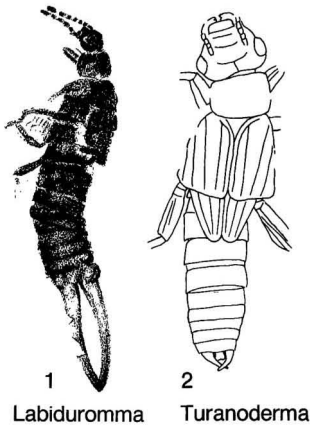


FIG. 93. Pygidicranidae and Labiduridae (p. 153).

Mesoforficula PING, 1935, p. 107 [**M. sinkianensis*; OD]. Little-known insect with short antennae and elytra. *Jur.*, China (Xinjiang).

Sinolabia ZHOU & CHEN, 1983, p. 62 [**S. longyouensis*; OD]. Little-known genus, based on poorly preserved specimen, apparently lacking tegmina. *Cret.*, China (Zhejiang).

Order ORTHOPTERA Olivier, 1789

[*nom. transl. et correct.* OLIVIER, 1811, p. 550, ex Orthopteres OLIVIER, 1789a, p. 12] [= *Pruvoostioptera* ZALESKY, 1928b, p. 381]

Fore wings typically tegminous, rarely membranous; costa submarginal, precostal area usually prominent; vein SC generally extending beyond midwing, with series of oblique veinlets directed to anterior margin beyond C; R with oblique veinlets or definite terminal branches; RS arising from R, usually having several branches; M typically with at least 2 main branches, which in some families may represent MA and MP; CUA well developed, commonly anastomosed with M or its branches; CUP and 1A nearly straight, unbranched. Hind wings membranous, with slender remigium and expanded anal lobe; costa reduced, usually marginal; anal lobe including several to many radiating anal veins. Crossveins usually well developed and numerous, in many forming reticulation, which may develop into series of weak intercalary veins. Fore wings or both fore and hind wings may be reduced or completely absent.

Mouthparts mandibulate; antennae well developed, commonly long; prothorax prominent; tarsi usually with from 3 to 5 segments; hind legs modified for jumping; female usually with ovipositor; cerci small, usually inconspicuous and unsegmented. Stridulatory organs usually present (generally alary or femoroalary) at least in males; tympanal organs on either abdomen or fore tibiae. *U. Carb.—Holo.*

As usually treated and as presented here, the order Orthoptera includes only the saltatorial orthopteroids. Lack of knowledge of the leg structure of a few Permian orthopteroids has made their ordinal positions uncertain. In these cases I have accepted SHAROV's conclusions, as given in his detailed account of the phylogeny of the orthopteroids (1968).

The venation of the Orthoptera has some controversial features. The topography (i.e., convexity or concavity) of veins C, SC, R, and CUP is retained, but the branches of RS and M, as well as of CUA, are usually flat or neutral in the fore wings. In certain extinct families, such as the Oedischiidae, however, MP is clearly preserved as a strongly concave vein and CUA as convex. MA does not occur in any known Orthoptera as a distinctly convex vein; its presence, as in the Protorthoptera, can only be assumed on the basis of the proximal position of the first fork of M. One area of controversy is the relationship between M and CUA. In the fore wings of most Orthoptera there is some kind of connection between CUA and M (Fig. 94, *Oedischia williamsoni*; see also Fig. 95, 4b). In others, CUA curves anteriorly from the stem of CU near the base of the wing and anastomoses with the stem of M for a brief interval before diverging posteriorly (see Fig. 110, 2, *Mesoeischia madygenica*). In most families, CUA has merged with M at the very base of the wing and is usually no longer visible as a distinct vein (see Fig. 103, 1, *Hagla gracilis*). Also, as noted by SHAROV (1968), some crossveins have tended to become relatively thick, functioning as struts (as in the Odonata), especially in the fore wings of the males,

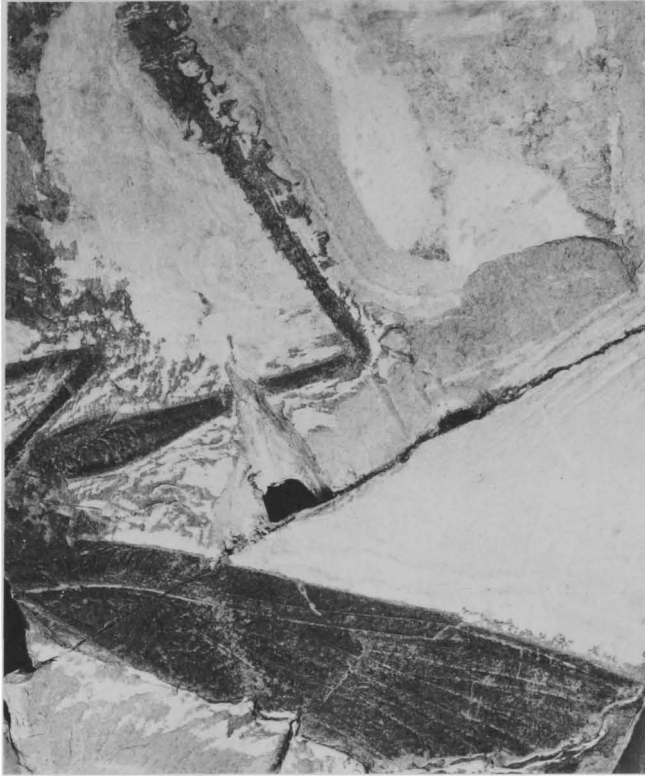


FIG. 94. Orthoptera; fore wing and hind leg of *Oedischia williamsoni*, Upper Carboniferous of France, $\times 1.6$ (Carpenter, new).

in which the venation has been much modified by the development of the stridulatory apparatus.

The evolution of the Orthoptera has apparently involved (1) increasing specializations of the fore wings as tegmina or wing covers, (2) development of stridulatory organs on the fore wings at least of the males, (3) expansion of the anal lobes of the hind wings, and (4) development of tympanal organs. The ability of the Orthoptera to jump and to stridulate has placed them among the most conspicuous of the existing insects. The saltatorial legs were well developed in the *Oedischiidae* of the Upper Carboniferous (Fig. 94). Stridulatory organs were thought by SHAROV (1968) to have been present on the wings of some *oedischiids*; they were obviously well developed on the wings of several Triassic genera of the related, existing family

Haglidae (see Figs. 104,1, *Archibagla* and 106,2, *Protshorkuphlebia*).

The order Orthoptera is here divided into two suborders, Ensifera and Caelifera.

Suborder ENSIFERA

Chopard, 1920

[Ensifera CHOPARD, 1920, p. 56]

Antennae long, filiform, commonly longer than body and consisting of at least 30 segments; tympanal (auditory) organs, when present, located on fore tibiae; stridulatory structures (if present) on the overlapping, horizontal part of the fore wings in resting position; ovipositor, when present, sword-shaped. *U. Carb.—Holo.*

The morphological features included in the diagnosis of the Ensifera are only rarely preserved in fossils. However, there are other

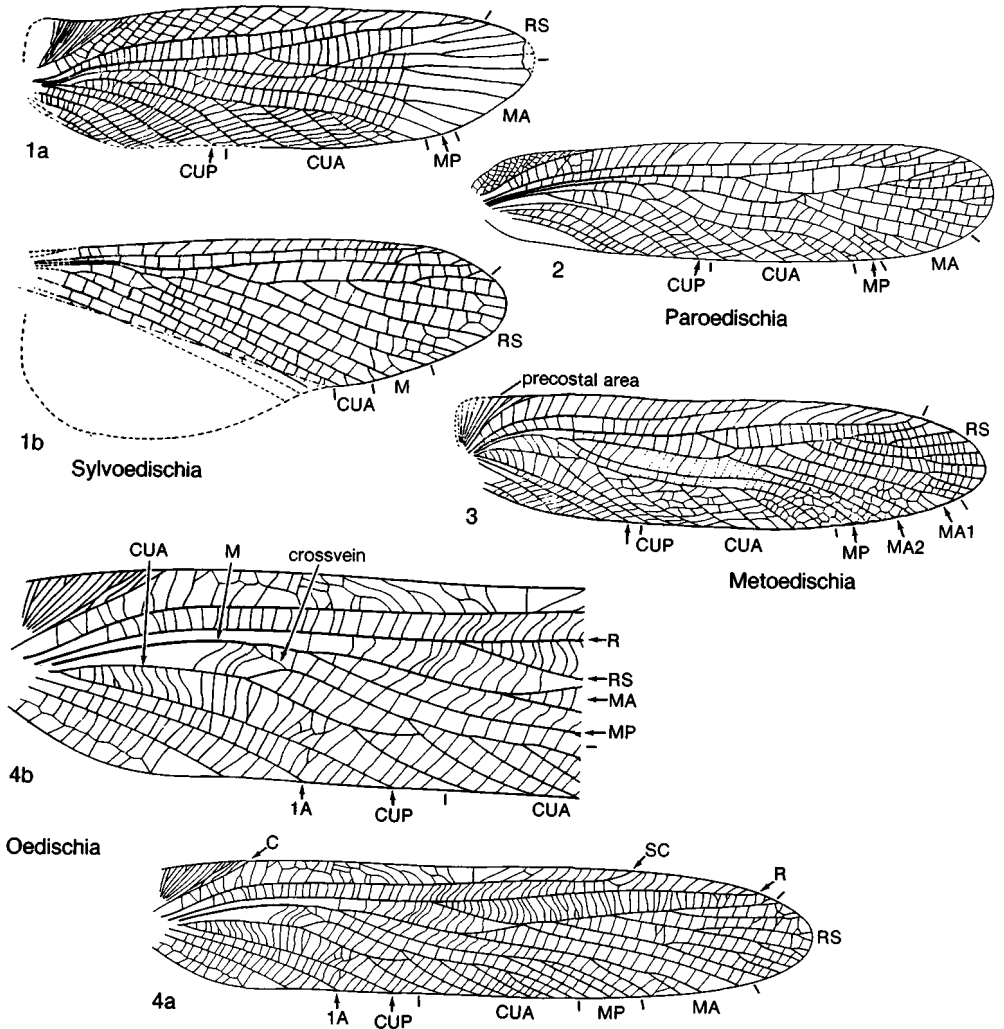


FIG. 95. Oedischiidae (p. 157–158).

characteristics, especially in the venational patterns, that are sufficiently associated with the body structures mentioned to enable sub-order classification in most instances.

Family OEDISCHIIDAE
Handlirsch, 1906

[Oedischiidae HANDLIRSCH, 1906a, p. 700] [=Anhomalophlebiidae HANDLIRSCH, 1919b, p. 547; Pruvostitidae ZALESSKY, 1928b, p. 381]

Fore wing weakly coriaceous; precostal area well developed; vein SC extending well beyond midwing; RS arising at about midwing, with several branches; stem of M inde-

pendent basally, dividing into MA and MP after a short interval; MA with a distinct anterior branch (MA1) diverging toward RS and commonly at least touching it; MP commonly unbranched; CUA and CUP separating close to wing base; CUA1 directed toward stem of M and typically connected to it by a thickened crossvein, just before origin of MP; CUA with several long branches; CUP and anal veins unbranched. Hind wing incompletely known (in *Sylvoedischia* and *Macroedischia*); remigium about same size as in fore wing; MA not anastomosed with

RS; anal area unknown. Body known only in *Oedischia* and *Sylvoedischia*; head hypognathous; pronotum long; legs long, posterior pair with enlarged femora (Fig. 94), tarsi with 5 segments; cerci and ovipositor short. *U. Carb.*—*Perm.*

The oedischiids are generally considered to be the most primitive of the known Orthoptera. At present thirteen genera are known, two from the Upper Carboniferous and the rest from Permian strata. It should be noted here that I have excluded from the Oedischiidae the Triassic genus *Mesoedischia* SHAROV, which seems to me to represent a distinct family. It is here placed in the category of family Uncertain.

Oedischia BRONGNIART, 1885a, p. 58 [**O. williamsoni*; OD]. Fore wing with SC terminating at about one-quarter wing length from apex; MA1 touching or nearly touching RS; MP branched. ZEUNER, 1939; CARPENTER, 1966; SHAROV, 1968. *U. Carb.*, Europe (France).—FIG. 94. **O. williamsoni*; fore wing and hind leg, $\times 1.6$ (Carpenter, new).—FIG. 95,4. **O. williamsoni*; a, fore wing, $\times 1.0$; b, proximal half of fore wing, $\times 1.7$ (both Carpenter, new).

Anhomalophlebia HANDLIRSCH, 1919b, p. 547 [**Homalophlebia couloni* MEUNIER, 1911a, p. 128; OD]. Fore wing as in *Oedischia* but relatively shorter and broader; MP unbranched; MA1 not quite reaching RS. [Type of family Anhomalophlebiidae HANDLIRSCH, 1919b.] *U. Carb.*, Europe (France).—FIG. 96,1. **A. couloni* (MEUNIER); fore wing, $\times 1.6$ (Carpenter, new).

Jasvia ZALESSKY, 1934, p. 150 [**J. reticulata*; OD]. Little-known genus, apparently similar to *Oedischia*, but crossveins forming a dense reticulation over most of wing; MP unbranched. *Perm.*, USSR (Asian RSFSR).—FIG. 96,2. **J. reticulata*; fore wing, $\times 1.0$ (Zalessky, 1934).

Macroedischia SHAROV, 1968, p. 159 [**M. elongata*; OD]. Fore wing as in *Jasvia*, but precostal area longer and more pointed; crossveins not forming a dense reticulation apically; anal area longer. *Perm.*, USSR (Asian RSFSR).—FIG. 96,6. **M. elongata*; fore wing, $\times 1.0$ (Sharov, 1968).

Metoedischia MARTYNOV, 1928b, p. 45 [**M. magnifica*; OD]. Fore wing as in *Jasvia*, but relatively broader; MA1 anastomosed with RS for longer interval; crossveins between branches of RS more nearly straight. [The small wing fragment of an oedischiid from the Permian of Portugal and described by LAURENTIAUX & TEIXEIRA (1958b, p. 212) as *Metoedischia lusitanica* obviously does not belong to this genus.] SHAROV, 1968. *Perm.*,

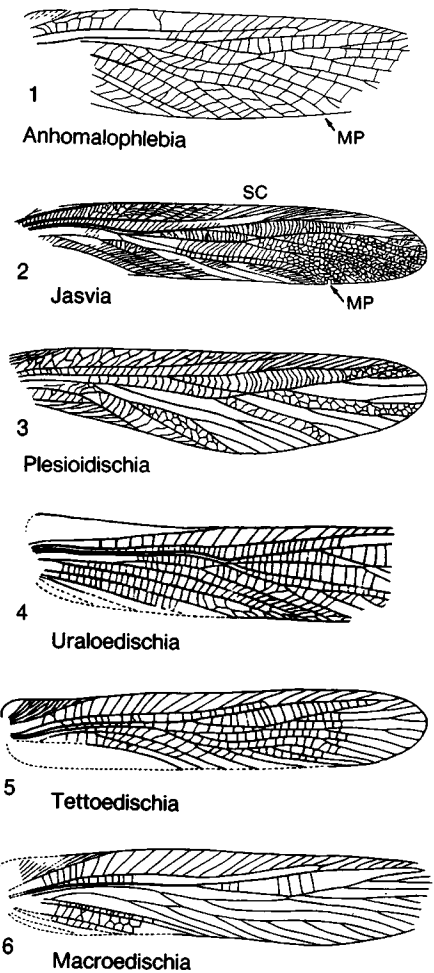


FIG. 96. Oedischiidae (p. 157–158).

USSR (European RSFSR).—FIG. 95,3. **M. magnifica*; fore wing, $\times 1.8$ (Martynov, 1928b). *Paroedischia* CARPENTER, 1966, p. 79 [**P. recta*; OD]. Similar to *Metoedischia*, but precostal area very long; SC long; crossveins not reticulate. *Perm.*, USA (Kansas).—FIG. 95,2. **P. recta*; fore wing, $\times 1.8$ (Carpenter, 1966). *Permoedischia* KUKALOVÁ, 1955a, p. 542 [**P. moravica*; OD]. Little-known fore wing; precostal area more extensive than in *Oedischia*; MP unbranched. SHAROV, 1968. *Perm.*, Europe (Czechoslovakia). *Plesioedischia* HANDLIRSCH, 1906b, p. 346 [**P. baentschi*; OD]. Fore wing as in *Oedischia* but markedly widened near middle; crossveins forming reticulation in region of RS. *Perm.*, Europe (Germany).—FIG. 96,3. **P. baentschi*; fore wing, $\times 1.0$ (Guthörl, 1934).

- Pruvostites** ZALESSKY, 1928b, p. 381 [**P. takbtachurensis*; OD]. Little-known genus, based on wing fragment with broad costal area. [Type of family Pruvostitidae and order Pruvostitoptera.] SHAROV, 1968. *Perm.*, USSR (European RSFSR).
- Rimnosentomon** ZALESSKY, 1955b, p. 349 [**R. grande*; OD]. Little-known genus, based on distal fragment of fore wing. SHAROV, 1962c. *Perm.*, USSR (Asian RSFSR).
- Sylvoedischia** SHAROV, 1968, p. 158 [**S. uralica*; OD]. Fore wing with large precostal area, nearly as long as in *Macroedischia*; costal veinlets connected by crossveins; crossveins very dense over most of wing. Hind wing with SC nearly straight. *Perm.*, USSR (Asian RSFSR).—FIG. 95, 1. **S. uralica*; *a*, fore and *b*, hind wings, both $\times 1.8$ (Sharov, 1968).
- Tettoedischia** SHAROV, 1968, p. 159 [**T. minuta*; OD]. Fore wing slender; precostal area large, tapering; costal veinlets not connected by crossveins. *Perm.*, USSR (Asian RSFSR).—FIG. 96, 5. **T. minuta*; fore wing, $\times 1.8$ (Sharov, 1968).
- Uraloedischia** SHAROV, 1968, p. 157 [**U. permiansis*; OD]. Little-known genus, based on proximal fragment of fore wing. Precostal area long and narrow, extending about halfway to origin of RS; subcostal veinlets not reticulate. *Perm.*, USSR (Asian RSFSR).—FIG. 96, 4. **U. permiansis*; fore wing, $\times 1.7$ (Sharov, 1968).

Family TCHOLMANVISSIIDAE Zalessky, 1934

[Tcholmanvissiidae ZALESSKY, 1934, p. 153] [=Tillyardiellidae HANDLIRSCH, 1937, p. 82]

Fore and hind wings similar to those of the Oedischiidae. Fore wing with vein MA1 not anastomosed with RS and without a sharp bend toward RS; branches of CUA nearly parallel and close together. Hind wing with 1A forked distally; anal area with about 12 radiating veins. Body as in the Oedischiidae; ovipositor well developed and bearing many small spines. SHAROV, 1968. *Perm.*

- Pinegia** MARTYNOV, 1928b, p. 47 [**P. oknowae*; OD] [= *Tbnetodes* MARTYNOV, 1928b, p. 5 (type, *T. craticus*); *Tcholmanvissia* ZALESSKY, 1929, p. 19 (type, *T. noinskii*); *Kamaites* ZALESSKY, 1929, p. 21 (type, *K. mirabilis*); *Tillyardiella* MARTYNOV, 1930a, p. 76 (type, *T. distincta*)]. Crossveins very numerous and close together, forming a reticulation only in distal part of wings; posterior margin of fore wing concave. SHAROV, 1962c, 1968. *Perm.*, USSR (Asian and European RSFSR).—FIG. 97, 1. *P. longipes* (MARTYNOV);

a, fore and *b*, hind wings, both $\times 1.0$ (Sharov, 1968).

- Jubilaeus** SHAROV, 1968, p. 161 [**J. beybienkoi*; OD]. Fore wing as in *Pinegia*, but subcostal area broader; precostal area bulging; posterior margin of wing straight or slightly convex. *Perm.*, USSR (Asian RSFSR).—FIG. 97, 2. **J. beybienkoi*; *a*, fore and *b*, hind wings, both $\times 0.8$ (Sharov, 1968).

Family PERMELCANIDAE Sharov, 1962

[Permecanidae SHAROV, 1962b, p. 112]

Fore wing more membranous than in Oedischiidae; vein SC extending at least to midwing; RS arising near midwing, with very short, oblique stem and anastomosed with MA for a considerable interval; MP diverging from MA before level of origin of RS; CUA separating from CUP near wing base; CUA forking before level of main fork of M; CUA diverging toward M and typically anastomosed with M and MP for a short interval; CUP arising from the common stem CU; several anal veins. Hind wing little known; costa submarginal; SC terminating near midwing; anal area apparently well developed; anal veins unknown. Body (known only in *Permecana*): antennae long, filiform; legs slender, hind femora thick basally; tarsi with 4 segments. SHAROV, 1968. *Perm.*

- Permecana** SHAROV, 1962b, p. 114 [**P. sojanense*; OD]. MA in fore wing anastomosed with RS for an interval almost equal to length of free part of MA. *Perm.*, USSR (European RSFSR).—FIG. 98, 1. *P. kukalovae* SHAROV; *a*, fore and *b*, hind wings, both $\times 5.0$ (Sharov, 1968).

- Meselcana** SHAROV, 1968, p. 162 [**P. madygenica*; OD]. Similar to *Permecana*, but SC much longer; branches of CUA1 in fore wing strongly curved. *Perm.*, USSR (Asian RSFSR).—FIG. 98, 4. **M. madygenica*; *a*, fore and *b*, hind wings, both $\times 5.3$ (Sharov, 1968).

- Proelcana** SHAROV, 1962b, p. 113 [**P. uralica*; OD]. Little-known genus, based on fragment of fore wing. MA anastomosed with RS for a very short interval. *Perm.*, USSR (Asian RSFSR).

- Promartynovia** TILLYARD, 1937a, p. 99 [**P. venicosta*; OD]. Similar to *Permecana*, but fore wing more broadly rounded distally; RS with only 2 terminal branches. Hind wing unknown. *Perm.*, USA (Kansas).—FIG. 98, 3. **P. venicosta*; fore wing, $\times 7.3$ (Carpenter, 1966).

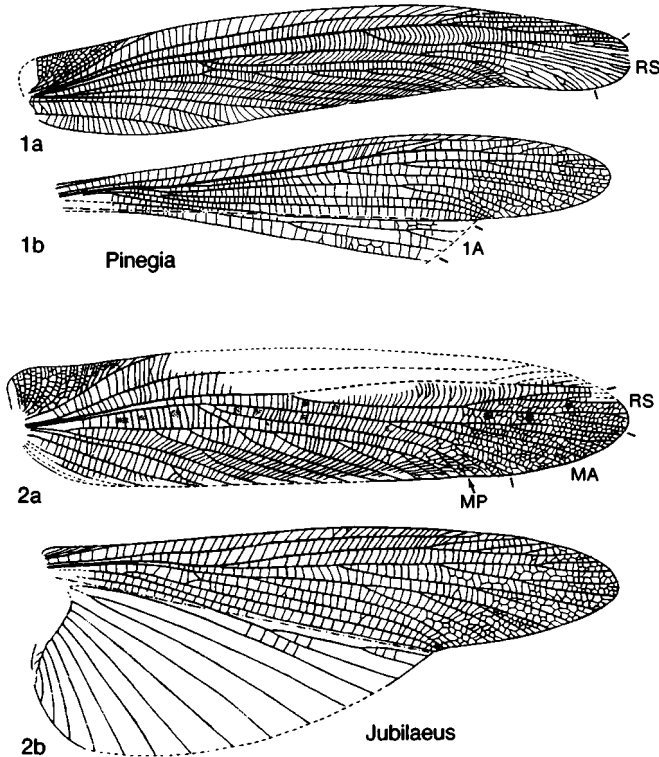


FIG. 97. Tcholmanvissiidae (p. 158).

Family ANELCANIDAE Carpenter, 1987

[Anelcanidae CARPENTER, 1987, p. 375, *nom. subst. pro* Parelcanidae CARPENTER, 1966, p. 84]

Fore wing as in Oedischiidae but more coriaceous; precostal area very large and very acute distally, extending about one-third wing length from wing base; vein SC remote from costal margin, terminating beyond midwing. Hind wing unknown. *Perm.*

Anelcana CARPENTER, 1987, p. 375, *nom. subst. pro* *Parelcana* CARPENTER, 1966, p. 84, *non* HANDLIRSCH, 1906b [**Parelcana dilatata*; OD]. Costal area about as wide as area between SC and R at midwing; crossveins numerous but not branched. *Perm.*, USA (Kansas).—FIG. 98,2. **A. dilatata* (CARPENTER); fore wing as preserved, $\times 2.8$ (Carpenter, 1966).

Petrelcana CARPENTER, 1966, p. 85 [**P. elongata*; OD]. Fore wing elongate, with many irregular veinlets; precostal area not so long or so broad as in *Anelcana*; costal area much wider than area

between SC and R; R with several irregular, oblique veinlets distally; basal piece of MA very long; crossveins forming a coarse reticulation in several areas of wing. *Perm.*, USA (Kansas).—FIG. 98,5. **P. elongata*; fore wing, $\times 2.2$ (Carpenter, 1966).

Family PERMORAPHIDIIDAE Tillyard, 1932

[Permorphidiidae TILLYARD, 1932a, p. 5]

Similar to Permelcanidae. Fore wing apparently lacking precostal area; vein SC with an anterior basal branch, connected to costal margin of wing by crossveins; MA anastomosed for a short interval with RS; crossveins numerous. Hind wing with MA anastomosed with RS; CUA1 anastomosed with M; anal area unknown. *Perm.*

Permorphidia TILLYARD, 1932a, p. 6 [**P. americana*; OD]. Costal area of fore wing much broader than subcostal area; CUP extending

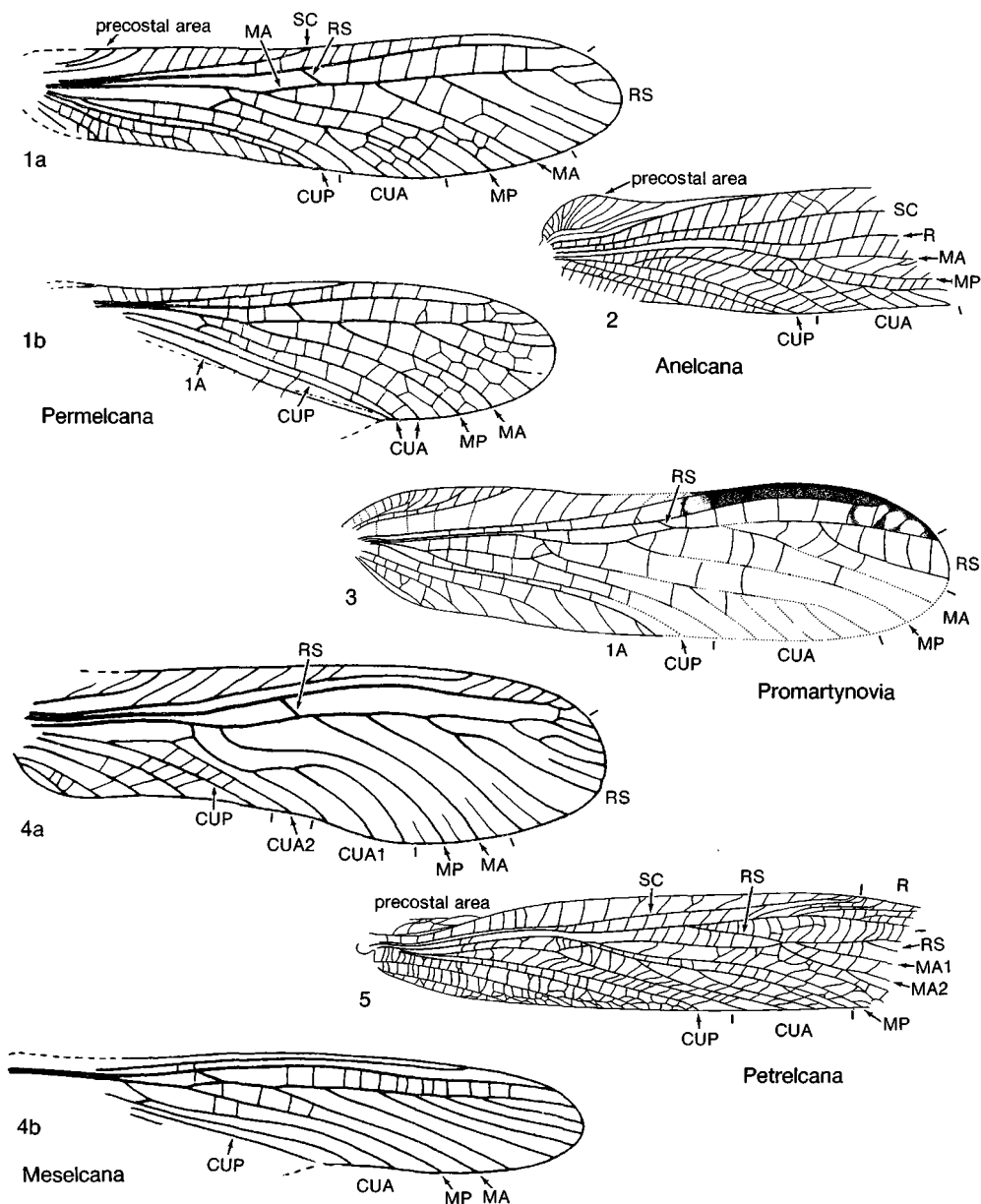


FIG. 98. Permelmcanidae and Anelcanidae (p. 158–159).

beyond midwing. CARPENTER, 1943a; SHAROV, 1968. *Perm.*, USA (Kansas).—FIG. 99, 1. **P. americana*; a, fore and b, hind wings, $\times 8.0$ (Carpenter, 1943a).

Family ELCANIDAE Handlirsch, 1906

[Elcanidae HANDLIRSCH, 1906b, p. 412]

Similar to Permelmcanidae, but fore wing with vein CUA forking much nearer wing

base; RS and MA in brief contact. SHAROV, 1968. *Jur.—Cret.*

Panorpidium WESTWOOD, 1854, p. 394 [**P. tessellatum*; OD] [= *Elcana* GIEBEL, 1856, p. 259, obj.; *Rapha* GIEBEL, 1856, p. 290 (type, *R. liasina*); *Clathrotermes* HEER, 1865, p. 85 (type, *C. signatus*); *Parelcana* HANDLIRSCH, 1906b, p. 420 (type, *P. tenuis*)]. Fore wing: submarginal part

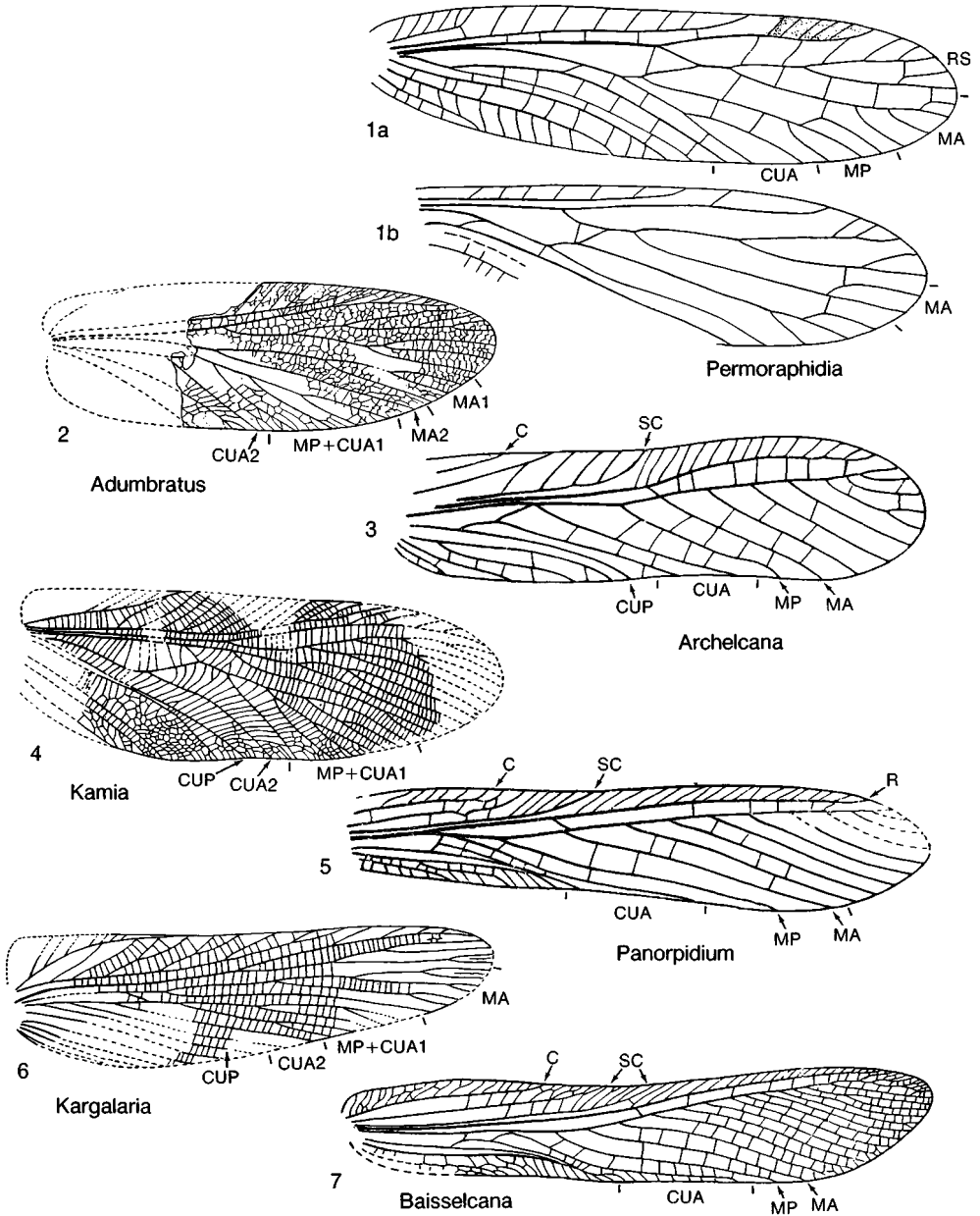


FIG. 99. Permoraphidiidae, Elcanidae, and Kamiidae (p. 159–162).

of C with several branches leading to front margin of wing; apex of wing rounded. ZEUNER, 1942d; BODE, 1953. *Jur.*, England, Europe (Germany, Switzerland), USSR (Kazakh).—FIG. 99,5. *P. karatavica* (SHAROV), USSR; fore wing, $\times 4.0$ (Sharov, 1968).

Archelcana SHAROV, 1968, p. 163 [**Elcana britannica* HANDLIRSCH, 1906b, p. 414; OD]. Fore wing as in *Panorpidium*, but submarginal part

of C without distinct branches. *Jur.*, England, USSR (Kirghiz).—FIG. 99,3. **A. britannica* (HANDLIRSCH), England; fore wing, $\times 4.5$ (Sharov, 1968).

Baisselcana SHAROV, 1968, p. 164 [**B. sibirica*; OD]. Fore wing: precostal area long, with many veinlets; apex of wing pointed. *Cret.*, USSR (Asian RSFSR).—FIG. 99,7. **B. sibirica*; fore wing, $\times 2.5$ (Sharov, 1968).

Family KAMIIDAE Sharov, 1968

[Kamiidae SHAROV, 1968, p. 165]

Related to Oedischiidae. Costal area of fore wing very broad; area between veins SC and R very narrow; MA not anastomosed with RS or even curved toward it and with 3 or more branches; crossveins very numerous. *Perm.*

Kamia MARTYNOV, 1928b, p. 4 [**K. angustovenosa*; OD] [= *Spongoneura* MARTYNOV, 1928b, p. 6 (type, *S. incerta*); *Permacridites* MARTYNOV, 1931c, p. 156 (type, *P. maximus*)]. Fore wing broad; crossveins mostly straight, not branched. SHAROV, 1968. *Perm.*, USSR (European and Asian RSFSR).—FIG. 99,4. **K. angustovenosa*; fore wing as preserved, $\times 1.3$ (Sharov, 1968).

Adumbratus SHAROV, 1961f, p. 246 [**A. extensus*; OD]. Similar to *Kamia*, but crossveins forming a dense reticulation over most of fore wing. SHAROV, 1968. *Perm.*, USSR (Asian RSFSR).—FIG. 99,2. **A. extensus*; fore wing as preserved, $\times 3.0$ (Sharov, 1961f).

Kargalaria SHAROV, 1968, p. 165 [**K. maculata*; OD]. Fore wing as in *Kamia* but more slender; crossveins not so dense; main veins and their branches nearly parallel. *Perm.*, USSR (Asian RSFSR).—FIG. 99,6. **K. maculata*; fore wing as preserved, $\times 1.0$ (Sharov, 1968).

Family VITIMIIDAE Sharov, 1968

[Vitimiidae SHAROV, 1968, p. 152]

Similar to Kamiidae, but anastomosis of MP and CUA in fore wing apparently occurring at base of wing; hind wing with large anal area. *Trias.—Cret.*

Vitimia SHAROV, 1968, p. 167 [**V. evoluta*; OD]. Crossveins mostly simple, unbranched. *Cret.*, USSR (Asian RSFSR).—FIG. 100,4. **V. evoluta*; fore wing as preserved, $\times 3.5$ (Sharov, 1968).

Fergania SHAROV, 1968, p. 167 [**F. reducta*; OD]. Fore wing similar to that of *Vitimia*, but pre-costal area much larger and CUP diverging from CU more proximally. Hind wing with a concave anterior margin. *Trias.*, USSR (Kirghiz).—FIG. 100,2. **F. reducta*; *a*, fore and *b*, hind wings, both $\times 2.8$ (Sharov, 1968).

Provitimia SHAROV, 1968, p. 166 [**P. pectinata*; OD]. Little-known genus, similar to *Vitimia*, but SC with many forked branches. *Trias.*, USSR (Kirghiz).

Family BINTONIPELLIDAE
Handlirsch, 1939

[Bintoniellidae HANDLIRSCH, 1939, p. 55]

Related to Vitimiidae. Fore wing with prominent pre-costal area; veinlets in costal 2009 area; SC extending well beyond midwing; MA

area commonly unbranched, without connecting crossveins; vein MA not anastomosed with RS and remote from it; M with 3 main, parallel branches. *Trias.—Jur.*

Bintoniella HANDLIRSCH, 1939, p. 55 [**B. brodiei*; OD]. Costal area of fore wing narrow, nearly as narrow as subcostal area; branches of vein RS curved and parallel. Remigium of hind wing relatively slender and pointed; crossveins very dense distally. Fore wings showing some sexual dimorphism, those of males being more sclerotized than those of females, as well as slightly larger. WHALLEY, 1982. *Jur.*, England.—FIG. 100,1. **B. brodiei*; *a*, fore and *b*, hind wings, both $\times 1.8$ (Sharov, 1968).

Probintoniella SHAROV, 1968, p. 168 [**P. triassica*; OD]. Fore wing as in *Bintoniella*, but costal area very broad, about twice as wide as subcostal area; branches of RS divergent and irregular. Remigium of hind wing broad, with rounded apex. *Trias.*, USSR (Kirghiz).—FIG. 100,3. **P. triassica*; *a*, fore and *b*, hind wings, both $\times 2.8$ (Sharov, 1968).

Family TRIASSOMANTEIDAE
Tillyard, 1922[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 809, ex Triassomantidae TILLYARD, 1922b, p. 449, *nom. imperf.*] [=Xenopteridae RIEK, 1955, p. 687]

Apparently related to the Oedischiidae. Precostal area of fore wing small and narrow; costal area very broad, its veinlets unbranched; subcostal area narrow; vein M much reduced; crossveins unbranched, except in anal area. Hind wing with large anal area, with CUA extending farther distally than in fore wing. [I have followed SHAROV (1968) in placing his genera *Ferganopterus*, *Ferganopterodes*, and *Triassomanteodes* in the family Triassomanteidae. However, because of the fragmentary nature of the unique specimen of the type genus, that placement is uncertain. The family diagnosis above is based in part on SHAROV's genera.] *Trias.*

Triassomantis TILLYARD, 1922b, p. 450 [**T. pygmaeus*; OD]. Little-known genus, based on fragment of fore wing. *Trias.*, Australia (Queensland).

Ferganopterodes SHAROV, 1968, p. 169 [**F. reductus*; OD]. Fore wing as in *Ferganopterus*, but MA not anastomosed with RS. *Trias.*, USSR (Kirghiz).—FIG. 101,1. **F. reductus*; fore wing, $\times 4.0$ (Sharov, 1968).

Ferganopterus SHAROV, 1968, p. 169 [**F. clarus*; OD]. Fore wing with long and tapering costal

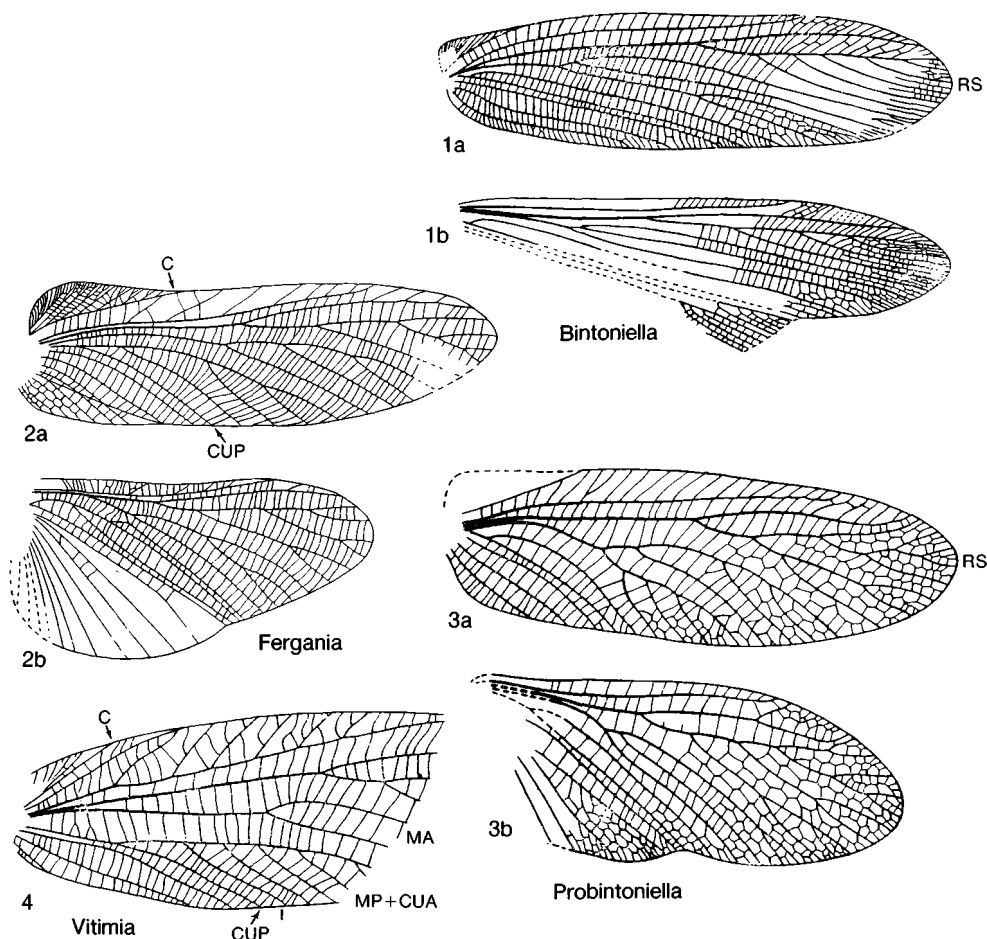


FIG. 100. Vitimiidae and Bintoniellidae (p. 162).

anastomosed with RS; crossveins between CUP and 1A very close together. Hind wing with MA and CUA close together and parallel. *Trias.*, USSR (Kirghiz).—FIG. 101,4. **F. clarus*; *a*, fore and *b*, hind wings, both $\times 3.0$ (Sharov, 1968).

Triassomanteodes SHAROV, 1968, p. 170 [**T. madygenicus*; OD]. Similar to *Ferganopterodes*, but SC terminating at about midwing, MA anastomosed with RS, and stem of CUA much shorter. *Trias.*, USSR (Kirghiz).—FIG. 101,3. **T. madygenicus*; fore wing, $\times 7.0$ (Sharov, 1968).

Xenopterum RIEK, 1955, p. 678 [**X. crosbyi*; OD]. Little-known genus, based on wing fragments. [Type of family Xenopteridae RIEK.] SHAROV, 1968. *Trias.*, Australia (Queensland).

Family TETTAVIDAE Sharov, 1968

[Tettavidae SHAROV, 1968, p. 171]

Wing venation similar to that of Oedischiidae; veins RS and MA anastomosed in hind

wing but not in fore wing; R in fore wing with several branches distally. *Perm.—Trias.*

Tettavus SHAROV, 1968, p. 171 [**Pinegia fenestrata* MARTYNOV, 1931c, p. 208; OD]. Fore wing (presumably of female): distal branches of R very long; RS with pectinate branching; crossveins in radial field forming a reticulation distally. *Perm.*, USSR (Asian RSFSR).—FIG. 101,5. **T. fenestrata*; *a*, fore wing as preserved, *b*, hind wing, both $\times 2.0$ (Sharov, 1968).

Madygenia SHAROV, 1968, p. 171 [**M. orientalis*; OD]. Female: fore wing as in *Tettavus*, but RS branched dichotomously; crossveins reticulate over most of wing; hind wing with branches of RS nearly parallel to MA, MP, and CUA. Male much smaller than female; venation little known. *Trias.*, USSR (Kirghiz).—FIG. 101,2. **M. orientalis*; *a*, fore and *b*, hind wings of female, *c*, fore wing of male as preserved, all $\times 2.0$ (Sharov, 1968).

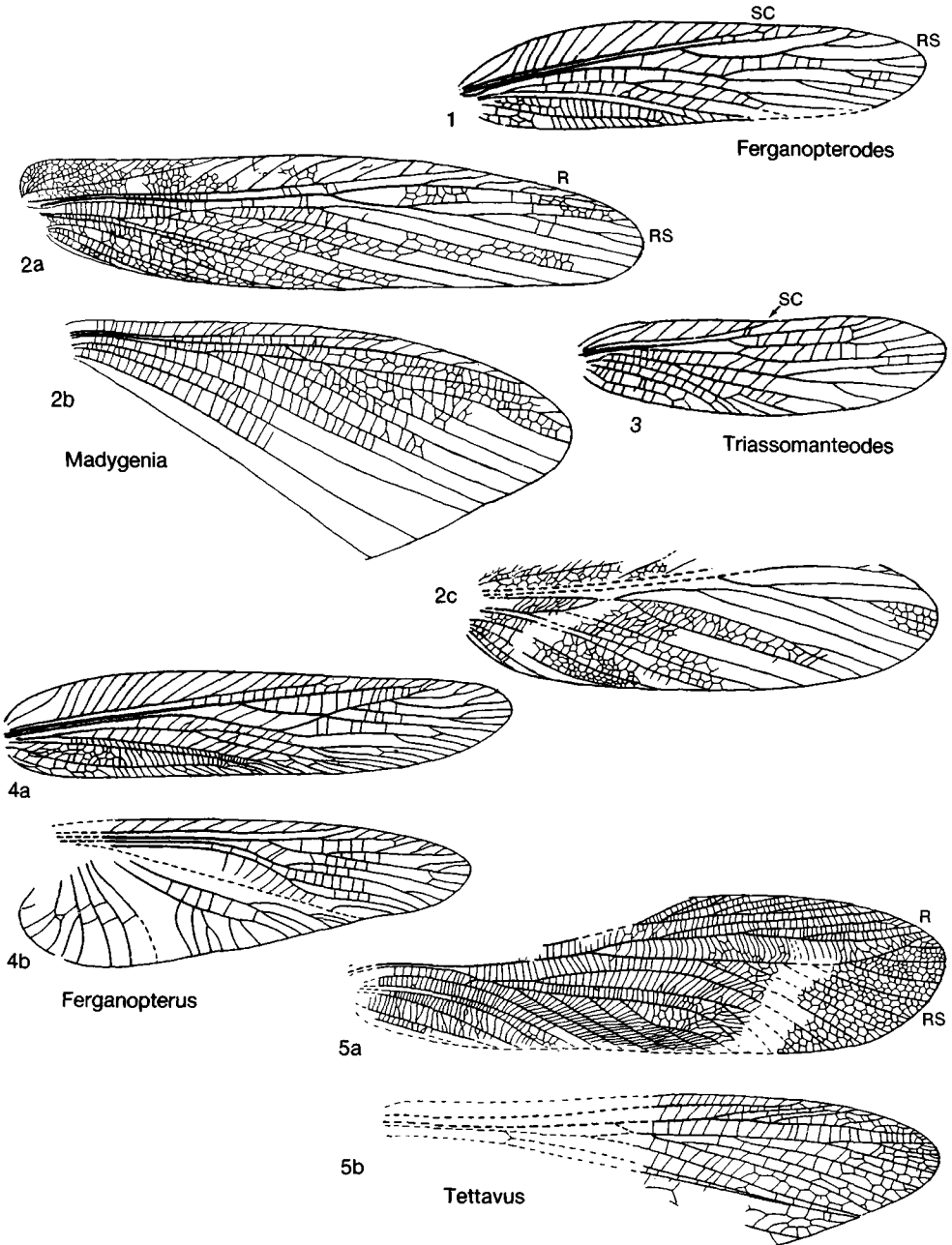


FIG. 101. Triassomanteidae and Tettavidae (p. 162–163).

Family TETTIGONIIDAE

Krauss, 1902

[Tettigoniidae KRAUSS, 1902, p. 538]

Similar in appearance to Oedischiidae and Tettavidae. Fore wings tegminous, their apices

folded together at rest; vein RS only rarely fused with MA, even for a short interval; CUA with an anterior branch coalescing with MP; stridulatory structures commonly well developed; right tegmen with a membranous

area between CUP and branches of CUA; left tegmen with a similar structure, but CUP larger and serrulate. Hind wings much as in Oedischiidae, but MA commonly anastomosed for a short interval; MP typically fused with an anterior branch of CUA. Body laterally compressed; antennae long, filiform; fore and middle legs relatively short; hind femora skittle-shaped; tarsi with 4 segments; ovipositor laterally flattened; auditory organs commonly present, situated on fore tibiae. *Eoc.*—*Holo.*

Tettigonia LINNÉ, 1758, p. 425. *Holo.* [A wing from the Miocene/Pliocene of France has been identified (BRICE & LAURENTIAUX, 1964) as belonging to a female of the existing species *Tettigonia viridissima* LINNÉ, but SHAROV (1968) reports that the wing is from a male and that the taxonomic identification is erroneous.]

Anabrus HALDEMANN, 1852, p. 372. Ovipositor only. [Generic position doubtful.] COCKERELL, 1908p. *Oligo.*, USA (Colorado)—*Holo.*

Arctolocusta ZEUNER, 1937, p. 157 [*Locusta groenlandica* HEER, 1883, p. 146; OD]. Little-known fore wing, female. SHAROV, 1968. *Eoc.*, Greenland.

Eodecticus PONGRÁČZ, 1928, p. 128 [*E. maculatus*; OD]. Fore wing similar to that of *Decticus* (recent) but with more branches of SC to costal margin and with irregular maculations. ZEUNER, 1939. *Mio.*, Europe (Austria).—FIG. 102,1. **E. maculatus*; fore wing, $\times 1.0$ (Zeuner, 1939).

Eomortoniellus ZEUNER, 1936b, p. 291 [*E. handlirshi*; OD]. Similar to *Mortoniellus* (recent) but pronotum smaller. ZEUNER, 1944b. *Oligo.*, Europe (Baltic).

Lipotactes BRUNNER, 1898, p. 274. Nymphal male. ZEUNER, 1936b. *Oligo.*, Europe (Baltic)—*Holo.*

Lithymnetes SCUDDER, 1878a, p. 532 [*L. guttatus*; OD]. Little-known genus, based on fore wing. THÉOBALD, 1937a; ZEUNER, 1939; SHAROV, 1968; KEVAN & WIGHTON, 1983. *Oligo.*, USA (Colorado).

Nymphomorpha HENRIKSEN, 1922b, p. 13 [*N. medialis*; OD]. Little-known hind wing. ZEUNER, 1939. *Eoc.*, Europe (Denmark).

Orchelimum SERVILLE, 1839, p. 522. Complete male and female. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Orphanina FISCHER, 1853, p. 222. Hind tibia. CHARPENTIER, 1825; ZEUNER, 1929, 1939. *Pleist.*, Europe (Poland)—*Holo.*

Platycleis FIEBER, 1852, p. 2. Fore wings, hind wings, and parts of body. ZEUNER, 1929, 1939. *Mio.*, Europe (Austria, Germany)—*Holo.*

Pseudotettigonia ZEUNER, 1937, p. 157 [**Tettigonia amoena* HENRIKSEN, 1929, p. 317; OD]. Similar to *Tettigonia*, but crossveins of fore wing

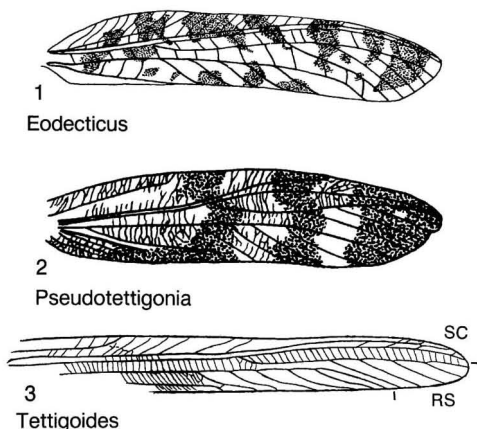


FIG. 102. Tettigoniidae (p. 165).

more regular. SHAROV, 1968. *Eoc.*, Europe (Denmark).—FIG. 102,2. **P. amoena* (HENRIKSEN); fore wing, $\times 0.8$ (Zeuner, 1939).

Rammea ZEUNER, 1931, p. 253 [**R. lateipes*; OD]. Similar to *Decticus* but with a conelike process between meso- and metasternum. ZEUNER, 1939. *Mio.*, Europe (Germany).

Tettigoides RIEK, 1952b, p. 20 [**T. pectinata*; OD]. Elytron very narrow, with long SC; RS arising at midwing; M nearly parallel to R. [Family position uncertain.] ?*Eoc.*, Australia (Queensland).—FIG. 102,3. **T. pectinata*; elytron, $\times 2.0$ (Riek, 1952b).

Family HAGLIDAE Handlirsch, 1906

[Haglidae HANDLIRSCH, 1906b, p. 425] [=Eospilopteronidae COCKERELL, 1915, p. 472; Pamphagopsidae MARTYNOV, 1925b, p. 577; Aboilidae MARTYNOV, 1925b, p. 581; Prophalangopsidae HANDLIRSCH, 1929, p. 724; Isfartopteridae MARTYNOV, 1937a, p. 61; Tshorkuphlebidae MARTYNOV, 1937a, p. 72]

Related to Oedischiidae but with the venation of the fore wings conspicuously different in males and females; fore wings of males with a more or less elaborate stridulatory organ. Fore wing, male: costal area very broad, at least basally, with numerous veinlets and crossveins; costal vein submarginal in specialized species, forming a long precostal area; R typically with several terminal branches; RS with numerous branches in generalized genera, but few in genera having elaborate stridulatory organs; CUA coalesced with M basally but diverging posteriorly before M divides into MA and MP; MA not anastomosed with RS; MA and MP commonly unbranched but strongly curved in specialized genera; CUP unbranched. Fore wing,

female: MA not directed toward RS or in contact with it; MA and MP much as in males but without curves. Hind wing known in only a few species; venation as in Oedischidae but with an enlarged anal area in some specialized genera. Antennae long, multisegmented; legs relatively short; 4 tarsal segments; auditory organs on fore tibiae; ovipositor broad and well developed. ZEUNER, 1939; SHAROV, 1968. *Trias.*—*Holo.*

SHAROV'S account (1968) of the fossil Haglidae shows that the family was very large and diverse during the early half of the Mesozoic. In contrast, there are only two recent genera, *Prophalangopsis* WALKER (India) and *Cyphoderis* UHLER (western North America), neither of which is represented in the fossil record.

Hagla GIEBEL, 1856, p. 265 [**H. gracilis*; SD ZEUNER, 1939, p. 139] [= *Haglodes* HANDLIRSCH, 1906b, p. 425 (type, *Hagla similis* GIEBEL, 1856, p. 265)]. Male: fore wing broadest before midwing. Female: fore wing with 5 to 6 terminal branches on RS. Hind wing unknown. ZEUNER, 1939; SHAROV, 1968. *Jur.*, England.—FIG. 103,1. **H. gracilis*; fore wings of *a*, male and *b*, female, $\times 2.0$ (Zeuner, 1939).

Aboilus MARTYNOV, 1925b, p. 581 [**A. fasciatus*; OD] [= *Pamphagopsis* MARTYNOV, 1925b, p. 578 (type, *P. maculata*); *Syndesmophyllum* MARTYNOV, 1934, p. 1004, *nom. nud.*]. Male: fore wing broadly oval; precostal area large; costal area very broad; RS arising just before midwing; MA and MP smoothly curved and parallel; hind wing with narrow costal area; RS arising nearer wing base than in fore wing; anal area unknown. Female: fore wing with nearly straight anterior margin, M forking before origin of RS. [Type of family Aboilidae MARTYNOV, 1925b.] ZEUNER, 1939; SHAROV, 1968. *Jur.*, USSR (Kazan).—FIG. 103,2. *A. columnatus* MARTYNOV; *a*, fore and *b*, hind wings of male, both $\times 1.7$ (Rohdendorf, 1962a); *c*, fore wing of female, $\times 0.2$ (Sharov, 1968).

Albertoilus KEVAN & WIGHTON, 1981, p. 1825 [**A. cervirufi*; OD]. Little-known genus, based on fragments of fore and hind wings, apparently related to *Aboilus*. KEVAN & WIGHTON, 1983. *Paleoc.*, Canada (Alberta).

Alloma HONG, 1982a, p. 79 [**A. facialata*; OD]. Female: fore wing as in *Hebeihagla* but broader near midwing. HONG, 1982b. *Jur.*—*Cret.*, China (Liaoning Province).

Archaboilus MARTYNOV, 1937a, p. 51 [**A. kisytkiensis*; OD]. Male: fore wing as in *Aboilus*, but

costal veinlets more numerous and closer together; precostal area much smaller. ZEUNER, 1939; SHAROV, 1968. *Jur.*, USSR (Kirghiz, Tadzhik).—FIG. 104,6. *A. shurabicus* MARTYNOV; fore wing of male, $\times 0.8$ (Rohdendorf, 1962a).

Archaeohagla LIN, 1965, p. 364 [**A. sinensis*; OD]. Little-known genus, based on proximal fragment of fore wing of female. [Probably a synonym of *Sinohagla*.] *Jur.*, China (Inner Mongolia).

Archihagla SHAROV, 1968, p. 175 [**A. zeuneri*; OD]. Male: fore wing very similar to that of *Hagla*, but front margin of fore wing smoothly curved and branching of R more extensive; subcostal veinlets mostly forked. Female unknown. *Trias.*, USSR (Kirghiz).—FIG. 104,1. **A. zeuneri*; fore wing, $\times 3.2$ (Sharov, 1968).

Cyrtophyllites OPPENHEIM, 1888, p. 223 [**C. rogeri*; OD]. Little-known genus. Male: fore wing broadly oval, with very wide costal area; RS with 3 or 4 long branches; crossveins close together and forming cellules distally. SHAROV, 1968. *Jur.*, Europe (Germany).—FIG. 104,2. **C. rogeri*; fore wing, $\times 1.2$ (Zeuner, 1939).

Eospilopteron COCKERELL, 1915, p. 472 [**E. ornatum*; OD]. Little-known genus, based on apical fragment of wing. [Family assignment doubtful. Type of family Eospilopteroidae.] SHAROV, 1968. *Jur.*, England.

Hebeihagla HONG, 1982b, p. 1121 [**H. songyingziensis*; OD]. Female: fore wing similar to that of *Parahagla*, but RS apparently with a few more branches; wing broadest basally. [Probably a synonym of *Parahagla*.] *Jur.*, China (Hebei Province).

Isfaroptera MARTYNOV, 1937a, p. 61 [**I. grylliformis*; OD]. Similar to *Cyrtophyllites*. Male: fore wing about as wide as long, almost circular; RS with only 1 or 2 branches. [Type of family Isfaropteridae MARTYNOV, 1937a.] ZEUNER, 1939; SHAROV, 1968. *Jur.*, USSR (Kirghiz).—FIG. 104,3. **I. grylliformis*; fore wing of male, $\times 2.0$ (Martynov, 1937a).

Jurassobatea ZEUNER, 1937, p. 154 [**J. gryllacroides*; OD]. Little-known genus, based on a poorly preserved specimen. Large species, similar to *Aboilus*. [Probably a synonym of *Pyncophlebia*. Placed by ZEUNER (1937, 1939) in Gryllacrididae; by SHAROV (1968) in Haglidae.] KEVAN & WIGHTON, 1981, 1983. *Jur.*, Europe (Germany).

Liassophyllum ZEUNER, 1935, p. 106 [**L. abbreviatum*; OD]. Little-known genus, based on distal fragment of fore wing of male; apex pointed; RS arising much nearer apex than in *Cyrtophyllites*; MA strongly arched anteriorly. [Family assignment doubtful.] ZEUNER, 1939; SHAROV, 1968. *Jur.*, England.—FIG. 104,5. **L. abbreviatum*; fore wing as preserved, $\times 0.8$ (Zeuner, 1935).

Mesogryllus HANDLIRSCH, 1906b, p. 523 [**Blattidium achelous* WESTWOOD, 1854, p. 390; OD]. Little-known genus, based on poorly preserved

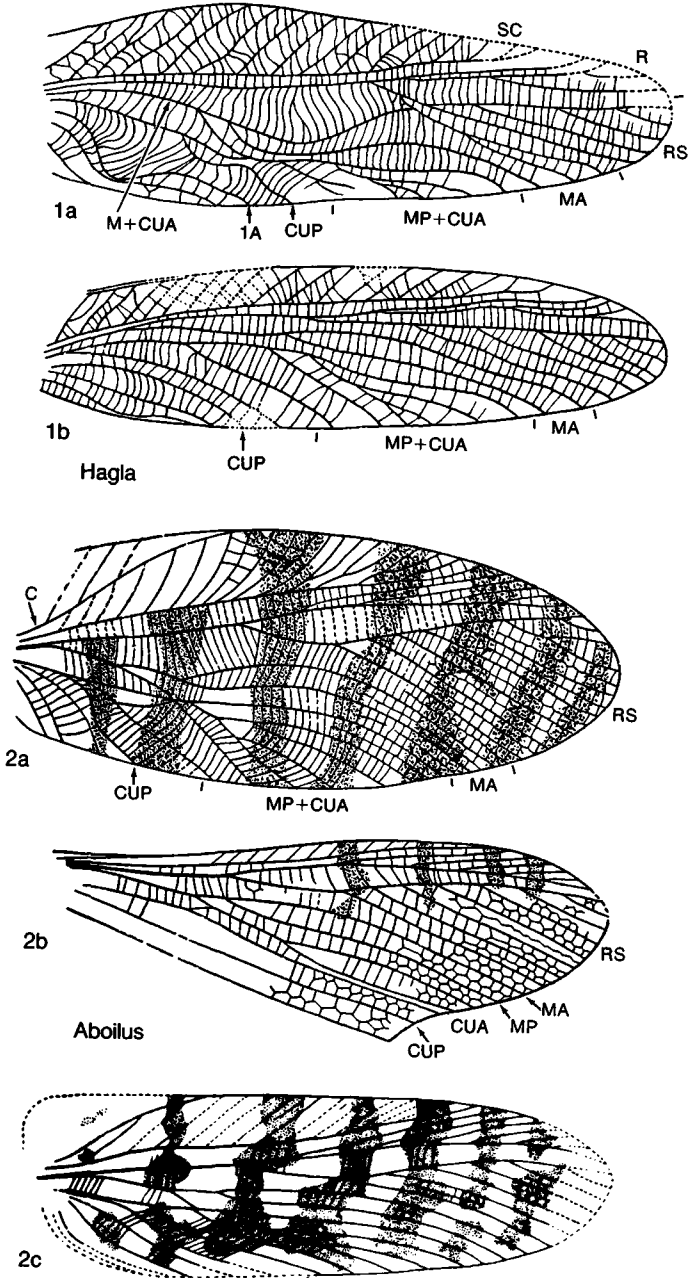


FIG. 103. Haglidae (p. 166).

wing. [Placed in Gryllidae by ZEUNER (1939) and in Haglidae by SHAROV (1968).] *Jur.*, England.
Neohagla RIEK, 1955, p. 683 [**N. sinuata*; OD]. Male: venation of fore wing as preserved similar

to that of *Hagla*, but with fewer branches on R; crossveins between R and RS more sinuous. SHAROV, 1968. *Trias.*, Australia (Queensland).
Nipponohagla FUJIIYAMA, 1978, p. 183 [**N. kaga*; OD]. Female: fore and hind wings apparently as

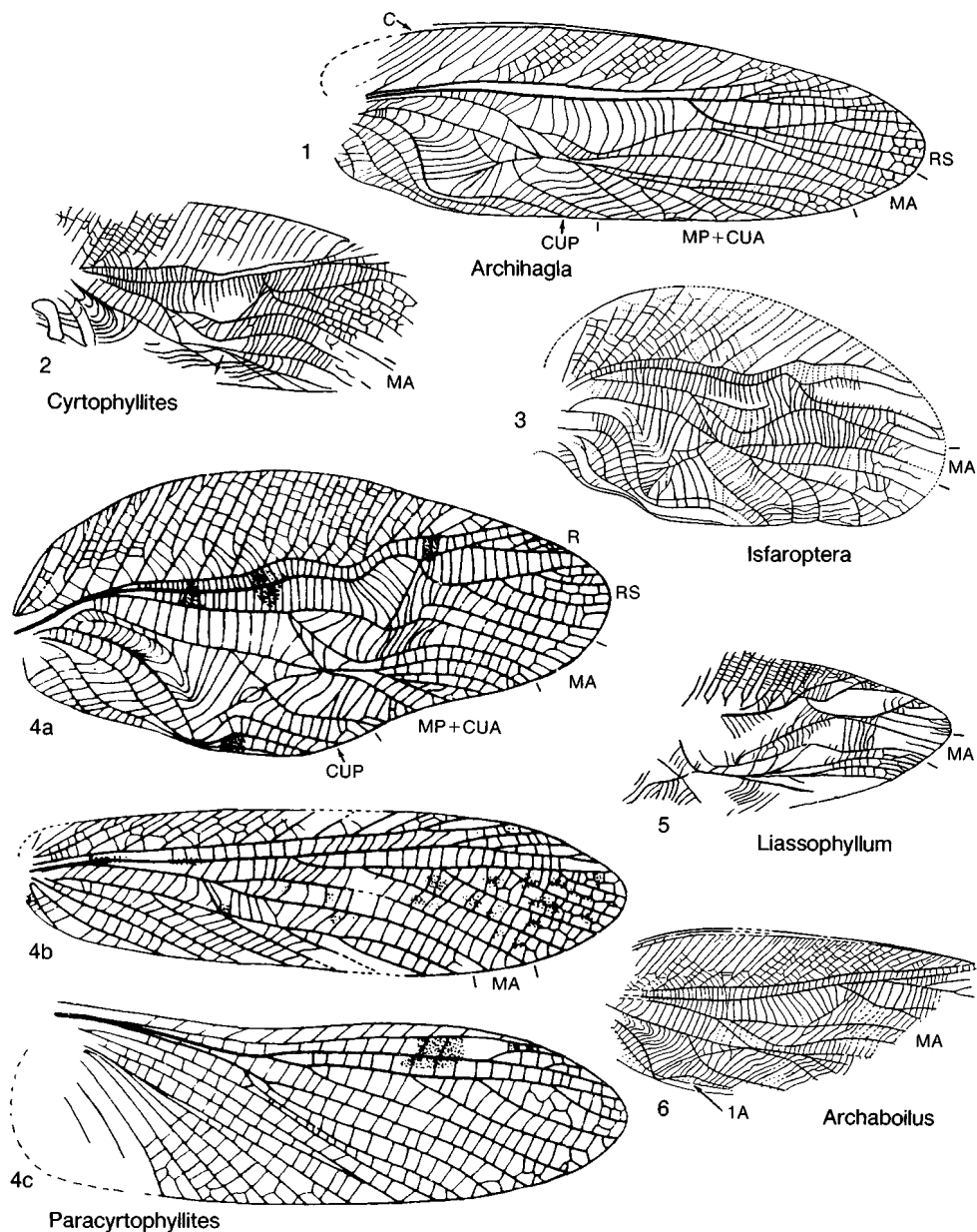


FIG. 104. Haglidae (p. 166–168).

in *Abolilus*, but fore wing much broader, with convex posterior margin. *Cret.*, Japan.

Notopamphagopsis CABRERA, 1928, p. 371 [**N. bolivari*; OD]. Little-known genus, based on apical fragment of wing. SHAROV, 1968. *Trias.*, Argentina (Mendoza).

Palaeorehnia COCKERELL, 1908t, p. 126 [**P. maculata*; OD] [= *Cymatomera maculata* SCUDDER, 1890, p. 230]. Little-known genus, based on

small proximal fragment of fore wing of female. ZEUNER, 1939; SHAROV, 1968; KEVAN & WIGHTON, 1983. *Paleog.*, Scotland; *Oligo.*, USA (Colorado).

Paracyrtophyllites SHAROV, 1968, p. 177 [**P. undulatus*; OD]. Similar to *Cyrtophyllites*, but male with stem MA of fore wing more remote from MP and deeply forked. Fore wing of female with normal costal area and shape. Hind wing

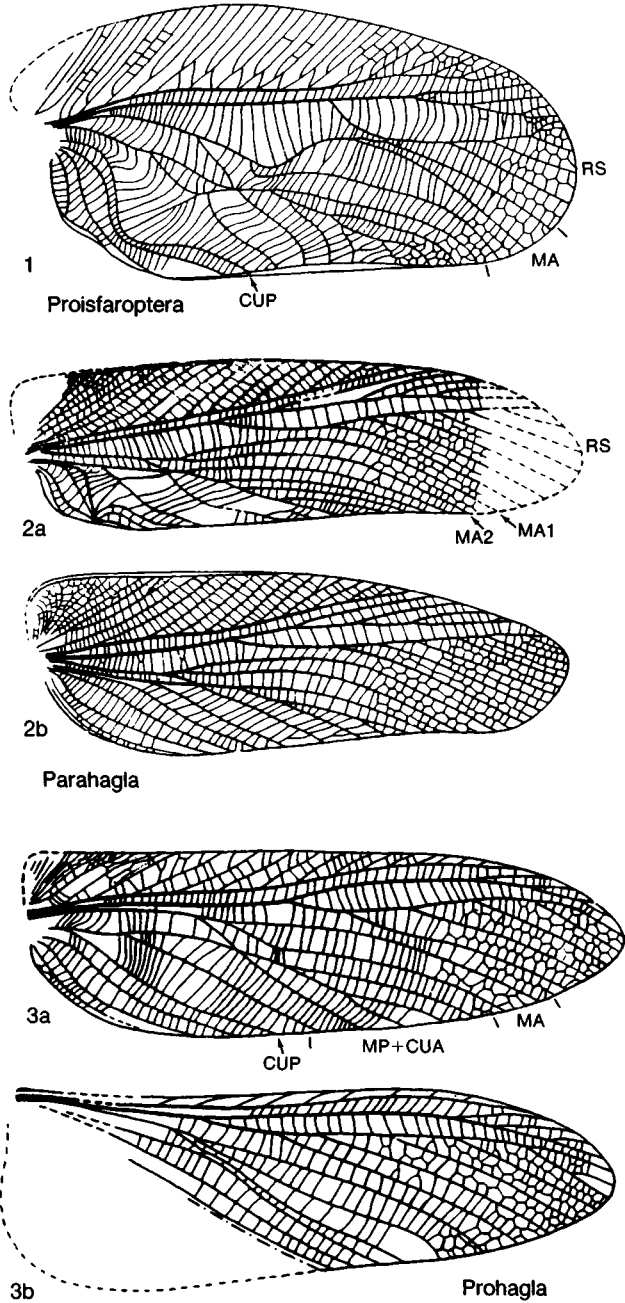


FIG. 105. Haglidae (p. 169–170).

with enlarged anal area. *Jur.*, USSR (Kazakh).
 —FIG. 104,4. **P. undulatus*; *a*, fore wing of male, $\times 4.0$; *b*, fore wing of female, $\times 3.2$; *c*, hind wing of female, $\times 4.0$ (Sharov, 1968).

Parahagla SHAROV, 1968, p. 178 [**P. sibirica*; OD].
 Similar to *Hagla*, but fore wing of male with MA1 and MA2 almost parallel and with a strong bend at midwing. *Cret.*, USSR (Asian RSFSR).

- FIG. 105,2. **P. sibirica*; *a*, fore wing of male, $\times 2.3$; *b*, fore wing of female, $\times 1.8$ (Sharov, 1968).
- Paratshorkuphlebia** SHAROV, 1968, p. 176 [**P. multivenosa*; OD]. Similar to *Tshorkuphlebia*. Male: costal area of fore wing very broad; MA curved anteriorly near midwing. *Jur.*, USSR (Kirghiz). — FIG. 106,3. **P. multivenosa*; fore wing of male as preserved, $\times 1.6$ (Sharov, 1968).
- Procyrtophyllites** ZEUNER, 1935, p. 106 [**P. britannicus*; OD]. Little-known genus, based on small wing fragment of male; similar to *Archaboilus*, but crossveins between RS and M more sigmoidal. ZEUNER, 1939; SHAROV, 1968. *Jur.*, England.
- Prohagla** RIEK, 1954c, p. 164 [**P. superba*; OD]. Female: fore wing relatively broad, with prominent precostal area; oblique costal veinlets as in *Protshorkuphlebia*. RS with only 5 terminal branches; vein 2A serrate. RIEK, 1955; SHAROV, 1968. *Trias.*, Australia (New South Wales, Queensland). — FIG. 105,3. **P. superba*; *a*, fore and *b*, hind wings of female, $\times 2.0$ (Sharov, 1968).
- Proisfaroptera** SHAROV, 1968, p. 173 [**P. martynovi*; OD]. Male: fore wing broadly oval, with wide costal area; MA strongly curved; stridulatory organ well developed. Female: fore wing similar to that of *Turkestanina*, but branches of R much shorter. *Trias.*, USSR (Kirghiz). — FIG. 105,1. **P. martynovi*; fore wing of male, $\times 3.0$ (Sharov, 1968).
- Prophalangopseides** SHAROV, 1968, p. 178 [**P. vitimicus*; OD]. Similar to *Prophalangopsis* (recent), but fore wing of male with branching of RS more extensive and that of M more reduced. *Cret.*, USSR (Asian RSFSR). — FIG. 106,7. **P. vitimicus*; fore wing of male, $\times 2.5$ (Sharov, 1968).
- Protohagla** ZEUNER, 1962a, p. 165 [**P. langi*; OD]. Little-known genus, based on proximal fragment of fore wing of male. Precostal area well developed; subcostal area with dense, parallel crossveins; longitudinal veins straight, except CUP. SHAROV, 1968. *Jur.*, England.
- Protshorkuphlebia** SHAROV, 1968, p. 174 [**P. triassica*; OD]. Male: fore wing elongate, pointed; R and RS branching at same level, almost symmetrically. Female: fore wing very similar to that of *Turkestanina*. *Trias.*, USSR (Kirghiz). — FIG. 106,2. **P. triassica*; fore wing of male, $\times 2.0$ (Sharov, 1968).
- Pseudohagla** SHAROV 1962g, p. 152 [**Hagla pospelovi* MARTYNOVA, 1949b, p. 923; OD]. Female: fore wing broader than in *Hagla* and precostal area longer; crossveins numerous but not reticulate. SHAROV, 1968. *Jur.*, USSR (Asian RSFSR). — FIG. 106,6. **P. pospelovi* (MARTYNOVA); fore wing of female, $\times 1.4$ (Sharov, 1962g).
- Pycnophlebia** DEICHMÜLLER, 1886, p. 20 [*Locusta speciosa* GERMAR, 1839, p. 198; OD]. Little-known genus, based on numerous but poorly preserved specimens; apparently similar to *Aboilus*. Large species; remigium of fore wing subtriangular; RS with about 10 parallel branches. Tympanal organ on fore tibia. [Placed by MARTYNOV (1937a) in Haglidae, by ZEUNER (1939) in Ensifera, *incertae sedis*, and by SHAROV (1968) in Haglidae.] *Jur.*, Europe (Germany).
- Sinohagla** LIN, 1965, p. 363 [**S. anthoides*; OD]. Little-known genus, based on distal portion of fore wing of female. Venation as in *Aboilus*, with some reticulate crossveins distally. SHAROV, 1968. *Jur.*, China (Inner Mongolia).
- Sunoprophalangopsis** HONG, 1982b, p. 1124 [**S. elegantis*; OD]. Similar to *Aboilus*, but fore wing with CUA more abruptly curved. [Probably a synonym of *Aboilus*.] *Jur.*, China (Hebei Province).
- Tshorkuphlebia** MARTYNOV, 1937a, p. 154 [**T. compressa*; OD]. Related to *Hagla*, but with fewer branches on RS. Male: costal area very broad basally; precostal area wide but short; stridulatory organ as in *Hagla*. Female: fore wing with branches of M and CUA parallel. [Type of family Tshorkuphlebiidae.] SHAROV, 1968. *Jur.*, USSR (Tadzhik). — FIG. 106,1. *T. shurabica* SHAROV; *a*, fore wing of male as preserved; *b*, fore wing of female, $\times 1.5$ (Sharov, 1968).
- Turkestanina** SHAROV, 1968, p. 173 [**T. deviata*; OD]. Female: fore wing as in *Zeunerophlebia*, but CUP nearly straight basally; crossveins very dense over entire wing. *Trias.*, USSR (Kirghiz). — FIG. 106,4. **T. deviata*; fore wing of female, $\times 0.75$ (Sharov, 1968).
- Zalmona** GIEBEL, 1856, p. 266 [**Z. brodiei*; OD]. Little-known genus, based on small fragment of fore wing of female, probably related to *Paracyrtophyllites*. ZEUNER, 1939; SHAROV, 1968. *Jur.*, England.
- Zalmonites** HANDLIRSCH, 1906b, p. 422 [**Z. geinirzi*; OD]. Little-known genus, based on small distal fragment of wing. [Placed in Locustidae by HANDLIRSCH (1906b) and in Haglidae by SHAROV (1968).] *Jur.*, Europe (Germany).
- Zeunerophlebia** SHAROV, 1968, p. 172 [**Z. gigas*; OD]. Male: costal area of fore wing very broad; RS with at least 7 branches; CUA with at least 6 branches; stridulatory organs present. Female: costal area of fore wing less broad; CUP curved basally, serrate. *Trias.*, USSR (Kirghiz). — FIG. 106,5. **Z. gigas*; *a*, fore wing of male, $\times 1.0$; *b*, fore wing of female, $\times 0.7$ (Sharov, 1968).

Family PHASMOMIMIDAE Sharov, 1968

[Phasmomimidae SHAROV, 1968, p. 179]

Related to the Haglidae. Fore wing elongate; precostal area small or absent; costal area narrow, with few veinlets; vein RS typ-

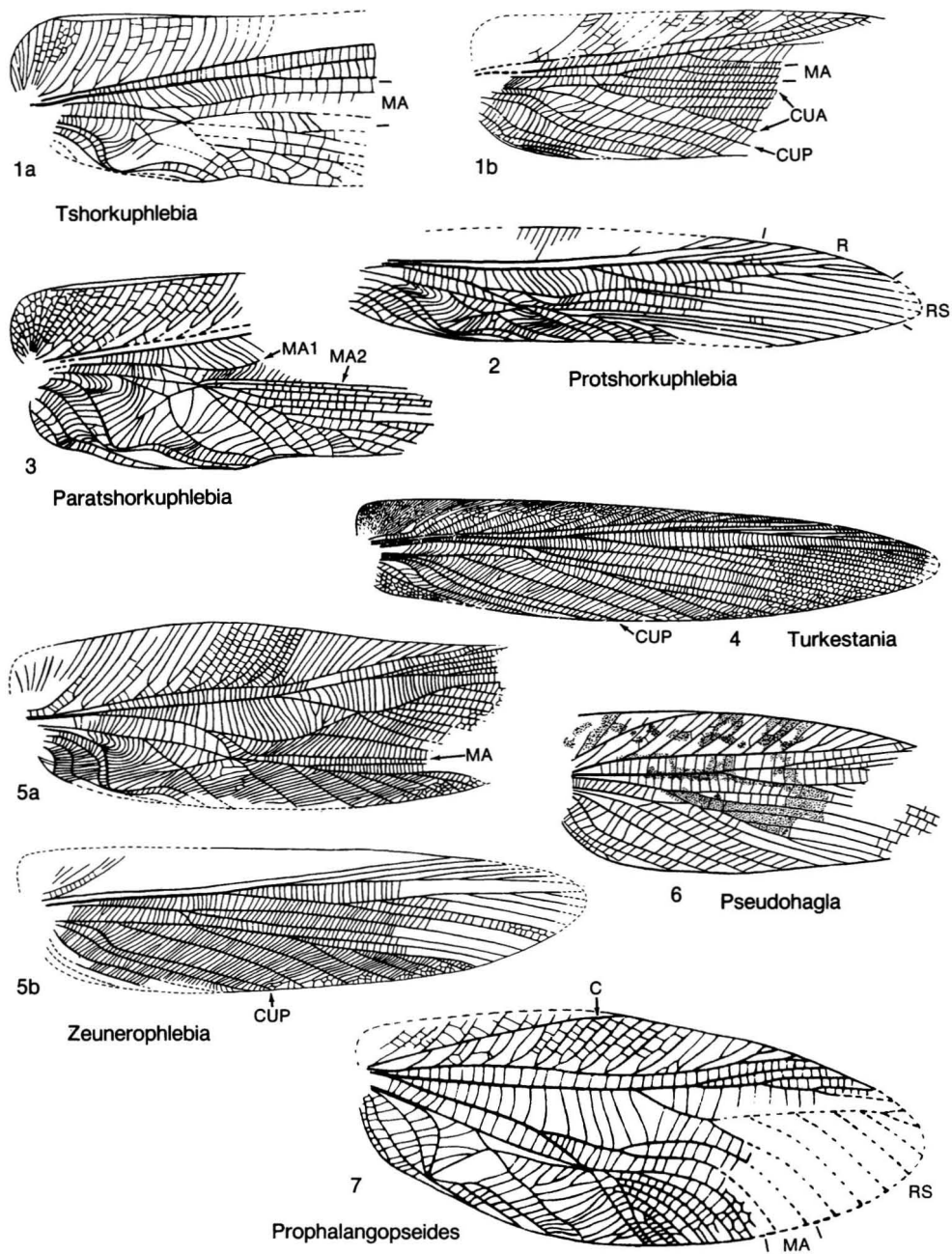


FIG. 106. Haglidae (p. 170).

ically with 2 or 3 terminal branches; MA and MP commonly unbranched; CUA not attached to stem of M. Hind wing much as in Haglidae but with a large anal fan. Ovipositor long, curved. *Jur.—Paleoc.*

Phasmomima SHAROV, 1968, p. 179 [**P. maculomarginata*; OD]. Fore wing: R and RS branched distally only; MA and MP ending almost at wing apex. *Jur.*, USSR (Kazakh).—FIG. 107,2. **P. maculomarginata*; a, fore and b, hind wings, both X2.0 (Sharov, 1968).

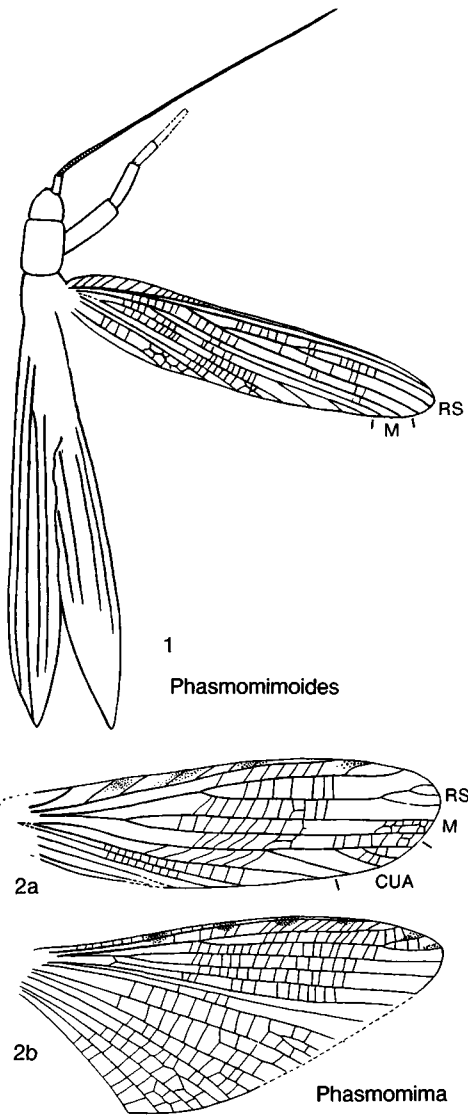


FIG. 107. Phasmomimidae (p. 171–172).

Palaeopteron RICE, 1969, p. 7 [**P. complexum*; OD]. Little-known genus, based on a fore wing fragment; similar to *Phasmomimella*, with veins SC, R, and RS1 convergent apically. [Originally placed in order Perlaria.] KEVAN & WIGHTON, 1983. *Cret.*, Canada (Labrador).

Phasmomimella KEVAN & WIGHTON, 1981, p. 1826 [**P. paskapoensis*; OD]. Little-known genus, based on fragments of fore and hind wings. Fore wing apparently as in *Phasmomimoides*, but stem of RS much longer; M apparently unbranched. *Paleoc.*, Canada (Alberta).

Phasmomimoides SHAROV, 1968, p. 180 [**P.*

lineatus; OD]. Fore wing as in *Phasmomimella*, but RS deeply forked and MA and MP ending below wing apex. *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).—FIG. 107, 1. **P. lineatus*, *Jur.*; fore wing, part of body, and antenna, X1 (Sharov, 1968).

Phasmomimula KEVAN & WIGHTON, 1981, p. 1828 [**P. enigma*; OD]. Little-known genus, based on fragments of fore and hind wings. Apparently similar to *Phasmomimella*, but RS unbranched in fore wing. *Paleoc.*, Canada (Alberta).

Family GRYLLACRIDAE

Stål, 1874

[Gryllacrididae STÅL, 1874, p. 4]

Related to the Haglidae. Fore wing with precostal area very long, submarginal costa extending typically beyond midwing; branches of main veins more or less parallel; few branches on vein RS. Hind wing with M apparently unbranched; anal fan larger than remigium. Stridulatory organs absent from both pairs of wings, but tympanal organs present on fore tibiae of some existing species. Tarsi with 4 segments; ovipositor as in Haglidae. *Paleoc.*—*Holo.*

Gryllacris SERVILLE, 1831, p. 138. *Holo.*

Macrelcana KARNY, 1932, p. 67 [**Gryllacris ungeri* HEER, 1849, p. 8; OD]. Little-known genus, based on poorly preserved fore wing and hind legs; apparently related to *Gryllacris* (recent), but spines in hind femora broadened to form flat plates. ZEUNER, 1939, SHAROV, 1968. *Mio.*, Europe (Germany).

Prorhaphidophora CHOPARD, 1936a, p. 163 [**P. antiqua*; OD]. Similar to *Rhaphidophora* (recent), but fore and middle femora armed only with a small geniculate spine. ZEUNER, 1939. *Oligo.*, Europe (Baltic).

Zeuneroptera SHAROV 1962g, p. 153 [**Palaeorehnia scotica* ZEUNER, 1939, p. 126; OD]. Little-known genus, based on fore wing fragment. Vein C terminating slightly before midwing. SHAROV, 1968; KEVAN & WIGHTON, 1983. *Paleoc.*, Scotland.

Family GRYLLIDAE Latreille, 1802a

[Gryllidae LATREILLE, 1802a, p. 274]

Related to the Haglidae. Male: fore wing tegminous, each tegmen with a longitudinal line of folding; tegmina at rest forming a boxlike cover over meso- and metanotum, hind wings, and abdomen; posterior branches of vein CUA modified as part of stridulatory

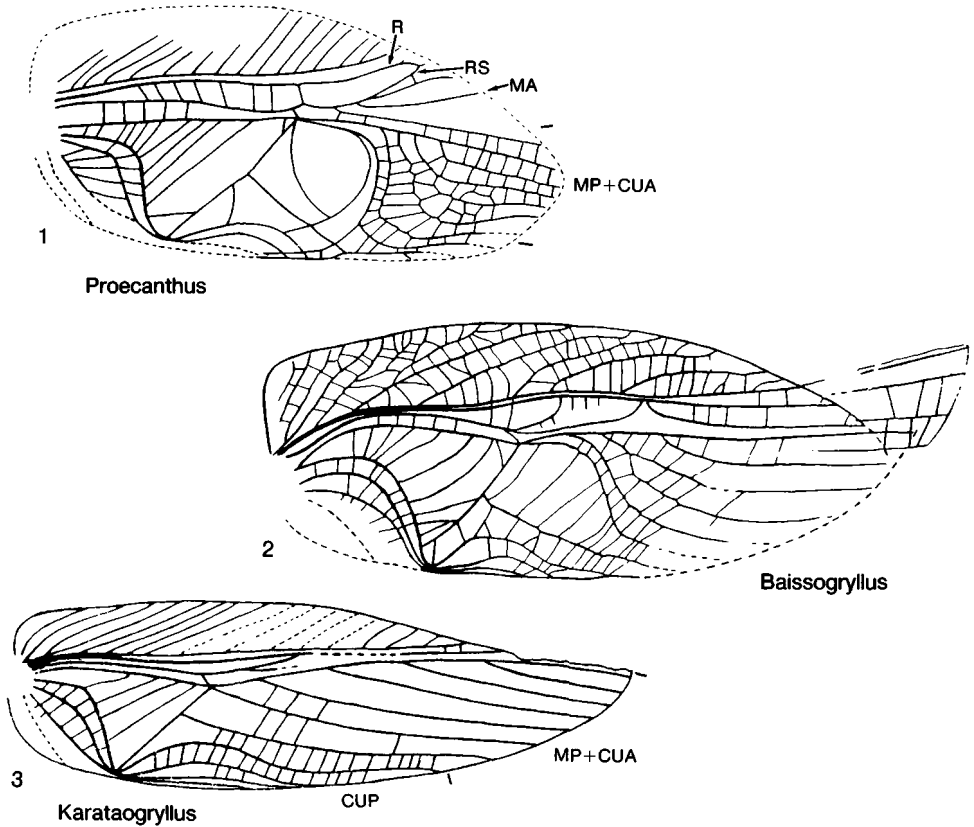


FIG. 108. Gryllidae (p. 173–174).

organ, extending almost to wing apex; stridulatory organ expanded distally and anteriorly, commonly occupying at least half of wing area, with an oblique secondary vein extending diagonally across central part of wing; CUP curving posteriorly, serrulate. Hind wing typically with an enlarged anal fan, as in Haglidae. Female: fore wing as in male in most respects, but lacking modifications of veins associated with stridulatory organ; branching of R and RS reduced, with loss of RS in highly specialized genera. Tarsi with 3 segments; cerci long, flexible; ovipositor cylindrical. ZEUNER, 1939, SHAROV, 1968. *Trias.*—*Holo.*

Gryllus LINNÉ, 1758, p. 425. Specimens of fore wings only. COCKERELL, 1925e; THÉOBALD, 1937a; ZEUNER, 1937, 1939; SHAROV, 1968. *Paleoc.*—*Plio.*, Argentina (Jujuy); *Oligo.*, England, Europe (France, Germany)—*Holo.*

Allopterites COCKERELL, 1920a, p. 275 [**A. multilineatus*; OD]. Little-known genus; similar to *Gryllus*, but M with more branches. *Oligo.*, England.

Baissogryllus SHAROV, 1968, p. 183 [**B. sibiricus*; OD]. Male: fore wing nearly oval in shape; costal area long and nearly of uniform width; branches of SC long, oblique. *Jur.*, USSR (Asian RSFSR). —FIG. 108,2. **B. sibiricus*; fore wing of male, ×4 (Sharov, 1968).

—FIG. 108,2. **B. sibiricus*; fore wing of male, ×4 (Sharov, 1968).

Eneopterotrypus ZEUNER, 1937, p. 156 [**E. chopardi*; OD]. Little-known genus, based on fragment of fore wing of male. ZEUNER, 1939. *Oligo.*, England.

Gryllavus SHAROV, 1968, p. 181 [**G. madygenicus*; OD]. Male: fore wing relatively slender; R with a few, short terminal branches; RS with a shallow fork; MA and MP parallel and nearly straight, terminating at wing apex; CUA with 8 terminal branches. Female: fore wing similar to that of male except for details in region of stridulatory organ; RS unbranched. *Trias.*, USSR (Kirghiz). —FIG. 109,1. **G. madygenicus*; fore wings of a, male and b, female, both ×4 (Sharov, 1968).

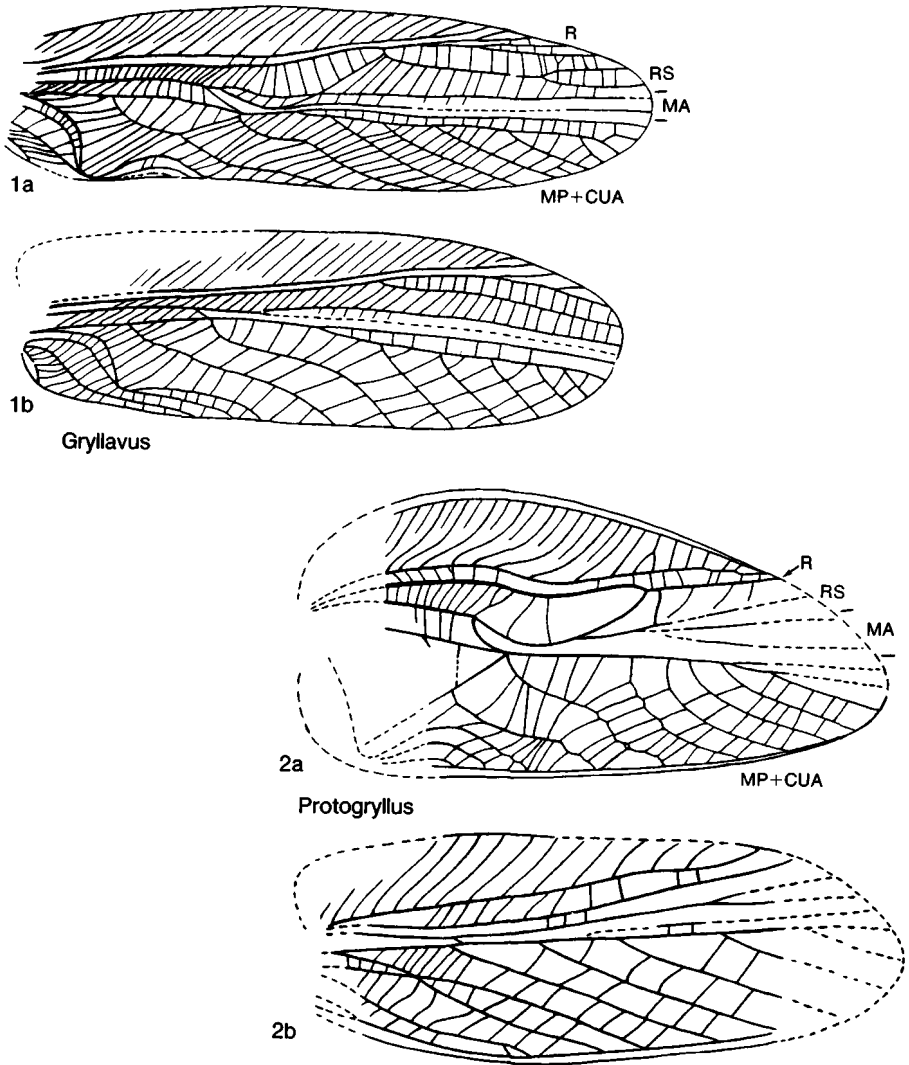


FIG. 109. Gryllidae (p. 173–175).

Heterotrypus SAUSSURE, 1878, p. 537. Whole adult male. CHOPARD, 1936b; WEIDNER, 1956. *Oligo.*, Europe (Baltic)—*Holo.*

Karataogryllus SHAROV, 1968, p. 182 [**K. gryllotalpiformis*; OD]. Male: fore wing as in *Protogryllus* but more elongate; anterior margin not so convex; branches of M and CUA parallel. *Jur.*, USSR (Kazakh).—FIG. 108,3. **K. gryllotalpiformis*; fore wing of male, $\times 4$ (Sharov, 1968).

Liassogrylloides BODE, 1953, p. 105 [**L. basifastigatus*; OD]. Little-known fore wing. [Family assignment doubtful.] *Jur.*, Europe (Germany).

Lithogryllites COCKERELL, 1908p, p. 64 [**L. lutzii*; OD]. Little-known genus, based on apterous male, probably immature. ZEUNER, 1939. *Oligo.*, USA (Colorado).

Madasumma WALKER, 1869, p. 64. Female adult. CHOPARD, 1936b; ZEUNER, 1939, 1944b. *Oligo.*, Europe (Baltic)—*Holo.*

Prooecanthus SHAROV, 1968, p. 184 [**P. caucasicus*; OD]. Little-known genus, based on fragment of fore wing of male. Similar to *Prooecanthus*, but costal area much narrower. *Mio.*, USSR (Asian RSFSR).

Prooecanthus SHAROV, 1968, p. 183 [**P. anatolicus*; OD]. Little-known genus, based on incomplete fore wing of male. Similar to *Baissogryllus* but with fewer crossveins in the stridulatory area. *Cret.*, USSR (Kazakh).—FIG. 108,1. **P. anatolicus*; fore wing of male as preserved, $\times 5$ (Sharov, 1968).

Pronemobius SCUDDER, 1890, p. 234 [**Nemobius*

tertiarius SCUDDER, 1878b, p. 774; SD ZEUNER, 1939, p. 227]. Related to *Nemobius* (recent), but hind tibiae without spines. ZEUNER, 1939. *Eoc.*, USA (Wyoming, Colorado).

Protogryllus HANDLIRSCH, 1906b, p. 424 [**Gryllus dobertlinensis* GEINITZ, 1880, p. 523; OD] [= *Achaetites* HANDLIRSCH, 1906b, p. 523 (type, *Acheta sedgwicki* BRODIE, 1845, p. 32); *Archaeogrylloides* HAUGHTON, 1924, p. 336 (type, *A. stormburgensis*)]. Male: fore wing very broad, about half as wide as long; anterior border of wing very convex; R unbranched; distal branches of CUA more curved than in *Gryllavus*. ZEUNER, 1939; SHAROV, 1968. *Trias.*, South Africa; *Jur.*, USSR (Kirghiz, Kazakh), England, Europe (Germany).—FIG. 109.2. *P. asiaticus* SHAROV, USSR; fore wings of *a*, male and *b*, female, both $\times 6$ (Sharov, 1968).

Stenogryllodes CHOPARD, 1936b, p. 382 [**S. brevipalpis*; OD]. Little-known genus, based on a male nymph. Similar to *Stenogryllus*, but spines of hind tibiae less numerous but more closely arranged. ZEUNER, 1939. *Oligo.*, Europe (Baltic).

Trichogryllus CHOPARD, 1936b, p. 378 [**Gryllus macrocercus* GERMAR & BERENDT, 1856, p. 36; OD]. Related to the recent *Pteroplistes*. Posterior tibiae with 4 widely separated spines on each side. ZEUNER, 1939. *Oligo.*, Europe (Baltic).

Family GRYLLOTALPIDAE

Leach, 1815

[Gryllotalpidae LEACH, 1815, p. 119]

Fore wing short, with a simple stridulatory organ on that of male; hind wing typically functional, but apterous species not uncommon. Forelegs well developed, adapted for digging; femora and tibiae broad and compressed; middle legs small; hind legs relatively short, with prominent femora; tarsi with 3 segments; external ovipositor absent. *Oligo.*—*Holo.*

Gryllotalpa LATREILLE, 1802, p. 275. Fore wing and whole specimen. COCKERELL, 1921d; ZEUNER, 1931, 1939; WEIDNER, 1968a. *Oligo.*, England; *Mio.*, Europe (Germany); *Plio.*, Europe (Germany)—*Holo.*

Neocurrilla KIRBY, 1906, p. 2. Foreleg only. ZEUNER, 1937, 1939. *Mio.*, Europe (Germany)—*Holo.*

Family PROPAGRYLLACRIDIDAE

Riek, 1956

[*nom. transl.* SHAROV, 1968, p. 185, ex Propagryllacridinae RIEK, 1956, p. 106]

Male: fore wing with vein C submarginal; precostal area long, as in Oedischiidae; R with several branches, some arising close to

origin of RS; RS with only 3 terminal branches; branches of RS, MA, MP, and CUA close together and parallel; stridulatory organ absent. Female: fore wing as in male, but RS with several long branches. Antennae long, filiform; prothorax of moderate length; hind legs long, with femora only slightly thickened; tarsi with 5 segments; arolium present; ovipositor broad, serrate; cerci long and thin. SHAROV, 1968. *Trias.*

The relationships of this family with others in the Ensifera are uncertain. The type genus is known only by small fragments. The preceding family diagnosis is based on SHAROV's account (1968) of the family, which was based mainly on two other genera that he placed in the family, *Mesogryllacris* RIEK and *Gryllacrimima* SHAROV.

Propagryllacris RIEK, 1956, p. 106 [**P. crassifemur*; OD]. Little-known genus, based on fragments of wings and body. Venation apparently similar to that of *Gryllacrimima*. SHAROV, 1968. *Trias.*, Australia (Queensland).

Gryllacrimima SHAROV, 1968, p. 185 [**G. perfecta*; OD]. Similar to *Propagryllacris*. Both MA and MP+CUA forked in fore wing of male. Body structure discussed under family. *Trias.*, USSR (Kirghiz).—FIG. 110.3. **G. perfecta*; fore wing of male, $\times 2.0$ (Sharov, 1968).

Mesogryllacris RIEK, 1955, p. 685 [**M. giganteus*; OD]. Large species. Costal area of fore wing broader than in *Propagryllacris*; M forked in basal half of wing; MA and MP apparently not forked. SHAROV, 1968. *Trias.*, Australia (Queensland).

Family UNCERTAIN

The following genera, apparently belonging to the Orthoptera, suborder Ensifera, are too poorly known to permit assignment to families.

Huabeius HONG, 1982b, p. 1128 [**H. suni*; OD]. Little-known genus, possibly related to the Haglidae. Cubital and anal areas of fore wing of female very narrow. *Cret.*, China (Hebei Province).

Lithymnetoides KEVAN & WIGHTON, 1983, p. 220, footnote [**Lithymnetes laurenti* THÉOBALD, 1937a, p. 113; OD]. Little-known genus, based on poorly preserved specimens. *Oligo.*, Europe (France).

Mesoedischia SHAROV, 1968, p. 160 [**M. madygenica*; OD]. Fore wing of male: precostal area very short; costal veinlets widely spaced, not reticulate; area between SC and R very narrow; crossveins numerous but reticulate only near wing

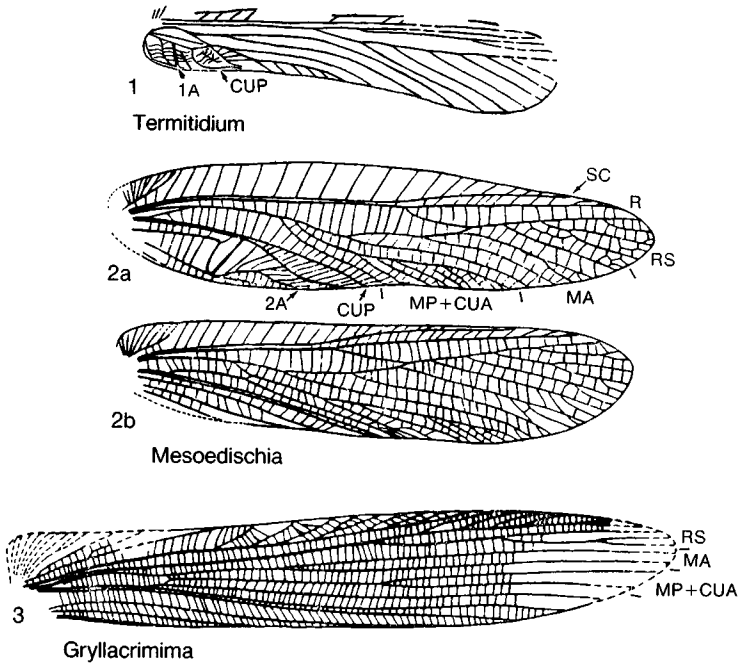


FIG. 110. Proparagryllacrididae and Uncertain (p. 175-176).

apex; CUA diverging basally from CUP and anastomosed with M for a considerable interval, before diverging off, usually in combination with MP; CUA with several branches; stridulatory apparatus well developed at base of wing. Fore wing of female similar to that of male but without local specializations near wing base. [This genus was placed by SHAROV (1968) in the Oedischiidae. The anastomosis of CUA with the stem of M, clearly shown at the base of the wing of the type specimen, and the presence of an advanced stridulatory apparatus at the base of the wing of the male seem to me to require a separate family. With regard to the structures mentioned, the genus seems more closely related to the Haglidae than to the Oedischiidae. So far as I am aware, however, this is the only extinct genus that shows the actual anastomosis of CUA1 with M at the base of the wing.] *Trias.*, USSR (Tadzhik).—FIG. 110.2. **M. madygenica*; fore wings of *a*, male and *b*, female, $\times 2.5$ (Sharov, 1968).

Proedischia PINTO & ORNELLAS, 1978c, p. 309 [**P. mezzalirai*; OD]. Little-known genus, possibly related to the Oedischiidae. Fore wing elongate; costal area slender; precostal area very small or absent, the main veins not curved posteriorly near wing base; anal area unknown. [Type of family Proedischiidae PINTO & ORNELLAS]. *U. Carb.*, Brazil (São Paulo).

Protachaeta HANDLIRSCH, 1939, p. 55 [**P. masculina*; OD]. Little-known genus, based on poorly

preserved fore wing. ZEUNER, 1939. *Jur.*, Europe (Germany).

Pseudohumbertiella HANDLIRSCH, 1906b, p. 522 [**Humbertiella grandis* BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 13; OD]. Little-known genus, based on distal fragment of wing. [Placed in Locustidae by HANDLIRSCH (1906b), and in Haglidae by SHAROV (1968).] *Jur.*, USSR (Asian RSFSR).

Termitidium WESTWOOD, 1854, p. 394 [**T. ignotum*; OD]. Fore wing with CUP remote from 1A. [Placed in Tettigoniidae by ZEUNER (1939) and in Haglidae by SHAROV (1968).] *Jur.*, England.—FIG. 110.1. **T. ignotum*; fore wing, $\times 1.5$ (Zeuner, 1939).

Thuringopteryx KUHN, 1937, p. 191 [**T. gimmi*; OD]. Little-known genus, based on hind wing fragment, possibly belonging to Haglidae. ZEUNER, 1939. *Trias.*, Europe (Germany).

Zhemengia HONG, 1982b, p. 1123 [**Z. sinica*; OD]. Little-known genus, based on wing fragment. *Jur.*, China (Inner Mongolia).

Suborder CAELIFERA Ander, 1936

[Caelifera ANDER, 1936, p. 93]

Antennae shorter than body, with not more than 30 segments; tympanal organs, when present, on first abdominal segment; strid-

ulatory mechanism diverse (rarely absent), hind tibiae or femora commonly scraped across ridges on abdomen or fore wings; ovipositor, when present, typically short. *Trias.*—*Holo.*

Family LOCUSTOPSEIDAE Handlirsch, 1906

[*nom. correct* ROHDENDORF, 1957, p. 83, *pro* Locustopsidae HANDLIRSCH, 1906b, p. 421]

Related to Acrididae. Fore wings long, commonly twice as long as body, typically broader distally than proximally; apex rounded; vein SC terminating near apex; M forking into MA and MP near level of origin of RS; MA typically with 2 long, parallel branches; CUA commonly with 3 terminal branches; CUP unbranched; crossveins not so numerous as in Acrididae. Stridulatory apparatus apparently absent. Hind wing as in Acrididae; M anastomosed with R basally. Body structures apparently similar to those of the Acrididae. ZESSIN, 1983a. *Trias.*—*Cret.*

Locustopsis HANDLIRSCH, 1906b, p. 421 [**L. elegans*; SD COCKERELL, 1915, p. 473] [= *Brodiana* ZEUNER, 1942d, p. 13 (type, *B. cubitalis*)]. Fore wing: RS with 3 to 5 branches; M with 3, rarely 2; crossveins forming an irregular network over at least part of wing. SHAROV, 1968; ZESSIN, 1983a. *Jur.*, England, Europe (Germany), USSR (Kazakh, Tadzhik, Kirghiz, Asian RSFSR).—FIG. 111,1. *L. karatavica* SHAROV; *a*, fore wing, *b*, hind wing, both $\times 3.5$; *c*, entire specimen, $\times 2.5$ (Sharov, 1968).

Conocephalella STRAND, 1926, p. 46, *nom. subst. pro* *Conocephalites* HANDLIRSCH, 1906b, p. 518, *non* BARRANDE, 1852 [**Conocephalus capito* DEICHMÜLLER, 1886, p. 24; OD] [= *Conocephalopsis* HANDLIRSCH, 1939, p. 154, *obj.*]. Large species; RS of fore wing with 6 or 7 branches. Strong spines on hind tibiae. ZEUNER, 1942d; SHAROV, 1968. *Jur.*, Europe (Germany).

Parapleurites BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 13 [**P. gracilis*; OD]. Fore wing as in *Locustopsis* but with a double row of cells between M and CU basally. ZEUNER, 1942d; SHAROV, 1968. *Jur.*, USSR (Asian RSFSR).—FIG. 111,4. *P. sibirica* SHAROV; fore wing, $\times 4.0$ (Sharov, 1968).

Praelocustopsis SHAROV, 1968, p. 187 [**P. mirabilis*; OD]. Fore wing: SC short; precostal area with very few veinlets and narrower than costal area below it; crossveins widely spaced distally. *Trias.*, USSR (Asian RSFSR).—FIG. 111,2. **P. mirabilis*; fore wing, $\times 9.0$ (Sharov, 1968).

Schwinzia ZESSIN, 1983a, p. 180 [**S. sola*; OD].

Fore wing similar to that of *Triassolocusta*, but CUA with 4 terminal branches. *Jur.*, Europe (Germany).

Triassolocusta TILLYARD, 1922b, p. 451 [**T. leptoptera*; OD]. Little-known genus, based on part of a fore wing; M with 4 terminal branches, CUA with 2. SHAROV, 1968. *Trias.*, Australia (Queensland).

Zeunerella SHAROV, 1968, p. 189 [**Z. arborea*; OD]. Fore wing as in *Locustopsis* but C longer, extending almost to level of origin of RS; C strongly curved anteriorly near wing base. KEVAN & WIGHTON, 1983. *Cret.*, USSR (Kazakh).—FIG. 111,3. **Z. arborea*; fore wing, $\times 4.5$ (Sharov, 1968).

Family LOCUSTAVIDAE Sharov, 1968

[Locustavidae SHAROV, 1968, p. 185]

Fore wing as in Locustopseidae, but vein CUA with 4 or 5 terminal branches. Body unknown. [Provisionally placed in Caelifera by SHAROV; lack of knowledge of body structure prevents definite assignment to either Caelifera or Ensifera.] *Trias.*

Locustavus SHAROV, 1968, p. 186 [**L. madygensis*; OD]. RS arising near midwing; forking of M at level of end of C. *Trias.*, USSR (Kirghiz).—FIG. 112,2. **L. madygensis*; fore wing, $\times 2.5$ (Sharov, 1968).

Ferganopsis SHAROV, 1968, p. 186 [**F. lanceolatus*; OD]. Fore wing as in *Locustavus*, but RS arising much nearer wing base; M forking well before origin of RS. *Trias.*, USSR (Kirghiz).—FIG. 112,4. **F. lanceolatus*; *a*, fore and *b*, hind wings, both $\times 3.0$ (Sharov, 1968).

Family EUMASTACIDAE Burr, 1899

[Eumastacidae BURR, 1899, p. 75]

Small species, with great diversity of structure. Fore and hind wings commonly reduced or absent; stridulatory structures and tympanal organs apparently absent; fore wing (when fully formed) with an unbranched CUA. *Cret.*—*Holo.*

Eumastax BURR, 1899, p. 94. *Holo.*

Archaeomastax SHAROV, 1968, p. 189 [**A. jurasicus*; OD]. Similar to *Erucius* (recent), but subcostal area broader and branches of M shorter. *Cret.*, USSR (Kazakh).—FIG. 112,1. **A. jurasicus*; fore wing, $\times 8.0$ (Sharov, 1968).

Taphacris SCUDDER, 1890, p. 226 [**T. reliquata*; OD] [= *Eobanksia* COCKERELL, 1909h, p. 384 (type, *E. bitaciformis*)]. Little-known genus, based on fragments of wings and body. [Family

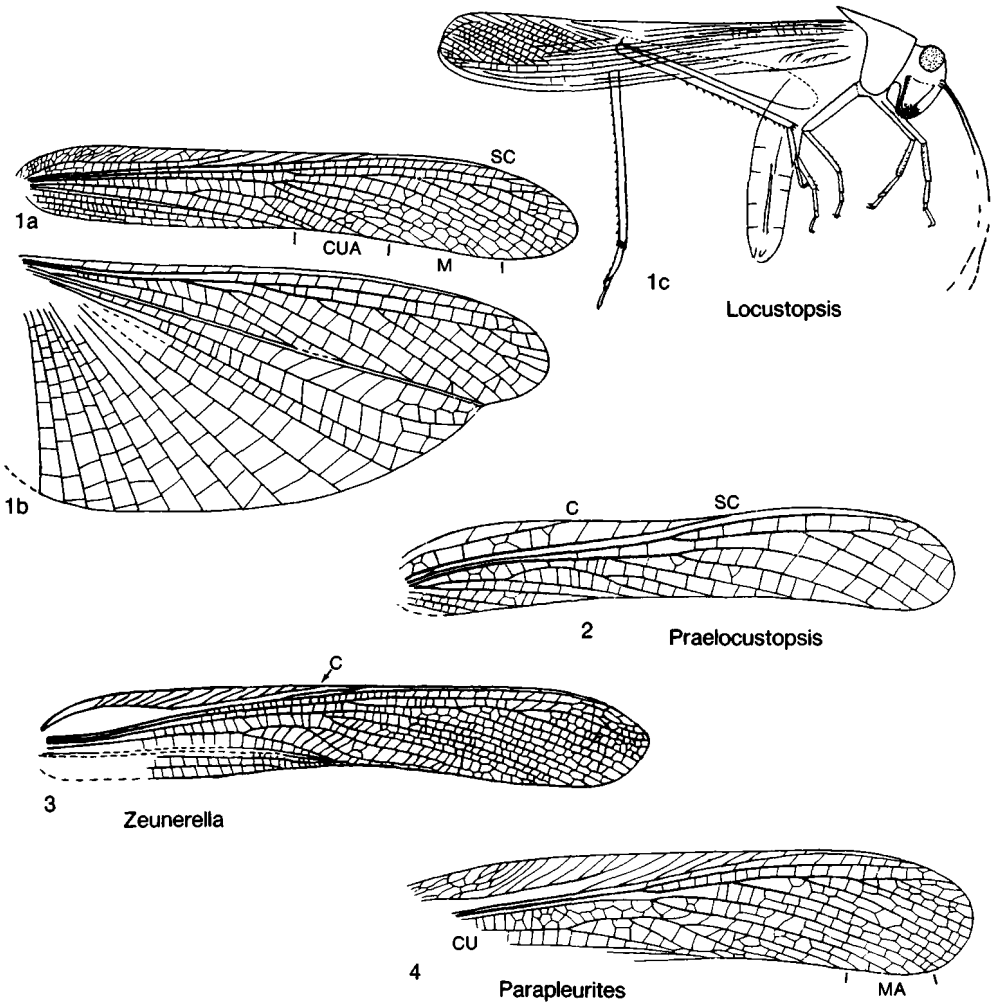


FIG. 111. Locustopseidae (p. 177).

assignment uncertain.] ZEUNER, 1944b. *Oligo.*, USA (Colorado).

Family PROMASTACIDAE

Kevan & Wighton, 1981

[Promastacidae KEVAN & WIGHTON, 1981, p. 1834]

Apparently similar to Erucidae (recent), but fore wings broader and less constricted near middle; stems of veins SC, R, RS, and M more widely separated from each other. *Paleoc.*—*Eoc.*

Promastax HANDLIRSCH, 1910b, p. 97 [**P. archaicus*; OD]. Little-known genus, based on distal fragment of fore wing. Branches of RS arising in distal third of wing; RS with 3 terminal

branches; MA unbranched. KEVAN & WIGHTON, 1981. *Eoc.*, Canada (British Columbia).—FIG. 112, 3. **P. archaicus*; fore wing, $\times 2.6$ (Handlirsch, 1910b).

Promastacoides KEVAN & WIGHTON, 1981, p. 1834 [**P. albertae*; OD]. Little-known genus, based on poorly preserved fore wing. Similar to *Promastax*, but branches of RS arising before midwing; RS with 5 terminal branches; MA forked. *Paleoc.*, Canada (Alberta).

Family TETRIGIDAE Rambur, 1838

[Tetrigidae RAMBUR, 1838, p. 64]

Small species. Fore wings short and thick, commonly scalelike or absent in existing species. Hind wings of moderate size, if present.

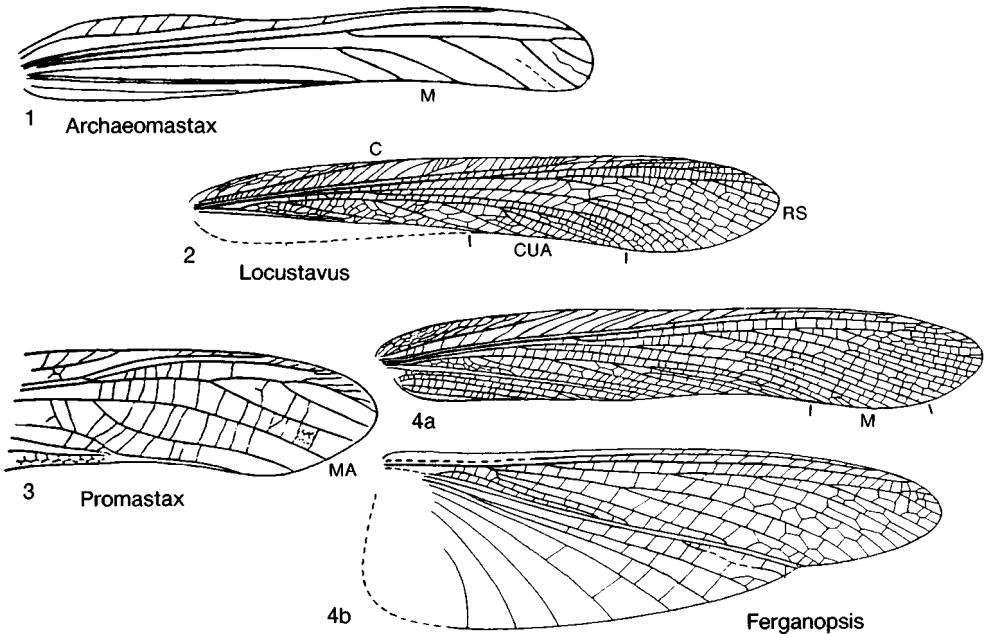


FIG. 112. Locustavidae, Eumastacidae, and Promastacidae (p. 177–178).

Pronotum projecting posteriorly at least to base of abdomen and commonly to or beyond apex of abdomen. Tympanal and stridulatory structures absent. *Cret.*–*Holo.*

Tetrix LATREILLE, 1802, p. 284. Adult male. ZEUNER, 1937. *Oligo.*, Europe (Baltic)–*Holo.*

Archaeotetrix SHAROV, 1968, p. 190 [**A. locustopseiformis*; OD]. Fore and hind wings fully formed. Fore wing tegminous, unusually thick; crossveins forming a coarse reticulation between longitudinal veins; precostal and costal areas nearly equally broad, the two combined about half width of wing; SC and stem of R very close together and parallel; M and CUA unbranched. Hind wing with MA and MP present. *Cret.*, USSR (Asian RSFSR).—FIG. 113, 3. **A. locustopseiformis*; a, fore and b, hind wings, both $\times 6.5$ (Sharov, 1968).

Prototetrix SHAROV, 1968, p. 190 [**P. reductus*; OD]. Fore wing with precostal area forming a small basal lobe; SC, R, and RS distinct; M and CU much reduced; CUA absent. *Cret.*, USSR (Asian RSFSR).—FIG. 113, 1. **P. reductus*; fore wing, $\times 13.0$ (Sharov, 1968).

Succinotetrix PITON, 1938, p. 227 [**S. chopardi*; OD]. Little-known genus, apparently related to *Paratetrix* (recent). Antennae with 19 segments; pronotum extending posteriorly slightly beyond end of abdomen. *Oligo.*, Europe (Baltic).

Tettigidea SCUDDER, 1862, p. 476. Whole insect.

[Generic assignment doubtful.] HEER, 1865; SCUDDER, 1890. *Mio.*, Europe (Germany)–*Holo.*

Family TRIDACTYLIDAE Brunner, 1882

[Tridactylidae BRUNNER, 1882, p. 453]

Small, highly specialized species. Fore wing tegminous and short, commonly not reaching apex of abdomen; venation in existing species reduced to 2 or 3 veins (SC, R, 1A). Hind wing with remigium reduced to narrow strip; all veins unbranched; anal fan very large. Hind femora greatly enlarged; hind tibiae of recent species with a pair of articulated plates. *Cret.*–*Holo.*

Tridactylus OLIVIER, 1789, p. 26. *Holo.*

Monodactyloides SHAROV, 1968, p. 191 [**M. curtipennis*; OD]. Similar to *Monodactylus*, but fore wings short, extending only to middle of abdomen. SC of fore wing with short branches. *Cret.*, USSR (Asian RSFSR).

Monodactylus SHAROV, 1968, p. 191 [**M. dolichopterus*; OD]. Fore wing well developed and long, with apices reaching end of abdomen; SC extending about three-fourths wing length from base, with several long branches; M and CUA unbranched. Pronotum with broad lateral lobes.

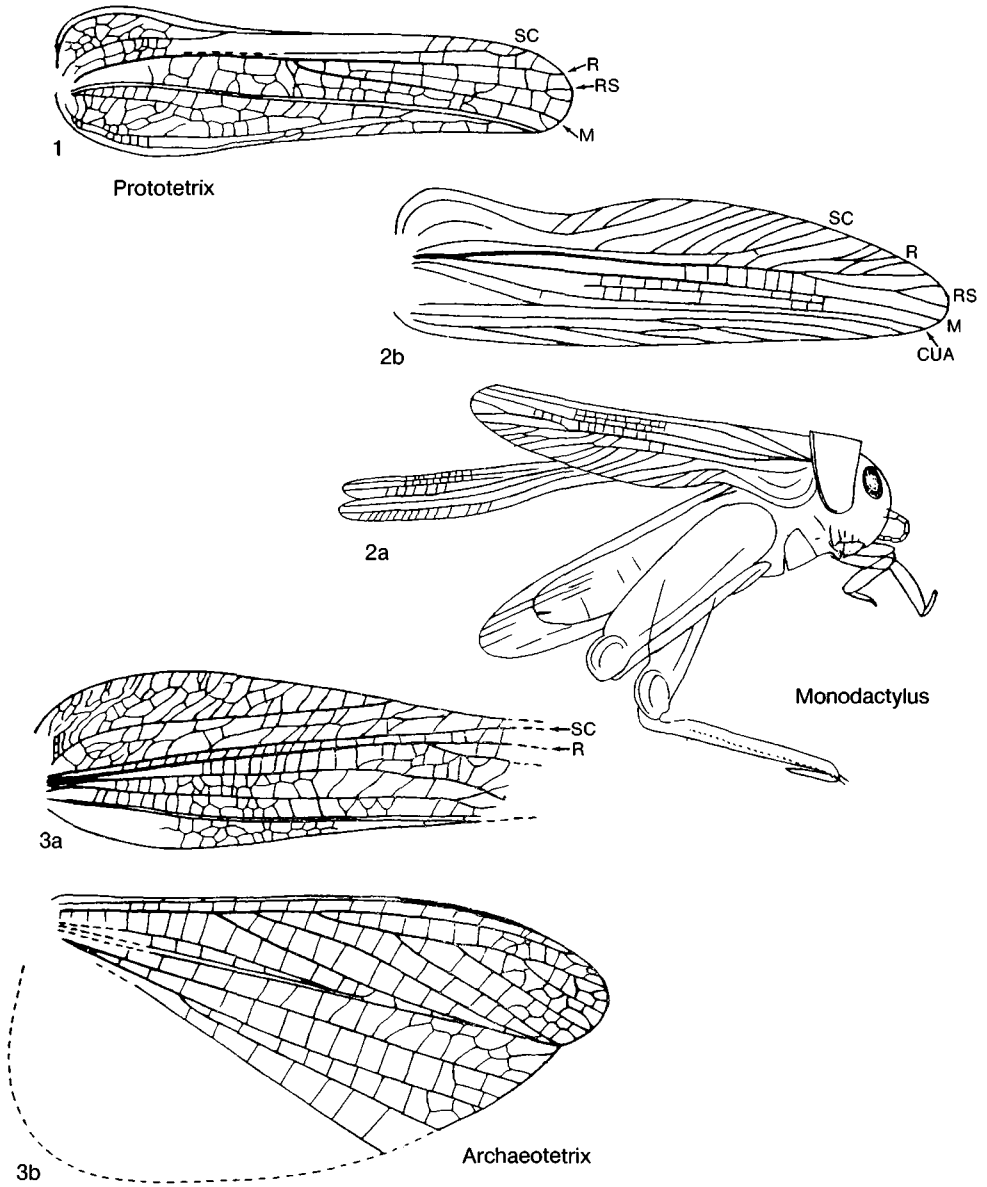


FIG. 113. Tettigidae and Tridactylidae (p. 178-180).

Cret., USSR (Asian RSFSR).—FIG. 113,2. **M. dolichopterus*; a, entire specimen as preserved, X4.5; b, fore wing, X7.3 (Sharov, 1968).

Family ACRIDIDAE Latreille, 1825

[Acrididae LATREILLE, 1825, p. 414]

Both pairs of wings typically well developed. Fore wing with basal parts of veins SC,

R, and M very close together; RS with numerous branches. Hind wing with R and M anastomosed basally. Tympanal organs on first abdominal segment. Stridulation by rubbing hind femora across posterior margin of fore wings, or by snapping hind wings in flight. *Eoc.-Holo.*

Acrida LINNÉ, 1758, p 425. *Holo.*

- Bryodema** FIEBER, 1853, p. 129. Parts of wings and body. PONGRÁ CZ, 1928; ZEUNER, 1942a. *Mio.*, Europe (Hungary)—*Holo.*
- Heeracris** ZEUNER, 1937, p. 159 [**Acridium oenigense* SCUDDER, 1895a, p. 118; OD]. Little-known genus, based on part of fore wing. [Possibly related to *Catanops* (recent).] *Mio.*, Europe (Germany).
- Mentacridium** PITON, 1936b, p. 78 [**M. eocenicum*; OD]. Little-known genus, based on poorly preserved fore wing. [Family assignment doubtful.] ZEUNER, 1944b. *Eoc.*, Europe (France).
- Miocaenacris** ZEUNER, 1931, p. 275 [**M. soergeli*; OD]. Little-known genus, based on general body form; probably related to *Catanops* (recent). ZEUNER, 1941b. *Mio.*, Europe (Germany).
- Nanthacia** SCUDDER, 1890, p. 224 [**N. torpida*; OD]. Little-known genus, based on single hind wing. ZEUNER, 1944b. *Oligo.*, USA (Colorado).
- Oedipoda** LATREILLE, 1829, p. 188. Fore wings and body. [Generic assignment of fossils uncertain.] ZEUNER, 1942a. *Mio.*, Europe (Hungary)—*Holo.*
- Proschistocerca** ZEUNER, 1937, p. 158 [**P. oligocaenica*; OD]. Similar to *Schistocerca* (recent), but costal area of fore wing abruptly narrowed just before first branch of RS. *Oligo.*, England.
- Protocatanops** ZEUNER, 1931, p. 262 [**P. gracilis*; OD]. Little-known genus, based on head and prothorax. [Probably synonymous with *Catanops* (recent).] *Mio.*, Europe (Germany).
- Taeniopodites** COCKERELL, 1909q, p. 283 [**T. pardalis*; OD]. Little-known genus, based on fragment of fore wing; probably related to *Catanops* (recent). ZEUNER, 1941b. *Oligo.*, USA (Colorado).
- Tyrbula** SCUDDER, 1885b, p. 768 [**T. russelli*; OD]. Little-known genus, based on body only. ZEUNER, 1944b. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado).

Family UNCERTAIN

The following genera, apparently belonging to the Orthoptera, suborder Caelifera, are too poorly known to permit assignment to families.

- Chresmoda** GERMAR, 1839, p. 201 [**C. obscura*; OD] [= *Locusta prisca* GERMAR, 1839, p. 200]. Little-known genus, probably related to Acrididae. [Type of family Chresmodidae HAASE, 1890a, p. 11. Placed in the Orthoptera by GERMAR and in the Hemiptera (Hydrometridae or Gerridae) by most entomologists before 1900; placed by HANDLIRSCH (1906b) and almost everyone else since then in the Phasmatodea. Frequently confused with *Pygolampis gigantea* (GERMAR). See HAGEN, 1862; VISHNIAKOVA, 1980b, p. 173, footnote; and CARPENTER, 1992.] *Jur.*, Europe (Germany).
- Miopyrgomorpha** KEVAN in KEVAN & AKBAR, 1964,

p. 152b, footnote [**Oedipoda fischeri* HEER, 1865, p. 367; OD]. Little-known genus, based on poorly preserved specimen. ZEUNER, 1944b; KEVAN, 1965. *Mio.*, Europe (Germany).

Suborder UNCERTAIN

The following genera, apparently belonging to the order Orthoptera, are too poorly known to permit assignment to suborders.

- Locustopsites** THÉOBALD, 1937a, p. 116 [**L. gigantea*; OD]. Little-known genus, based on fore wing fragment. ZEUNER, 1942d. *Oligo.*, Europe (France).
- Phaneropterites** HANDLIRSCH, 1906b, p. 519 [**Phaneroptera germari* MÜNSTER in GERMAR, 1842, p. 81; OD]. Little-known genus, based on a poorly preserved specimen. ZEUNER, 1942d. *Jur.*, Europe (Germany).

Order GRYLLOBLATTODEA

Brues & Melander, 1915

[*nom. correct.* BRUES & MELANDER, 1932, *pro* Grylloblattoidea BRUES & MELANDER, 1915, p. 13]

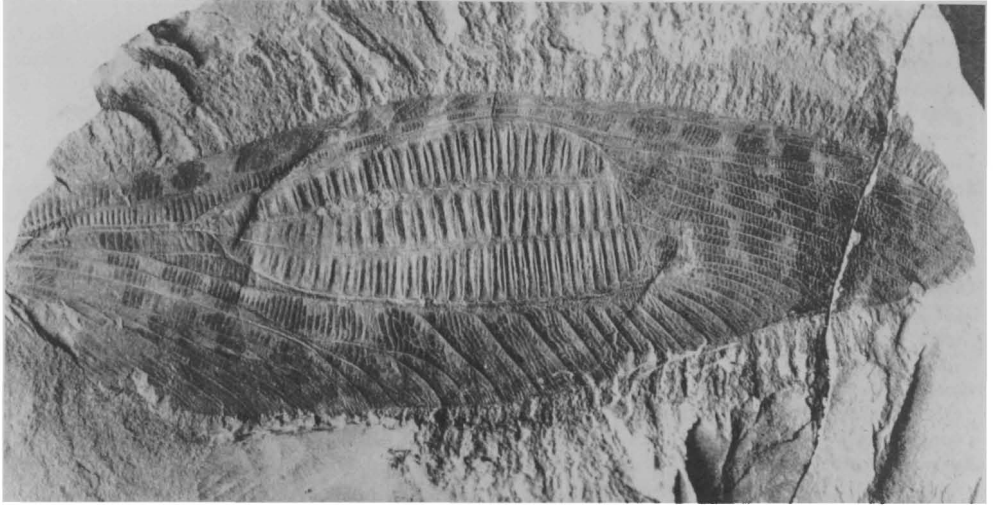
Wingless; antennae long, multisegmented; compound eyes absent or small; ocelli absent; legs cursorial; tarsi five-segmented; cerci well developed, segmented; ovipositor conspicuous. *Holo.*

Order TITANOPTERA

Sharov, 1968

[Titanoptera SHAROV, 1968, p. 122]

Orthopteroid insects of moderate to large size. Fore wing with or without a precostal area; spaces between veins RS, MA, and MP commonly wide, in some genera much enlarged and forming a stridulatory area, apparently in both sexes; CUP commonly branched; 2A with pectinate branching for its entire length, directed posteriorly. Hind wing with MP+CUA1 branched; 2A branched much as in fore wing; anal area large and forming a lobe in some genera but relatively small in others. Antennae very long, slender, and filiform; head hypognathous, with long, serrate mandibles; prothorax relatively short; forelegs prehensile, spinose; hind



Mesotitan

FIG. 114. Mesotitanidae (p. 182).

legs cursorial, relatively short; all tarsi with 5 segments; arolium present; cerci short, unsegmented; ovipositor also short. Wings at rest folded flat over abdomen, not inclined as in the Orthoptera (Saltatoria). Nymphs unknown. *Trias*.

TILLYARD (in TILLYARD & DUNSTAN, 1916) originally placed the genus *Mesotitan* in the Protorthoptera, but he later (TILLYARD, 1925c) transferred it to the Protohemiptera, where it was also placed by McKEOWN (1937), who had much better specimens for study (Fig. 114). ZEUNER (1939) transferred the genus and its family to the Orthoptera, in which they were also later placed by RIEK (1954c). SHAROV (1962b) assigned the Mesotitanidae to the Paraplecoptera, but in 1968, after study of a very extensive collection of Mesotitanidae and related families from the Triassic of the USSR, he designated the new order Titanoptera for their reception. More recently, RASNITSYN (1980c) treated the Titanoptera as a suborder of the Orthoptera. However, since in the present work the order Orthoptera is restricted to the saltatorial orthopteroids, the Titanoptera have ordinal status.

Family MESOTITANIDAE Tillyard, 1925

[Mesotitanidae TILLYARD, 1925c, p. 376] [=Clathrotitanidae RIEK, 1954c, p. 165]

Large insects. Fore wing with areas between veins RS and MA1, MA1 and MA2, MA2 and MP+CUA1 commonly broad; crossveins in those areas straight, unbranched, alternately convex and concave, and forming a stridulatory apparatus; RS arising from R about one-third wing length from base and very close to R for most of its length; MA forking at about level of origin of RS. Venation of hind wing similar to that of fore wing except for the stridulatory area. *Trias*.

Mesotitan TILLYARD in TILLYARD & DUNSTAN, 1916, p. 40 [**M. giganteus*; OD] [=Clatrotitan McKEOWN, 1937, p. 32 (type, *C. andersoni*, =*M. scullyi* TILLYARD, 1925c, p. 376)]. Fore wing broadest at level of midwing; precostal area apparently absent; stridulatory area about half the width of entire wing. SHAROV, 1968. *Trias.*, Australia (New South Wales).—FIG. 114. *M. scullyi* TILLYARD (type specimen of *C. andersoni* McKEOWN); fore wing, ×1 (McKeown, 1937). **Mesotitanodes** SHAROV, 1968, p. 197 [**M. tillyardi*; OD]. Fore wing very broad, especially medially; precostal area present; area between MA1 and MA2 about twice as wide as that

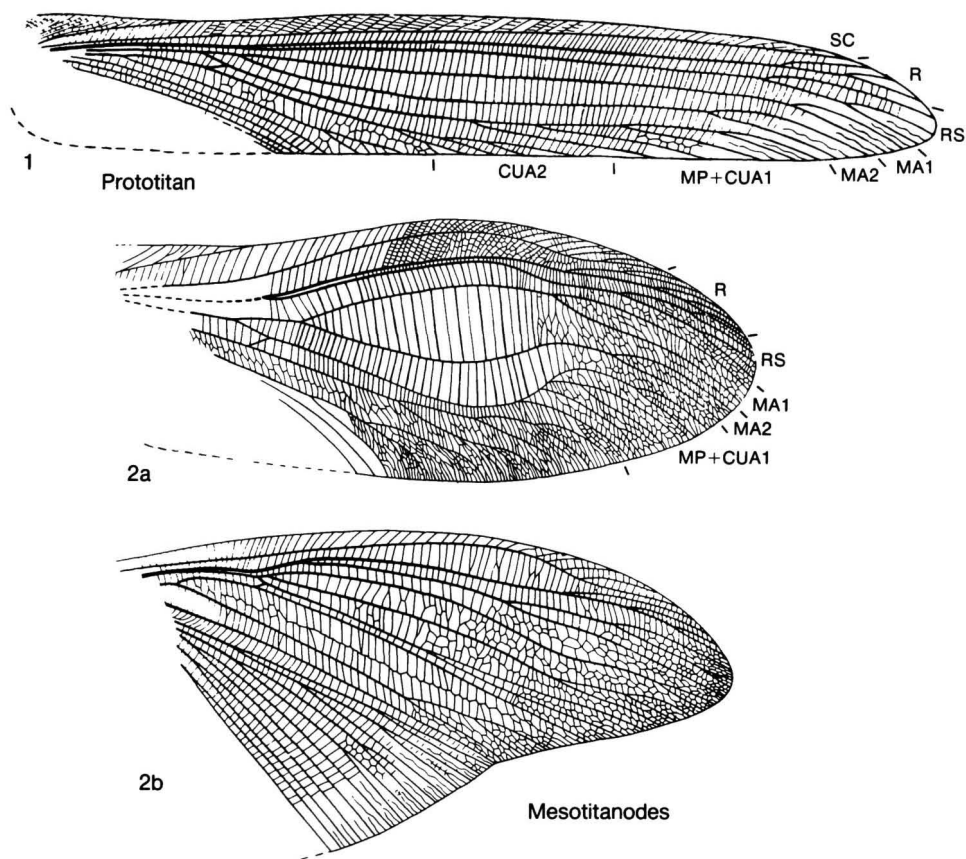


FIG. 115. Mesotitanidae (p. 182–183).

between RS and MA1. *Trias.*, USSR (Kirghiz).
 —FIG. 115,2. **M. tillyardi*; a, fore and b, hind wings, $\times 1$ (Sharov, 1968).

Prototitan SHAROV, 1968, p. 196 [**P. primitivus*; OD]. Fore wing nearly uniform in width, not increased medially; precostal area present; areas between RS and MP+CUA1 only slightly widened. *Trias.*, USSR (Kirghiz). —FIG. 115,1.

**P. primitivus*; fore wing, $\times 1.5$ (Sharov, 1968).
Ultratan SHAROV, 1968, p. 198 [**U. superior*; OD]. Little-known genus, based on distal fragment of wing. Stridulatory area extending nearly to wing apex. *Trias.*, USSR (Kirghiz).

Family PARATITANIDAE Sharov, 1968

[Paratitanidae SHAROV, 1968, p. 198]

Fore wing with anterior margin uniformly curved; space between veins MA2 and MP+CUA1 very narrow; precostal area

present; base of M anastomosed with R; RS arising from R in distal third of wing. Hind wing with enlarged anal lobe. *Trias.*

Paratitan SHAROV, 1968, p. 199 [**P. libelluloides*; OD]. Fore wing with subcostal area nearly as broad as costal area; M branching from R nearer to forking of M than to wing base; MA2 slightly sigmoidal in distal half. *Trias.*, USSR (Kirghiz).

—FIG. 116, a, b. **P. libelluloides*; a, fore and b, hind wings, $\times 1.6$ (Sharov, 1968). —FIG. 116, c. *P. ovalis* SHAROV; fore wing, $\times 1.5$ (Sharov, 1968).

Family GIGATITANIDAE Sharov, 1968

[Gigatitanidae SHAROV, 1968, p. 199]

Very large species. Fore wing with pre-costal area present; vein RS arising basally or near midwing; area between MA2 and

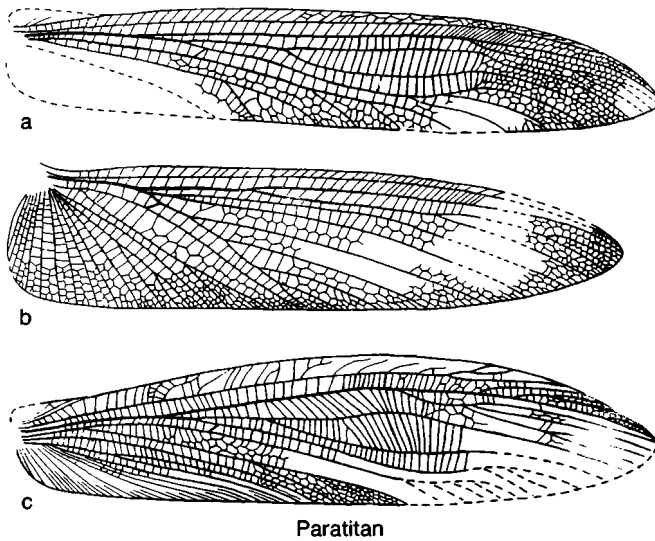


FIG. 116. Paratitanidae (p. 183).

MP+CUA1 the only broad space in the stridulatory area of the wing. *Trias*.

Gigatitan SHAROV, 1968, p. 200 [**G. vulgaris*; OD]. Fore wing: SC with basal branch extending about one-third wing length from base; RS arising from R near wing base. *Trias*, USSR (Kirghiz).—FIG. 117,3. **G. vulgaris*; a, reconstruction, $\times 0.8$; b, fore wing, $\times 0.6$; c, hind wing, $\times 0.6$; d, foreleg, $\times 2.0$; e, head, antennae, pronotum, $\times 1$ (all Sharov, 1968).

Nanotitan SHAROV, 1968, p. 202 [**N. magnificus*; OD]. Fore wing with large precostal area; RS arising near wing base; MA1 and MA2 unbranched; MA2 and MP+CUA1 anastomosed at base of wing. *Trias*, USSR (Kirghiz).—FIG. 117,1. *N. extensus* SHAROV; fore wing, $\times 1$ (Sharov, 1968).

Ootitan SHAROV, 1968, p. 201 [**O. curtis*; OD]. Fore wing very short and broad; RS arising at about midwing. *Trias*, USSR (Kirghiz).—FIG. 117,2. **O. curtis*; fore wing, $\times 1$ (Sharov, 1968).

Order PHASMATODEA Brunner, 1893

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 102, *pro* Phasmodea BRUNNER, 1893, p. 76] [=Aeroplanoptera TILLYARD, 1923b, p. 481]

Moderate-sized to large insects, with much diversity of wing and body form. Mouthparts mandibulate, mandibles strong; eyes small; antennae typically long, slender, and multi-

segmented, less commonly short, with few to many segments; legs gressorial, long, and diversely modified; 5 tarsomeres. Fore wings typically reduced or absent in existing species but normally developed in some Mesozoic families. Hind wings of existing species rarely absent, commonly large; remigium tegminous; anal area greatly enlarged, fan-shaped. Venation of fore wings and of remigium of hind wings of existing species reduced, with dense reticulation, and a series of strong, parallel longitudinal veins, with very few branches. Abdomen long, slender, and cylindrical in Phasmatidae and most Mesozoic species, shorter and dorsoventrally compressed in Phylliidae; cerci unsegmented, typically short. Existing species foliage-feeders. Eggs deposited in ground litter or more rarely inserted in soil. *Trias*.—*Holo*.

For many years the Phasmatodea were considered to be a family within the order Orthoptera. However, their gressorial hind legs, five-segmented tarsi, unsegmented cerci, as well as several venational features, support the conclusion of BEIER (1967) that they represent a separate order within the orthopteroid complex. The order is now relatively small, with only two families, Phasmatidae and Phylliidae, generally recognized. The

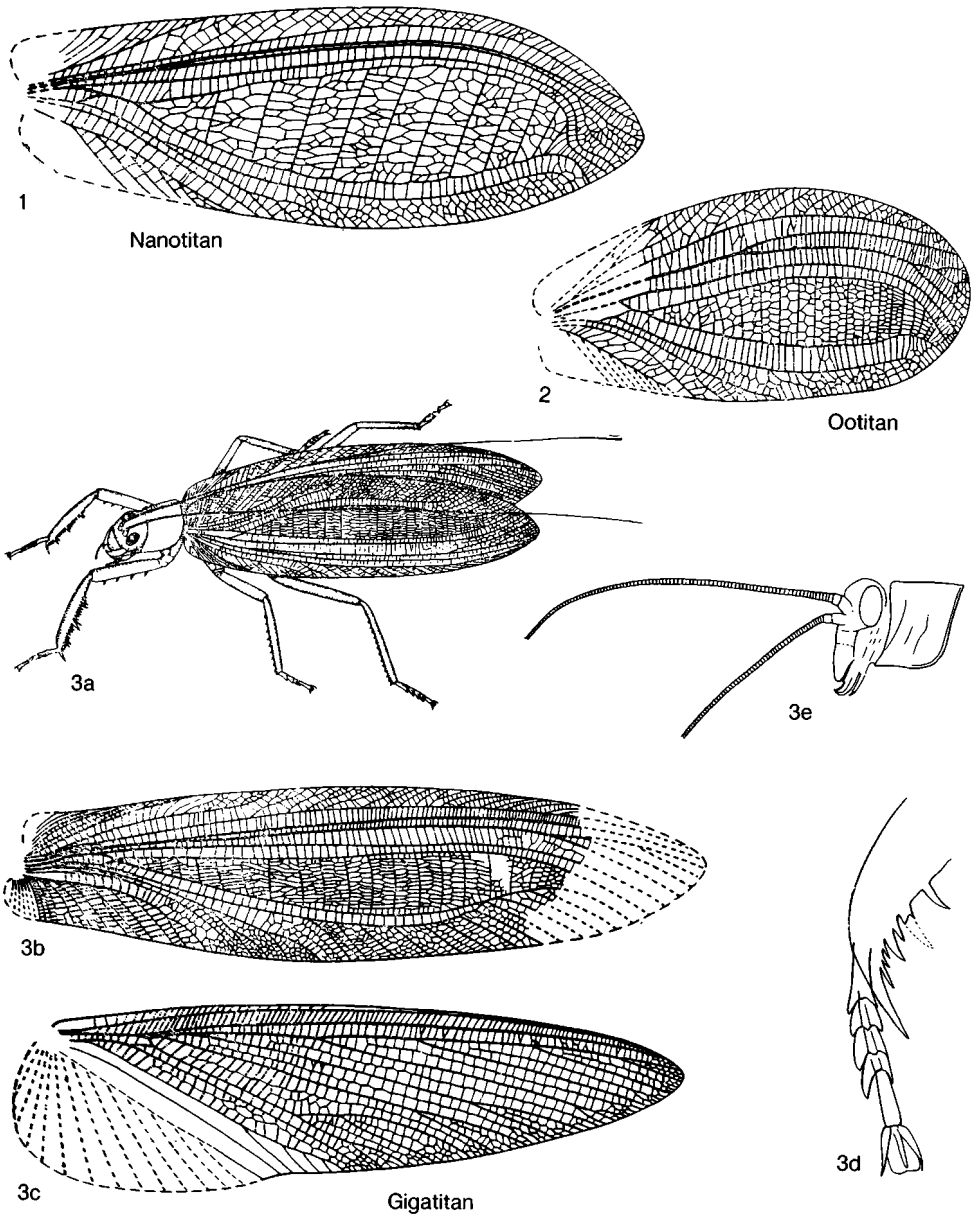


FIG. 117. Gigatitanidae (p. 184).

phasmatids, with long and cylindrical bodies, resemble twigs and small sticks; the phylliids, with dorsoventrally compressed bodies and flat extensions of the legs, resemble leaves.

SHAROV (1968) has made the most significant contribution to our knowledge of the geological record of the order, and in partic-

ular to what appears to have been its early stages, with a study of a series of Mesozoic specimens. The geological record of the two existing families is limited to nymphs of one species of each family in Baltic amber. The early Mesozoic members of the order bear little resemblance, in general form, to the

Phasmatidae or Phylliidae. They do, however, have very long and narrow fore wings, with the longitudinal veins straight and parallel as in the phasmatids. Similarly, the remigium of the hind wing is long, narrow, and tegminous, with the longitudinal veins as in the fore wings. The compound vein, MP+CUA1, is present in the Mesozoic species and similar in form to that in both Phasmatidae and Phylliidae. The cerci in the Mesozoic fossils are unsegmented, as in the existing Phasmatodea. These features are indeed indicative of relationship, but more structural details are probably needed for conviction. At present, the Mesozoic record includes only five small families of these insects.

Family XIPHOPTERIDAE

Sharov, 1968

[Xiphopteridae SHAROV, 1968, p. 192]

Little-known family. Fore wing membranous; precostal area well developed; vein C with many fine branches; RS arising from R in distal half of wing, branched; MA forked; MP+CUA1 with a comb of branches directed posteriorly. Hind wing unknown. [Ordinal assignment doubtful.] *Trias*.

Xiphopterum SHAROV, 1968, p. 192 [**X. curvatum*; OD]. Fore wing broadest distally and curved posteriorly in distal area; precostal area forming a prominent bulge basally; MA forking in proximal part of wing. *Trias*, USSR (Kirghiz).—FIG. 118,2. **X. curvatum*; fore wing, $\times 1.3$ (Sharov, 1968).

Family AEROPLANIDAE

Tillyard, 1918

[Aeroplanidae TILLYARD, 1918c, p. 425]

Fore wing: precostal area long, but vein C without branches; longitudinal veins mostly parallel; crossveins unbranched, except in the anal area; RS arising from R near wing base; MP+CUA1 forked near level of origin of RS, with at most 5 branches. Hind wing unknown. MARTYNOV, 1928a; SHAROV, 1968; VISHNIAKOVA, 1980b. *Trias*.

Aeroplana TILLYARD, 1918c, p. 426 [**A. mirabilis*; OD]. Little-known genus, based on basal half of fore wing; CUA2, CUP, and 1A sigmoidal. [Originally placed in Protodonata, later in new

order Aeroplanoptera (TILLYARD, 1923b).] *Trias*, Australia (New South Wales).—FIG. 118,1. **A. mirabilis*; fore wing, $\times 2$ (Sharov, 1968; after Tillyard, 1923b).

Paraplana SHAROV, 1968, p. 193 [**P. affinis*; OD]. Fore wing similar to that of *Aeroplana*, but the short, oblique base of CUA1 absent; MP+CUA1 with 3 branches. *Trias*, USSR (Kirghiz).—FIG. 118,4. **P. affinis*; fore wing, $\times 1.5$ (Sharov, 1968).

Family AEROPHASMATIDAE

Martynov, 1928

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 809, *pro* Aerophasmidae MARTYNOV, 1928a, p. 320]

Similar to Aeroplanidae, but fore wing lacking precostal area; vein MP+CUA1 with only 3 branches. Hind wing with RS and M anastomosed near wing base. *Jur*.

Aerophasma MARTYNOV, 1928a, p. 320 [**A. prynadai*; OD]. Fore wing with dense covering of hair; MA with 2 branches. SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur*, USSR (Kazakh).—FIG. 118,3. **A. prynadai*; *a*, fore and *b*, hind wings, $\times 1.3$ (Sharov, 1968).

Family PROCHRESMODIDAE

Vishniakova, 1980

[Prochresmodidae VISHNIAKOVA, 1980b, p. 173, footnote]

Apparently related to Aeroplanidae. Antennae long and filiform. Fore wing: precostal area broad, with fine archidictyon; vein SC extending to wing apex; MP+CUA1 and branches of MA curved; 2A ending well before midwing. Hind wing: anal area very broad, branches of 2A directed to posterior margin of wing. Legs very long; male apparently with broad and spiny hind femora. *Trias*.

Prochresmoda SHAROV, 1968, p. 194 [**P. longipoda*; OD]. Precostal area extending nearly to midwing; crossveins very numerous, mostly straight, rarely branched. VISHNIAKOVA, 1980b. *Trias*, USSR (Kirghiz).—FIG. 119. **P. longipoda*; *a*, fore and *b*, hind wings, $\times 2$; *c*, whole insect, $\times 1$ (Sharov, 1968).

Family CRETOPHASMATIDAE

Sharov, 1968

[Cretophasmatidae SHAROV, 1968, p. 193]

Fore wing much as in Aeroplanidae, but precostal area extending nearly to level of midwing; archidictyon present between veins

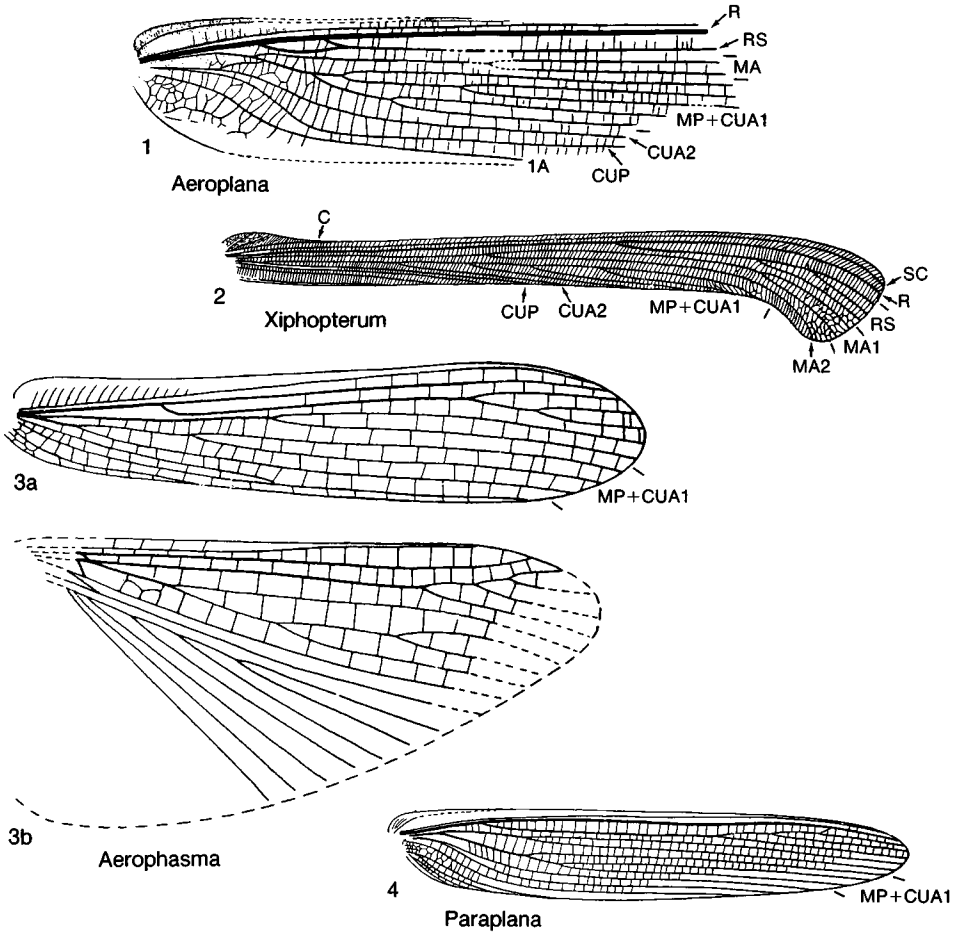


FIG. 118. Xiphopteridae, Aeroplanidae, and Aerophasmatidae (p. 186).

C and SC; RS unbranched; MA with 3 branches. *Cret.*

Cretophasma SHAROV, 1968, p. 193 [**C. raggei*; OD]. RS arising from R near base of wing. Anterior margin of wing slightly concave. *Cret.*, USSR (Kazakh).—FIG. 120,4. **C. raggei*; fore wing, $\times 2$ (Sharov, 1968).

Family PHASMATIDAE Leach, 1815

[*nom. correct.* ROBERTS, 1941, p. 16, *pro* Phasmidae LEACH, 1815, p. 119]

Antennae commonly short and slender; fore wings coriaceous, commonly reduced or absent; hind wing typically well developed, with small coriaceous remigium and large anal fan, folded over the abdomen at rest; fore wing venation reduced, with a few, weakly developed, parallel veins; remigium

of hind wings with a series of well-developed, parallel veins and numerous crossveins. Body commonly elongate; legs typically long, often spinose; middle and hind tibiae with a ventral, triangular, areolate area distally. *Oligo.*—*Holo.*

Phasma LICHTENSTEIN, 1796, p. 49. *Holo.*

Pseudoperla PICTET, 1854, p. 364 [**P. gracilipes*; OD]. Nymph, with small wing pads. Mesothorax slightly longer than pronotum. BACHOFEN-ECHT, 1949. *Oligo.*, Europe (Baltic).—FIG. 120,2. **P. gracilipes*; whole insect, $\times 2.5$ (Germar & Berendt, 1856).

Family PHYLLIIDAE Brunner, 1893

[Phylliidae BRUNNER, 1893, p. 101]

Similar to Phasmatidae, but body flattened dorsoventrally; legs and abdominal

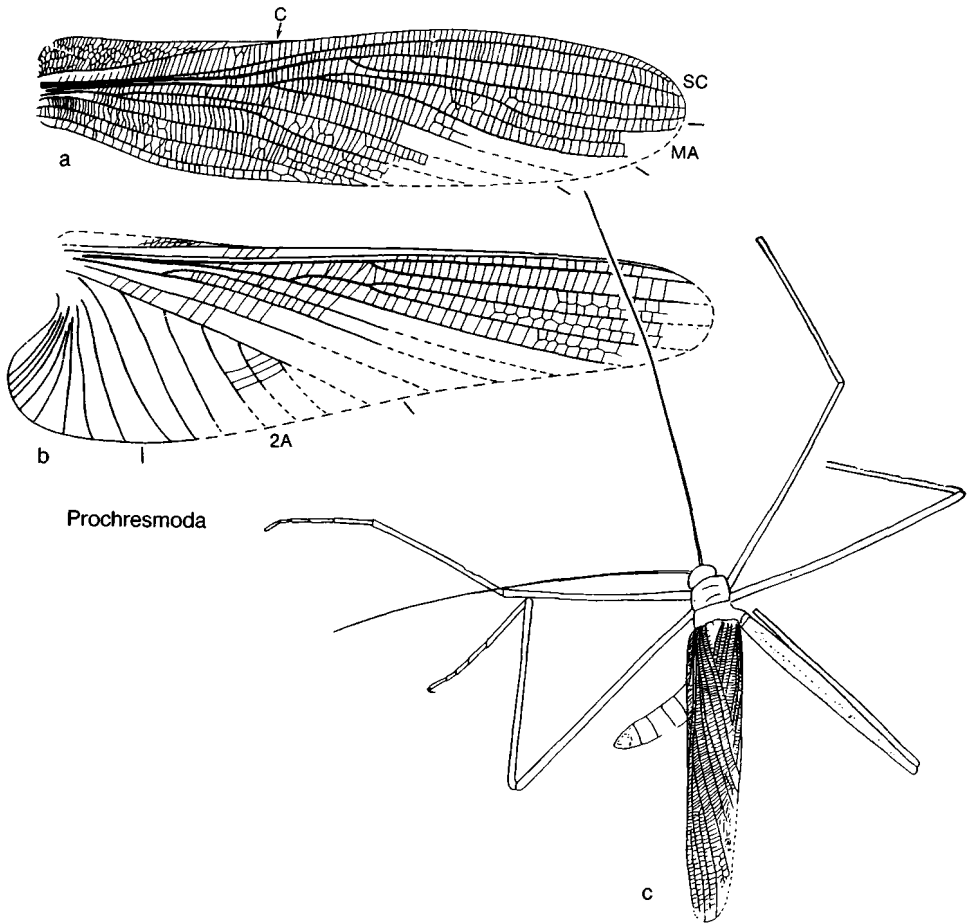


FIG. 119. Prochresmodidae (p. 186).

segments with lamellate extensions; fore wings reduced; hind wings commonly well developed, resting flat, not folded, over abdomen. *Oligo.*, Europe (Baltic)—*Holo.*

Phyllium ILLIGER, 1798, p. 499. *Holo.*

Electrobaculum SHAROV, 1968, p. 195 [**E. gracile*; OD]. Little-known genus, based on nymph. Ovipositor and cerci longer than those of other genera in family. *Oligo.*, Europe (Baltic).—FIG. 120,3. **E. gracile*; whole insect, $\times 3$ (Sharov, 1968).

Family UNCERTAIN

The following genera, apparently belonging to the order Phasmatodea, are too poorly known to permit assignment to families.

Chresmodella BODE, 1953, p. 108 [**C. integra*; OD]. Little-known genus, based on fore wings, but details not clear; probably related to Halo-

metridae (recent). SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur.*, Europe (Germany).—FIG. 120,1. **C. integra*; fore wing, $\times 2.5$ (after Bode, 1953). *Coniphasma* BIRKET-SMITH, 1981, p. 245 [**C. rosenkrantzi*; OD]. Little-known genus, based on incomplete fore wing. R, RS, MA, MP, CUA, and CUP nearly straight and parallel; costa marginal; SC ending just beyond midwing; MA, MP, CUA, and CUP unbranched. [Ordinal assignment doubtful.] *Cret.*, Greenland.

Propygotlampis WEYENBERGH, 1874, p. 84 [**P. bronni*; OD] [= *Halometra* OPPENHEIM, 1888, p. 230 (type, *Pygotlampis gigantea* GERMAR, 1839, p. 207); *Sternarthron* HAASE, 1890b, p. 655 (type, *S. zitteli*)]. Little-known genus, similar to *Prochresmoda*, but antennae very short; longitudinal veins of fore wing straight and close together, much as in *Aeroplanidae*. Hind wing unknown. [*Propygotlampis* and *Halometra* were originally placed in the order Hemiptera and have been confused with *Chresmoda* (Orthoptera). *Sternarthron* was placed by HAASE in the Araneae, but

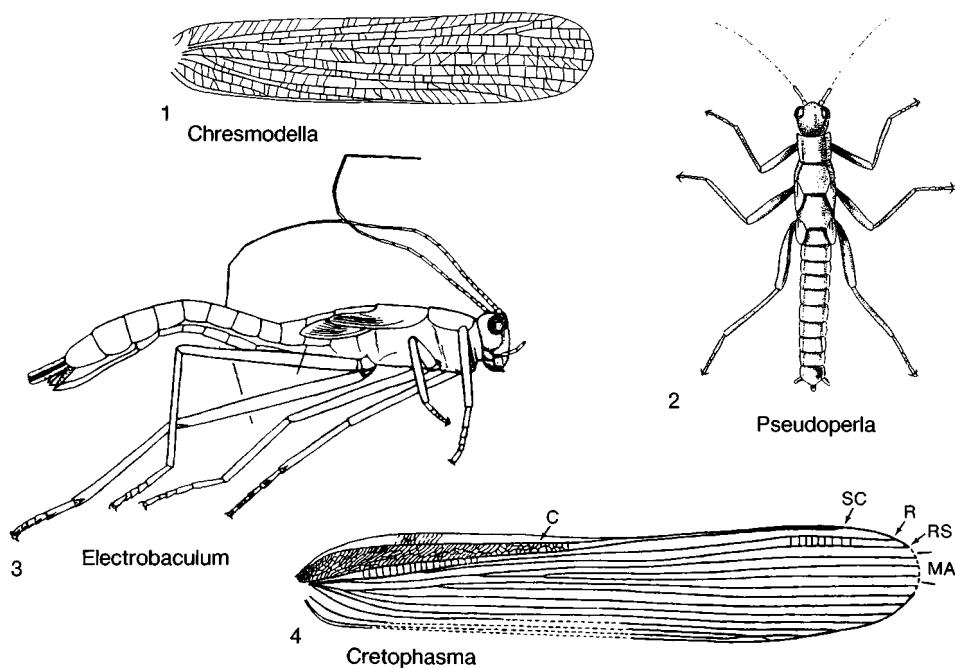


FIG. 120. Cretophasmatidae, Phasmatidae, Phylliidae, and Uncertain (p. 187–188).

as noted by HANDLIRSCH (1906b) the type specimens were insects; they were probably nymphs of *Propygodlampis*.] HAGEN, 1862; HANDLIRSCH, 1906b, 1920; MARTYNOV, 1928a; CARPENTER, 1932a, 1992; ESAKI, 1949; SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur.*, Europe (Germany); *Cret.*, China (Inner Mongolia).—FIG. 121. **Propygodlampis gigantea* (GERMAR), *Jur.*, Germany; ventral view of whole insect, including antennae and cerci, specimen in Museum of Comparative Zoology, MCZ 6105, $\times 0.9$ (Carpenter, new).

Order EMBIOPTERA

Shiple, 1904

[Embioptera SHIPLEY, 1904, p. 261]

Small, subsocial insects with mandibulate mouthparts; tarsi with 3 segments, first segment of fore tarsi containing silk glands and much enlarged; hind femora enlarged; females apterous; males commonly winged; wings homonomous; veins except R and CUP usually weak; R and CUP thickened; SC short and not reaching midwing; RS typically forked before midwing; M simple or branched; CU usually with weak anterior branch and stronger CUP; anal lobes absent;

cerci typically with 2 segments, generally asymmetrical in males. Ross, 1970. *Oligo.*—*Holo.*

The Embioptera are orthopteroids, apparently closely related to the Isoptera, although their precise ancestry is far from clear. Their morphological specializations, such as the slender body, short legs, and tendency for aptery, are adaptations to living in galleries. Lined with silk, produced by glands in the fore tarsi, the galleries are made on irregular surfaces of trees, rocks, moss, and even termite mounds. All existing Embioptera are subsocial, the female guarding the eggs and newly hatched nymphs in her galleries. The homonomous condition of the fore and hind wings is obviously secondary and the venation is much reduced.

The geological history of the Embioptera is poorly known. Two Permian genera, *Prot-embia* TILLYARD (1937b) and *Tillyardembia* ZALESSKY (1937d), originally placed in the order Embioptera, have been shown to be members of the Protorthoptera (MARTYNOV, 1940; CARPENTER, 1950; ROSS, 1956); and another Permian genus, *Sheimia* MARTYNOVA-

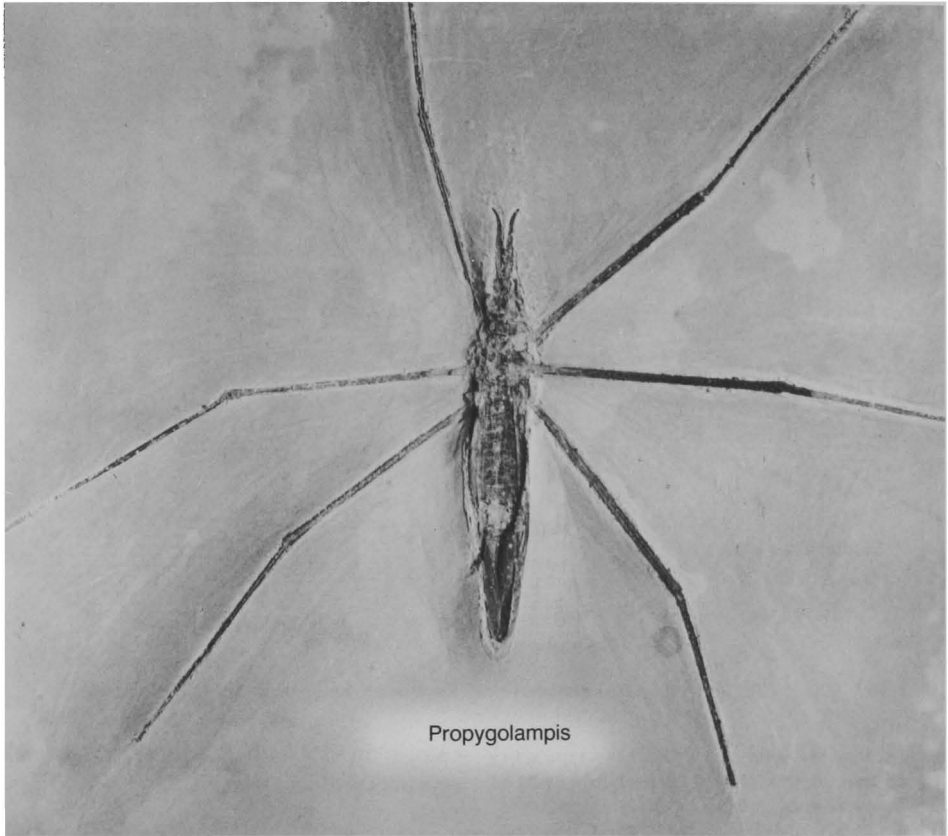


FIG. 121. Phasmatodea, Uncertain (p. 188–189).

(1958), also placed in the Embioptera, is known only by a poorly preserved wing that does not show sufficient structural features to justify assignment to the order (CARPENTER, 1976; ROSS, personal communication, 1977). The earliest record of the Embioptera, in the Baltic amber, consists of two apterous males belonging to the genus *Electroembia*. The genus is extinct but it is more specialized than some living genera. In all probability Embioptera will eventually be found in Cretaceous deposits.

Family EMBIIDAE Burmeister, 1838

[Embiidae BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 768]

Male wing (if present) with vein RS3+4 forked; hind tarsi with 1 or 2 ventral papillae (sole-bladders) on first segment; left cercus with 2 segments. *Oligo.*—*Holo.*

Embia LATREILLE, 1829, p. 257. *Holo.*

Electroembia ROSS, 1956, p. 77 [**Embia antiqua* PICTET, 1854, p. 370; OD]. Male apterous; basal segment of left cercus spiculate; hind basitarsus elongate and having 2 ventral papillae. *Oligo.*, Europe (Baltic).—FIG. 122,2. **E. antiqua* (PICTET); *a*, abdominal terminalia, *b*, hind basitarsus, $\times 30$ (ROSS, 1956).

Lithembia ROSS, 1984, p. 83 [**Embia florissantensis* COCKERELL, 1908e, p. 230; OD]. Little-known genus, based on relatively large male, with typical embiid venation. DAVIS, 1939b. *Oligo.*, USA (Colorado).

Family NOTOLIGOTOMIDAE Davis, 1940

[Notoligotomidae DAVIS, 1940a, p. 681]

Male left cercus with 1 segment. *Mio.*—*Holo.*

Notoligotoma DAVIS, 1936, p. 244. *Holo.*

Burmitembia COCKERELL, 1919d, p. 194 [**B. ve-*

nosa; OD]. Male winged; veins strong; RS3+4 and M single; several strong oblique crossveins. DAVIS, 1939b, 1940a. *Mio.*, Burma.—FIG. 122, 1. **B. venosa*; a, right fore wing, $\times 20$; b, hind legs and abdomen from below, $\times 16$ (both Davis, 1939b).

Order PSOCOPTERA

Shiple, 1904

[Psocoptera SHIPLEY, 1904, p. 261]

Small or minute insects, with short body; head relatively large; eyes large, ocelli usually present; antennae slender and commonly long, with numerous segments (12 to 50); mandibles well developed; laciniae forming sclerotized rods partially sunk into head and moved by muscles; labial palps vestigial in recent species; prothorax ordinarily small; meso- and metathorax usually distinct but may be fused to form compact unit; wings commonly present, reduced or absent in some, membranous and transparent, with distinct pterostigma. Fore wing commonly bearing conspicuous setae or scales; vein SC usually very short or absent; R and RS strongly developed, R enclosing distal end of pterostigma; RS usually forked; M arising from base, and in existing genera commonly coalesced with CUA basally and in contact with stem of R for short distance, terminating in several branches distally; CUA ordinarily forking near wing margin to form prominent cell, areola postica; CUP weakly developed, unbranched; usually only 1 anal vein. Hind wing generally smaller than fore wing, markedly so in some; in recent species, M, CUA, and CUP generally unbranched. Legs mostly homonomous, cursorial; tarsi in recent forms with 2 or 3 segments, in Permian Psocidiidae with 5 segments; abdomen with 9 or 10 distinct segments; cerci absent in recent forms, obsolescent in some Permian species. *Perm.*—*Holo.*

The Psocoptera constitute a very distinct and homogeneous group at present. Numerous recent families are now usually recognized, based on wing venation as well as tarsal and antennal segmentation, but much difference of opinion exists about character-

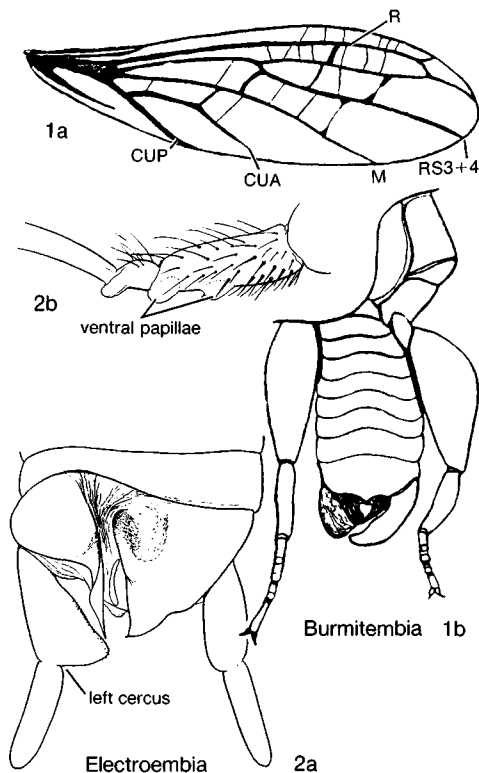


FIG. 122. Embiidae and Notoligotomidae (p. 190–191).

istics of the families. The classification used here is based on the systems of ROESLER (1944) and SMITHERS (1965, 1972). The families of Psocoptera are usually grouped into three or four suborders; but since there is little agreement among specialists regarding characteristics of the suborders or about the families included, the subordinal grouping is omitted here. In any case, most characteristics on which suborders are based are actually known in very few of the extinct genera.

The venation of the Psocoptera presents no problems in homology, except for the median system, which shows neither convexity nor concavity and which is accordingly designated here as the media (M). The evolution of the Psocoptera has involved extensive modifications of the wing venation; these have included varying degrees of anastomosis of RS and M, the branching of the media,

and especially the form of the areola postica and its relationship to the media. Similar patterns have been developed independently in various lines of evolution within the order. Moreover, the Permian species seem to have evolved along lines very unlike those of recent families; none of the Permian groups seems to suggest an approach to any living family.

The discovery of Psocoptera in Permian deposits of Kansas in 1926 (TILLYARD, 1926f) was followed by finds of a similar nature in Australian and Russian beds. These fossils have revealed a fauna that is surprisingly diverse for Permian age and have indicated some lines of psocopterous evolution. On the basis of all evidence now available, the Permian Psocidiidae seem to be the most primitive members of the order known; they had homonomous wings, a relatively generalized venational pattern, five-segmented tarsi, and short but distinct cerci. Little is known of Mesozoic Psocoptera, but the order is well represented in the Oligocene of the Baltic amber. Fortunately, also, the amber species have been studied by several major workers on recent Psocoptera (HAGEN, ENDERLEIN, ROESLER), with the result that the systematics of the amber fauna is on as firm a basis as that of the recent one. It is clear that the Psocoptera in Baltic amber, although including several extinct genera, are remarkably modern, some of the species being as highly specialized as the most extensively modified recent species.

The Psocoptera are usually regarded as more closely related to the Hemiptera than to any other order. The mouthparts, although of a chewing type, are modified in several respects that are suggestive of the hemipterous pattern. In this connection, the prolongation of the head in *Dichentomum* (BECKER-MIGDISOVA, 1962a, p. 103) is especially interesting; it suggests the possibility that in these Permian species there was a tendency for the formation of a beaklike extension of the head. Relationship to the Hemiptera is also suggested by the close resemblance between the venation of the Pso-

coptera and that of the Permian Archescytinidae (Hemiptera). In any event, although the Psocoptera as now known were almost certainly not ancestral to the Hemiptera, in all probability these two orders did arise from common ancestral stock.

Family PSOCIDIIDAE Tillyard, 1926

[Psocidiidae TILLYARD, 1926f, p. 319] [=Dichentomidae CARPENTER, 1932b, p. 61]

Fore wing usually slender; vein SC terminating on R; pterostigma commonly distinct; RS with 2 or 3 branches; M with at least 4 branches; length of areola postica about 3 times as long as its height. Hind wing similar to fore wing, usually about same size. Body structure known in *Dichentomum* only; head relatively large; antennae long, filamentous, with about 50 segments; head forming short rostrum; maxillary palpi long, with 3 segments; labial palpi shorter; fore tarsi with 4 segments; ovipositor prominent.

Perm.

Dichentomum TILLYARD, 1926f, p. 320 [**D. tinctum*; OD] [=Psocidium TILLYARD, 1926f, p. 321 (type, *P. permianum*); *Chaetopsocidium* TILLYARD, 1926f, p. 331 (type, *C. sellardsi*); *Metapsocidium* TILLYARD, 1926f, p. 333 (type, *M. loxineurum*); *Pentapsocidium* TILLYARD, 1926f, p. 334 (type, *P. indistinctum*); *Permentomum* TILLYARD, 1926f, p. 335 (type, *P. tenuiforme*); *Parapsocidium* ZALESSKY, 1937d, p. 847 (type, *P. uralicum*)]. Pterostigma oval; M with 4 branches. *Perm.*, USA (Kansas), USSR (European RSFSR), Australia (New South Wales).—FIG. 123,2. **D. tinctum*, *Perm.*, Kansas; *a*, whole insect, $\times 7$ (Laurentiaux, 1953); *b*, fore wing, $\times 12$ (Carpenter, 1933a).

Austropsocidium TILLYARD, 1935a, p. 267 [**A. pincombei*; OD]. R more remote from costa than in *Dichentomum*; pterostigma triangular. *Perm.*, Australia (New South Wales).—FIG. 123,1. **A. pincombei*; *a*, fore and *b*, hind wings, $\times 6$ (Tillyard, 1935a).

Megapsocidium TILLYARD, 1935a, p. 269 [**M. australe*; OD]. Little-known wing apex; cross-vein between base of pterostigma and RS. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).

Stenopsocidium TILLYARD, 1935a, p. 270 [**S. elongatum*; OD]. Similar to *Dichentomum*, but M with 5 branches; pterostigma small. *Perm.*, Australia (New South Wales).—FIG. 123,5. **S. elongatum*; fore wing, $\times 9$ (Tillyard, 1935a).

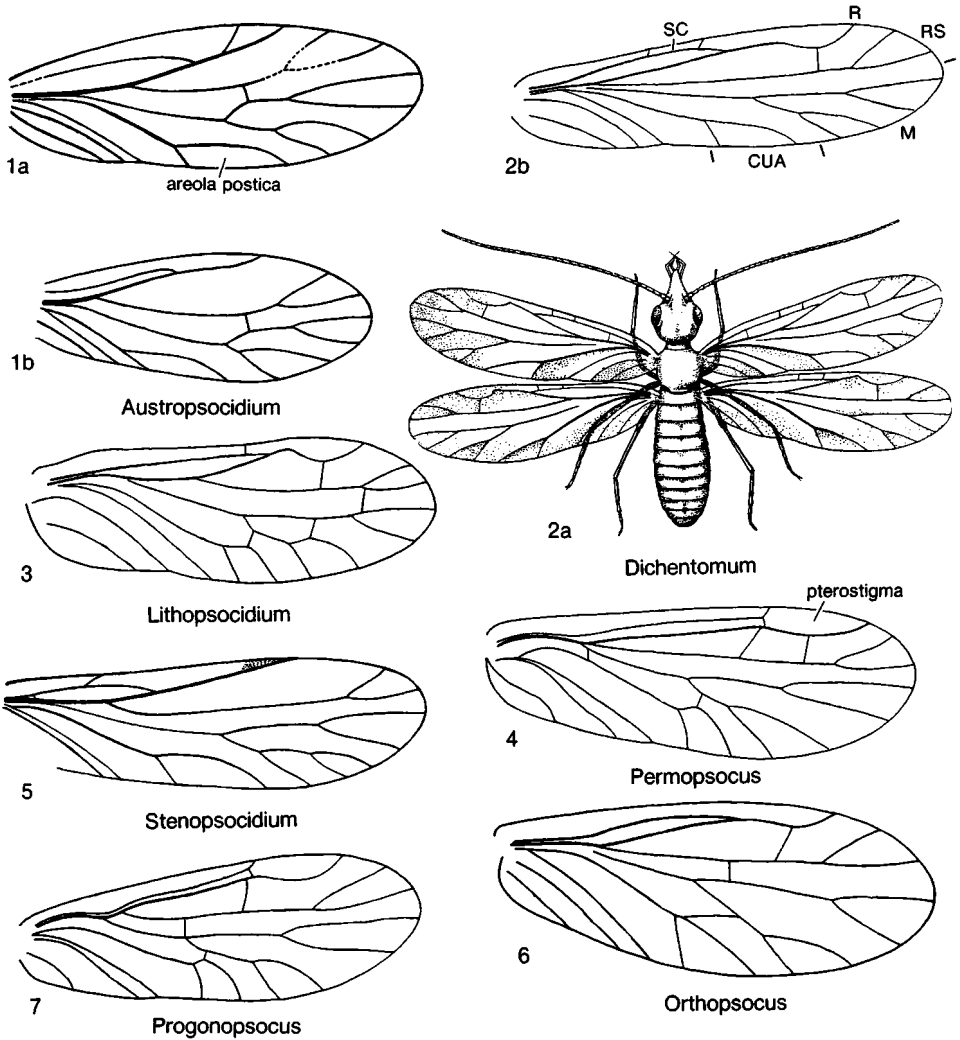


FIG. 123. Psocidiidae and Permopsocidae (p. 192-194).

Family PERMOPSOCIDAE
Tillyard, 1926

[Permopsocidae TILLYARD, 1926f, p. 340]

Fore wing broader than in Psocidiidae; veins SC and R close together and parallel; pterostigma well developed; fork of CUA high, with crossvein between CUA1 and M3 + 4. Hind wing similar to fore wing; fork of CUA slightly higher. Body structure little known; antennae much shorter than in Psocidiidae. *Perm.*

Permopsocus TILLYARD, 1926f, p. 339 [**P. latipennis*; OD] [= *Ancylopsocus* TILLYARD, 1926f, p. 344 (type, *A. insolitus*)]. End of SC connected to base of pterostigma by short crossvein; RS and stem of M divergent; fore wing with small sclerotized lobe near base of posterior margin. *Perm.*, USA (Kansas). — FIG. 123, 4. **P. latipennis*; hind wing, $\times 11$ (Carpenter, 1932b).

Lithopsocidium CARPENTER, 1932b, p. 14 [**L. permianum*; OD]. Hind wing: SC clearly terminating on R near pterostigma; RS arising near middle of wing. *Perm.*, USA (Kansas). — FIG. 123, 3. **L. permianum*; hind wing, $\times 17$ (Carpenter, 1933a).

Orthopsocus CARPENTER, 1932b, p. 15 [**O. singularis*; OD]. Hind wing: SC terminating on R near pterostigma; RS arising nearer wing base than in *Lithopsocidium*; fork of CUA triangular. *Perm.*, USA (Kansas).—FIG. 123,6. **O. singularis*; hind wing, $\times 12$ (Carpenter, 1933a).

Progonopsocus TILLYARD, 1926f, p. 337 [**P. permianus*; OD]. Very similar to *Permopsocus*, but RS and stem of M parallel. *Perm.*, USA (Kansas).—FIG. 123,7. **P. permianus*; hind wing, $\times 14$ (Carpenter, 1933a).

Family MARTYNOPSOCIDAE

Karny, 1930

[Martynopsocidae KARNY, 1930, p. 446, *nom. subst. pro* Dinopsocidae MARTYNOV, 1928b, p. 40]

Fore wing with vein SC terminating on R; pterostigma very slender; RS and M each with 3 branches. Hind wing and body unknown. *Perm.*

Martynopsocus KARNY, 1930, p. 446, *nom. subst. pro* *Dinopsocus* MARTYNOV, 1928b, p. 39, *non* BANKS, 1920 [**Dinopsocus arcuatus* MARTYNOV, 1928b, p. 40; OD] [= *Idelopsocus* ZALESSKY, 1929, p. 17 (type, *I. tartaricus*)]. RS with RS1, RS2, and RS3 + 4; fork of CUA shallow. *Perm.*, USSR (European RSFSR).—FIG. 124,1. **M. arcuatus* (MARTYNOV); fore wing, $\times 6$ (Martyinov, 1928b).

Family ARCHIPSYLLIDAE

Handlirsch, 1906

[Archipsyllidae HANDLIRSCH, 1906b, p. 502]

Antennae filiform, with at least 13 segments; mandibles elongate; fore and hind wings slender, very similar in shape and venation; vein SC short, coalesced with stem R at wing base, but almost immediately diverging towards and fusing with C, finally diverging back and joining R more distally; pterostigma well developed; RS forked distally; M with 4 branches; CU dividing basally; CUA forked distally; CUP well developed. VISHNIAKOVA, 1976. *Perm.*—*Cret.*

Archipsylla HANDLIRSCH, 1906b, p. 503 [**A. primitiva*; SD ENDERLEIN, 1909, p. 772]. Fore wing with pterostigma relatively short, about as long as wide; crossvein between RS and M1 + 2 near midwing. ENDERLEIN, 1929; VISHNIAKOVA, 1976. *Jur.*, Europe (Germany), USSR (Kazakh).—FIG. 124,2. *A. turanica* MARTYNOV, USSR; fore wing, $\times 10$ (adapted from Martyinov, 1926b and Vishniakova, 1976).

Archipsyllodes VISHNIAKOVA, 1976, p. 83 [**A. speciosis*; OD]. Pterostigma short; crossvein rs + m

as in *Eopsylla*; areola postica very slender. *Cret.*, USSR (Asian RSFSR).

Archipsyllopsis VISHNIAKOVA, 1976, p. 83 [**A. basica*; OD]. Very similar to *Archipsyllodes*, but pterostigma longer. *Cret.*, USSR (Asian RSFSR).

Eopsylla VISHNIAKOVA, 1976, p. 78 [**Dichentomum sojanensis* BECKER-MIGDISOVA, 1962a, p. 102; OD]. Similar to *Archipsylla*, but pterostigma more slender and crossvein from RS joining M before it divides into M1 + 2 and M3 + 4. *Perm.*, USSR (European RSFSR).

Family SURIJOKOPSOCIDAE

Becker-Migdisova, 1961

[Surijokopsocidae BECKER-MIGDISOVA, 1961b, p. 284]

Fore wing much wider distally than basally; vein M with 5 branches; basal parts of CUA and R + M thickened, forming cell at wing base; anal area very narrow. Hind wing and body unknown. *Perm.*

Surijokopsocus BECKER-MIGDISOVA, 1961b, p. 284 [**S. radtschenkoi*; OD]. SC close to R; costal area very wide at base; distal branches of CUA recurved. *Perm.*, USSR (Asian RSFSR).—FIG. 124,3. **S. radtschenkoi*; fore wing, $\times 7$ (Becker-Migdisova, 1961b).

Family LOPHIONEURIDAE

Tillyard, 1921

[Lophioneuridae TILLYARD, 1921c, p. 417] [=Cyphoneuridae CARPENTER, 1932b, p. 18; Zoropsocidae TILLYARD, 1935a, p. 273]

Fore wing with vein SC short or absent, extending at most slightly beyond level of origin of RS and terminating on costal margin; RS with 2 branches; stem of M coalesced with stem R; M with 2 branches; CUA with weak posterior branch or unbranched. Hind wing little known, only about two-thirds length of fore wing; CUP and 1A apparently absent. Head broad, without prolongation as in Psocidiidae; antennae reaching only to about midwing. *Perm.*

Lophioneura TILLYARD, 1921c, p. 417 [**L. ustulata*; OD]. RS3 + 4 directed posteriorly, terminating at wing apex; M forked more deeply than RS. *Perm.*, Australia (New South Wales).—FIG. 124,4. **L. ustulata*; fore wing, $\times 10$ (Tillyard, 1921c).

Austrocypha TILLYARD, 1935a, p. 277 [**A. abrupta*; OD]. Fore wing with SC apparently absent; distal part of R strongly bent anteriorly; stems of RS, M, and CUA arising from stem R and continuing nearly parallel; CUA strongly curved sigmoidally. Hind wing about half length of fore wing; RS and M forked; CU and 1A

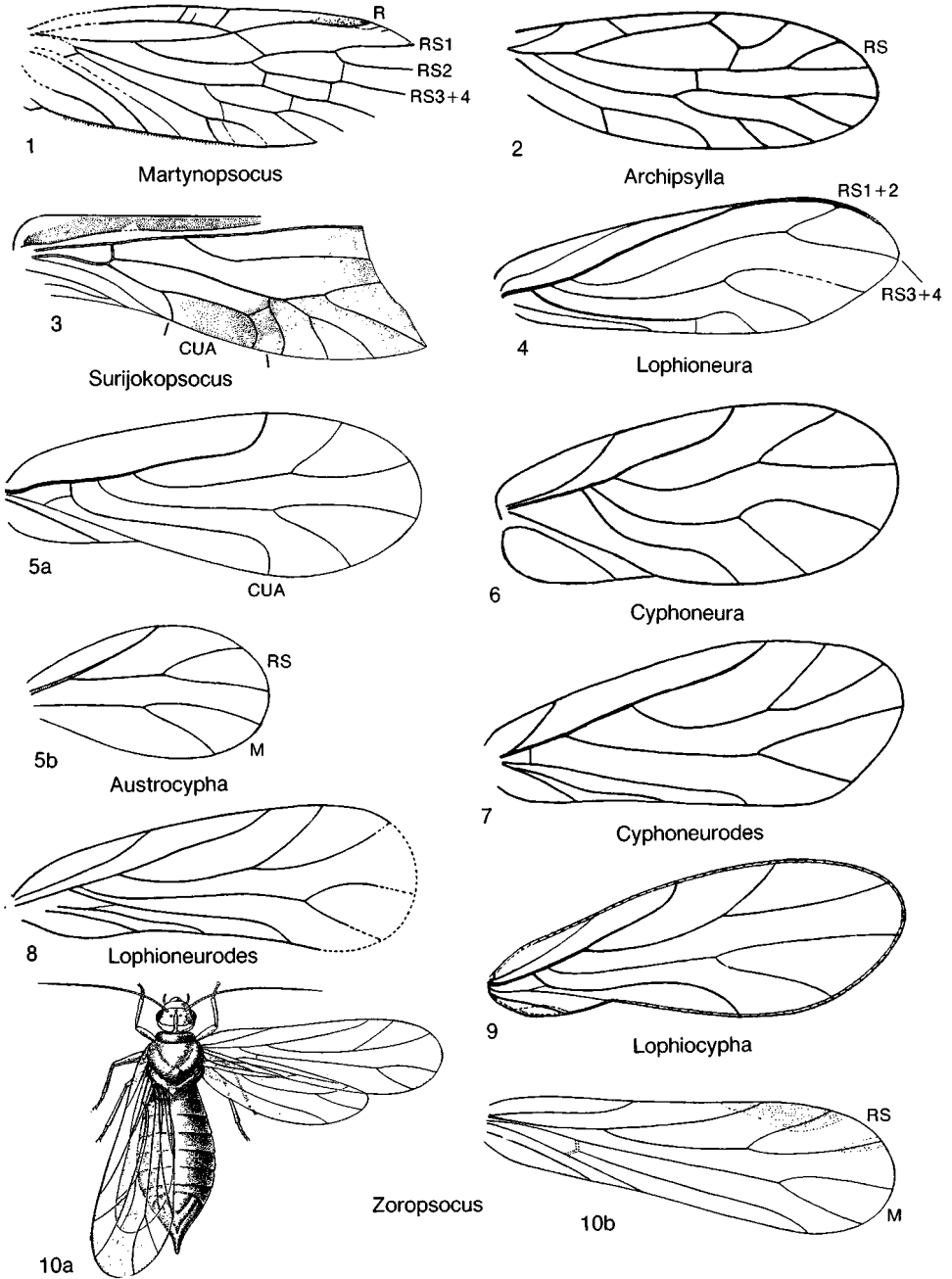


FIG. 124. Martynopsocidae, Archipsyllidae, Surijokopsocidae, and Lophioneuridae (p. 194–197).

absent. *Perm.*, Australia (New South Wales).

—FIG. 124,5. **A. abrupta*; *a*, fore and *b*, hind wings, X18 (Tillyard, 1935a).

Cyphoneura CARPENTER, 1932b, p. 18 [**C. permiana*; OD]. Fore wing nearly oval; R curved

strongly toward anterior margin; branches of M directed posteriorly; CUA unbranched, sigmoidally curved. *Perm.*, USA (Kansas). — FIG. 124,6. **C. permiana*; fore wing, X26 (Carpenter, 1932b).

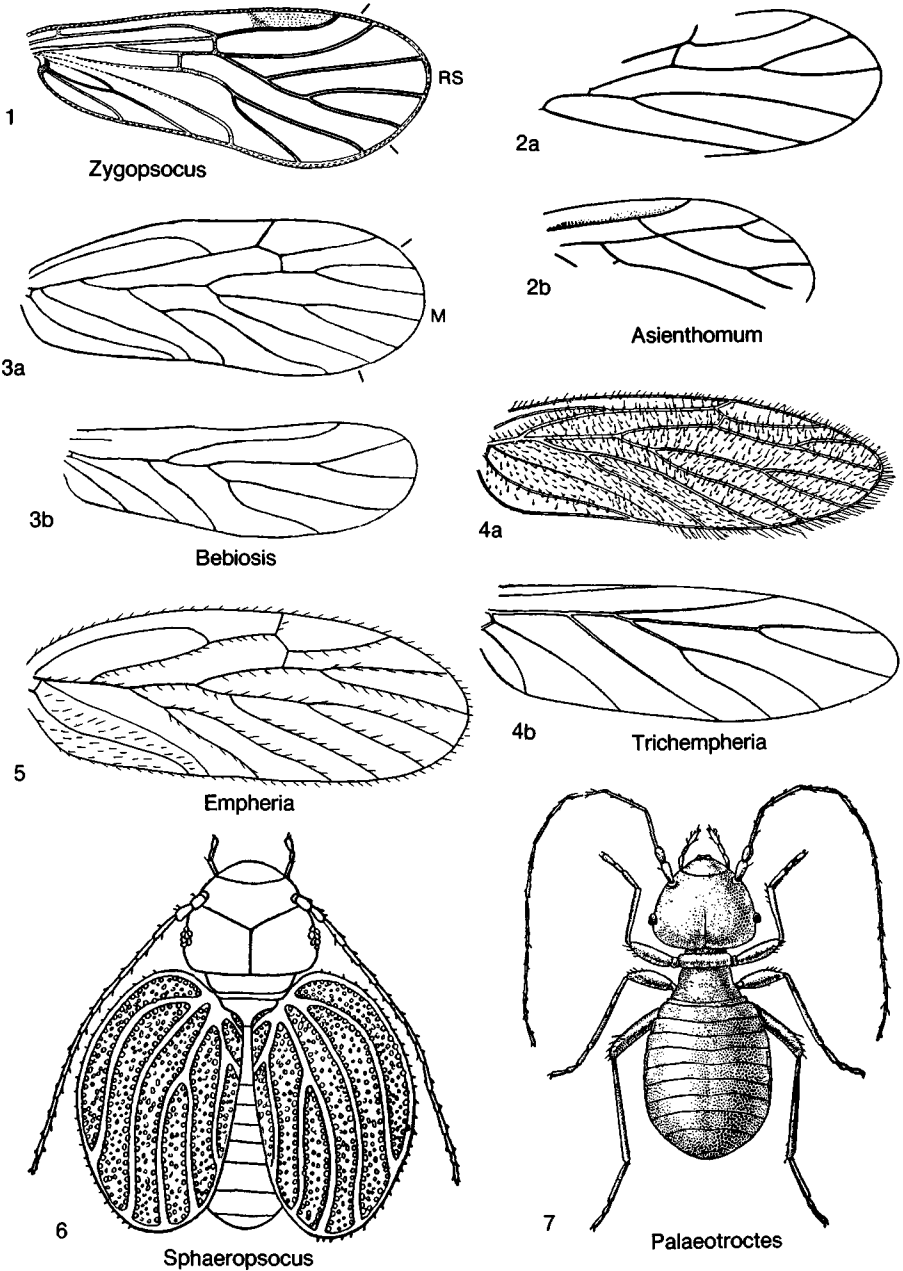


FIG. 125. Zygosocidae, Asienthomidae, Trogiidae, and Pachytroctidae (p. 197–198).

Cyphoneurodes BECKER-MIGDISOVA, 1953b, p. 281 [**Cyphoneura reducta* CARPENTER, 1932b, p. 19; OD]. Fore wing subtriangular; R not so strongly curved as in *Cyphoneura*; branches of M directed distally; CUA straight. *Perm.*, USA (Kansas). —FIG. 124, 7. **C. reducta* (CARPENTER); fore wing, $\times 22$ (Carpenter, 1932b).

Lophiocypha TILLYARD, 1935a, p. 274 [**L. permiana*; OD]. Similar to *Lophioneura* but with RS arising much farther from base of wing, and SC extending about to level of origin of RS. *Perm.*, Australia (New South Wales). —FIG. 124, 9. **L. permiana*; fore wing, $\times 18$ (Tillyard, 1935a).

Lophioneurodes BECKER-MIGDISOVA, 1953b, p. 280 [**L. sarbalensis*; OD]. CUA arising from stem of R+M; both branches of RS directed anteriorly; RS forked more deeply than *M. Perm.*, USSR (Asian RSFSR). — FIG. 124,8. **L. sarbalensis*; fore wing, $\times 18$ (Becker-Migdisova, 1962a).

Zoropsocus TILLYARD, 1935a, p. 273 [**A. delicatulus*; OD]. CUA independent of R+M, arising from common CU stem and connected to M by short crossvein; branches of RS directed anteriorly. *Perm.*, USSR (Asian RSFSR), Australia (New South Wales). — FIG. 124,10a. *Z. tomienis* BECKER-MIGDISOVA, USSR; whole insect, $\times 22$ (Becker-Migdisova, 1962a). — FIG. 124,10b. **Z. delicatulus*, Australia; fore wing, $\times 22$ (Tillyard, 1935a).

Family ZYGOPSOCIDAE

Tillyard, 1935

[Zygopsocidae TILLYARD, 1935a, p. 271]

Fore wing membranous with heavy veins; vein RS with 4 branches; M with 2 branches; CUA unbranched. Hind wing unknown. *Perm.*

Zygopsocus TILLYARD, 1935a, p. 271 [**Z. permianus*; OD]. SC terminating on R near midwing; CUA strongly curved distally; wing margin thick. *Perm.*, Australia (New South Wales). — FIG. 125,1. **Z. permianus*; fore wing, $\times 14$ (Tillyard, 1935a).

Family ASIETHOMIDAE

Martynov, 1926

[Asienthomidae MARTYNOV, 1926b, p. 1364, footnote, *nom. subst. pro Lithentomidae* MARTYNOV, 1926b, p. 1364]

Fore wing with vein CUA unbranched, M deeply forked, and RS forked. *Jur.*

Asienthomum MARTYNOV, 1926b, p. 1364, footnote, *nom. subst. pro Lithentomum* MARTYNOV, 1926b, p. 1364, *non* SCUDDER, 1867 [**Lithentomum praecox* MARTYNOV, 1926b, p. 1364; OD] [= *Lithopsocus* KARNY, 1930, p. 435, obj.]. Little-known wings. Fore wing with pterostigma about 4 times longer than wide; RS connected to R by an oblique crossvein at base of pterostigma. *Jur.*, USSR (Kazakh). — FIG. 125,2. **A. praecox* (MARTYNOV); *a*, fore and *b*, hind wings, $\times 24$ (Rohdendorf, 1962a).

Family TROGIIDAE Enderlein, 1911

[Trogidae ENDERLEIN, 1911, p. 295]

Antennae with more than 20 segments; tarsi with 3 segments, claws smooth, without teeth; scales absent from body and wings;

fore wing commonly broadly rounded distally, rarely absent. *Oligo.*—*Holo.*

Trogium ILLIGER, 1798, p. 500. *Holo.*

Bebiosis ENDERLEIN, 1911, p. 344 [**B. pertinens*; OD]. Similar to *Empheria*, but last segment of maxillary palpus much enlarged and broadened. *Oligo.*, Europe (Baltic). — FIG. 125,3. **B. pertinens*; *a*, fore and *b*, hind wings, $\times 3$ (Enderlein, 1911).

Empheria HAGEN, 1854, p. 225 [**E. reticulata*; OD]. Hairs on membrane of fore wing restricted to area between CUP and anal margin. PICTET & HAGEN, 1856. *Oligo.*, Europe (Baltic). — FIG. 125,5. **E. reticulata*; fore wing, $\times 35$ (Enderlein, 1911).

Trichempferia ENDERLEIN, 1911, p. 345 [**Empheria villosa* HAGEN, 1882, p. 221; OD]. Hairs generally distributed on fore wing membrane. *Oligo.*, Europe (Baltic). — FIG. 125,4. **T. villosa* (HAGEN); *a*, fore and *b*, hind wings, $\times 26$ (Becker-Migdisova & Vishniakova, 1962).

Family LEPIDOPSOCIDAE

Enderlein, 1903

[Lepidopsocidae ENDERLEIN, 1903, p. 206]

Antennae and tarsi as in Trogiidae, but claws with preapical tooth; scales usually present on wings and body. *Pleist.*—*Holo.*

Lepidopsocus ENDERLEIN, 1903, p. 328. *Holo.*

Thylacella ENDERLEIN, 1911, p. 349 [**T. everisiana*; OD]. Wings and body without scales; hind margin of fore wing evenly curved for its entire length. *Pleist.*, Africa.

Thylax HAGEN, 1866b, p. 172 [**T. fimbriatum*; OD]. Similar to *Thylacella*, but hind margin of fore wing angular near middle. ENDERLEIN, 1911. *Pleist.*, Africa.

Family PSYLLIPSOCIDAE Kolbe, 1884

[*nom. transl.* ENDERLEIN, 1903, p. 208, *ex* Psyllipsocini KOLBE, 1884, p. 381]

Antennae and tarsi as in Trogiidae, but veins CUP and 1A meeting at point at wing margin. *Mio.*—*Holo.*

Psyllipsocus SELYS-LONGCHAMPS, 1872, p. 136. Parts of fore and hind wings. [Generic assignment doubtful.] COCKERELL, 1916a. *Mio.*, Burma—*Holo.*

Family PACHYTROCTIDAE

Enderlein, 1905

[*nom. transl.* PEARMAN, 1936, p. 60, *ex* Pachytroctinae ENDERLEIN, 1905a, p. 461]

Antennae usually with 15 segments; tarsi with 3 segments; body normally convex,

short; legs long and slender; hind femur not broadened. Wings often reduced or absent. *Oligo.*—*Holo.*

Pachytroctes ENDERLEIN, 1905, p. 46. *Holo.*

Palaeotroctes ENDERLEIN, 1911, p. 350 [**Atropos succinica* HAGEN, 1882, p. 231; OD]. Eyes very small; meso- and metathorax fused. *Oligo.*, Europe (Baltic).—FIG. 125,7. **P. succinicus* (HAGEN); complete insect, $\times 60$ (Becker-Migdisova, 1962b).

Psylloneura ENDERLEIN, 1903, p. 317. Complete insect. [Generic assignment doubtful.] COCKERELL, 1919e. *Mio.*, Burma—*Holo.*

Sphaeropsocus HAGEN, 1882, p. 226 [**S. kunowi*; OD]. Fore wings forming short, broad elytra extending to end of abdomen; venation much reduced. *Oligo.*, Europe (Baltic).—FIG. 125,6. **S. kunowi*; complete insect, $\times 54$ (Becker-Migdisova & Vishniakova, 1962).

Family LIPOSCOLIDAE Enderlein, 1911

[Liposcolidae ENDERLEIN, 1911, p. 350]

Similar to Pachytroctidae, but body flattened and long; legs short; hind femur broad and flat; commonly wingless. *Oligo.*—*Holo.*

Liposcelis MOTSCHULSKY, 1852, p. 19. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Family AMPHIENTOMIDAE Enderlein, 1903

[Amphientomidae ENDERLEIN, 1903, p. 332]

Antennae with 12 or 13 segments; tarsi with 3 segments; body and wings usually scaled; fore femora with row of teeth; vein CUA attached to M. *Oligo.*

Amphientomum PICTET, 1854, p. 376 [**A. paradoxum*; OD]. Claws with 2 teeth; abdomen with very small scales. *Oligo.*, Europe (Baltic).—FIG. 126,1. **A. paradoxum*; *a*, fore and *b*, hind wings; $\times 35$ (Enderlein, 1911).

Electrentomum ENDERLEIN, 1911, p. 337 [**E. klebsianum*; OD]. Wings and body entirely without scales. SMITHERS, 1972. *Oligo.*, Europe (Baltic).—FIG. 126,2. **E. klebsianum*; fore wing, $\times 15$ (Enderlein, 1911).

Parelectrentomum ROESLER, 1940a, p. 228 [**P. priscum*; OD]. Similar to *Electrentomum*, but hind wing with closed middle cell; microtrichia on wing membranes very weakly developed. SMITHERS, 1972. *Oligo.*, Europe (Baltic).—FIG. 126,4. **P. priscum*; *a*, fore and *b*, hind wings, $\times 15$ (Roesler, 1940a).

Family EIPSOCIDAE Pearman, 1936

[Eipsocidae PEARMAN, 1936, p. 60]

Antennae usually with 13 segments; tarsi with 2 segments; fore wing completely lacking a crossvein from vein R to RS below pterostigma; 1 anal vein. *Oligo.*—*Holo.*

Eipsocus HAGEN, 1866c, p. 203. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Family PSOCIDAE Leach, 1815

[*nom. transl.* STEPHENS, 1829a, p. 312, ex Psocides LEACH, 1815, p. 139]

Antennae usually with 13 segments; tarsi with 2 segments; vein CUA1 in fore wing united with M by brief coalescence or by short crossvein. *Oligo.*—*Holo.*

Psocus LATREILLE, 1796, p. 99. ENDERLEIN, 1911; COCKERELL, 1921d. *Oligo.*, Europe (Baltic), England—*Holo.*

Copostigma ENDERLEIN, 1903, p. 229. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Trichadenotecnum ENDERLEIN, 1909, p. 329. ENDERLEIN, 1911, 1929. *Oligo.*, Europe (Baltic)—*Holo.*

Family MESOPSOCIDAE Enderlein, 1903

[Mesopsocidae ENDERLEIN, 1903, p. 206]

Similar to Psocidae, but tarsi with 3 segments; vein CUA1 not united with M or absent. *Oligo.*—*Holo.*

Mesopsocus KOLBE, 1880, p. 184. *Holo.*

Elipsocus HAGEN, 1866, p. 207. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Philotarsus KOLBE, 1880, p. 184. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Family PSEUDOCAECILIIDAE Pearman, 1936

[Pseudocaeciliidae PEARMAN, 1936, p. 60]

Similar to Mesopsocidae, but tarsi with 2 segments. *Oligo.*—*Holo.*

Pseudocaecilius ENDERLEIN, 1903, p. 260. *Holo.*

Archipsocus HAGEN, 1882, p. 222. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)—*Holo.*

Electropsocus ROESLER, 1940b, p. 244 [**E. unguidentis*; OD]. Veins and margin of fore wing hairy; antennae shorter than body; 3 pairs of gonapophyses in female; hypandrium of male evenly rounded. SMITHERS, 1972. *Oligo.*, Europe (Baltic).

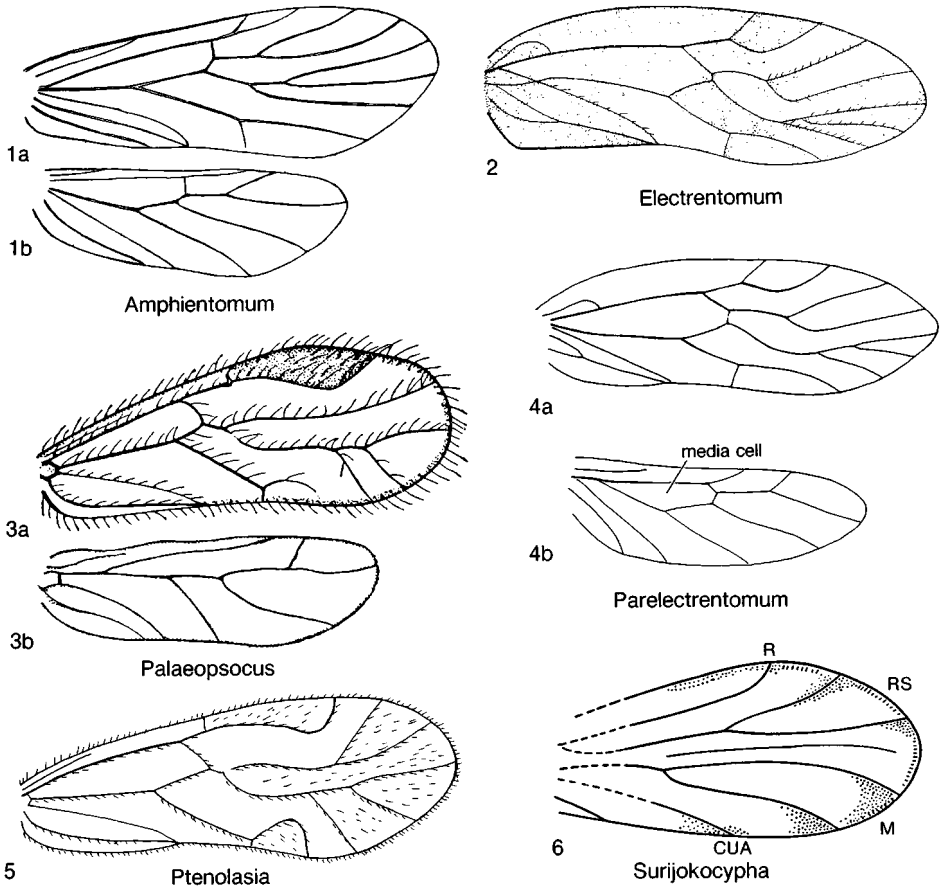


FIG. 126. Amphientomidae, Pseudocaeciliidae, Polypsocidae, and Uncertain (p. 198–200).

Palaeopsocus KOLBE, 1883, p. 190 [**Psocus tener* HAGEN in PICTET & HAGEN, 1856, p. 60; OD]. Veins of fore wing each with single row of hairs; antennae twice as long as fore wing. *Oligo.*, Europe (Baltic). — FIG. 126.3. **P. tener* (HAGEN); *a*, fore and *b*, hind wings, $\times 40$ (Becker-Migdisova & Vishniakova, 1962).

Ptenolasia ENDERLEIN, 1911, p. 321 [**Caecilius pilosus* HAGEN, 1882, p. 283; OD]. Distal half of fore wing membrane covered with hairs. *Oligo.*, Europe (Baltic). — FIG. 126.5. **P. pilosa* (HAGEN); fore wing, $\times 15$ (Enderlein, 1911).

Family POLYPSOCIDAE
Pearman, 1936

[Polypsocidae PEARMAN, 1936, p. 60]

Antennae usually with 13 segments; tarsi with 2 or 3 segments; vein CUA2 of fore wing very short. *Oligo.*–*Holo.*

Polypsocus HAGEN, 1866, p. 211. *Holo.*
Caecilius CURTIS, 1837, p. 648. ENDERLEIN, 1911; NAVÁS, 1914. *Oligo.*, Europe (Baltic)–*Holo.*
Kolbea BERTKAU, 1883, p. 128. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)–*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the order Psocoptera, are too poorly known to permit assignment to families.

Parapsocus SCUDDER, 1890, p. 117 [**P. disjunctus*; OD]. Little-known insect, probably psocopterous. SMITHERS, 1972. *Eoc.*, USA (Colorado).
Psococicadellopsis BECKER-MIGDISOVA, 1962a, p. 101 [**P. primitiva*; OD]. Little-known wing; RS apparently unbranched. *Trias.*, USSR (Issik-Kul).
Surijokocypha BECKER-MIGDISOVA, 1961b, p. 280 [**S. surijokovens*; OD]. Little-known wings;

M forked more deeply than RS; CUA unbranched. SMITHERS, 1972. *Perm.*, USSR (Asian RSFSR). — FIG. 126,6. **S. surijokovens*; fore wing, $\times 20$ (Becker-Migdisova, 1961b).

Vitriala BECKER-MIGDISOVA, 1961b, p. 282 [**V. nigriapex*; OD]. Little-known wing; M apparently unbranched. *Perm.*, USSR (Asian RSFSR).

Order ZORAPTERA Silvestri, 1913

[Zoraptera SILVESTRI, 1913b, p. 205]

Very small insects, with mandibulate, chewing mouthparts; antennae moniliform, with 9 segments; maxillae and labium normal; prothorax well developed, larger than mesothorax and metathorax; legs well developed; tarsi with 2 segments; most individuals apterous, but winged individuals of both sexes appear in nearly all species; fore wing with greatly reduced venation, consisting of 3 unbranched veins (R, RS, and M) and a forked CUA; hind wing much smaller and with only 2 veins (RS and M); both wings may be shed along basal fracture lines; abdomen with 11 distinct segments and a pair of short cerci. Nymphs similar to adults in general form, some with developing wing buds. Adults and nymphs occur chiefly in decaying wood and rich humus and are apparently fungivorous. *Holo.*

This is a very small order, all known species belonging to one genus, *Zorotypus*. They appear to be highly specialized relicts of a basically primitive group, probably related to the Psocoptera.

Order MALLOPHAGA Nitzsch, 1818

[Mallophaga NITZSCH, 1818, p. 280]

Small, apterous insects, with body dorsoventrally compressed; head large but diversely shaped; eyes reduced; antennae with 3 to 5 segments, either filiform or capitate; mouthparts with prominent, biting, dentate mandibles; prothorax well developed; mesothorax and metathorax small and frequently fused; legs moderately short, the tarsi with 1 or 2 segments and usually with 2 claws;

abdomen with 8 to 10 segments. Nymphs and adults similar in general appearance, both ectoparasites on birds or, more rarely, mammals; they feed on fragments of epidermal products, such as feathers or hairs. *Holo.*

This is a small order of ectoparasites, with somewhat fewer specializations than the Anoplura. They appear to be related to the Anoplura and Psocoptera.

Order ANOPLURA Leach, 1815

[Anoplura LEACH, 1815, p. 64]

Small, apterous insects, the body dorsoventrally compressed; head relatively small; eyes usually much reduced or absent; antennae short, with 3 to 5 segments; mouthparts highly modified for sucking blood, with 3 piercing stylets; thorax small, segmentation indistinct; legs short but well developed, the single tarsal segment bearing a strong claw; abdomen with 9 segments; cerci absent. The nymphs and adults, which are similar in general appearance, are ectoparasites on mammals and feed on blood. *Holo.*

This is a small order of highly specialized ectoparasites, often treated as a suborder of the order Phthiraptera, with the Mallophaga constituting a second suborder. In either case, the ancestral stock of the Anoplura is uncertain, although the Psocoptera are probably nearer to that ancestral line than any other known order (KRISTENSEN, 1981).

Although the Anoplura are not known prior to the Holocene, two well-preserved males of *Neobaematopinus relictus* DUBININ have been found on the frozen body of a gopher (*Citellus*) in Indigirka, USSR (Asian RSFSR). The age of the gopher was determined as about 10,000 years (DUBININ, 1948).

Order CALONEURODEA Handlirsch, 1937

[*nom. transl.* MARTYNOV, 1938a, p. 75, ex Caloneuroidea HANDLIRSCH, 1937, p. 64]

Fore and hind wings commonly similar in venation and texture, hind wings lacking an

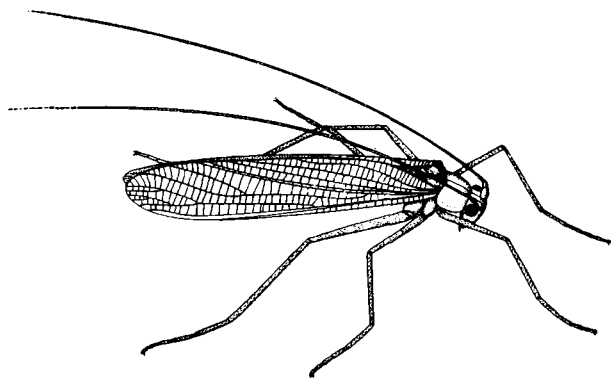


FIG. 127. Caloneurodea; restoration of *Paleuthygramma tenuicornis* MARTYNOV, Paleuthygrammatidae, Permian of USSR, $\times 1.8$ (Sharov, 1966a).

expanded anal area; base of vein CUA coalesced with stem of M for short distance; M commonly with 2 branches; CUA and CUP typically very close together, parallel, and unbranched; 2 or more unbranched anal veins; crossveins numerous, evenly distributed. Body slender; antennae filiform, multisegmented (Fig. 127); head hypognathous or prognathous; mouthparts mandibulate; legs long and slender; tarsi with 5 segments. Females with short, one-segmented cerci. Immature stages unknown. *U. Carb.—Perm.*

The Caloneurodea have generally been regarded as relatives of the Protorthoptera (HANDLIRSCH, 1906b; MARTYNOV, 1938a; CARPENTER, 1943a, 1961, 1970; MARTYNOVA, 1962b; BURNHAM, 1984). However, SHAROV (1966a) and RASNITSYN (1980b) consider them to have been endopterygote insects, close to the base of the neuropteroids and the Coleoptera. Evidence for the affinities of the Caloneurodea is admittedly inconclusive and will probably remain so until much more is known about their body structure. At present, the few morphological features of the body mentioned above are known only in two genera (*Paleuthygramma* and *Synomaloptila*). However, since the case for the endopterygote status of the Caloneurodea seems to me to be very weak, I have followed here the more generally accepted view of the order's position.

Although the fore and hind wings do not

usually show much difference in texture, in one family, the Caloneuridae, the fore wings are at least slightly tegminous, both membrane and veins being thicker than those of the hind wings. The wing venation throughout the order is considerably more reduced than that of the Protorthoptera and most other generalized orthopteroids. The convexities and concavities of the veins are unusually strong except for the media. The media is neutral, nearly flat, as in most other neopteran insects. The most prominent feature of the venation in most species is the close proximity of the strongly convex CUA and the strongly concave CUP.

This is one of the small extinct orders of insects, including only 16 genera distributed among 9 families. The genus *Genopteryx* SCUDDER (1885d), placed by RICHARDSON (1956) in the Caloneurodea, has recently been synonymized by BURNHAM (1983) with *Gerarus* SCUDDER (1885d) of the order Protorthoptera.

Family CALONEURIDAE Handlirsch, 1906

[Caloneuridae HANDLIRSCH, 1906b, p. 140]

Wings with vein SC terminating well before apex of wing; CUA and CUP very close together and nearly parallel. M forked dichotomously; 4 anal veins; crossveins numerous. *U. Carb.*

Caloneura BRONGNIART, 1885a, p. 59 [**C. dawsoni*; OD] [= *Confusio* HANDLIRSCH, 1919b, p. 547 (type, *Homaloneura royeri* MEUNIER, 1911a, p. 119)]. Fore wing with costal space abruptly narrowed basally; RS with 5 or 6 main branches; CUA and CUP unbranched. *U. Carb.*, Europe (France).—FIG. 128,8. **C. dawsoni*; *a*, fore and *b*, hind wings, $\times 1.2$ (Carpenter, 1961).

Family ANOMALOGRAMMATIDAE Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Anomalogrammatidae CARPENTER, 1943a, p. 74]

Vein SC terminating at midwing; M deeply forked; 3A absent. *Perm.*

Anomalogramma CARPENTER, 1943a, p. 75 [**A. parvum*; OD]. RS forked to about half length of fork of M. *Perm.*, USA (Kansas).—FIG. 128,10. **A. parvum*; wing, $\times 6$ (Carpenter, 1943a).

Family APSIDONEURIDAE Carpenter, 1961

[Apsidoneuridae CARPENTER, 1961, p. 151]

Wings with vein SC extending about to wing apex; M forked broadly, the anterior branch (M1+2) arching strongly away from posterior branch; 3 anal veins. *U. Carb.*—*Perm.*

Apsidoneura CARPENTER, 1943a, p. 72 [**A. flexa*; OD]. Fore wing much more slender than in *Caloneura* and narrowed basally; RS with 2 or 3 main branches. BURNHAM, 1984. *U. Carb.*, Europe (France); *Perm.*, USA (Kansas).—FIG. 128,9. **A. flexa*; fore wing, $\times 2$ (Carpenter, 1943a).

Homaloptila HANDLIRSCH, 1919b, p. 546 [**Homaloneura similis* MEUNIER, 1911a, p. 118; OD]. Fore wing nearly as broad as in *Caloneura*; RS with 4 main branches. *U. Carb.*, Europe (France).—FIG. 128,7. **H. similis* (MEUNIER); *a*, fore and *b*, hind wings, $\times 2$ (Carpenter, 1961).

Family EUTHYGRAMMATIDAE Martynov, 1928

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Euthygrammatidae MARTYNOV, 1928b, p. 49]

Similar to Paleothygrammatidae but with vein CUA remote from CUP and CUP very close to 1A. *Perm.*

Euthygramma MARTYNOV, 1928b, p. 50 [**E. paralletum*; OD]. RS unbranched. *Perm.*, USSR (European RSFSR).—FIG. 128,6. **E. paralletum*; wing, $\times 2.7$ (Martynov, 1938a).

Family PALEUTHYGRAMMATIDAE Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Paleothygrammatidae CARPENTER, 1943a, p. 70]

Wings long and slender; vein SC terminating not far from wing apex; RS arising near midwing, with 2 or 3 branches; M separating from stem R well before origin of RS; CUA and CUP straight and very close together. *Perm.*

Paleothygramma MARTYNOV, 1930b, p. 42 [**P. tenuicornis*; OD]. RS branched only at wing apex. *Perm.*, USSR (Asian RSFSR), USA (Kansas).—FIG. 128,5a. **P. tenuicornis*, USSR; wing of holotype as preserved, $\times 2.5$ (Martynov, 1930b) (see also FIG. 127).—FIG. 128,5b,c. *P. acutum* CARPENTER, Kansas; *b*, fore and *c*, hind wings, $\times 3$ (Carpenter, 1943a).

Pseudogramma CARPENTER, 1943a, p. 70 [**Euthygramma aberrans* MARTYNOV, 1938a, p. 73; OD]. M unbranched. *Perm.*, USSR (European RSFSR).—FIG. 128,4. **P. aberrans* (MARTYNOV); wing, $\times 3$ (Martynov, 1938a).

Vilvia ZALESSKY, 1933, p. 137 [**V. densinervosa*; OD]. Crossveins numerous and very close together. *Perm.*, USSR (Asian RSFSR).

Vilviopsis MARTYNOV, 1938a, p. 73 [**V. extensa*; OD]. RS with 2 long branches. [Probably synonymous with *Paleothygramma*.] *Perm.*, USSR (European RSFSR).—FIG. 128,3. **V. extensa*; wing, $\times 2$ (Martynov, 1938a).

Family PERMOBIELLIDAE Tillyard, 1937

[*nom. transl.* MARTYNOV, 1938b, p. 76, *ex* Permobiellinae TILLYARD, 1937a, p. 101]

Wings moderately slender; vein SC terminating slightly beyond midwing; RS with 3 branches; CUA and CUP close together proximally but diverging distally. *U. Carb.*—*Perm.*

Permobiella TILLYARD, 1937a, p. 101 [**P. perspicua*; OD]. R extending to wing apex; M forking well beyond origin of RS; crossveins strongly convex. CARPENTER, 1943a. *Perm.*, USA (Kansas).—FIG. 129,3. **P. perspicua*; wing as preserved, $\times 5$ (Carpenter, 1943a).

Pseudobiella CARPENTER, 1970, p. 407 [**P. fasciata*; OD]. Similar to *Permobiella*, but crossveins relatively weak, not strongly convex; front margin of wing concave near end of SC; wings with dark transverse band. *U. Carb.*, USA (New Mexico).—FIG. 129,1. **P. fasciata*; fore wing, $\times 5$ (Carpenter, 1970).

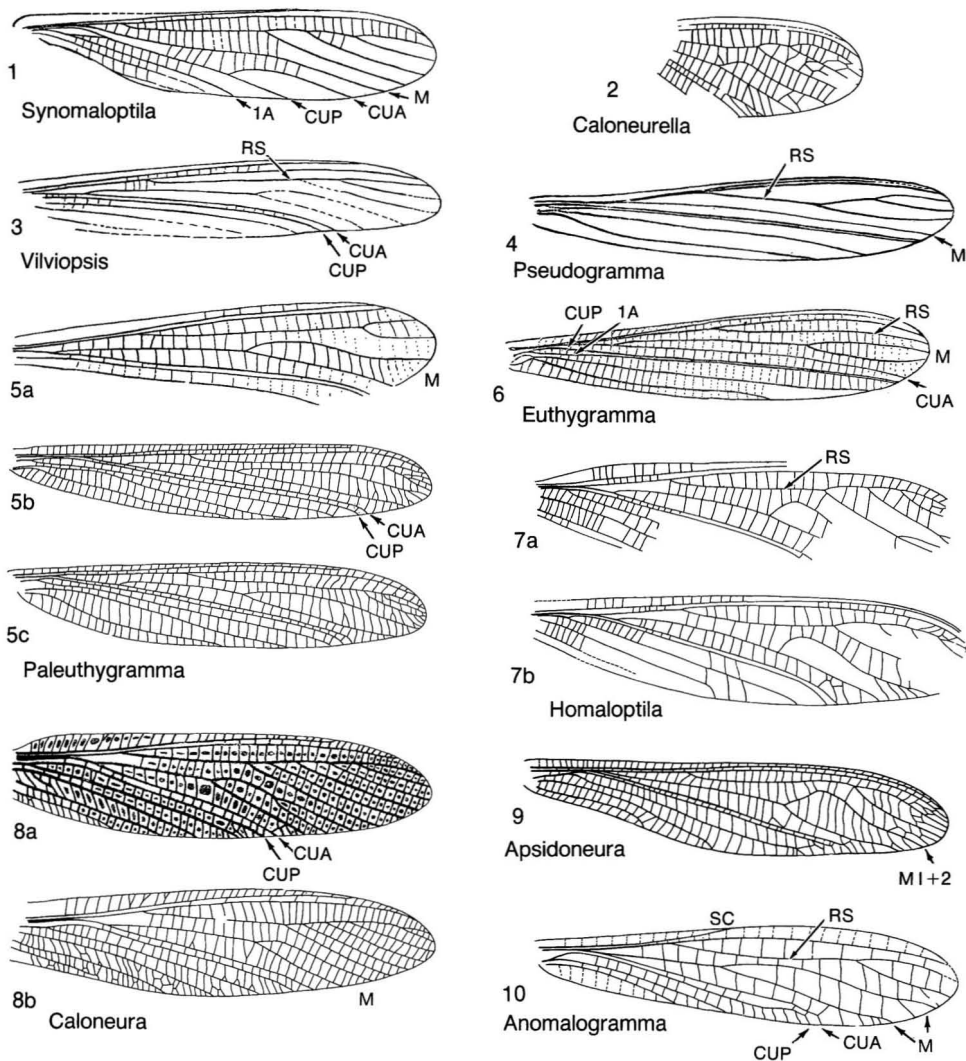


FIG. 128. Caloneuridae, Anomalogrammatidae, Apsidoneuridae, Euthygrammatidae, Paleothygrammatidae, Synomaloptilidae, and Uncertain (p. 202–204).

Family AMBONEURIDAE
Carpenter, 1980

[Amboneuridae CARPENTER, 1980, p. 111]

Apparently related to the Permobiellidae, but veins CUA and CUP not close together; crossveins forming a coarse network in strong relief over the wing. [Ordinal assignment uncertain.] *U. Carb.*

Amboneura CARPENTER, 1980, p. 112 [**A. klosei*; OD]. Vein RS with 5 terminal branches; M forked

to level of midwing. *U. Carb.*, USA (Pennsylvania). —FIG. 129, 4a, b. **A. klosei*; a, photograph of wing showing strong relief of crossveins, $\times 2.4$; b, drawing of venation as preserved in holotype, $\times 2.4$ (both Carpenter, 1980).

Family PLEISIOGRAMMATIDAE
Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Pleisiogrammatidae CARPENTER, 1943a, p. 73]

Wings nearly oval, broader than in Paleothygrammatidae, narrowed basally; vein

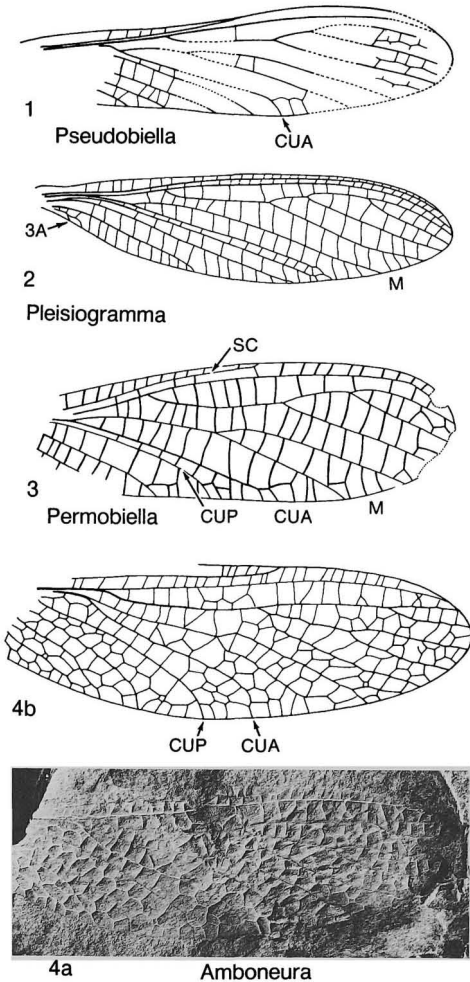


FIG. 129. Permobiellidae, Amboneuridae, and Pleisiogrammatidae (p. 202–204).

SC extending well beyond midwing; 3A vestigial or absent. *Perm.*

Pleisiogramma CARPENTER, 1943a, p. 73 [**P. mediale*; OD]. M unbranched. *Perm.*, USA (Kansas). —FIG. 129,2. **P. mediale*; wing, $\times 3.2$ (Carpenter, 1943a).

Family SYNOMALOPTILIDAE
Martynov, 1938

[Synomaloptilidae MARTYNOV, 1938a, p. 76]

Related to Euthygrammatidae, but veins CUA and CUP anastomosed for a considerable distance. *Perm.*

Synomaloptila MARTYNOV, 1938a, p. 76 [**S. longipennis*; OD]. SC terminating well before wing

apex; separation of CUA and CUP at about level of midwing. *Perm.*, USSR (Asian RSFSR). —FIG. 128,1. **S. longipennis*; wing, $\times 2$ (Martynov, 1938a).

Family UNCERTAIN

The following genera, apparently belonging to the order Caloneuroidea, are too poorly known to permit assignment to families.

Caloneurella CARPENTER, 1934, p. 324 [**C. carbonaria*; OD]. Apical wing fragment, probably related to *Caloneura*. *U. Carb.*, USA (Pennsylvania). —FIG. 128,2. **C. carbonaria*; $\times 1.8$ (Carpenter, 1934).

Pruvostiella HANDLIRSCH, 1922, p. 82 [**Euthyneura lecomtei* PRUVOST, 1919, p. 115; OD]. Small wing fragment. *U. Carb.*, Europe (France).

Order MIOMOPTERA
Martynov, 1927

[Miomoptera MARTYNOV, 1927d, p. 101, *emend.* MARTYNOV, 1938b, p. 138]

Small to very small insects, with wings nearly homonomous. Fore wing with vein SC ending before or at midwing; R commonly with a distal twig; RS arising before midwing, with at least 3 terminal branches; M commonly coalesced with CUA basally to varying amounts, but diverging in basal third of wing; M deeply forked; CUA with 2 or 3 terminal branches; CUP unbranched; 2 anal veins typically present. Hind wing similar in form to fore wing, without an anal lobe or fan; M usually arising from CU very near wing base. Body structure little known; head of moderate size; mouthparts apparently mandibulate; antennae conspicuous, relatively thick, with 15 to 20 segments; tarsi with 4 segments (*Palaeomantis*); cerci short. Immature stages unknown. *U. Carb.*—*Perm.*

The status of this order is uncertain. As originally proposed by MARTYNOV (1927d) it included five Permian families, previously placed in the order Protorthoptera, but it was based mainly on one of them, the Palaeomanteidae (=Delopteridae). The following year TILLYARD (1928b), obviously unaware of MARTYNOV's article, proposed the new order Protoperlaria for the same series of families except the Palaeomanteidae. Subsequent studies of extensive collections of

Palaeomanteidae and Lemmatophoridae (CARPENTER, 1933a, 1935a; MARTYNOV, 1938b; MARTYNOVA, 1958, 1961b, 1962a) supported the view that the Palaeomanteidae were sufficiently distinctive to justify ordinal separation and that the Lemmatophoridae and related families were in reality part of the order Protorthoptera.

The Miomoptera, as exemplified by the Palaeomanteidae, stand apart from the protorthopterous families, with which they have been associated, by two distinct features. One of these is the absence of the anal lobe or fan on the hind wing, probably a secondary condition, as in the Isoptera and Embioptera. The other is the very small number of crossveins and their virtual absence from the costal area of both wings.

Several families have been added to the Miomoptera since MARTYNOV's original publication on the order. Two of these, Archaeomipteridae (GUTHÖRL, 1939) and Metroptoridae HANDLIRSCH (1906a) almost certainly belong in the order (MARTYNOVA, 1958, 1961b; CARPENTER, 1965). The evidence for the others, however, is very weak and in my opinion insufficient to justify their inclusion in the Miomoptera. The family Permembiiidae TILLYARD (1937b), originally described in the Psocoptera, has been transferred to the Miomoptera by KUKALOVÁ (1963a) and RIEK (1973, 1976a); *Permembia* itself is known from a very few, poorly preserved specimens (CARPENTER, 1976), with a venation that has little in common with that of the Palaeomanteidae. Some details of body structure are preserved in two specimens, but since almost nothing is known of the body of the Palaeomanteidae we have no basis for comparing those details. The family Permosialidae MARTYNOV (1928b), originally in the Neuroptera, has been placed in the Miomoptera by RIEK (1976a) and RASNITSYN (1977c), as have the families Permonkidae RASNITSYN (1977c) and Palaeomantiscidae RASNITSYN (1977c). These families, however, are characterized by broadened anal areas or anal lobes on the hind wings and numerous crossveins on both wings including the costal areas. Since no revisions

of the definition or diagnosis of the Miomoptera have been proposed for the accommodation of these families, the order is treated here essentially as it was defined by MARTYNOV (1938b) and MARTYNOVA (1961b, 1962a). The families Permembiiidae, Permosialidae, Permonkidae, and Palaeomantiscidae, along with a nymphal form, *Permonympha* SHAROV (1957b), are included under Neoptera, Order Uncertain.

The homologies of the wings of the Miomoptera have not been definitely determined. In the fore wing, veins R and CUA are clearly convex, but RS and M show no definite topography. Whether the branches of M represent MA and MP (KUKALOVÁ, 1963a) or only one of these veins is uncertain; they are designated here as M1+2 and M3+4. The amount of anastomosis of M with CUA in the fore wing varies from genus to genus; in some species (e.g., *Permodelopterum obscurum* KUKALOVÁ; see Fig. 131,4a), M appears to arise independently of CUA, which joins it later; in others (e.g., *Palaeomantis minutum* (SELLARDS); see Fig. 131,1b) the stem of M seems to be coalesced with that of CUA from the very base of the wing. In all species, however, M diverges from CUA before midwing. In some individual wings, M1+2 seems to arise from RS or RS3+4; this may be a specific or even a generic characteristic, and there is some evidence that it occurs as an individual variation (CARPENTER, 1939).

The Miomoptera are among the smallest insects known from the Upper Carboniferous and Permian. However, their affinities are not clear. They are generally considered to have been related to the Psocoptera, although RASNITSYN (1980b) believes them to have been endopterygote insects, close to the ancestral stock of the Hymenoptera. MARTYNOV concluded (1938b) that they were an early, aberrant branch of protorthopterous or perlarian stock.

Family METROPATORIDAE Handlirsch, 1906

[Metroptoridae HANDLIRSCH, 1906a, p. 681]

Hind wing nearly oval; vein SC short, weakly developed, and close to R; RS forked

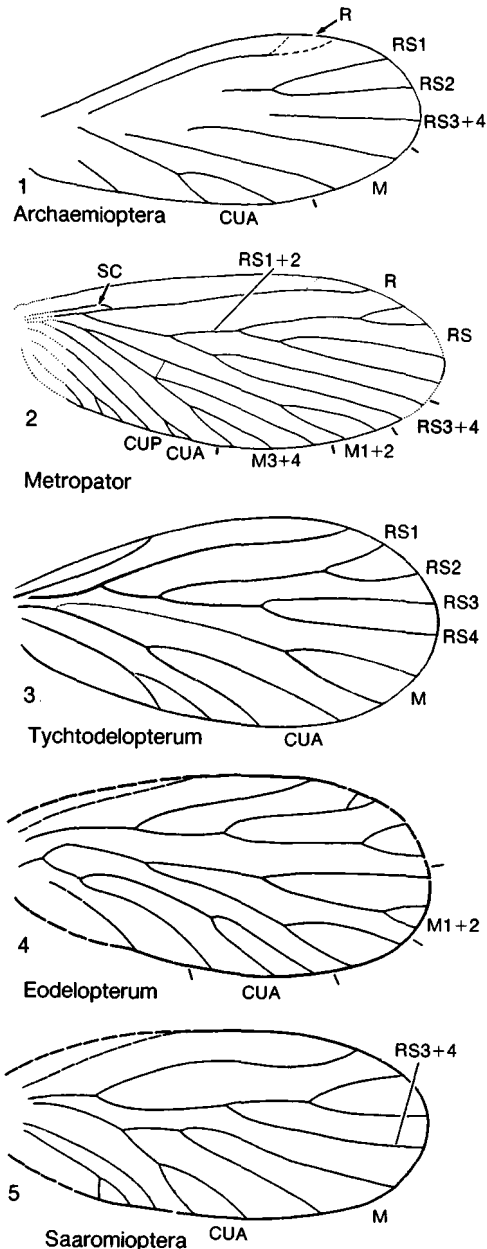


FIG. 130. Metropatoridae and Archaemiopteri-
dae (p. 206).

before midwing; RS1+2 with 4 terminal branches; RS3+4 forked once; M apparently arising from CUA at base of wing and forked almost to level of origin of RS; CUA with short terminal fork. Fore wing and body unknown. *U. Carb.*

Metropator HANDLIRSCH, 1906a, p. 681 [**M. pusillus*; OD]. RS3+4 more deeply forked than RS1+2; M1+2 forked distally; M3+4 forked twice. TILLYARD, 1926c; CARPENTER, 1965. *U. Carb.*, USA (Pennsylvania).—FIG. 130,2. **M. pusillus*; hind wing, $\times 6.5$ (Carpenter, 1965).

Family ARCHAEMIOPTERIDAE Guthörl, 1939

[Archaemiopteridae GUTHÖRL, 1939, p. 320]

Fore and hind wings broadly oval; vein RS1+2 forked, at least distally. Body unknown. *U. Carb.*—*Perm.*

Archaemioptera GUTHÖRL, 1939, p. 320 [**A. carbonaria*; OD]. RS3+4 unbranched; M forked to more than half its length; CUA with distal fork only. *U. Carb.*, Europe (Germany).—FIG. 130,1. **A. carbonaria*; fore(?) wing, $\times 10$ (Carpenter, new, based on holotype).

Eodelopterum SCHMIDT, 1962, p. 838 [**E. priscum*; OD]. Similar to *Tychtodelopterum*, but CUA with 3 terminal branches; M1+2 terminating at wing apex. GUTHÖRL, 1963. *U. Carb.*, Europe (Germany).—FIG. 130,4. **E. priscum*; hind wing, $\times 12$ (Guthörl, 1963).

Saaromioptera GUTHÖRL, 1963, p. 22 [**S. jordani*; OD]. Similar to *Tychtodelopterum*, but RS3+4 unbranched. *U. Carb.*, Europe (Germany).—FIG. 130,5. **S. jordani*; fore(?) wing, $\times 11$ (Guthörl, 1963).

Tychtodelopterum MARTYNOVA, 1958, p. 70 [**T. relictum*; OD]. Similar to *Archaemioptera*, but RS3+4 deeply forked; CUA forked to at least half its length. *Perm.*, USSR (Asian RSFSR).—FIG. 130,3. **T. relictum*; hind wing, $\times 16$ (Martynova, 1962a).

Family PALAEOMANTEIDAE Handlirsch, 1906

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 811, *pro* Palaeomantidae HANDLIRSCH, 1906b, p. 348] [=Delopteridae SEL-
LARDS, 1909, p. 168]

Fore wing membranous or coriaceous; vein SC usually ending before midwing, less commonly near midwing; RS usually with 3 terminal branches; basal stem of M apparently independent of both R and CU in some genera, but anastomosed with one of these in other genera; M forked deeply, usually to midwing; rarely, M1+2 apparently anastomosed with stem of RS (or connected by crossvein), resembling additional branch of RS; CUA with 2 or 3 terminal branches; distinct marginal indentation at end of CUP in some genera. Hind wing similar to fore

wing except for differences characteristic of the order. Antennae with about 15 short segments; tarsi with 4 segments; abdomen short, with wings projecting far beyond abdomen at rest; cerci very short. *U. Carb.—Perm.*

Palaeomantis HANDLIRSCH, 1904b, p. 4 [**P. schmidii*; OD] [= *Delopterum* SELLARDS, 1909, p. 168 (type, *D. minutum*); *Pseudodelopterum* MARTYNOV, 1928b, p. 66 (type, *Delopterum latum* SELLARDS, 1909); *Pseudomantis* MARTYNOV, 1928b, p. 73 (type, *P. minuta*); *Leptoneurula* MARTYNOV, 1928b, p. 77 (type, *L. insignis*); *Delopsocus* TILLYARD, 1928f, p. 474 (type, *D. elongatus*); *Miomantisca* ZALESSKY, 1956a, p. 275 (type, *M. clara*); *Miomatoneurites* ZALESSKY, 1956a, p. 278 (type, *M. sylvanensis*); *Delopteriella* ZALESSKY, 1956a, p. 284 (type, *D. graciosa*); *Stefanomioptera* GUTHÖRL, 1962a, p. 67 (type, *S. hangardi*)]. Fore wing slender, membranous; SC terminating at about midwing; RS diverging from R in basal third of wing and usually with branches RS1, RS2, and RS3 + 4; M separating from CUA near level of origin of RS; M1 + 2 and M3 + 4 diverging near midwing; CUA forked; crossveins very few and weakly developed; posterior margin of wing either smoothly curved or with an indentation at end of CUP. Hind wing slightly shorter than fore wing; SC short, usually terminating about one-third wing length from base. Hind wing similar in form to fore wing but apparently lacking a separate and distinct CUP; CUA not preserved as a definite, convex vein as in fore wing, but forming with CUP a compound vein (CU) and preserved as a strong ridge within a furrow. Head with large compound eyes; first tarsal segment longer than others; cerci short. CARPENTER, 1933a, 1967c; GUTHÖRL, 1962a; MARTYNOVA, 1962a; KUKALOVÁ, 1963a. *U. Carb.*, Europe (Germany); *Perm.*, USA (Kansas, Oklahoma), Europe (Czechoslovakia), USSR (European RSFSR).—FIG. 131,1a. *P. hangardi* (GUTHÖRL), *U. Carb.*, Germany; fore wing, $\times 9$ (Carpenter, 1967c).—FIG. 131,1b,c. **P. minutum* (SELLARDS), *Perm.*, Kansas; b, fore and c, hind wings, $\times 12$ (Carpenter, 1933a).

Miomatoneura MARTYNOV, 1927d, p. 106 [**M. frigida*; OD]. Fore wing as in *Palaeomantis*, but M1 + 2 arising from stem of RS or connected to it by crossvein; CUA with 2 or 3 terminal branches. Hind wing unknown. MARTYNOVA, 1961b, 1962a; KUKALOVÁ, 1963a. *Perm.*, USSR (European RSFSR), Europe (Czechoslovakia).—FIG. 131,2a. **M. frigida*, *Perm.*, USSR; fore wing, $\times 8$ (Martynova, 1962a).—FIG. 131,2b. *M. candida* KUKALOVÁ, *Perm.*, Czechoslovakia; fore wing, $\times 14$ (Kukalová, 1963a).

Miomatoneurella MARTYNOVA, 1958, p. 71 [**M. reducta*; OD]. Fore wing similar to that of *Miomatoneura*, but RS1 + 2 unbranched. MARTYNOVA, 1961b. *Perm.*, USSR (Asian RSFSR).—FIG.

131,3. **M. reducta*; fore wing, $\times 15$ (Martynova, 1962a).

Permodelopterum KUKALOVÁ, 1963a, p. 25 [**P. obscurum*; OD]. Fore wing similar to that of *Perunopterum* but broader and base of M apparently coalesced with R basally. Hind wing and body unknown. *Perm.*, Europe (Czechoslovakia).—FIG. 131,4a. **P. obscurum*; fore wing, $\times 8$ (Kukalová, 1963a).—FIG. 131,4b. *P. lumbiforme* KUKALOVÁ; fore wing, $\times 12$ (Kukalová, 1963a).

Perunopterum KUKALOVÁ, 1963a, p. 16 [**P. peruni*; OD]. Fore wing membranous or distinctly coriaceous, densely covered with minute hairs, and more slender than in *Palaeomantis*; indentation of hind margin at end of CUP pronounced; SC terminating near midwing; R with distal twig; RS arising before midwing, typically with branches RS1, RS2, and RS3 + 4; stem of M free from R basally; M arising from CUA at about level of origin of RS, with 2 long branches; CUA forked. Hind wing similar to fore but with SC shorter and weaker and costal area narrower; M separating from CUA nearer wing base. Both wings tend to show more crossveins than in *Palaeomantis*, even having reticulation in anal area. Body structure apparently much as in *Palaeomantis*; short cerci present. *Perm.*, Europe (Czechoslovakia).—FIG. 131,5a. **P. peruni*; fore wing, $\times 12$ (Kukalová, 1963a).—FIG. 131,5b. *P.(?) corium* KUKALOVÁ; fore wing, $\times 8$ (Kukalová, 1963a).

Order THYSANOPTERA Haliday, 1836

[Thysanoptera HALIDAY, 1836, p. 439]

Small or minute insects, with slender body (Fig. 132); head usually quadrangular; compound eyes small but prominent, with relatively large, rounded facets; ocelli commonly present; antennae with 6 to 10 segments; labrum and labium forming a short cone, containing as stylets the left mandible (right one absent or vestigial) and extensions of the 2 maxillae; maxillary and labial palpi present; prothorax free from mesothorax and well developed; wings usually present, nearly homonomous, membranous but very narrow, often strap-shaped, with not more than 2 longitudinal veins; wings fringed with long setae, at least along posterior margins; both brachypterous and apterous individuals may occur in some species; legs short, with 1 to 2 tarsal segments; abdomen elongate, seg-

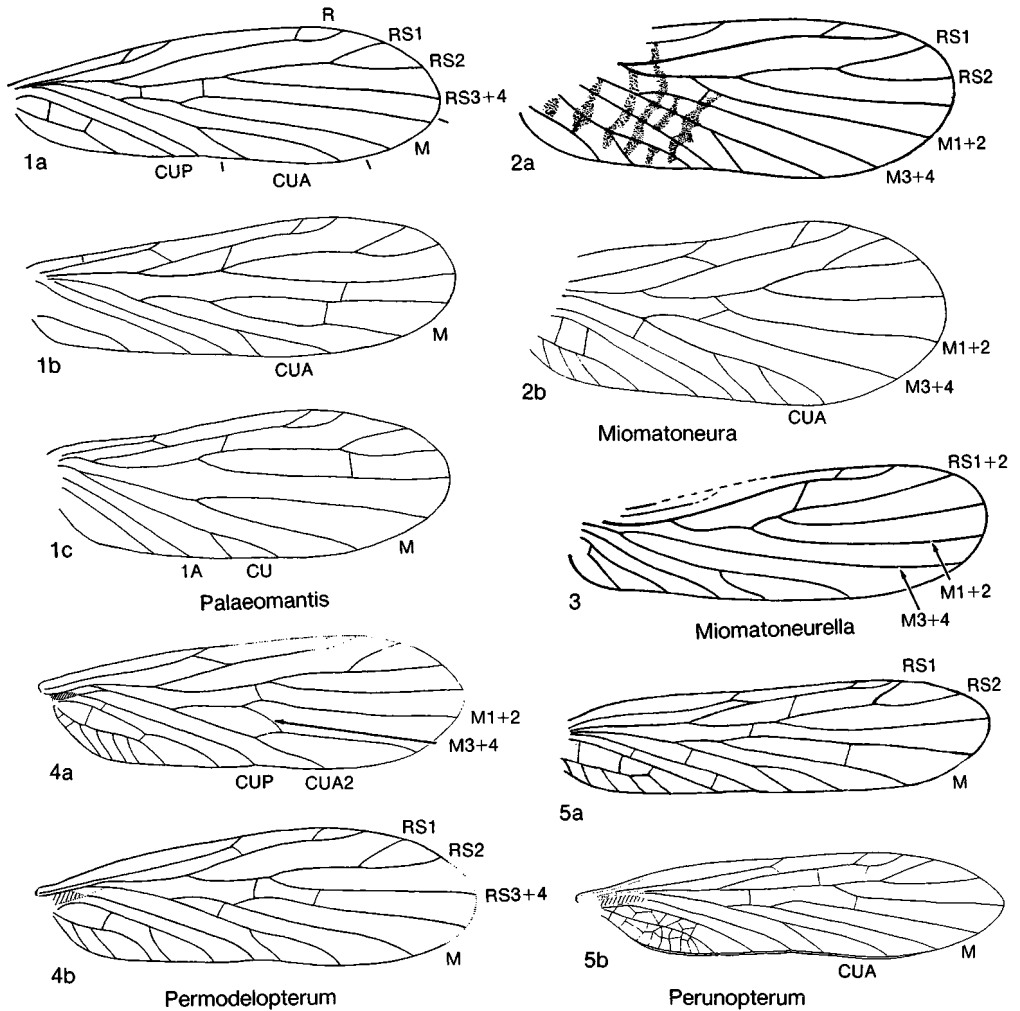


FIG. 131. Palaeomanteidae (p. 206–207).

mentation distinct; ovipositor present (Terebrantia) or absent (Tubulifera); cerci absent. *Perm.—Holo.*

The Thysanoptera, or thrips, feed by lacerating the surface of plants with their stylets and drawing the plant juices through the mouth cone. Some species are predaceous on small arthropods. The nymphs hatch from eggs laid on or in plant tissue; they resemble the adults in general form and feeding habits. Nymphs of most species pass through two or three quiescent stages (prepupa and pupa) in which wing pads occur.

The thrips, like the Psocoptera, are a dis-

trictive and homogeneous order of insects. Two suborders, Terebrantia and Tubulifera, are generally recognized; the most obvious differences between them are in the presence or absence of the ovipositor in the female, and in the shape of the terminal abdominal segment. However, other differences, of more phylogenetic significance, are found in the detailed structure of the mouthparts and wings. Such morphological evidence indicates that the Terebrantia are more primitive than the Tubulifera and that the family Aeolothripidae of the Terebrantia is the most primitive of the recent families.

Thysanoptera are well represented in the Tertiary deposits, mainly the Baltic amber; these Oligocene species have been studied in detail by two authorities on recent thrips, BAGNALL and PRIESNER. Two pre-Tertiary thrips have been described, one (*Liassothrips*) from the Jurassic (MARTYNOV, 1927b) and the other (*Permothrips*) from the Permian (MARTYNOV, 1935a). That these are thrips seems almost certain, although their subordinal positions are obscure. The fossil record of the Thysanoptera shows little to date about the evolution of the order. The Permian species appear to have had somewhat larger wings than any existing species, but no veins are preserved and the structure of the mouthparts is unknown. The classification used here is that of PRIESNER (1949).

Suborder TEREBRANTIA

Haliday, 1836

[Terebrantia HALIDAY, 1836, p. 439]

Terminal abdominal segment conical (rarely tubular) in females, bluntly rounded in male; female with sawlike ovipositor; fore wings nearly always with at least 1 longitudinal vein (in addition to costal vein) extending to apex. *Perm.—Holo.*

Family PERMOTHRIPIDAE

Martynov, 1935

[Permothripidae MARTYNOV, 1935a, p. 334]

Head somewhat extended; pronotum transverse; legs short, tibiae more slender than femora; wings broad and long, extending beyond abdomen; ovipositor apparently present. [Subordinal position of the family uncertain; it probably represents an extinct suborder.] *Perm.*

Permothrips MARTYNOV, 1935a, p. 334 [**P. longipennis*; OD]. Abdomen narrowed distally, not tubular. *Perm.*, USSR (Asian RSFSR).—FIG. 133, 5. **P. longipennis*; general form of body and wings, $\times 16$ (Martynov, 1935a).

Family AEOLOTHRIPIDAE Uzel, 1895

[Aeolothripidae UZEL, 1895, p. 42]

Wings broad and rounded at apex; ovipositor curved upward; antennae with 9 segments. *Eoc.—Holo.*

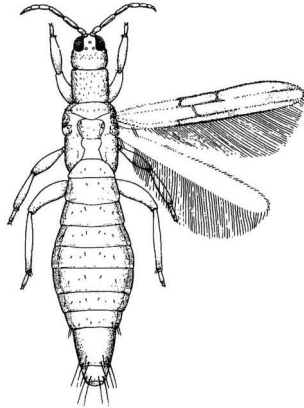


FIG. 132. Thysanoptera; dorsal view of whole insect, *Desmothrips propinquus*, Holocene, $\times 20$ (CSIRO, 1970).

Aeolothrips HALIDAY, 1836, p. 451. COCKERELL, 1917b; BAGNALL, 1924a; PRIESNER & QUIÉVREUX, 1935. *Oligo.*, England, Europe (France, Germany)—*Holo.*

Archanothrips PRIESNER, 1924, p. 132 [**A. pugionifer*; OD]. Similar to *Ankothrips* (recent), but hind angles of prothorax with short bristles; ninth antennal segment with 4 pale, transverse sutures. PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Eocranothrips BAGNALL, 1926, p. 17 [**Melanothrips annulicornis* BAGNALL, 1923, p. 36; OD]. Similar to *Cranothrips* (recent), but all antennal segments simple, without projections. PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Lithadothrips SCUDDER, 1875b, p. 221 [**L. vetusta*; OD]. Similar to *Orothrips* (recent), but fore wings widened toward apex. BAGNALL, 1924a; PRIESNER, 1949. *Eoc.*, USA (Utah); *Oligo.*, Europe (Germany).

Melanthrips HALIDAY, 1836, p. 450. SCUDDER, 1890. ?*Eoc.*, USA (Colorado)—*Holo.*

Palaeothrips SCUDDER, 1875b, p. 222 [**P. fossilis*; OD]. Apparently related to *Rhipidothrips* (recent); antennae with 7 segments, apical segments not conical. PRIESNER, 1949. *Eoc.*, USA (Utah).

Promelanthrips PRIESNER, 1930, p. 113 [**P. spiniger*; OD]. Similar to *Ankothrips* (recent), but hind angles of prothorax with one long bristle only. USINGER, 1942. *Oligo.*, Europe (Baltic).

Rhipidothripoides BAGNALL, 1923, p. 36 [**R. abdominalis*; OD]. Similar to *Rhipidothrips* (recent), but ninth segment of abdomen unusually elongate and third, fourth, and fifth antennal segments of about equal length. *Oligo.*, Europe (Baltic).

Stenurothrips BAGNALL, 1914, p. 483 [**S. succineus*; OD]. Ovipositor straight or nearly so; terminal abdominal segment tubular; setae of hind margin of fore wing wavy. [Family position

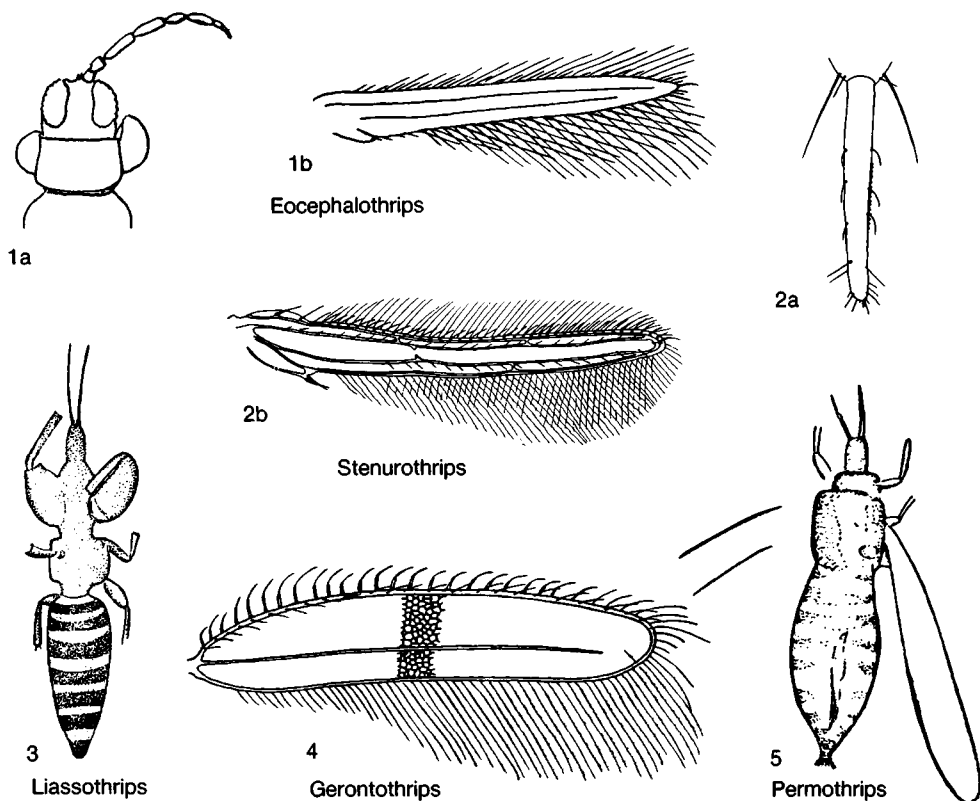


FIG. 133. Permothripidae, Aeolothripidae, Thripidae, Uncertain, and Liassothripidae (p. 209–212).

uncertain; possibly belonging to Heterothripidae.] BAGNALL, 1923; PRIESNER, 1949; STANNARD, 1956. *Oligo.*, Europe (Baltic).—FIG. 133,2. *S. bagnalli* STANNARD; *a*, terminal abdominal segment, $\times 66$; *b*, fore wing, $\times 55$ (Stannard, 1956).

Family THIRIPIDAE Stephens, 1829

[Thripidae STEPHENS, 1829b, p. 363]

Similar to Heterothripidae, but antennae with 6 to 9 segments and with slender sense cones; cones simple or forked; tarsal claws, if present, at apex of first or second tarsal segment. *Oligo.*—*Holo.*

Thrips LINNÉ, 1761, p. 266. *Holo.*

Amorphothrips BAGNALL, 1924c, p. 252 [**A. klebsi*; OD]. Similar to *Procerothrips*, but eye occupying whole side of head; pronotum transverse, without setae; hind legs very long and stout. BAGNALL, 1923; PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Anaphothrips UZEL, 1895, p. 142. PRIESNER, 1930; PALMER, 1957. *Oligo.*, Europe (Baltic); *Mio.*, USA (California)—*Holo.*

Frankliniella KARNY, 1910, p. 46. PRIESNER & QUIÉVREUX, 1935. *Oligo.*, Europe (France)—*Holo.*
Gerontothrips PRIESNER, 1949, p. 41, *nom. subst. pro Archaeothrips* PRIESNER, 1924, p. 138, *non* FIELD, 1910 [**Archaeothrips latipennis* PRIESNER, 1924, p. 138; OD]. Wings very broad, entire surface reticulate. PRIESNER, 1930. *Oligo.*, Europe (Baltic).—FIG. 133,4. **G. latipennis* (PRIESNER); fore wing, $\times 66$ (Priesner, 1924).

Heliothrips HALIDAY, 1836, p. 443. BAGNALL, 1924b. *Oligo.*, Europe (Baltic)—*Holo.*

Hercinothrips BAGNALL, 1932, p. 506. STANNARD, 1956. *Oligo.*, Europe (Baltic)—*Holo.*

Homothrips BAGNALL, 1915, p. 588. BAGNALL, 1924b. *Oligo.*, Europe (Baltic)—*Holo.*

Lipsanothrips PRIESNER, 1930, p. 119 [**L. skewarvae*; OD]. Antennae with 8 segments, sixth segment much shorter than fifth; wing with 1 or 2 longitudinal veins. *Oligo.*, Europe (Baltic).

Oxythrips UZEL, 1895, p. 141. PRIESNER, 1924, 1930. *Oligo.*, Europe (Baltic)—*Holo.*

Praedendrothrips PRIESNER, 1924, p. 139 [**P. avus*; OD]. Antennae with 9 segments, last 4 clearly separate from one another; posterior angles of

pronotum with at least 1 conspicuous bristle. PRIESNER, 1930. *Oligo.*, Europe (Baltic).

Procerothrips BAGNALL, 1924c, p. 252 [**P. cylindricornis*; OD]. Antennae with 8 segments and style with 2 segments; third through sixth antennal segments with parallel sides and of same width. BAGNALL, 1923. *Oligo.*, Europe (Baltic).

Selenothrips KARNY, 1911, p. 180. BAGNALL, 1923. *Oligo.*, Europe (Baltic)—*Holo.*

Taeniothrips SERVILLE, 1843, p. 644. BAGNALL, 1924b; PRIESNER, 1930, 1949. *Oligo.*, Europe (Baltic)—*Holo.*

Telothrips PRIESNER, 1930, p. 116 [**T. klebsi*; OD]. Similar to *Praedendrotthrips* but with sixth antennal segment large and stout and seventh, eighth, and ninth segments minute. PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Family HETEROTHRIPIDAE

Bagnall, 1912

[Heterothripidae BAGNALL, 1912, p. 222] [=Hemithripidae BAGNALL, 1923, p. 37; Stenurothripidae BAGNALL, 1923, p. 37; Opadothripidae BAGNALL, 1927, p. 562]

Wings narrow, usually pointed distally; ovipositor curved downward; antennae with 9 or 10 segments; fore tarsi usually with clawlike appendage at base of second segment. *Oligo.*—*Holo.*

Heterothrips HOOD, 1908, p. 361. *Holo.*

Electrothrips BAGNALL, 1924c, p. 251 [**E. bystrix*; OD]. Cephalic, pronotal, and wing bristles abnormally long and stout; wings and legs long and slender. *Oligo.*, Europe (Baltic).

Hemithrips BAGNALL, 1923, p. 37 [**H. femoralis*; OD]. Similar to *Heterothrips* (recent), but third and fourth antennal segments cylindrical. BAGNALL, 1924a; PRIESNER, 1949. *Oligo.*, Europe (Baltic, Germany).

Opadothrips PRIESNER, 1924, p. 133 [**O. fritschianus*; OD]. Similar to *Oligothrips* (recent), but antennal segments more elongate; terminal segment slender. BAGNALL, 1924a, 1927; PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Family MEROTHRIPIDAE

Hood, 1914

[Merothripidae HOOD, 1914, p. 17]

Wings narrow, pointed distally, surface smooth (not pubescent); ovipositor curved downward; pronotum with dorsal longitudinal sutures; anterior and posterior femora greatly enlarged. *Oligo.*—*Holo.*

Merothrips ZIMMERMANN, 1900, p. 12. Antennae with 8 segments. PRIESNER, 1924. *Oligo.*, Europe (Baltic)—*Holo.*

Praemerothrips PRIESNER, 1930, p. 130 [**P. boodi*; OD]. Antennae with 9 segments. PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Family UNCERTAIN

The following genera, apparently belonging to the order Thysanoptera, suborder Terebrantia, are too poorly known to permit assignment to families.

Calothrips OUSTALET, 1873, p. 24 [**C. scudderii*; OD]. Little-known thysanopteron, probably belonging to the Terebrantia. *Oligo.*, Europe (France).

Eucephalothrips BAGNALL, 1924a, p. 161 [**Thrips capito* SCHLECHTENDAL, 1887, p. 579; OD] [=Protothrips PRIESNER, 1924, p. 136 (type, *P. speratus*)]. Head quadrate; wings moderately broad, apex pointed. PRIESNER, 1949. *Oligo.*, Europe (Baltic).—FIG. 133, 1. *E. speratus* (PRIESNER); *a*, head and prothorax; $\times 66$; *b*, fore wing, $\times 66$ (Priesner, 1924).

Suborder TUBULIFERA

Haliday, 1836

[Tubulifera HALIDAY, 1836, p. 459]

Terminal abdominal segments of both sexes almost always tubular; female without ovipositor; fore wing without definite costal vein and with only a vestige of another longitudinal vein, long fringe present. *Oligo.*—*Holo.*

Family PHLAEOTHRIPIDAE

Uzel, 1895

[Phlaeothripidae UZEL, 1895, p. 42]

Characteristics of suborder. *Oligo.*—*Holo.*

Phlaeothrips HALIDAY, 1836, p. 441. SCHLECHTENDAL, 1887; BAGNALL, 1924a, 1929. *Oligo.*, Europe (Baltic)—*Holo.*

Cephenothrips PRIESNER, 1930, p. 135 [**C. laticeps*; OD]. Similar to *Pygidothrips* (recent), but wing bristles short and knobbed. USINGER, 1942; PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Hoplothrips AMYOT & SERVILLE, 1843, p. 640. BAGNALL, 1929; PRIESNER, 1949. *Oligo.*, Europe (Baltic)—*Holo.*

Liotrichothrips BAGNALL, 1929, p. 97 [**L. bystrix*; OD]. Head longer than pronotum, broader than long; cheeks with few prominent setae; antennae long, with third and fourth segments subequal. Similar to *Ethirothrips* (recent), but legs as in *Liothrips* (recent). PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Necrothrips PRIESNER, 1924, p. 147 [**N. nanus*;

- OD]. Similar to *Austrothrips* (recent), but eyes very large, protruding, and consisting of many facets. USINGER, 1942; PRIESNER, 1949. *Oligo.*, Europe (Baltic).
- Proleuwenia** PRIESNER, 1924, p. 148 [**P. succini*; OD]. Wings reduced (female); similar to *Idiothrips* (recent), but antennae with 8 segments. USINGER, 1942; PRIESNER, 1949. *Oligo.*, Europe (Baltic).
- Schlechtendalia** BAGNALL, 1929, p. 96 [**S. longitubus*; OD]. Similar to *Pblaeothrips*, but tenth abdominal segment substantially longer than head; fifth antennal segment with a projection; wing bristles blunt. PRIESNER, 1949. *Oligo.*, Europe (Baltic).
- Symphiothrips** HOOD & WILLIAMS, 1915, p. 131. PRIESNER, 1924, 1949. *Oligo.*, Europe (Baltic)—*Holo.*
- Treherniella** WATSON, 1923, p. 81. PRIESNER, 1930, 1949. *Oligo.*, Europe (Baltic)—*Holo.*

Suborder UNCERTAIN

The genus described below, apparently belonging to the order Thysanoptera, is too poorly known to permit assignment to suborders.

Family LIASSOTHRIPIDAE Priesner, 1949

[Liassothripidae PRIESNER, 1949, p. 34] [=Mesothripidae MARTYNOV, 1927b, p. 768]

Antennae thin, with at least 7 segments; head narrow; anterior femora very broad; wings unknown. *Jur.*

Liassothrips PRIESNER, 1949, p. 34, *nom. subst. pro Mesothrips* MARTYNOV, 1927b, p. 768, *non* ZIMMERMANN, 1900 [**Mesothrips crassipes* MARTYNOV, 1927b, p. 768; OD]. Little-known thysanopteron; abdomen apparently constricted basally. *Jur.*, USSR (Kazakh).—FIG. 133,3. **L. crassipes* (MARTYNOV); body, $\times 16$ (Martynov, 1927b).

HEMIPTEROID EXOPTERYGOTES

Order HEMIPTERA Linné, 1758

[Hemiptera LINNÉ, 1758, p. 434] [=Hemipsocoptera ZALESSKY, 1937e, p. 51; Palaeohemiptera HANDLIRSCH, 1904b, p. 2]

Exopterygote Neoptera, mostly small to very small, with much morphological diversity. Head opisthognathous or prognathous; compound eyes usually present but diverse

in size; two ocelli commonly present, rarely three or none; antennae typically with five segments or less, rarely with as many as ten; mouthparts haustellate, consisting of two pairs of maxillary stylets in a segmented, rostrate labium. Pronotum of moderate size, often diversely modified; meso- and metathorax well developed. Legs usually cursorial, but forelegs of some genera raptorial, vestigial, or absent; tarsi commonly with three segments, rarely with two or one. Wings usually present, but very different in the two suborders. Wing venation quite generalized in primitive forms but much reduced in most families; fore wings of suborder Homoptera usually of uniform texture, those of suborder Heteroptera partly membranous and partly coriaceous. Abdomen well developed; ovipositor usually present. Nymphs resembling adults in basic body structure. *Perm.—Holo.*

This is the largest of the exopterygote orders, and it has apparently been a major order at least since the Triassic. All available evidence suggests that the Hemiptera are most closely related to the Psocoptera, which were well represented in the Permian. The order Hemiptera has traditionally been divided into two suborders, Homoptera and Heteroptera, the members of both groups having the same distinctive, haustellate mouthparts. Both suborders are also represented in the Permian, but the Homoptera have by far the more extensive record in that period.

The wings provide the best means of distinguishing the members of the two suborders. The homologies of the main veins are clear throughout both suborders, even in those in which the venation is much reduced. However, there has been much convergence in the reduction process. In part because of this, the family and generic classifications of the Hemiptera, especially of the Homoptera, have been based mainly on body features, such as the detailed structure of the rostrum, number and size of ocelli, tarsal segmentation, and integumentary details. Since fossils do not usually show such structures, the family position of many of the extinct genera is uncertain.

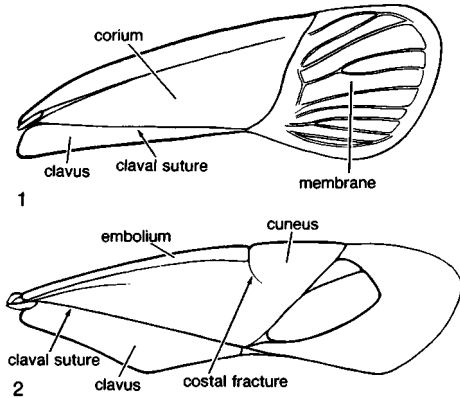


FIG. 134. Hemiptera; wing structure of the suborder Heteroptera. —1. *Nazara* sp., Pentatomidae. (adapted from CSIRO, 1970). —2. *Megacoelum* sp., Miridae (adapted from CSIRO, 1970).

The fore wings of the two suborders, except for a few primitive families in each one, differ mainly in texture. Those of the Homoptera are usually of a uniform or nearly uniform texture. Exceptions are found in a few primitive families, such as the Palaeontinidae and Prosbolidae, in which the fore wing is partly divided into two areas by an irregular nodal line (see Figs. 137,1 and 139,4a). The proximal area is usually more coriaceous than the distal part. A slight break (costal break or indentation) in the costal margin appears to be functionally associated with the nodal line. The anal area, commonly termed the clavus in the Hemiptera, is usually a distinct region of the fore wing. The fore wings of the Heteroptera, usually termed hemelytra, have a more complex structure. The distal portion of the wing is membranous, but the proximal part is coriaceous, consisting of a large, anterior, triangular section (corium) and a relatively small region (clavus), separated from the corium by the claval suture (Fig. 134,1). These areas are diverse in form and size in families and genera. The costal area of the corium may be separated from the rest of it by vein M+R, forming the embolium; and a more distal part (cuneus) of the corium may be separated by a costal fracture (Fig. 134,2). The hind wings of the Hemiptera

are generally more specialized than the fore pair, often with a very different shape. Polymorphism of wings, including aptery, occurs commonly in the order.

The great majority of the Hemiptera are phytophagous, but some Heteroptera are active predators. Immature stages have essentially the same feeding habits as the adults.

The geological record of the Hemiptera is very extensive, including almost a hundred families, two-thirds of which are Homoptera. A surprisingly large number of entomologists, specialists on the systematics of existing Hemiptera, have contributed to our knowledge of this fossil record and of the phylogeny of the order. There is, however, much difference of opinion among them about the systematic position of many of the extinct genera.

Suborder HOMOPTERA

Leach, 1815

[Homoptera LEACH, 1815, p. 124]

Fore wing of uniform texture or nearly so, not sharply differentiated into membranous and coriaceous areas; wings typically held sloping over the sides of the body at rest. *Perm.—Holo.*

Family DUNSTANIIDAE

Tillyard, 1916

[Dunstaniidae TILLYARD in TILLYARD & DUNSTAN, 1916, p. 31]

Fore wing sharply separated into tegminous basal part and membranous distal area; nodal break prominent; vein SC long, terminating on costal margin; R and RS curved; RS unbranched; clavus broad, triangular; 1A and 2A long, extending to hind margin. Hind wing little known, smaller than fore wing, with rounded anal area. Head, compound eyes, and pronotum relatively large. Relatively large insects. Affinities uncertain, but apparently closely related to the Palaeontinidae. TILLYARD, 1918d; BECKER-MIGDISOVA, 1949b; EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965; RIEK, 1976b. *Trias.*

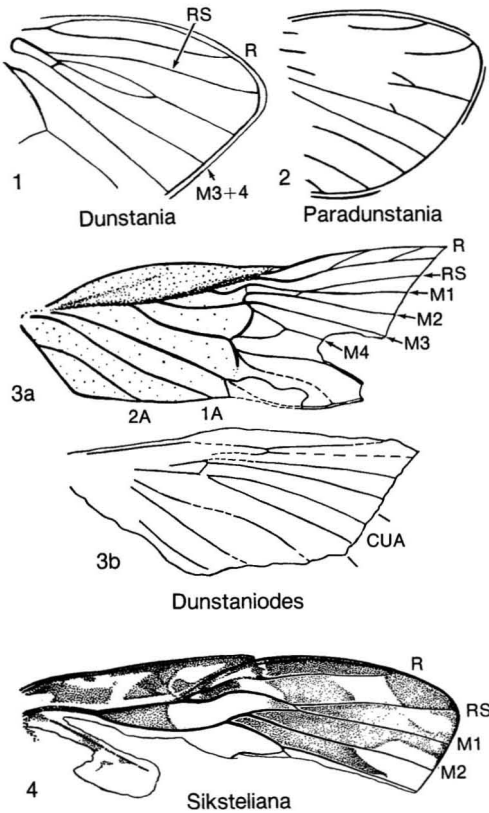


FIG. 135. Dunstaniidae (p. 214).

Dunstania TILLYARD in TILLYARD & DUNSTAN, 1916, p. 31 [**D. pulchra*; OD]. M3+4 not forked, RS apparently joined to M by a short, oblique crossvein. [The genus has been reported from South Africa (RIEK, 1976b), but the generic position of the species described is very uncertain.] *Trias.*, Australia (Queensland).—FIG. 135,1. **D. pulchra*; fore wing as preserved, $\times 1.5$ (Evans, 1956).

Dunstaniodes BECKER-MIGDISOVA & WOOTTON, 1965, p. 64 [**D. elongatus*; OD]. Fore wing elongate; costal margin of basal half of wing strongly convex. *Trias.*, USSR (Kirghiz).—FIG. 135,3. **D. elongatus*; a, fore and b, hind wings as preserved, $\times 3.0$ (Becker-Migdisova & Wootton, 1965).

Dunstaniopsis TILLYARD, 1918d, p. 584 [**D. triassica*; OD]. Little-known genus, based on incomplete fore wing; apex apparently more pointed than in *Dunstania*. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Trias.*, Australia (Queensland).

Paradunstania TILLYARD, 1918d, p. 585 [**P. affinis*; OD]. Little-known genus, based on fragment of fore wing; probably a synonym of *Dunstania*. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON,

1965. *Trias.*, Australia (Queensland).—FIG. 135,2. **P. affinis*; fore wing as preserved, $\times 1.5$ (Evans, 1956).

Siksteliiana BECKER-MIGDISOVA & WOOTTON, 1965, p. 68 [**S. popovi*; OD]. Little-known genus, based on fore wing. Similar to *Dunstaniodes*, but costal margin of basal half nearly straight. *Trias.*, USSR (Kirghiz).—FIG. 135,4. **S. popovi*; fore wing, $\times 3$ (Becker-Migdisova & Wootton, 1965).

Family PALAEONTINIDAE Handlirsch, 1906

[Palaeontinidae HANDLIRSCH, 1906b, p. 618] [=Cicadomorphae EVANS, 1956, p. 222]

Fore wing as in Dunstaniidae, with membranous, distal part of wing broader and longer than basal, tegminous part; vein SC usually weakly developed, commonly with branches or suggestions of branches; R and M separating before or close to midwing; R and RS nearly straight. Hind wing with a prominent indentation on costal margin; M1 commonly coalesced for short interval with RS; M with 4 branches. Head small, narrow, pronotum wide; body generally with numerous hairs. *Perm.*—*Jur.*

Palaeontina BUTLER, 1873, p. 126 [**P. oolitica*; OD]. Little-known genus, based on fore wing. M with 4 branches, M1+2 and M3+4 forking at about same level. [The genus was excluded from Homoptera by EVANS (1956) but included here by BECKER-MIGDISOVA (1962b) and POPOV (1980b).] *Jur.*, England.—FIG. 136,1. **P. oolitica*; fore wing, $\times 0.8$ (Handlirsch, 1906b).

Asiocossus BECKER-MIGDISOVA, 1962a, p. 89 [**A. subcostalis*; OD]. Little-known genus, based on fragment of fore wing. SC free from R+M except for very base, branched; R+M and stem of R very short. *Trias.*, USSR (Kirghiz).—FIG. 136,3. **A. subcostalis*; fore wing base, $\times 2.5$ (Becker-Migdisova, 1962b).

Cicadomorpha MARTYNOV, 1926b, p. 1357 [**C. punctulata*; OD]. SC coalesced with R+M at base; area between M and CUA very broad, without crossveins; CU slightly arched at base. *Jur.*, USSR (Kazakh).—FIG. 136,7. **C. punctulata*; fore wing, $\times 1.0$ (Becker-Migdisova, 1962b).

Fletcheriana EVANS, 1956, p. 224 [**F. triassica*; OD]. Fore wing as in *Pseudocossus*, but costal area much broader; SC lying alongside R basally; RS arising from R remote from wing base. [The assignment of a species from the Triassic of South Africa (RIEK, 1976b) to this genus is very uncertain.] *Trias.*, Australia (New South Wales).—FIG. 136,2. **F. triassica*; a, fore wing; b, hind wing, $\times 1.0$ (Evans, 1956).

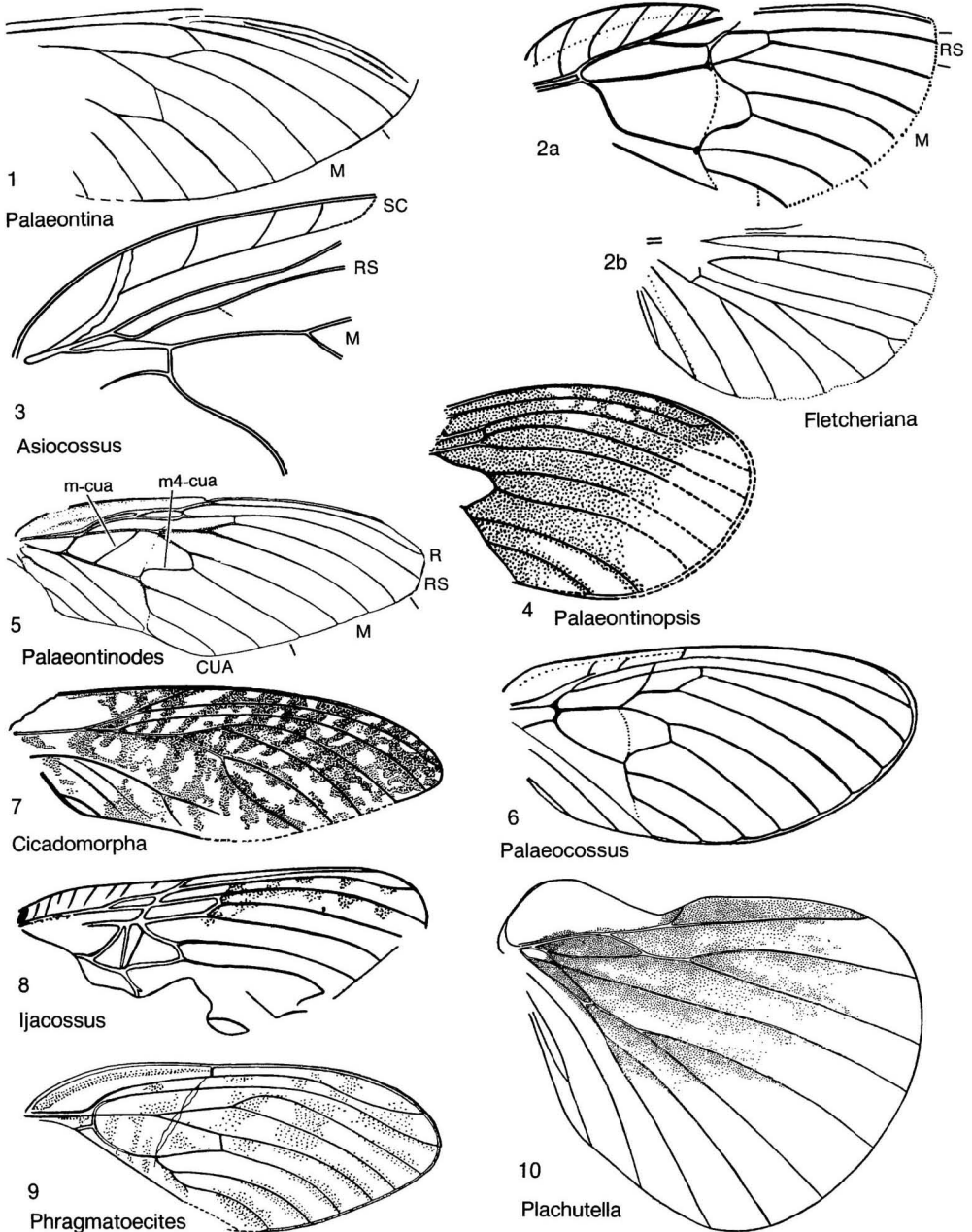


FIG. 136. Palaeontinidae (p. 214–216).

Ijacossus BECKER-MIGDISOVA, 1950, p. 1106 [*I. suchanovae*; OD]. Little-known genus, based on fore wing. Similar to *Palaeontinodes*, but SC with several branches. [Family assignment uncertain.] *Jur.*, USSR (Asian RSFSR).—FIG. 136, 8. *I. suchanovae*; fore wing, $\times 1$ (Becker-Migdisova, 1962b).

Palaeocicadopsis T'AN, 1980, p. 161 [**P. chinensis*; OD]. Fore wing similar to that of *Cicadomorpha*, but M branching near wing base. *Perm.*, China (Inner Mongolia).

Palaeocossus OPPENHEIM, 1885, p. 333 [**P. jurassicus*; OD]. Fore wing without nodal indentation; wing broadly oval; distal margin of basal median

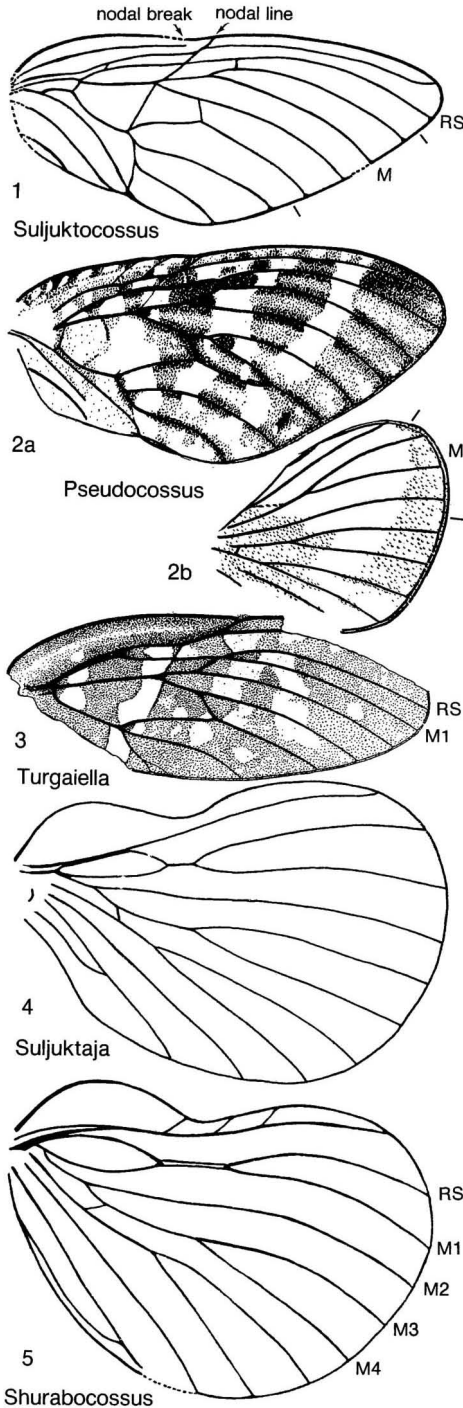


FIG. 137. Palaeontinidae (p. 216–217).

cell (between M and CUA) smoothly curved; hind margin strongly convex. *Jur.*, USSR (Asian RSFSR).—FIG. 136,6. **P. jurassicus*; fore wing, $\times 1.5$ (Evans, 1956).

Palaeontinodes MARTYNOV, 1937a, p. 166 [**P. shabarovi*; OD]. Fore wing triangular; costal indentation weak; SC without branches; crossvein m-cua long; basal median cell divided by crossveins (not shown in figure). BECKER-MIGDISOVA, 1949b; EVANS, 1956. *Jur.*, USSR (Tadzhik, Asian RSFSR).—FIG. 136,5. *P. angarensis* BECKER-MIGDISOVA & WOOTTON; fore wing, $\times 1$ (Becker-Migdisova & Wootton, 1965).

Palaeontinopsis MARTYNOV, 1937a, p. 167 [**P. latipennis*; OD]. Little-known genus. Fore wing apparently oval and with rounded apex. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Tadzhik).—FIG. 136,4. **P. latipennis*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Phragmatocites OPPENHEIM, 1885, p. 333 [**P. damesi*; OD]. Fore wing with costal margin straight or only slightly curved; nodal indentation weak. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Asian RSFSR).—FIG. 136,9. **P. damesi*; fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).

Plachutella BECKER-MIGDISOVA, 1949b, p. 11 [**P. rotundata*; OD]. Little-known genus, based on hind wing. M2 close to M3+4 at one point but not coalesced with it. BECKER-MIGDISOVA, 1950; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Kazakh, Tadzhik).—FIG. 136,10. **P. rotundata*; hind wing, $\times 2.5$ (Becker-Migdisova, 1949b).

Pseudocossus MARTYNOV, 1931d, p. 94 [**P. zemcuznicovi*; OD]. Fore wing triangular, with pronounced indentation of costal margin at nodal break; SC free from R+M at base, branched; RS arising from R near wing base; distinct bands of coloration. Hind wing rounded, much smaller than fore wing. *Jur.*, USSR (Asian RSFSR, Kazakh).—FIG. 137,2. *P. turgaiensis* BECKER-MIGDISOVA & WOOTTON, Kazakh; a, fore and b, hind wings, $\times 1.5$ (Becker-Migdisova & Wootton, 1965).

Shurabocossus BECKER-MIGDISOVA, 1949b, p. 15 [**S. gigas*; OD]. Hind wing similar to that of *Plachutella*, but M2 coalesced with M3+4 for a considerable interval before separating. *Jur.*, USSR (Tadzhik).—FIG. 137,5. **S. gigas*; hind wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Suljuktaja BECKER-MIGDISOVA, 1949b, p. 17 [**S. turkestanensis*; OD]. Hind wing as in *Shurabocossus* but with the coalesced parts of 1A and 2A at least as long as the free portions. *Jur.*, USSR (Kirghiz).—FIG. 137,4. **S. turkestanensis*; hind wing, $\times 2$ (Becker-Migdisova, 1962b).

Suljuktocossus BECKER-MIGDISOVA, 1949b, p. 8 [**S.*

prosboloides; OD]. Fore wing as in *Phragma-toectites* but more nearly triangular and with apex nearly pointed. *Jur.*, USSR (Kirghiz).—FIG. 137,1. **S. prosboloides*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Turgaiella BECKER-MIGDISOVA & WOOTTON, 1965, p. 70 [**T. pomerantsevae*; OD]. Fore wing as in *Palaeontinodes*, but wing oval and basal median cell not divided by crossveins; crossvein m4-cua very short. *Jur.*, USSR (Kazakh).—FIG. 137,3. **T. pomerantsevae*; fore wing, $\times 1.5$ (Becker-Migdisova & Wootton, 1965).

Family MESOGEREONIDAE Tillyard, 1921b

[Mesogereonidae TILLYARD, 1921b, p. 272]

Fore wing slender, with well-developed submarginal (ambient) vein and coriaceous border; veins SC and R close together and to costal margin; RS arising before fork of M1 + 2; crossvein m4-cua near wing base and almost longitudinal in position. Hind wing little known, much smaller than fore wing. Body structure unknown. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Trias.*

Mesogereon TILLYARD in TILLYARD & DUNSTAN, 1916, p. 33 [**M. neuropunctatum*; OD]. RS joined to M1 by a short crossvein; M3 + 4 forking more basally than M1 + 2. *Trias.*, Australia (New South Wales).—FIG. 138,1a. *M. superbum* TILLYARD; fore wing, $\times 1.2$ (Evans, 1956).—FIG. 138,1b. *M. shepherdii* TILLYARD; hind wing, $\times 1.2$ (Evans, 1956).

Triassogereon RIEK, 1976b, p. 808 [**T. distinctum*; OD]. Fore wing as in *Mesogereon*, but fork of M3 + 4 close to fork of M1 + 2. *Trias.*, South Africa.—FIG. 138,2. **T. distinctum*; fore wing, $\times 1.6$ (Riek, 1976b).

Family PROSBOLIDAE Handlirsch, 1906

[Prosbolidae HANDLIRSCH, 1906b, p. 390 [=Sojaneuridae BECKER-MIGDISOVA, 1946, p. 730]

Fore wing: distal part commonly membranous; costal area broad; vein SC usually forming an anterior branch submarginal to costal margin and more rarely an indistinct, short branch that parallels R + M and even part of R; forks of M and CUA usually shallow. Hind wing: costal margin usually deeply excised near middle, convex basally and dis-

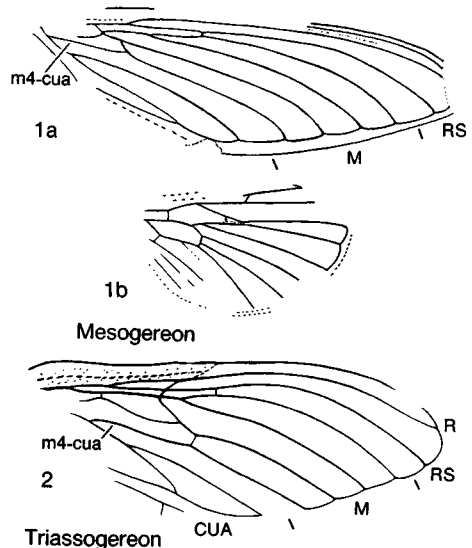


FIG. 138. Mesogereonidae (p. 217).

tally; anal region extended posteriorly. Body structure unknown. BECKER-MIGDISOVA, 1940, 1947, 1962b; EVANS, 1956. *Perm.*—*Trias.*

Prosbolole HANDLIRSCH, 1904b, p. 2 [**P. hirsuta*; OD] [=*Prosbolina* HANDLIRSCH, 1937, p. 132 (type, *Prosbolole biexcisa* MARTYNOV, 1928b, p. 7)]. Fore wing: nodal break and nodal line present; R, M, and CUA dividing at about same level. Hind wing: M with at least 4 branches. *Perm.*, USSR (European and Asian RSFSR).—FIG. 139,4a. **P. hirsuta*; fore wing, $\times 1.6$ (Evans, 1956).—FIG. 139,4b. *P. reducta* MARTYNOV; fore wing, $\times 3.5$ (Becker-Migdisova, 1940).—FIG. 139,4c. *P. breviata* BECKER-MIGDISOVA; hind wing, $\times 2.6$ (Becker-Migdisova, 1940).

Austroprosbolole EVANS, 1943b, p. 181 [**A. maculata*; OD]. Fore wing with nodal break and nodal line; RS curved posteriorly, touching M1 + 2 at point of fork; CUA with a shallow, distal fork. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 139,5. **A. maculata*; fore wing, $\times 4$ (Evans, 1943b).

Austroprosboloides RIEK, 1973, p. 527 [**A. vandijki*; OD]. Little-known genus; fore wing similar to *Austroprosbolole*, but RS touching M1 beyond fork and M3 + 4 connected to CUA distally. RIEK, 1976a. *Perm.*, South Africa.—FIG. 140,6. **A. vandijki*; fore wing, $\times 4$ (Riek, 1973).

Beaufortiscus RIEK, 1976a, p. 779 [**B. dixi*; OD]. Fore wing very similar to that of *Prosbolole*; anal

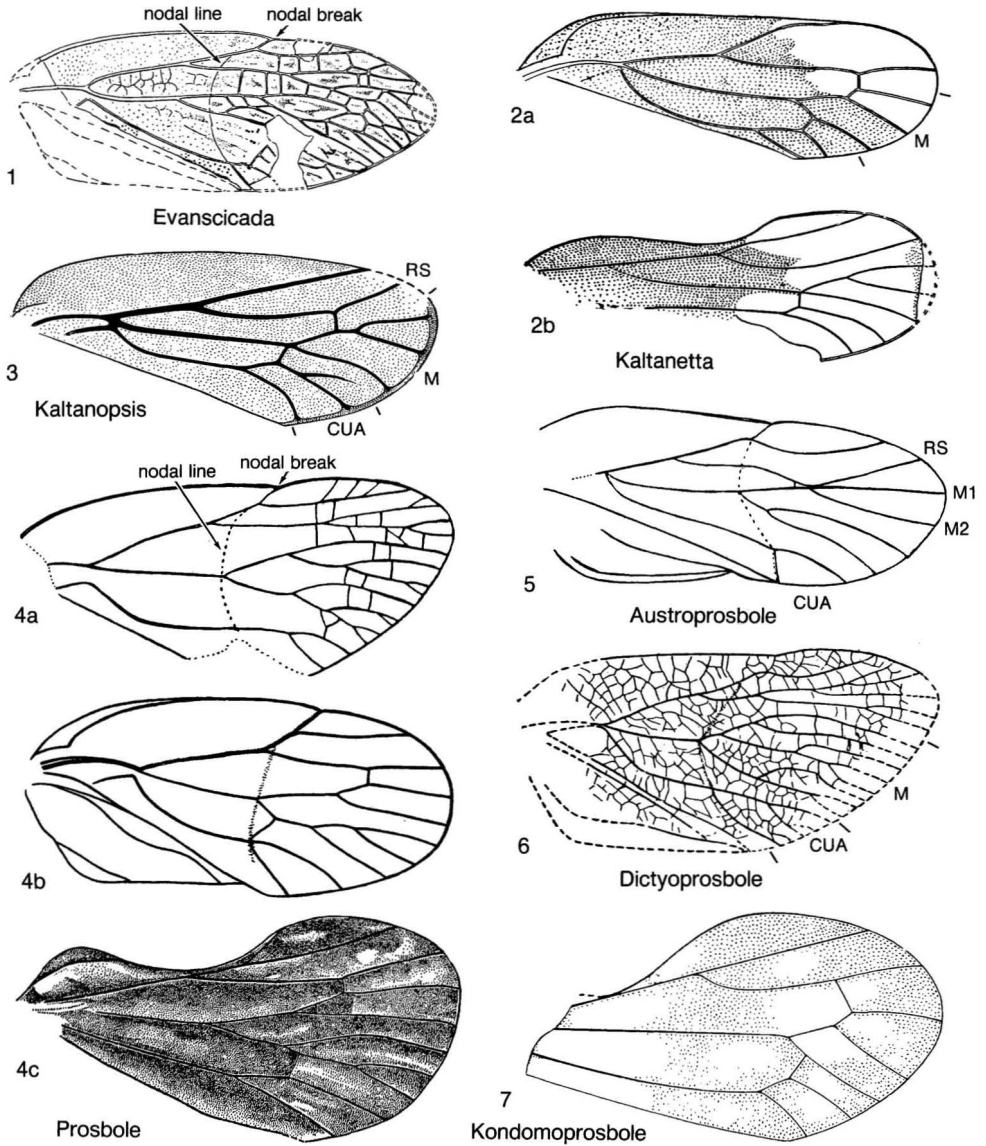


FIG. 139. Prosbolidae (p. 217–220).

area with 3 veins. [Probably a synonym of *Prosbole*.] *Perm.*, South Africa.
Dictyoprosbole MARTYNOV, 1935d, p. 443 [**D. membranosa*; OD]. Fore wing membranous, covered with a network of crossveins; M and CUA dividing at level of origin of RS; RS, M, and CUA with branching as in *Orthoprosbole*. EVANS, 1956. *Perm.*, USSR (Asian RSFSR). —FIG. 139,6. **D. membranosa*; fore wing, $\times 1.5$ (Becker-Migdisova, 1960).
Evanscicada BECKER-MIGDISOVA, 1962b, p. 170,

nom. subst. pro Evansia BECKER-MIGDISOVA, 1961c, p. 323, non CAMBRIDGE, 1900 [**Evansia speciosa* BECKER-MIGDISOVA, 1961c, p. 323; OD]. Fore wing narrow; basal part tegminous; RS arising at level of forking of M; numerous crossveins distally and indication of network near basal-central part of wing. *Perm.*, USSR (Asian RSFSR). —FIG. 139,1. **E. speciosa*; fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).

Falsia BECKER-MIGDISOVA, 1946, p. 750 [**F. chimaera*; OD]. Similar to *Sojanoneura*, but first

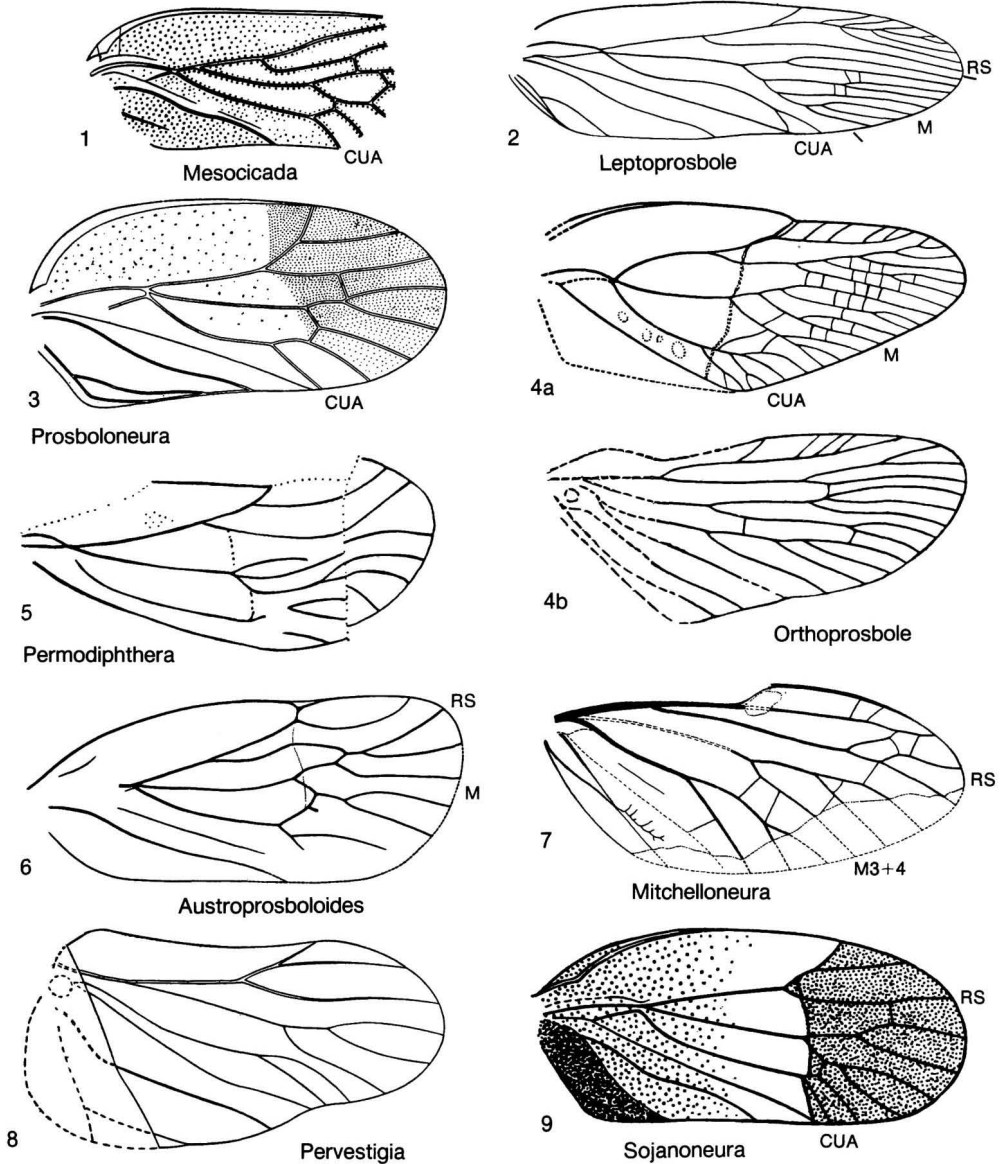


FIG. 140. Prosbolidae (p. 217–221).

and second tarsal segments of same size. BECKER-MIGDISOVA, 1946. *Perm.*, USSR (European RSFSR).

Kaltanetta BECKER-MIGDISOVA, 1961c, p. 303 [**K. nigra*; OD]. Fore wing slender, apex symmetrically curved; RS arising well before level of forking of M and of CUA; M with 3 branches. Hind wing slender distally; marginal indentation deep and wide; M with 3 branches. *Perm.*, USSR (Asian RSFSR).—FIG. 139,2. **K. nigra*; a,

fore and b, hind wings, $\times 6.5$ (Becker-Migdisova, 1961c).

Kaltanopsis BECKER-MIGDISOVA, 1961c, p. 300 [**K. ornata*; OD]. Fore wing similar to that of *Kaltanetta*, but costal margin strongly curved and R continuing in a straight line from its stem; longitudinal veins unusually thick. *Perm.*, USSR (Asian RSFSR).—FIG. 139,3. **K. ornata*; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Kondomoprosbole BECKER-MIGDISOVA, 1961c, p.

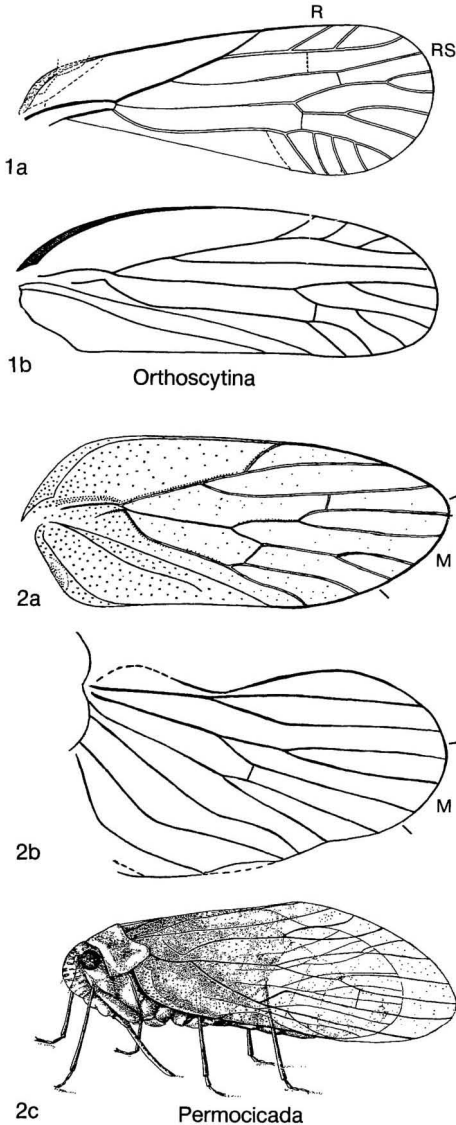


FIG. 141. Prosboldidae (p. 220).

315 [**K. pictata*; OD]. Hind wing: anterior margin with prominent bulge distally; R a straight continuation of stem R; M with 3 short branches. *Perm.*, USSR (Asian RSFSR).—FIG. 139,7. **K. pictata*; hind wing, $\times 8.5$ (Becker-Migdisova, 1962b).

Leptoprosbole RIEK, 1976b, p. 812 [**L. lepida*; OD]. Fore wing elongate; M with 8 terminal branches. [Family assignment doubtful.] *Trias.*, South Africa.—FIG. 140,2. **L. lepida*; fore wing, $\times 1.5$ (Riek, 1976b).

Mesocicada BECKER-MIGDISOVA, 1962a, p. 90 [**M.*

verrucosa; OD]. Little-known fore wing; nodal break absent; M with 4 branches; CUA with small fork. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).—FIG. 140,1. **M. verrucosa*; fore wing, $\times 14$ (Becker-Migdisova, 1962a).

Mitchelloneura TILLYARD, 1921c, p. 414 [**M. permiana*; OD]. Little-known hind wing; RS with irregular distal branches; M with M1, M2, and M3+4; CUA deeply forked. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 140,7. **M. permiana*; hind wing, $\times 3.2$ (Tillyard, 1921c).

Neurobole RIEK, 1976a, p. 779 [**N. ramosa*; OD]. Little-known genus, based on small apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa.

Orthoprosbole MARTYNOV, 1935d, p. 445 [**O. congesta*; OD]. Fore wing strongly narrowed in distal half; RS and M with numerous branches; nodal break prominent. Hind wing little known; distal part elongate; M and CUA with numerous branches. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 140,4a. *O. triangularis* (MARTYNOV); fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).—FIG. 140,4b. **O. congesta*; hind wing, $\times 3.5$ (Becker-Migdisova, 1962b).

Orthoscytina TILLYARD, 1926a, p. 9 [**O. mitchelli*; OD]. Fore wing slender, oval; anal area long; RS arising just before midwing; M and CUA forked at distal third of wing; R with several oblique branches to costal margin. Hind wing little known. EVANS, 1956; RIEK, 1976a. *Perm.*, Australia (New South Wales), Africa (South Africa), USSR (Asian RSFSR).—FIG. 141,1a. **O. mitchelli*, Australia; fore wing, $\times 6$ (Tillyard, 1926a).—FIG. 141,1b. *O. suchovi* BECKER-MIGDISOVA, USSR; fore wing, $\times 6$ (Becker-Migdisova, 1961c).

Permocicada MARTYNOV, 1928b, p. 19 [**P. umbrata*; SD BECKER-MIGDISOVA, 1940, p. 29] [= *Permocicadopsis* BECKER-MIGDISOVA, 1940, p. 54 (type, *Permocicada angusta* MARTYNOV, 1935c, p. 15)]. Fore wing with weak venation; RS arising before forking of M and CUA; M with 3 or 4 branches. Hind wing with deeply indented costal margin having nearly symmetrical slopes. ZALESSKY, 1929, 1932b; EVANS, 1956; BECKER-MIGDISOVA, 1961c, 1962b. *Perm.*, USSR (European and Asian RSFSR).—FIG. 141,2. *P. integra* BECKER-MIGDISOVA; a, fore wing, $\times 4$; b, hind wing, $\times 4$; c, reconstruction, $\times 3$ (Becker-Migdisova, 1940).

Permodiphthera TILLYARD, 1926a, p. 24 [**P. robusta*; OD]. Little-known genus. Fore wing with RS unbranched; branches of M apparently strongly curved. *Perm.*, Australia (New South Wales).—FIG. 140,5. **P. robusta*; fore wing, $\times 6$ (Evans, 1956).

Pervestigia BECKER-MIGDISOVA, 1961c, p. 318 [**P.*

veteris; OD]. Hind wing: anterior margin without distal hump; M with 3 branches; CUA with narrow fork distally. *Perm.*, USSR (Asian RSFSR).—FIG. 140,8. **P. veteris*; hind wing, $\times 3$ (Becker-Migdisova, 1961c).

Prosbolomorpha RIEK, 1974c, p. 21 [**P. clara*; OD]. Fore wing as in *Austroprosbolole*, but RS not coalesced with M; M3+4 forking at its point of origin. [Probably a synonym of *Austroprosbolole*.] *Trias.*, South Africa.

Prosboloneura BECKER-MIGDISOVA, 1961c, p. 305 [**P. colorata*; OD]. Fore wing shaped as in *Sojanoneura*, but CUA more deeply forked and M with 3 branches. *Perm.*, USSR (Asian RSFSR).—FIG. 140,3. *P. kondonensis* BECKER-MIGDISOVA; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Sojanoneura MARTYNOV, 1928b, p. 22 [**S. edemskii*; SD BECKER-MIGDISOVA, 1940, p. 44]. Fore wing oval, bluntly rounded; RS arising nearer wing apex than in *Dictyoprosbole*; M with 3 or 4 branches. Hind wing little known, with only a slight bulging of the costal margin basally; M with 2 or 3 branches. MARTYNOV, 1935c; EVANS, 1956. *Perm.*, USSR (European and Asian RSFSR).—FIG. 140,9. *S. stigmata* MARTYNOV; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Family CICADOPROSBOLIDAE

Evans, 1956

[Cicadoprobsolidae EVANS, 1956, p. 222]

Apparently related to Probsolidae. Fore wing with vein M forking at midwing; RS arising before midwing; short, supplementary veins between branches of R; nodal line distinct, crossing RS remote from origin of RS and crossing M beyond its first fork. *Trias.*

Cicadoprobsolole BECKER-MIGDISOVA, 1947, p. 445 [**C. sogutensis*; OD]. Fore wing oval, apex slightly asymmetrical; branches of M and CUA slightly curved and parallel. [Originally placed in the family Probsolidae but transferred to a new family, Cicadoprobsolidae, by EVANS (1956) and later to the Tettigarctidae by BECKER-MIGDISOVA, 1962b.] *Trias.*, USSR (Kirghiz).—FIG. 142,4. **C. sogutensis*; fore wing, $\times 3.5$ (Becker-Migdisova, 1947).

Family TETTIGARCTIDAE

Distant, 1905

[Tettigarctidae DISTANT, 1905, p. 280]

Fore wing with transparent membranous area; costa broadly sclerotized; apical border narrow; venation much as in *Cicadidae*; vein SC with a short, hook-shaped anterior branch

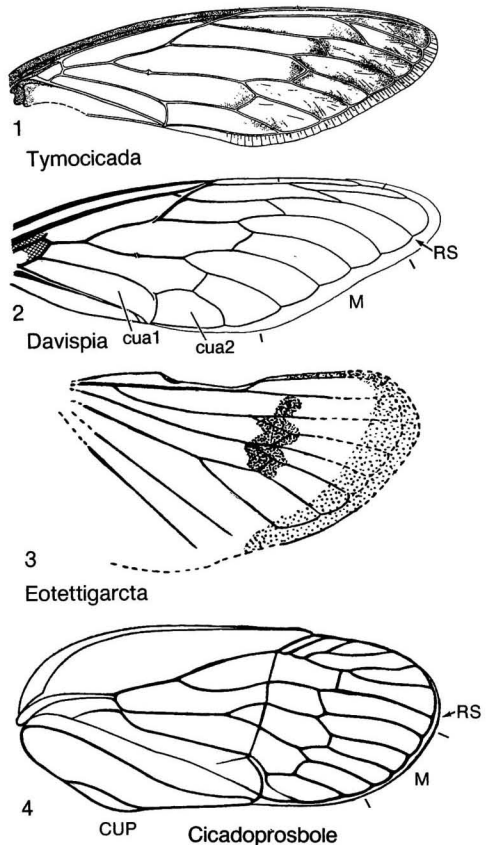


FIG. 142. Cicadoprobsolidae, Tettigarctidae, and Cicadidae (p. 221–222).

basally and a posterior branch coalesced with R+M and R. Hind wing: front margin with shallow indentation and convex area. Body structure: stridulatory organ present in both sexes. [This family is known by only one living genus, *Tettigarcta*, occurring in Australia. There is a reliable Tertiary record of the family, but the several Mesozoic genera that have been placed here are very poorly known and are assigned in this account to the category, family uncertain.] EVANS, 1956; WHALLEY, 1983. *Eoc.*—*Holo.*

Tettigarcta WHITE, 1845, p. 412. *Holo.*

Eotettigarcta ZEUNER, 1944a, p. 110 [**E. scotica*; OD]. Hind wing similar to that of *Tettigarcta* (recent), but indentation of costal margin much longer; origin of posterior branch of RS more remote from base of wing. Fore wing unknown.

WHALLEY, 1983. *Eoc.*, Scotland.—FIG. 142,3.
**E. scotica*; hind wing, $\times 2.5$ (Zeuner, 1944a).

Family CICADIDAE Leach, 1815

[Cicadidae LEACH, 1815, p. 124]

Fore wing with costal area reduced to a narrow strip or absent; apical parts of distal forks of veins aligned to form a submarginal vein along the outer and hind margins; anal area narrow and short. Hind wing much smaller than fore wing; anterior margin smooth; submarginal vein formed as in fore wing; anal-jugal area slightly broader than in fore wing. Stridulatory organs (tymbals) present on dorsum of first abdominal segment, at least in males. [A fragmented specimen from the Eocene of France was described as *beauchampi* by Piton (1940a); this species was placed in the existing genus *Chemsitica* STÅL (= *Ribana* DISTANT). However, the fossil does not show enough structural detail for family assignment. See also *Liassocicada* under Homoptera, family Uncertain.] COOPER 1941; WHALLEY, 1983. *Paleoc.*—*Holo.*

Cicada LINNÉ, 1758, p. 434. COOPER, 1941; WHALLEY, 1983. *Oligo.*, USA (Colorado); *Mio.*, Europe (Yugoslavia, Germany)—*Holo.*

Davisia COOPER, 1941, p. 288 [**D. bearcreekensis*; OD]. Similar to *Tibicen*; cell *cua2* broad but slightly more than twice as long as wide; apical margin of cell *cua1* evenly and shallowly curving into cell *cua2*. WHALLEY, 1983. *Paleoc.*, USA (Montana).—FIG. 142,2. **D. bearcreekensis*; fore wing, $\times 1.0$ (Cooper, 1941).

Lithocicada COCKERELL, 1906c, p. 457 [**L. perita*; OD]. Similar to *Cicada*, but cubital cell of fore wing with pointed or narrowly truncate apex. COOPER, 1941. *Oligo.*, USA (Colorado).

Platypedia UHLER, 1888, p. 23. COCKERELL, 1908a; COOPER, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Tibicen LATREILLE, 1825, p. 426. SCUDDER, 1892; COOPER, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Tymocicada BECKER-MIGDISOVA, 1954, p. 799 [**T. gorbunovi*; OD]. Fore wing similar to that of *Cosmopsaltivia* (recent), but CUA with longer anterior branch; cell between R and RS slightly broader. *Mio.*, USSR (Asian RSFSR).—FIG. 142,1. **T. gorbunovi*; fore wing, $\times 1.4$ (Becker-Migdisova, 1954).

Family SCYTINOPTERIDAE Handlirsch, 1906b

[Scytinopteridae HANDLIRSCH, 1906b, p. 391]

Fore wing tegminous; costal margin commonly thickened basally; veins usually thin;

vein SC obsolescent; branches of M and CUA short; crossveins few; only a few closed cells between R, M, and CUA. Hind wing with costal margin with at most a shallow convexity at base of wing; RS unbranched; M and CUA distally branched. Body little known, apparently as in Cicadellidae. *Perm.*—*Trias.*

Scytinoptera HANDLIRSCH, 1904b, p. 3 [**S. kokeni*; OD] [= *Anomoscyta* MARTYNOV, 1928b, p. 34 (type, *A. reducta*); *Permocixius* MARTYNOV, 1928b, p. 36 (type, *P. kazanensis*); *Scytinoptera curta* ZALESKY, 1929, p. 28)]. Fore wing with posterior branch of SC short, forming a sharp curve at level of R+M, or absent; M and CUA with distal forks, forming series of small, marginal cells, usually subequal; anal-jugal region strongly widened. Hind wing with costal margin with conspicuous but gradual convexity near base; no prominent marginal concavity or excision. Pronotum with lateral projections. [RIEK (1976b) has described a late Triassic species (*distorta*) in the genus *Scytinoptera*, but there is really no evidence to justify that placement.] *Perm.*, USSR (European and Asian RSFSR).—FIG. 143,5a,b. *S. kaltanica* BECKER-MIGDISOVA; a, fore and b, hind wings, $\times 10$ (Becker-Migdisova, 1962b).—FIG. 143,5c. *S. picturata* BECKER-MIGDISOVA; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Anaprosbole BECKER-MIGDISOVA, 1960, p. 28 [**A. ivensis*; OD]. Fore wing with costal margin relatively broad basally; RS arising well beyond midwing; branches of M1+2 much longer than branches of M3+4; CUA with 3 terminal branches. [Family assignment uncertain.] *Perm.*, USSR (European RSFSR).—FIG. 143,6. **A. ivensis*; fore wing, $\times 5.0$ (Becker-Migdisova, 1960).

Anomaloscytina DAVIS, 1942, p. 112 [**A. metapteryx*; OD]. Hind wing with costal margin with distinct but gentle concavity; SC short but distinct; anal area extensive. [Family position uncertain.] *Perm.*, Australia (New South Wales).—FIG. 143,7. **A. metapteryx*; hind wing, $\times 6.5$ (Davis, 1942).

Elliptoscarta TILLYARD, 1926a, p. 16 [**E. ovalis*; OD]. Fore wing oval, with apex evenly rounded; costal area (between C and R) broad; R dichotomously forked; M with 5 branches; CUA forked. *Perm.*, Australia (New South Wales).—FIG. 143,1. **E. ovalis*; fore wing, $\times 8.2$ (Tillyard, 1926a).

Homaloscytina TILLYARD, 1926a, p. 16 [**H. plana*; OD]. Fore wing as in *Anaprosbole*, but CUA with only 2 terminal branches and connected to M by a crossvein; apex of wing bluntly rounded. EVANS, 1943b. *Trias.*, Australia (New South Wales).—FIG. 143,4. **H. plana*; fore wing, $\times 8$ (Evans,

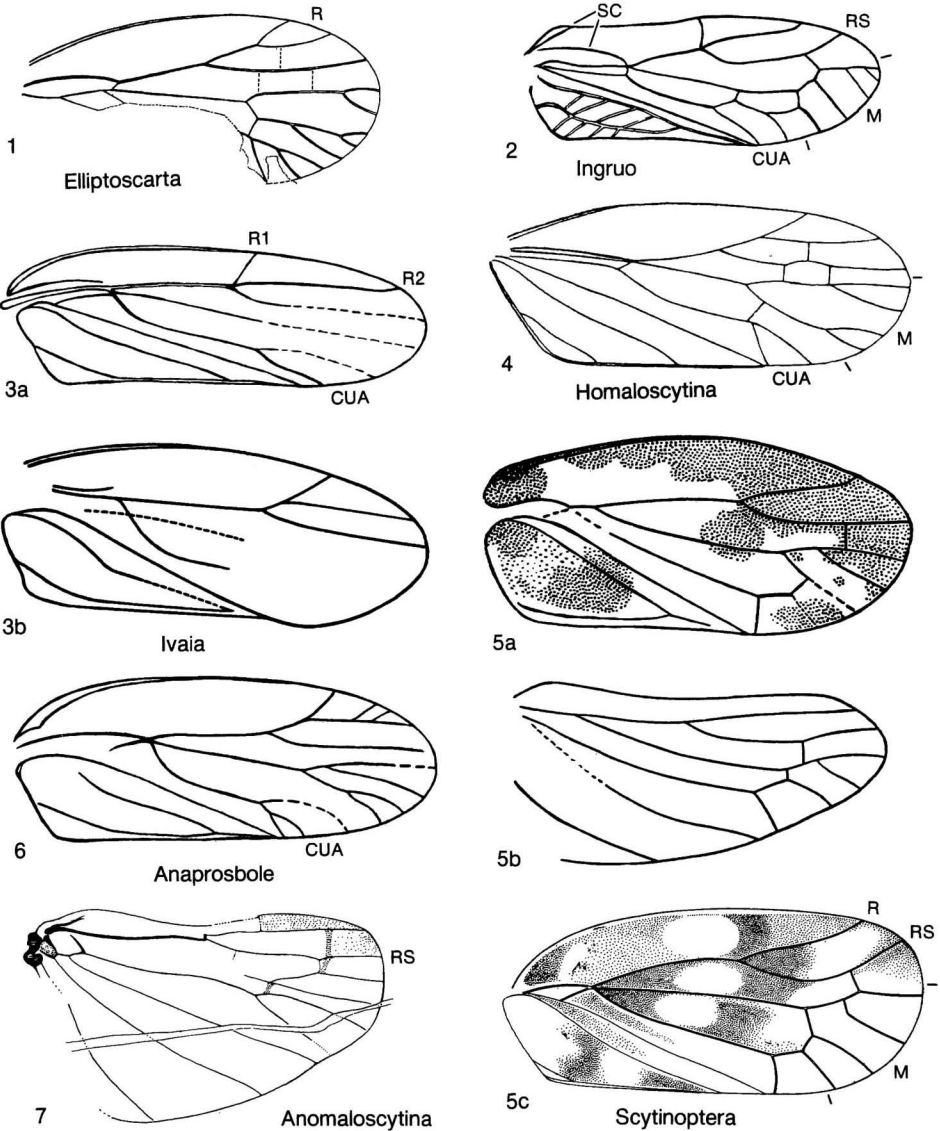


FIG. 143. Scytinopteridae (p. 222–223).

Ingruo BECKER-MIGDISOVA, 1960, p. 19 [*I. lanceolata*; OD]. Fore wing very narrow; posterior branch of SC short, merging with R; CUA dividing at level of origin of RS; fork of CUA large. [Family assignment doubtful]. *Perm.*, USSR (European RSFSR).—FIG. 143,2. **I. lanceolata*; fore wing, $\times 16$ (Becker-Migdisova, 1960).

Ivaia BECKER-MIGDISOVA, 1960, p. 25 [*I. indistincta*; OD]. Fore wing moderately broad; costal area (between C and R) broad; R straight; CUA in brief contact with M, then diverging; M apparently unbranched. *Perm.*, USSR (European RSFSR).—FIG. 143,3a. *I. procucopoides* BECKER-MIGDISOVA; fore wing, $\times 6.5$ (Becker-

Migdisova, 1960).—FIG. 143,3b. **I. indistincta*; fore wing, $\times 8$ (Becker-Migdisova, 1962b). **Kaltanospes** BECKER-MIGDISOVA, 1961c, p. 344 [**K. kuznetskiensis*; OD]. Fore wing as in *Ingruo*, but CUA dividing much further distally of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 144,6. **K. kuznetskiensis*; fore wing and body, $\times 10$ (Becker-Migdisova, 1961c).

Mesonirvana EVANS, 1956, p. 191 [**M. abrupta*; OD]. Fore wing: R with several branches; crossvein m-cu joined to CUA1; RS unbranched. *Trias.*, Australia (Queensland).—FIG. 144,7. **M. abrupta*; fore wing, $\times 5$ (Evans, 1956).

Mesothymbris EVANS, 1956, p. 191 [**M. perkinsi*; OD]. Fore wing: R with several branches; crossvein m-cu joined to CUA1; RS unbranched. *Trias.*, Australia (Queensland).—FIG. 144,8. **M. perkinsi*; fore wing, $\times 5$ (Evans, 1956).

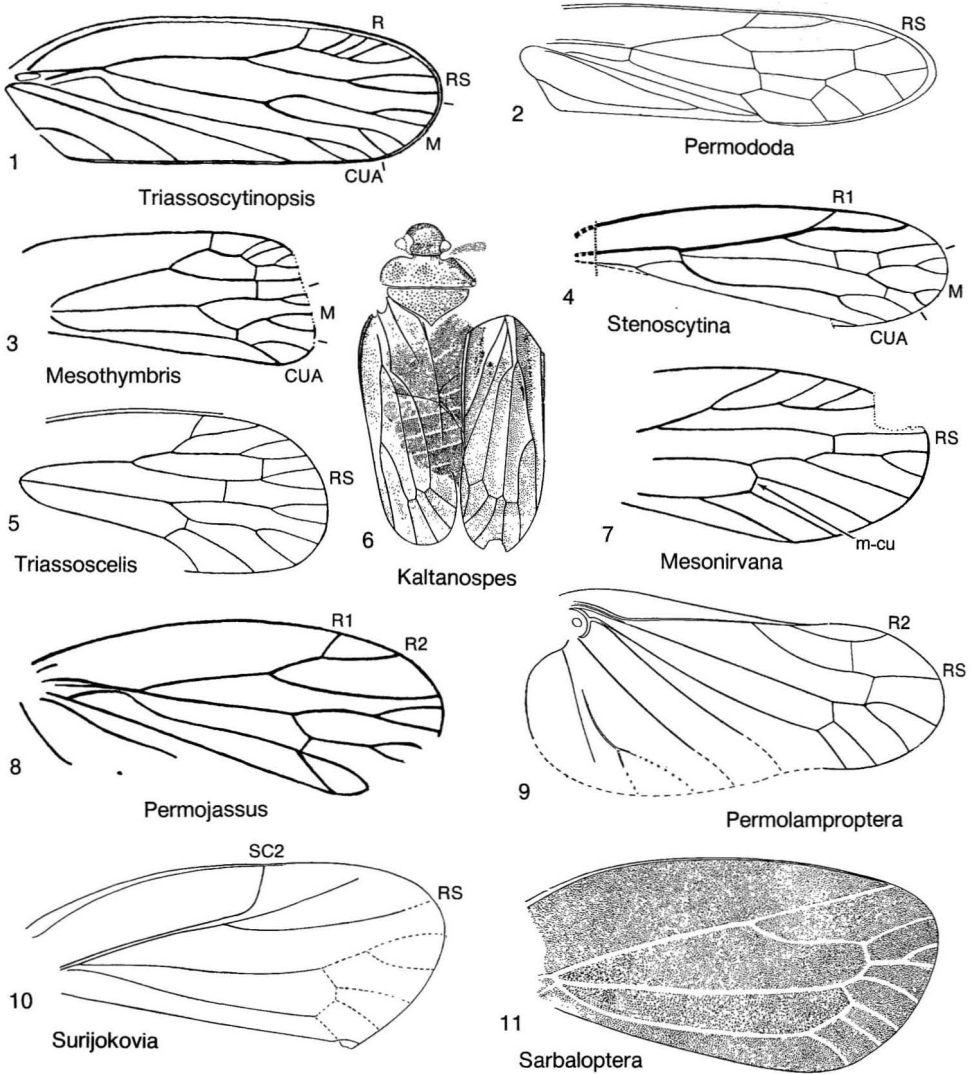


FIG. 144. Scytinopteridae (p. 223–225).

OD]. Fore wing as in *Triassoscytinopsis*, but M1+2 forming almost straight continuation of M; M3+4 bent towards CUA; crossvein m-cu joined to CUA. *Trias.*, Australia (Queensland). —FIG. 144,3. **M. perkinsi*; fore wing, $\times 6$ (Evans, 1956).

Permododa BECKER-MIGDISOVA, 1961c, p. 347 [**P. membracoides*; OD]. Fore wing very slender; several closed cells between RS and M and between M and CUA. *Perm.*, USSR (Asian RSFSR). —FIG. 144,2. **P. membracoides*; fore wing, $\times 10$ (Becker-Migdisova, 1961c).

Permojassus TILLYARD, 1926a, p. 7 [**P. australis*; OD] [= *Permojassula* HANDLIRSCH, 1937, p. 115, obj.] Fore wing similar to that of *Homaloscytina*, but anal area apparently much narrower. EVANS,

1956. *Perm.*, Australia (New South Wales). —FIG. 144,8. **P. australis*; fore wing, $\times 8$ (Evans, 1956).

Permolamproptera BECKER-MIGDISOVA, 1961c, p. 340 [**P. grandis*; OD]. Hind wing similar to that of *Scytinoptera* but with R2 curved distally; anal area extended. *Perm.*, USSR (Asian RSFSR). —FIG. 144,9. **P. grandis*; hind wing, $\times 5.7$ (Becker-Migdisova, 1961c).

Sarbaloptera BECKER-MIGDISOVA, 1961c, p. 328 [**S. sarbalensis*; OD]. Fore wing with asymmetrical apex; costal area (between C and R) very broad. *Perm.*, USSR (Asian RSFSR). —FIG. 144,11. **S. sarbalensis*; fore wing, $\times 6.5$ (Becker-Migdisova, 1961c).

Stenoscytina TILLYARD, 1926a, p. 15 [**S. aus-*

traliensis; OD]. Little-known genus. Fore wing narrow; M with 4 branches; CUA curving abruptly posteriorly after diverging from M. [Family assignment uncertain.] *Perm.*, Australia (New South Wales).—FIG. 144,4. **S. australiensis*; fore wing, $\times 6.5$ (Tillyard, 1926a).

Surijokovia BECKER-MIGDISOVA, 1961c, p. 342 [**S. lata*; OD]. Little-known fore wing; posterior branch of SC long, mostly parallel to R, then diverging anteriorly to termination on costal margin; RS apparently unbranched. *Perm.*, USSR (Asian RSFSR).—FIG. 144,10. **S. lata*; fore wing, $\times 16$ (Becker-Migdisova, 1961c).

Triassoscelis EVANS, 1956, p. 192 [**T. anomala*; OD]. Fore wing as in *Mesonirvana*, but RS forked. *Trias.*, Australia (Queensland).—FIG. 144,5. **T. anomala*; fore wing, $\times 5$ (Evans, 1956).

Triassoscytina EVANS, 1956, p. 179 [**T. incompleta*; OD]. Fore wing as in *Homaloscytina*, but M forking just beyond level of origin of RS. [Family position uncertain.] *Trias.*, Australia (Queensland).

Triassoscytinopsis EVANS, 1956, p. 190 [**T. stenulata*; OD]. Fore wing with apex evenly rounded; R with at least 4 parallel branches distally; RS with from 2 to 4 branches; M with 4 branches. *Trias.*, Australia (Queensland).—FIG. 144,1. *T. aberrans* EVANS; fore wing, $\times 6$ (Evans, 1956).

Tychoscytina BECKER-MIGDISOVA, 1952, p. 179 [**T. kuznetskiensis*; OD]. Fore wing little known, with wide costal area; R1 straight. *Perm.*, USSR (Asian RSFSR).

Family BITURRITIIDAE Metcalf, 1951

[Biturritiidae METCALF, 1951, p. 11]

Fore wing sclerotized; no marginal border; vein M unbranched; radial cell divided by a crossvein. Hind wing nearly of uniform width, with very slight concavity of costal margin. *Trias.—Holo.*

Biturritia GODING, 1930, p. 39. *Holo.*

Absoluta BECKER-MIGDISOVA, 1962a, p. 92 [**A. distincta*; OD]. Hind wing with base of CUA nearly or completely coalesced with stem of M. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).—FIG. 145,1. **A. distincta*; hind wing, $\times 12$ (Becker-Migdisova, 1962b).

Family CICAPELLIDAE Latreille, 1802

[Cicadellidae LATREILLE, 1802a, p. 257] [=Jasscopidae HAMILTON, 1971, p. 943]

Fore wing tegminous; several to many closed cells; CUA usually with wide distal fork. Hind wing narrowed distally; submar-

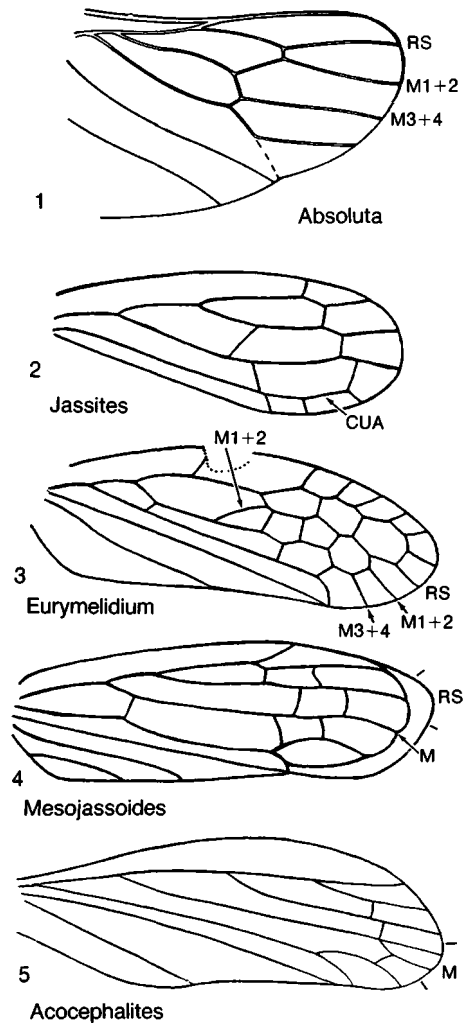


FIG. 145. Biturritiidae and Cicadellidae (p. 225–227).

ginal vein conspicuous, with relatively wide margin; ano-jugal area broad. *Trias.—Holo.*

Cicadella DUMÉRIl, 1806, p. 266. BEROVETS, 1910; COCKERELL, 1920c; BECKER-MIGDISOVA, 1951. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Baltic); *Mio.*, USSR (European RSFSR)—*Holo.*

Acocephalites MEUNIER, 1904e, p. 119 [**A. bred dini*; OD]. Little-known genus, based on fore wing with strongly arched costal margin and a venation similar to that of *Mesojassoides*; M with distal fork. *Jur.*, Europe (Spain).—FIG. 145,5. **A. bred dini*; fore wing, $\times 14$ (Handlirsch, 1907).

Agallia CURTIS, 1833, p. 193. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Aphrodes CURTIS, 1833, p. 193. SCUDDER, 1890;

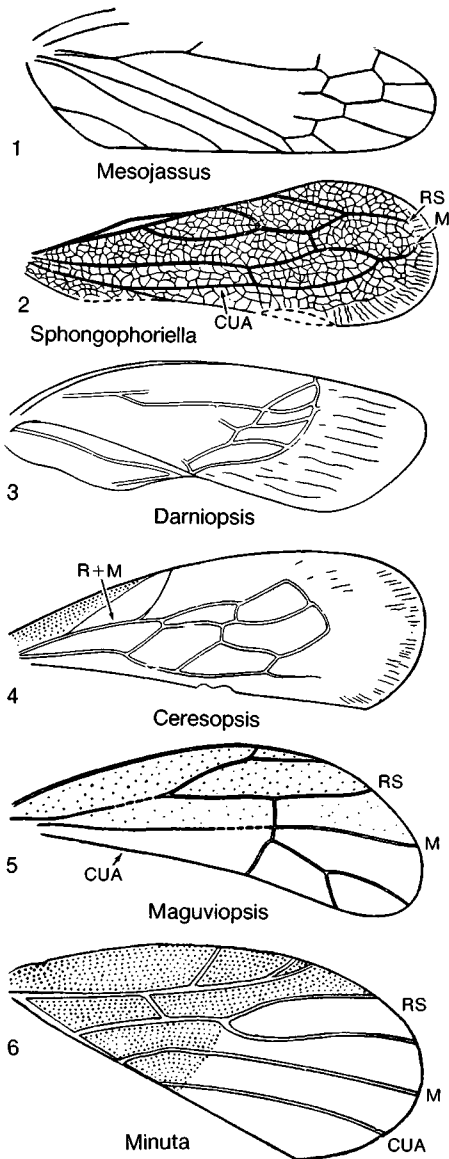


FIG. 146. Eurymelidae and Membracidae (p. 227–228).

- STATZ, 1950a. *Eoc.*, USA (Wyoming); *Oligo.*–*Mio.*, Europe (Germany)–*Holo.*
- Batrachomorphus** LEWIS, 1834, p. 51, *nom. correct.* AGASSIZ, 1846, *ex Batrachomorphus* LEWIS, 1834. STATZ, 1950a. *Oligo.*, Europe (Germany)–*Holo.*
- Cicadula** ZETTERSTEDT, 1838, p. 296. SCUDDER, 1890. *Eoc.*, USA (Wyoming)–*Holo.*
- Coelidia** GERMAR, 1821, p. 75. SCUDDER, 1890, 1895b. *Eoc.*, USA (Wyoming), Canada (British Columbia); *Oligo.*, USA (Colorado)–*Holo.*

- Deltocephalus** BURMEISTER, 1838, p. 5. STATZ, 1950a. *Oligo.*, Europe (Germany)–*Holo.*
- Durgades** DISTANT, 1912, p. 608. BECKER-MIGDISOVA & MARTYNOVA, 1951. *Mio.*, USSR (Kirghiz)–*Holo.*
- Eurymelidium** TILLYARD, 1919c, p. 884 [**E. australe*; OD]. SC apparently absent; M1 + 2 anastomosed with part of RS. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 145, 3. **E. australe*; fore wing, $\times 10$ (Evans, 1956).
- Euscelis** BRULLÉ, 1832, p. 109. STATZ, 1950a; PIERCE, 1963. *Oligo.*, Europe (Germany); *Mio.*, USA (California)–*Holo.*
- Gypona** GERMAR, 1821, p. 73. [Generic assignment of fossil doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)–*Holo.*
- Gyponites** STATZ, 1950a, p. 10 [**G. pronota*; OD]. Little-known cicadellid; head short and broad; ocelli large; pronotum long, with parallel sides; scutellum shorter than pronotum. *Oligo.*, Europe (Germany).
- Homopterulum** HANDLIRSCH, 1907, p. 641 [**Cercopidium signoreti* WESTWOOD, 1854, p. 396; SD CARPENTER, herein]. Little-known genus, based on fore wing. [Family assignment doubtful.] EVANS, 1956. *Jur.*, England.
- Idiocerus** LEWIS, 1834, p. 47. STATZ, 1950a. *Oligo.*, Europe (Germany)–*Holo.*
- Jascopus** HAMILTON, 1971, p. 944 [**J. notabilis*; OD]. Little-known genus, based on nymph. [Type of family *Jascopidae* HAMILTON.] EVANS, 1972. *Cret.*, Canada (Manitoba).
- Jassites** HANDLIRSCH, 1907, p. 642 [**Cicada punctatus* BRODIE, 1845, p. 33; OD]. Little-known genus, based on fore wing. CUA with very short branches. EVANS, 1956. *Jur.*, England.—FIG. 145, 2. **J. punctatus*; fore wing, $\times 5.5$ (Evans, 1956).
- Jassopsis** SCUDDER, 1890, p. 312 [**J. evidens*; OD]. Little-known genus, similar to *Thamnotettix*. Scutellum not more than half the length of thorax. *Oligo.*, USA (Colorado).
- Jassus** FABRICIUS, 1803, p. 85. BERVOETS, 1910; MEUNIER, 1920c; PITON, 1940a; STATZ, 1950a. *Eoc.*, Europe (France); *Oligo.*, Europe (Baltic, Germany)–*Holo.*
- Lavrushinia** COCKERELL, 1925g, p. 10 [**L. elegantula*; OD]. Little-known genus, based on long and narrow fore wing; marginal vein very close to wing margin. *Mio.*, USSR (Asian RSFSR).
- Macropsis** LEWIS, 1834, p. 49. BERVOETS, 1910; STATZ, 1950a. *Oligo.*, Europe (Baltic, Germany)–*Holo.*
- Maleojassus** ZEUNER, 1941a, p. 90 [**M. primitivus*; OD]. Fore wing as in *Stonastla* (recent), but RS smoothly curved, not bent at junction with M1; M almost straight. *Eoc.*, Scotland.
- Megophthalmus** CURTIS, 1833, p. 193. STATZ, 1950a. *Oligo.*, Europe (Germany)–*Holo.*
- Mesojassoides** OMAN, 1937, p. 38 [**M. gigantea*;

OD]. Fore wing as in *Coelidia* but with additional crossveins; M unbranched. *Cret.*, USA (Colorado).—FIG. 145, 4. **M. gigantea*; fore wing, $\times 4.5$ (Evans, 1956).

Miochlorotettix CARPENTER, herein [**M. gibroni* PIERCE, 1963, p. 73; OD]. Similar to *Chlorotettix* (recent), but prothorax strongly arched forward and scutellum extending back between wings about as far as forwards. The original generic name, *Miochlorotettix*, was a *nomen nudum* (PIERCE, 1963.) *Mio.*, USA (California).

Miomesamia PIERCE, 1963, p. 81 [**M. juliae*; OD]. Similar to *Ulope* (recent). Face wide, eyes prominent; antennae at sides of front sutures, opposite outer corners of eyes. *Mio.*, USA (California).

Oligogypona STATZ, 1950a, p. 8 [**O. haupiti*; OD]. Similar to *Gypona*, but head broad, somewhat narrower than pronotum; costal margin of fore wing strongly arched. *Oligo.*, Europe (Germany).

Oligoidiocerus STATZ, 1950a, p. 15 [**O. pronotalis*; OD]. Similar to *Idiocerus* but with richer venation and unmarked fore wing. *Oligo.*, Europe (Germany).

Oligopenthimia STATZ, 1950a, p. 9 [**O. ovalis*; OD]. Similar to *Penthimia* (recent). Head short, as wide as pronotum; scutellum long, reaching to the middle of the abdomen. *Oligo.*, Europe (Germany).

Phlepsius FIEBER, 1866, p. 503. PIERCE, 1963. *Mio.*, USA (California)—*Holo.*

Prochlorotettix PIERCE, 1963, p. 78 [**P. calico*; OD]. Similar to *Chlorotettix* (recent), but with last sternum completely divided. *Mio.*, USA (California).

Tetigonia BLANCHARD, 1852, p. 282. STATZ, 1950a. *Oligo.*, Europe (Germany)—*Holo.*

Tettigella CHINA & FENNAH, 1945, p. 711. SCUDDER, 1890; STATZ, 1950a. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*

Thamnotettix ZETTERSTEDT, 1838, p. 292. COCKERELL, 1920c, 1924a, 1925a; STATZ, 1950a. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany); *Mio.*, USA (Colorado)—*Holo.*

Typhlocyba GERMAR, 1833, p. 180. GERMAR & BERENDT, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

Family EURYMELIDAE

Amyot & Serville, 1843

[Eurymelidae AMYOT & SERVILLE, 1843, p. 554]

Fore wing hyaline or opaque and coriaceous; venation often reticulate; vein RS absent; M1+2 retained as separate vein, extending to apex; M3+4 usually unbranched; CUA forked. *Trias.*—*Holo.*

Eurymela LE PELETIER & SERVILLE, 1828, p. 603. *Holo.*

Mesojassus TILLYARD in TILLYARD & DUNSTAN, 1916,

p. 34 [**M. ipswiciensis*; OD]. Little-known genus, based on fore wing. Fork of CUA marginal, very shallow. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 146, 1. **M. ipswiciensis*; fore wing, $\times 8.4$ (Evans, 1956).

Family MEMBRACIDAE

Rafinesque, 1815

[Membracidae RAFINESQUE, 1815, p. 121]

Fore wing usually membranous, except for basal region; clavus distinct, claval suture along vein 1A; ends of veins usually forming a scalloped submarginal line, the terminal marginal membrane (limbus) extending beyond the veins; veins usually clear and marked by punctures; M either free basally or coalesced in part with stem of R or CUA; cells usually irregular; venation highly diverse. Hind wing well developed, but usually shorter than fore wing; limbus usually present; venation usually similar to that of fore wing. Pronotum extensively developed, often prolonged posteriorly and concealing the scutellum, the wings, and even the entire abdomen; antennae minute, bristlelike; tarsi with 3 segments. *Trias.*—*Holo.*

This is a very large and diversified family. Fossil forms, which are usually known only from wings, are often difficult to classify because of the variability in the venation, especially that of the fore wings. Much difference of opinion exists among specialists in Homoptera about the generic lines. The taxonomic groups used here are essentially those employed in the *General Catalogue of the Homoptera* (METCALF & WADE, 1966).

Membracis FABRICIUS, 1775, p. 675. *Holo.*

Ceresopsis BECKER-MIGDISOVA, 1958, p. 66 [**C. costalis*; OD]. Fore wing broader than in *Darniopsis*, with conspicuous sclerotized area between costal margin and R+M basally; 3 apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146, 4. **C. costalis*; fore wing, $\times 10$ (Becker-Migdisova, 1958).

Darniopsis BECKER-MIGDISOVA, 1958, p. 65. [**D. tragopea*; OD]. Fore wing elongate, with very wide limbus; costal margin only slightly convex; 4 apical cells; M and CUA with common stem; anal area large, triangular. *Trias.*, USSR (Kirghiz).—FIG. 146, 3. **D. tragopea*; fore wing, $\times 10$ (Becker-Migdisova, 1958).

Maguviopsis BECKER-MIGDISOVA, 1953c, p. 463 [**M. kotchnevi*; OD]. Fore wing with costal-

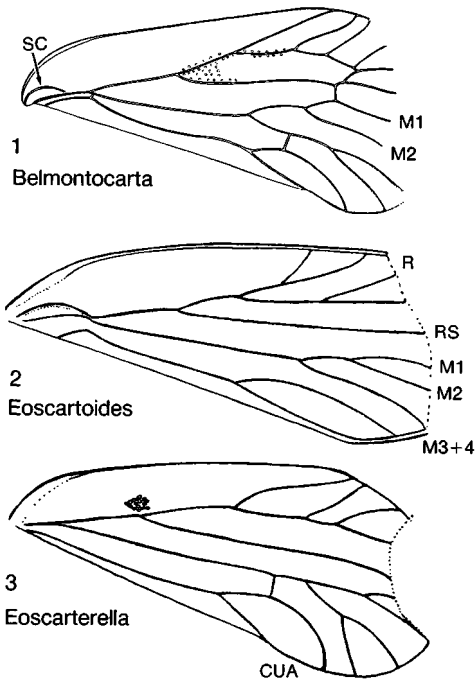


FIG. 147. Eoscarterellidae (p. 228).

distal margin broadly curved; anterior half of wing sclerotized; R and M not coalesced with CUA; M unbranched, straight. *Jur.*, USSR (Asian RSFSR).—FIG. 146,5. **M. kotchnevi*; fore wing, $\times 16$ (Becker-Migdisova, 1953c).

Minuta BECKER-MIGDISOVA, 1958, p. 64 [**M. heteropterata*; OD]. Little-known genus; fore wing short, sclerotized from midwing to front margin; R, M, and CUA merged with CUP basally; CUA long; no apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146,6. **M. heteropterata*; fore wing, $\times 20$ (Becker-Migdisova, 1958).

Sphongophoriella BECKER-MIGDISOVA, 1958, p. 63 [**S. reticulata*; OD]. Fore wing elongate, reticulate; M and CUA not coalesced to form a common stem; venation reduced; cells elongate-oval; anal area narrow, 3 apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146,2. **S. reticulata*; fore wing, $\times 34$ (Becker-Migdisova, 1958).

Family AETALIONIDAE Spinola, 1850

[Aetalionidae SPINOLA, 1850, p. 53]

Similar to Cicadellidae; fore wing with vein RS absent; M1+2 (or M1 and M2) extending to apex of wing; M3+4 usually forked; CUA unbranched. Hind wing with RS absent. *Oligo.*—*Holo.*

Aetalion LATREILLE, 1810, p. 263. STATZ, 1950a. *Oligo.*, Europe (Germany)—*Holo.*

Family EOSCARTERELLIDAE

Evans, 1956

[Eoscarterellidae EVANS, 1956, p. 220]

Fore wing with vein RS arising from R about one-third wing length from base; R with at least 2 branches; CUA separate from M. *Perm.*—*Trias.*

Eoscarterella EVANS, 1956, p. 220 [**E. media*; OD] [= *Prosbolopsites* BECKER-MIGDISOVA, 1960, p. 90 (type, *P. illyardi*)]. Fore wing tegminous and rugose, broadest in distal half; RS and M parallel for most of their lengths; M with 4 branches. EVANS, 1961. *Trias.*, Australia (Queensland).—FIG. 147,3. **E. media*; fore wing, $\times 5.5$ (Evans, 1956).

Belmontocarta EVANS, 1958, p. 112 [**B. perfecta*; OD]. Fore wing with SC very short, curving distally towards R+M; M1 and M2 longer than M3 and M4; CUA curved and joined to base of M by short crossvein. *Perm.*, Australia (New South Wales).—FIG. 147,1. **B. perfecta*; fore wing, $\times 4.5$ (Evans, 1958).

Eoscartoides EVANS, 1956, p. 220 [**E. bryani*; OD]. Fore wing with complete marginal border; R and M arched basally; M1+2 forked. EVANS, 1961. *Trias.*, Australia (Queensland).—FIG. 147,2. **E. bryani*; fore wing, $\times 4.5$ (Evans, 1961).

Family PROCERCOPIDAE

Handlirsch, 1906

[Procercopidae HANDLIRSCH, 1906b, p. 500]

Fore wing slender, at least three times as long as wide; vein RS arising in basal third of wing; M and CUA branching in distal third of wing, their branches short. Hind wing very little known. EVANS, 1956. *Trias.*—*Jur.*

Procercopis HANDLIRSCH, 1906b, p. 500 [**P. alutacea*; SD BECKER-MIGDISOVA, 1962b, p. 180]. Fore wing elongate, about 4 times as long as broad; M with at least 3 branches; several crossveins in distal part of wing. *Trias.*, USSR (Kirghiz); *Jur.*, Europe (Germany).—FIG. 148,3. *P. longipennis* BECKER-MIGDISOVA, *Trias.*; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Procercopina MARTYNOV, 1937a, p. 99 [**P. asiatica*; OD]. Fore wing as in *Procercopis* but relatively broader; only one crossvein between adjacent veins. EVANS, 1956. *Jur.*, USSR (Kirghiz).—FIG. 148,5. **P. asiatica*; fore wing, $\times 4.6$ (Becker-Migdisova, 1962b).

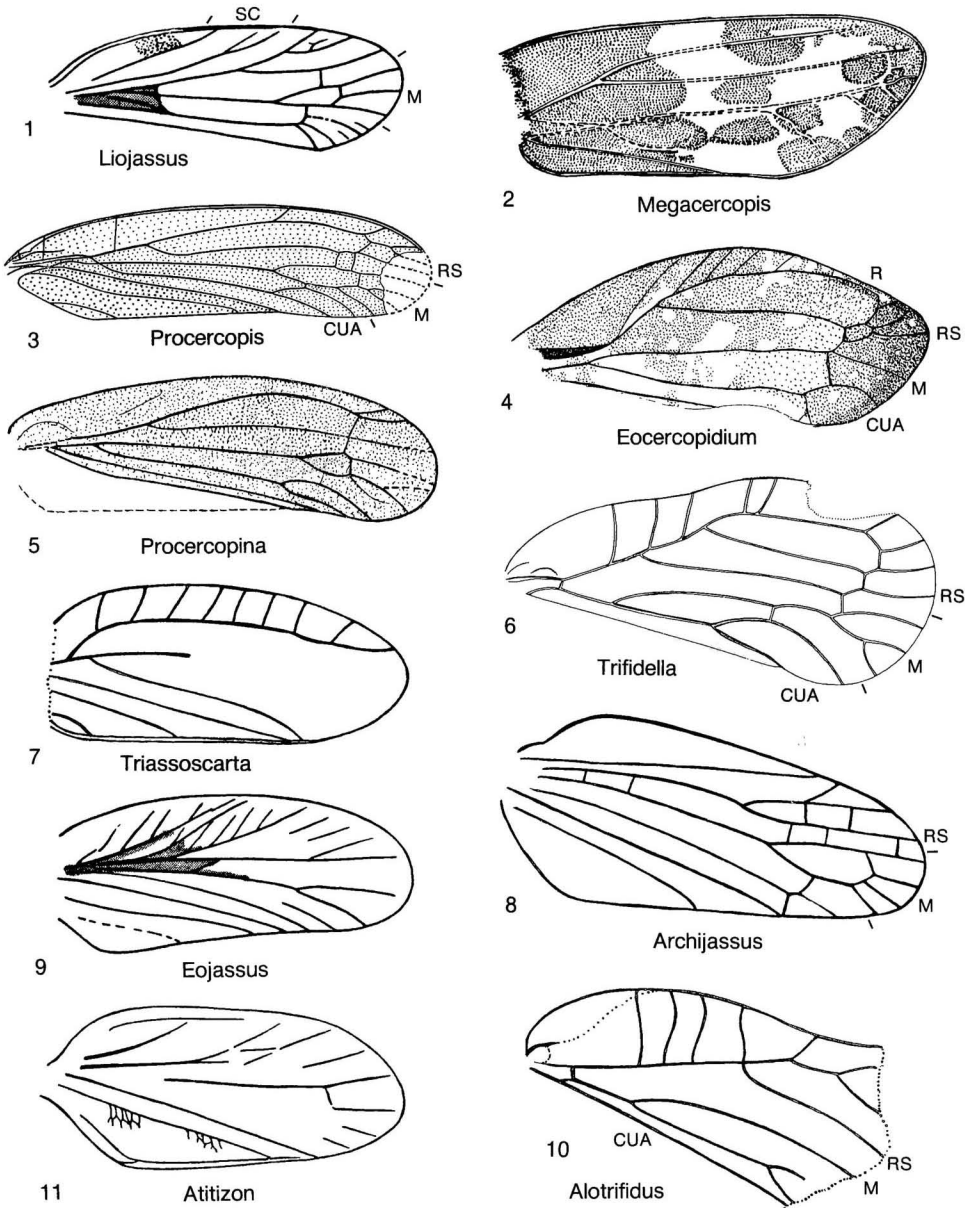


FIG. 148. Procercopidae, Cercopidae, and Archijassidae (p. 228-233).

Family DYSMORPHOPTILIDAE
Handlirsch, 1906

[Dysmorphoptilidae HANDLIRSCH, 1906b, p. 492]

Tegmen of irregular form, abruptly narrowed distally, strongly sclerotized; vein SC apparently fused with R; several short

branches from R to costal margin; RS arising before midwing. EVANS, 1956. *Trias.-Jur.*

Dysmorphoptila HANDLIRSCH, 1906b, p. 492 [**Belostoma liasina* GIEBEL, 1856, p. 371; OD]. Broad portion of tegmen extending only to about midwing; M with only one distal fork. EVANS, 1956. *Jur.*, Europe (Germany).

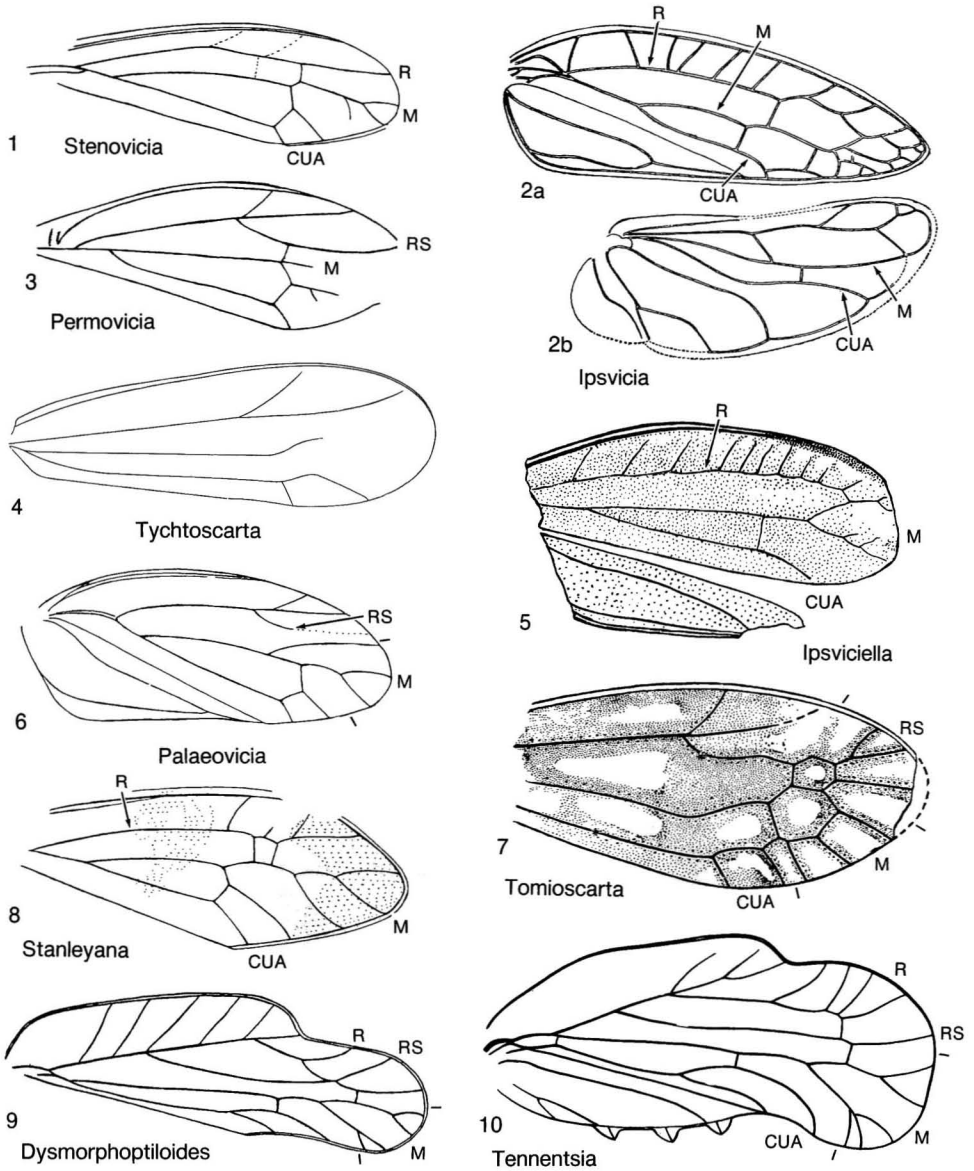


FIG. 149. Dymorphoptilidae and Ipsviciidae (p. 230–233).

Dymorphoptiloides EVANS, 1956, p. 218 [**D. elongata*; OD]. Tegmen as in *Dymorphoptila*, but broad portion extending nearer to apex; M with 2 distal forks. RIEK, 1974b. *Trias.*, Australia (Queensland), South Africa.—FIG. 149,9. **D. elongata*; tegmen, $\times 3.4$ (Evans, 1956).

Mesoatraxis BECKER-MIGDISOVA, 1949b, p. 40 [**M. reducta*; OD]. Tegmen as in *Dymorphoptiloides* but with shorter distal area; M with 3 terminal

branches. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Tadzhik).

Tennentsia RIEK, 1976b, p. 813 [**Dymorphoptiloides protuberans* RIEK, 1974c, p. 22; OD]. Fore wing similar to that of *Dymorphoptiloides*, but SC with several distal branches and RS unbranched; M and CU apparently connected basally by a crossvein. *Trias.*, South Africa.—FIG. 149,10. **T. protuberans*; fore wing, $\times 2.3$ (Riek, 1976b).

Family CERCOPIDAE

Westwood, 1838

[Cercopidae WESTWOOD, 1838, p. 39]

Head narrower than pronotum, usually as wide as anterior margin of scutellum; ocelli on disc of crown, each at posterior end of sulcus; length and width of eyes almost equal; antennae originating in cavities below anterior margin of head; postclypeus commonly protuberant. Fore wings usually coriaceous. [The Aphrophoridae are included here, as a subfamily, because of the difficulty of recognizing the distinguishing features in the fossils.] EVANS, 1956. *Trias*.—*Holo*.

Cercopis FABRICIUS, 1775, p. 688. [Numerous extinct species from Tertiary deposits and described before 1900 were placed in the genus, but their assignment to *Cercopis* has not been generally accepted (see HANDLIRSCH, 1907, p. 1072–1074). However, a few, well-preserved specimens appear to justify at least tentative placement in the genus.] SCUDDER, 1890; COCKERELL, 1920a, 1927b; EVANS, 1956. *Eoc.*, Canada (British Columbia), USA (Colorado, Wyoming), USSR (Asian RSFSR)—*Holo*.

Alotritifidus EVANS, 1956, p. 216 [**A. interruptus*; OD]. Fore wing as in *Trifidella*, but costal margin arching basally and RS arising further distally. *Trias.*, Australia (Queensland).—FIG. 148, 10. **A. interruptus*; fore wing, $\times 10$ (Evans, 1956).

Aphrophora GERMAR, 1821, p. 48. COCKERELL, 1922f, 1925g; PONGRÁZ, 1928; PITON, 1936c; THÉOBALD, 1937a; BECKER-MIGDISOVA, 1964. *Eoc.*, Europe (Baltic, France), Canada (British Columbia); *Oligo.*, England, Europe (France); *Mio.*, USSR (Asian RSFSR)—*Holo*.

Cercopites SCUDDER, 1890, p. 316 [**C. calliscens* SCUDDER, 1890, p. 316; SD CARPENTER, herein]. Head relatively small; thorax hexagonal; fore wing more than twice as long as broad. *Eoc.*, USA (Wyoming), Canada (British Columbia).

Clastoptera GERMAR, 1839, p. 187. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo*.

Dawsonites SCUDDER, 1895b, p. 18 [**D. veter.*; OD]. Similar to *Palecphora*, but RS arising at mid-wing. *Mio.*, Canada (British Columbia).

Eocercopidium ZEUNER, 1944a, p. 116, *nom. subst. pro Eocercopis* ZEUNER, 1941a, p. 88, *non* HANDLIRSCH, 1939 [**Eocercopis maculata* ZEUNER, 1941a, p. 88; OD]. Fore wing similar to that of *Aphrophora*, but R strongly bent anteriorly near base; preradial part of wing very wide, crossed by pectinate branches from R; radial-median area very broad; M separating from CUA very near to base. *Eoc.*, Scotland.—FIG. 148, 4. **E.*

maculata (ZEUNER); fore wing, $\times 6.4$ (Zeuner, 1944a).

Megacercopis COCKERELL, 1925g, p. 9 [**M. optima*; OD]. Little-known fore wing with venation similar to that of *Stenecphora*, but apex much more pointed. *Mio.*, USSR (Asian RSFSR).—FIG. 148, 2. **M. optima*; fore wing, $\times 2.5$ (Cockerell, 1925g).

Palaeoptysma SCUDDER, 1895b, p. 21 [**P. venosa*; OD]. Little-known fore wing, related to *Aphrophora* but very slender. *Eoc.*, Canada (British Columbia).

Palaphrodes SCUDDER, 1890, p. 333 [**P. irregularis* SCUDDER, 1890, p. 333; SD CARPENTER, herein]. Fore wing as in *Cercopis*, but head very obtuse and rounded in front, narrower distally than thorax. COCKERELL, 1908k. *Oligo.*, USA (Colorado).

Palecphora SCUDDER, 1890, p. 324 [**P. communis* SCUDDER, 1890, p. 324; SD CARPENTER, herein]. Fore wing longer and more slender than that of *Palaphrodes*; costal margin less arched. COCKERELL, 1908k. *Oligo.*, USA (Colorado).

Petrolystra SCUDDER, 1878a, p. 530 [**P. gigantea* SCUDDER, 1878a, p. 530; SD CARPENTER, herein]. Large insects; head large, flat dorsally, twice as broad as long, the front broadly convex; scutellum very small, about half as long as thorax. SCUDDER, 1890. *Oligo.*, USA (Colorado).

Philagra STÅL, 1863, p. 593. COCKERELL, 1925g. *Mio.*, USSR (Asian RSFSR)—*Holo*.

Ptyelus LE PELETIER & SERVILLE, 1828, p. 608. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo*.

Ptysmaphora SCUDDER, 1895b, p. 21 [**P. fleischeri*; OD]. Fore wing as in *Palaeoptysma* but with costal margin straighter. *Eoc.*, Canada (British Columbia).

Sinophora MELICHAR, 1902, p. 113 [**S. maculosa*; OD]. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (Asian RSFSR)—*Holo*.

Stenecphora SCUDDER, 1895b, p. 17 [**S. punctulata*; OD]. Fore wing with very broad apex, slender clavus; RS arising near base. *Eoc.*, Canada (British Columbia).

Stenolocris SCUDDER, 1895b, p. 19 [**S. venosa*; OD]. Little-known fore wing, with very strong costal vein and RS arising at wing base. [Family assignment doubtful.] *Mio.*, Canada (British Columbia).

Triassoscarta TILLYARD, 1919c, p. 874 [**T. subcostalis*; OD]. Little-known genus, based on incomplete tegmen. SC apparently absent; R long, nearly parallel with costal margin and connected to costal margin by about 8 subequal crossveins. [Originally placed in the *Scytinopteridae* but transferred to *Cercopidae* by EVANS (1956).] *Trias.*, Australia (Queensland).—FIG. 148, 7. **T. subcostalis*; fore wing, $\times 6$ (Evans, 1956).

Triecphora AMYOT & SERVILLE, 1843, p. 561. WOODWARD, 1879. *Eoc.*, England—*Holo*.

Trifidella EVANS, 1956, p. 215 [**T. perfecta*; OD]. Fore wing tegminous, coarsely rugose; several long veinlets between wing margin and R; M and CUA fused basally; CUA forked. *Trias.*, Australia (Queensland).—FIG. 148,6. **T. perfecta*; fore wing, $\times 10$ (Evans, 1961).

Family IPSVICIIDAE Tillyard, 1919

[Ipsviciidae TILLYARD, 1919c, p. 878] [=Stenoviciidae EVANS, 1956, p. 205]

Fore wing uniformly sclerotized; costal margin thick and flattened; vein R consisting usually of R and less commonly of RS; R joined to M by a prominent crossvein; M and CUA usually arising from a common basal stem; M typically branched; CUA and CUP apparently unbranched. Hind wing (known only in *Ipsvicia*) strongly curved anteriorly in distal area; CUA branched. Body unknown. *Perm.*—*Trias.*

The systematic position of this family is obscure. TILLYARD (1919c) originally assigned it to the Homoptera, close to the extinct family Syntonopteridae, but later (1926d) transferred it to the Fulgoroidea of the Homoptera. Subsequently, it has been placed in the Heteroptera by EVANS (1956), in the Homoptera (Auchenorrhyncha) by BECKER-MIGDISOVA (1962b), in the Homoptera (Peloridioidea) by CHINA (1962), and in the Homoptera (Cercopoidea) by EVANS (1963). Also, eight of the genera discussed below (*Stenovicia*, *Permocentrus*, *Permagra*, *Permonia*, *Stanleyana*, *Palaeovicia*, *Apheloscya*, and *Permoscarta*) were placed in a new family, Stenoviciidae, by EVANS (1956), although most of these were previously assigned to the Ipsviciidae (EVANS, 1943b). BECKER-MIGDISOVA (1962b) concluded that the new family is unnecessary, and I have followed her treatment in retaining these genera in the Ipsviciidae.

Ipsvicia TILLYARD, 1919c, p. 878 [**I. jonesi*; OD]. R with several anterior branches to costa near middle of tegmen. TILLYARD, 1923b. *Trias.*, Australia (Queensland).—FIG. 149,2. **I. jonesi*; *a*, tegmen; *b*, hind wing, $\times 4$ (Evans, 1956).

Apheloscya TILLYARD, 1922b, p. 458 [**A. mesocampa*; OD]. Branches of all veins of tegmen very short. [Family assignment doubtful.] EVANS,

1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Ipsviciella BECKER-MIGDISOVA, 1962a, p. 100 [**I. asiatica*; OD]. Tegmen with rounded apex; R nearly straight, with several parallel branches to costal margin; CUA unbranched, merging with M basally. *Trias.*, USSR (Kirghiz).—FIG. 149,5. **I. asiatica*; tegmen, $\times 6.5$ (Becker-Migdisova, 1962b).

Ipsviciopsis TILLYARD, 1922b, p. 464 [**I. elegans*; OD]. RS separating from R near base of tegmen. EVANS, 1963. *Trias.*, Australia (Queensland).

Palaeovicia EVANS, 1943b, p. 189 [**P. incerta*; OD]. Tegmen: RS short; M with 3 branches. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).—FIG. 149,6. **P. incerta*; tegmen, $\times 8$ (Evans, 1943b).

Permagra EVANS, 1943a, p. 7 [**P. distincta*; OD]. Tegmen as in *Tomioscarta* but lacking closed cells. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Permocentrus EVANS, 1956, p. 207 [**Permoscarta trivenulata* TILLYARD, 1926a, p. 19; OD]. Tegmen with M and CUA independent basally. BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Permoscarta TILLYARD, 1918b, p. 726 [**P. Mitchellii*; OD]. Little-known genus. Tegmen as in *Permocentrus* but with 2 crossveins between M and CUA. EVANS, 1943a, 1956; BECKER-MIGDISOVA, 1962b. *Trias.*, Australia (Queensland).

Permovicia EVANS, 1943b, p. 189 [**P. obscura*; OD]. Tegmen with RS broadly curved. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 149,3. **P. obscura*; $\times 10$ (Evans, 1943b).

Stanleyana EVANS, 1943b, p. 188 [**S. pulchra*; OD]. Tegmen with RS apparently absent; M and CUA coalesced basally; M with 3 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 149,8. **S. pulchra*; tegmen, $\times 6.5$ (Evans, 1943b).

Stenovicia EVANS, 1943b, p. 188 [**S. angustata*; OD]. Tegmen as in *Ipsvicia* but much more slender; R long, arising at about midwing; M with 2 very short branches; CUA and M coalesced basally. [Type of family Stenoviciidae EVANS, 1956.] *Perm.*, Australia (New South Wales).—FIG. 149,1. **S. angustata*; fore wing, $\times 8$ (Evans, 1943b).

Tomioscarta BECKER-MIGDISOVA, 1961c, p. 350 [**T. surijokovensii*; OD]. Tegmen with R branched at point of origin of RS; several closed cells between M, CUA, and RS. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 149,7. **T. surijokovensii*; fore wing, $\times 6.5$ (Becker-Migdisova, 1961c).

Tychoscarta BECKER-MIGDISOVA, 1961c, p. 350 [**T. sokolovensii*; OD]. Little-known genus.

Tegmen long and narrow; RS unbranched and continuing in a straight line from stem of R; M unbranched; CUA forked distally. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 149,4. **T. sokolovensis*; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Family ARCHIJASSIDAE Becker-Migdisova, 1962

[Archijassidae BECKER-MIGDISOVA, 1962a, p. 95]

Fore wing very wide, in some species with triangular costal area traversed by vein SC; SC usually divided into 2 long branches; RS present; numerous crossveins between branches of R and M; anal area wide, triangular. *Jur.*

Archijassus HANDLIRSCH, 1906b, p. 501 [**Cercopidium beeri* GEINITZ, 1880, p. 529; SD CARPENTER, herein]. Fore wing with costal margin strongly angular; RS arising beyond midwing; M with 4 branches. EVANS, 1956. *Jur.*, Europe (Germany).—FIG. 148,8. **A. beeri* (GEINITZ); fore wing, $\times 8$ (Evans, 1956).

Atitizon HANDLIRSCH, 1939, p. 144 [**A. jassoides*; OD]. Fore wing very broad; costal margin strongly curved but not angular basally; RS arising at midwing. *Jur.*, Europe (Germany).—FIG. 148,11. **A. jassoides*; fore wing, $\times 8$ (Handlirsch, 1939).

Eojassus HANDLIRSCH, 1939, p. 145 [**E. indistinctus*; OD]. Little-known genus, based on fore wing; costal margin smoothly curved. *Jur.*, Europe (Germany).—FIG. 148,9. **E. indistinctus*; fore wing, $\times 6.5$ (Handlirsch, 1939).

Liojassus HANDLIRSCH, 1939, p. 146 [**L. affinis*; OD]. Fore wing: SC with 2 long branches; RS arising at midwing; costal margin smoothly curved; M with 3 branches. [Family assignment doubtful.] *Jur.*, Europe (Germany).—FIG. 148,1. **L. affinis*; fore wing, $\times 6.5$ (Handlirsch, 1939).

Family HYLICELLIDAE Evans, 1956

[Hylcellidae EVANS, 1956, p. 195]

Fore wing as in Hylcidae (recent), with M coalesced basally with CUA, but CUA1 present and coalesced with part of M3+4 distally. *Trias.*

Hylcella EVANS, 1956, p. 195 [**H. colorata*; OD] [= *Hylcellites* BECKER-MIGDISOVA, 1962a, p. 95, (type, *Hylcella reducta* EVANS)]. CUA with abrupt basal bend; 2 crossveins between RS and M1+2; 1 crossvein between M1+2 and M3+4. *Trias.*, Australia (Queensland).—FIG. 150,6. **H. colorata*; fore wing, $\times 5$ (Evans, 1956).

Family MUNDIDAE Becker-Migdisova, 1960

[Mundidae BECKER-MIGDISOVA, 1960, p. 31]

Fore wing weakly tegminous, without pits; veins thick; RS, M, and CUA with prominent projections; costal area and anal area broad. *Perm.*

Mundus BECKER-MIGDISOVA, 1960, p. 31 [**M. nodosus*; OD]. Fore wing relatively broad, with asymmetrical, blunt apex; R diverging abruptly at midwing toward costal margin, forking; R2 parallel to RS. *Perm.*, USSR (European RSFSR).—FIG. 150,5. **M. nodosus*; fore wing, $\times 8$ (Becker-Migdisova, 1960).

Family PEREBORIIDAE Zalessky, 1930

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 813 (pro Pereboridae ZALESSKY, 1930, p. 1026)] [= Permoglyphidae EVANS, 1943b, p. 183]

Fore wing membranous; veins R, RS, and CUA with extensive branching. BECKER-MIGDISOVA, 1962b. *Perm.*—*Trias.*

Pereboria ZALESSKY, 1930, p. 1021 [**P. bella*; OD]. Little-known genus, based on fore wing. R with close pectinate branching; crossveins numerous, irregular; wing large, about 40 mm long. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 150,9. **P. bella*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Crosbella EVANS, 1956, p. 192 [**C. elongata*; OD]. Fore wing as in *Permobrachus*, but M more extensively branched. *Trias.*, Australia (Queensland).—FIG. 150,1. **C. elongata*; fore wing, $\times 4.5$ (Evans, 1956).

Kaltanopibrocha BECKER-MIGDISOVA, 1961c, p. 357 [**K. boreoscytinoides*; OD]. Little-known genus, based on hind wing fragment. Costal margin almost straight; R directed posteriorly in apical region, pectinately branched; M forking before RS. [Family assignment doubtful.] *Perm.*, USSR (Asian RSFSR).—FIG. 150,10. **K. boreoscytinoides*; hind wing, $\times 4.5$ (Becker-Migdisova, 1961c).

Neuropibrocha BECKER-MIGDISOVA, 1961c, p. 356 [**N. ramisubcostalis*; OD]. Fore wing as in *Pereboria*, but R with fewer pectinate branches and less dense reticulation of branches of RS, M, and CUA; area between stems R and M with few crossveins. *Perm.*, USSR (Asian RSFSR).—FIG. 150,7. **N. ramisubcostalis*; fore wing, $\times 2.0$ (Becker-Migdisova, 1961c).

Permobrachus EVANS, 1943b, p. 183 [**Permopdipthera dubia* TILLYARD, 1926a, p. 24; OD]. Fore wing shaped as in *Scytophara*, but R1 curv-

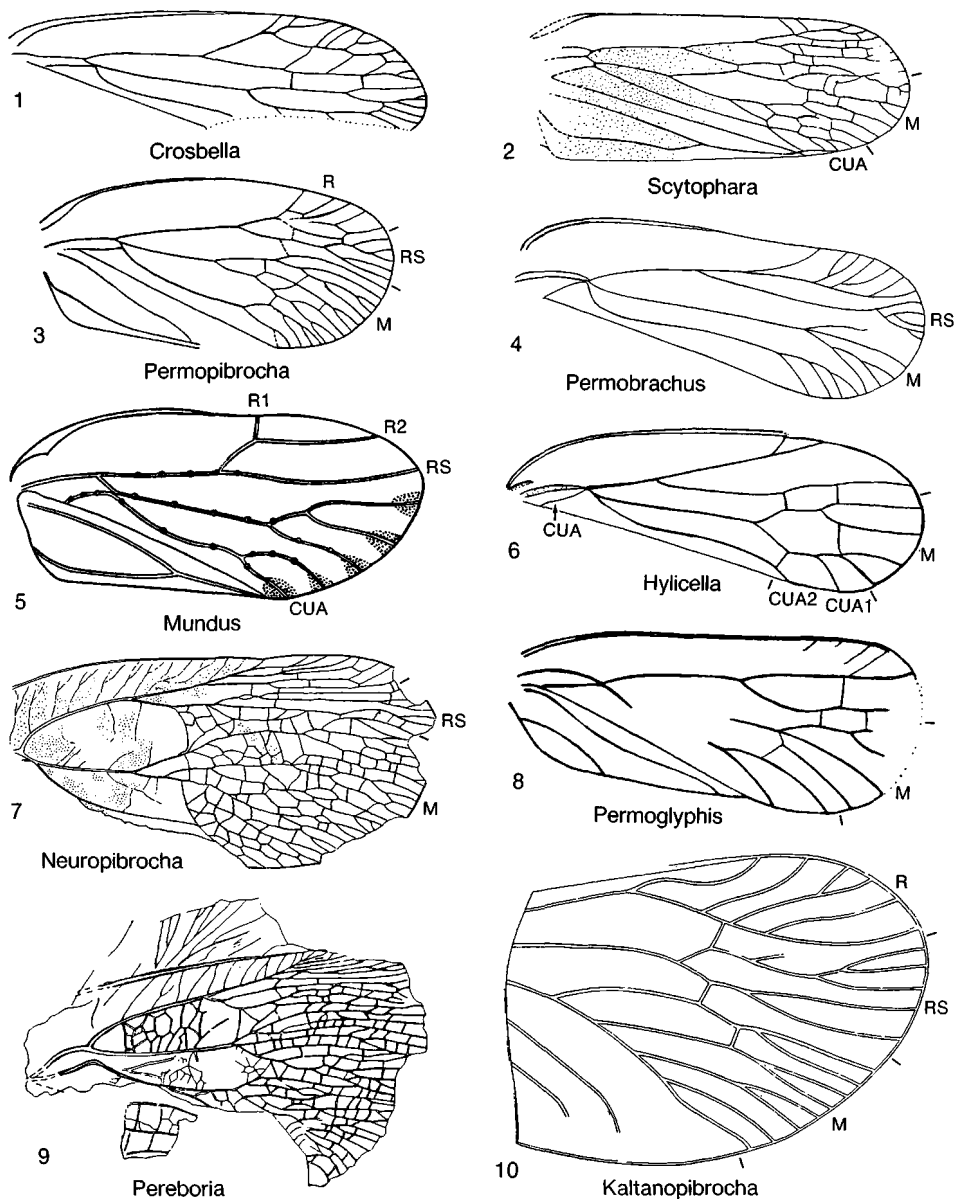


FIG. 150. Hylicellidae, Mundidae, and Pereboriidae (p. 233–235).

ing abruptly to anterior margin; branching of R2 pectinate; M branching well beyond midwing. *Perm.*, Australia (New South Wales).—FIG. 150.4. *P. magnus* EVANS; fore wing, $\times 3.5$ (Evans, 1943b).

Permoglyphis TILLYARD, 1926a, p. 22 [**P. belmontensis*; OD]. Little-known genus, based on fore wing; similar to *Permopibrocha* but apparently with less branching of R, RS, and M; costal margin nearly straight. *Trias.*, Australia (New

South Wales).—FIG. 150.8. **P. belmontensis*; fore wing, $\times 4.5$ (Evans, 1956).

Permopibrocha MARTYNOV, 1935c, p. 18 [**P. ramosa*; OD]. Fore wing as in *Pereboria*, but R with fewer branches; M more deeply forked than CUA; fore wing small. *Perm.*, USSR (European RSFSR).—FIG. 150.3. **P. ramosa*; fore wing, $\times 3.5$ (Martynov, 1935c).

Scytophara MARTYNOV, 1937b, p. 36 [**S. extensa*; OD]. Fore wing more slender than in *Permopi-*

brocha; costal margin straight beyond base; M forking at about level of origin of RS. *Perm.*, USSR (European RSFSR).—FIG. 150,2. **S. extensa*; fore wing, $\times 6.5$ (Martynov, 1937b).

Family FULGORIDIIDAE

Handlirsch, 1939

[*nom. transl.* BECKER-MIGDISOVA, 1962b, p. 184, ex Fulgoridiinae HANDLIRSCH, 1939, p. 122]

Fore wing tegminous; costal margin only slightly arched; vein SC long, without branches; RS arising at about midwing; CUA forking well before origin of RS; crossveins few. Hind wing a little shorter than fore wing; anal area very broad; RS simple or with short fork; 1A arched away from CUP. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*

Fulgoridium HANDLIRSCH, 1906b, p. 496 [**Pbyrganidium balticum* GEINITZ, 1880, p. 527; OD] [= *Fulgoridulum* HANDLIRSCH, 1939, p. 140 (type, *F. egens*)]. Fore wing slender; usually with maculations; SC close to margin; R with a series of short branches distally; CUA with several long branches. BODE, 1953; EVANS, 1956. *Jur.*, Europe (Germany).—FIG. 151,2a. *F. punctatum* HANDLIRSCH; fore wing, $\times 10$ (Handlirsch, 1939).—FIG. 151,2b. *F. reductum* HANDLIRSCH; hind wing, $\times 10$ (Handlirsch, 1939).

Metafulgoridium CARPENTER, herein [**M. spilotum* HANDLIRSCH, 1939, p. 139; OD]. Fore wing as in *Fulgoridium*, but CUA2 unbranched. [The original generic name, *Metafulgoridium*, was a *nomen nudum* (HANDLIRSCH, 1939).] *Jur.*, Europe (Germany).—FIG. 151,1. **M. spilotum*; fore wing, $\times 6.5$ (Handlirsch, 1939).

Family LOPHOPIDAE Stål, 1866

[Lophopidae Stål, 1866, p. 130]

Head markedly narrower than pronotum; vertex usually narrow; pronotum short and broad, tricarinate. Fore wing coriaceous, with conspicuous venation and supernumerary longitudinal veins and crossveins; wing usually elongate; apical margin broadly rounded; claval veins united before apex. Fore and middle tibiae usually compressed. *Jur.*—*Holo.*

Lophops SPINOLA, 1838, p. 205. *Holo.*

Eofulgoridium MARTYNOV, 1937a, p. 164 [**E. kirsylkiense*; OD]. Fore wing with SC about midway between C and R; M dividing at midwing; M with 3 branches. Hind wing little known; costal margin concave; RS arising beyond midwing; M and CUA dividing beyond midwing. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*, USSR

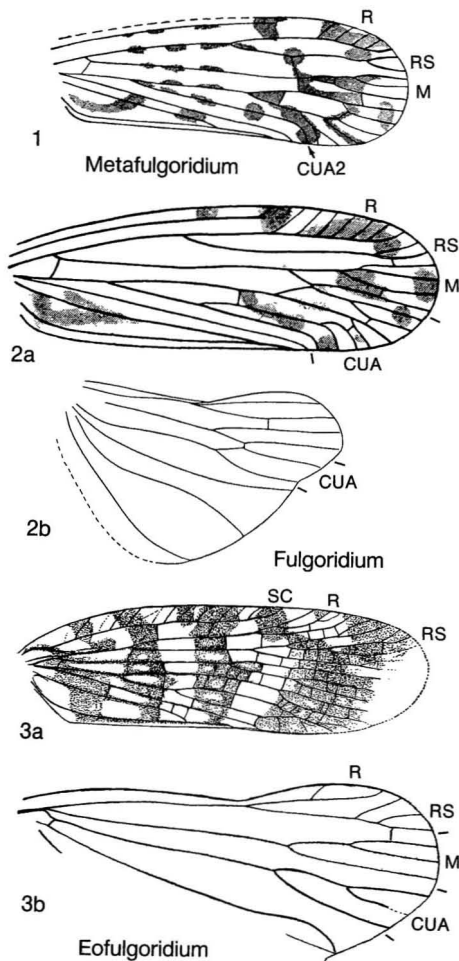


FIG. 151. Fulgoridiidae and Lophopidae (p. 235).

(Kirghiz).—FIG. 151,3a. **E. kirsylkiense*; fore wing, $\times 4.2$.—FIG. 151,3b. *E. proximum* MARTYNOV; hind wing, $\times 5$ (Martynov, 1937a). **Scoparidea** COCKERELL, 1920c, p. 243 [**S. nebulosa*; OD]. Fore wing with RS parallel to R; apical region with numerous, parallel veins; no regular gradate series of veins. [Family assignment doubtful.] *Eoc.*, USA (Colorado).

Family CIXIIDAE Spinola, 1838

[Cixiidae SPINOLA, 1838, p. 204]

Head not elongate; antennae with 2 segments, bearing flagella; wings unusually well developed. In fore wing, veins SC, R, and M with common stem; claval suture distinct; claval veins united into a claval stem. *Perm.*—*Holo.*

- Cixius** LATREILLE, 1804, p. 168. [The assignment of a Jurassic species from England to this genus is very doubtful (FENNAH, 1961), as is that of the several species in Baltic amber (GERMAR & BERENDT, 1856).] SCUDDER, 1890. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado)—*Holo.*
- Asiocixius** BECKER-MIGDISOVA, 1962a, p. 97 [**A. fulgorooides*; OD]. Fore wing membranous, except at base; costal margin smoothly rounded; R2 curved toward RS and giving rise to several veinlets; RS forked distally; M forking beyond midwing and with extensive pectinate branching; CUA with a long fork. *Trias.*, USSR (Kirghiz).—FIG. 152,6. **A. fulgorooides*; fore wing, $\times 5$ (Becker-Migdisova, 1962b).
- Boreocixius** BECKER-MIGDISOVA, 1955, p. 1100 [**B. sibiricus*; OD]. Fore wing with costal margin strongly thickened; RS arising very near wing base; R and RS with very short branches; fork of CUA long and curved. *Trias.*, USSR (Asian RSFSR).—FIG. 152,12. **B. sibiricus*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).
- Cixiella** BECKER-MIGDISOVA, 1962a, p. 98 [**C. reducta*; OD]. Fore wing weakly tegminous, distal portion membranous; RS arising near midwing; M forking beyond level of origin of RS, with 3 terminal branches, and forming a large, closed cell; CUA curved basally. *Trias.*, USSR (Kirghiz).—FIG. 152,8. **C. reducta*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).
- Cyclocyrtina** MARTYNOV, 1926b, p. 1349 [**C. delutinervis*; OD]. Fore wing tegminous, elongate; costal margin only slightly curved; R with a series of branches as in *Mesocixiella* but shorter; M joined to RS distally by a recurved branch. Hind wing little known; M with 2 long branches, arising before midwing. EVANS, 1956. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Kazakh, Tadzhik).—FIG. 152,3. **C. delutinervis*, *Jur.*, Kazakh; fore wing, $\times 6$ (Becker-Migdisova, 1962b).
- Diaplegma** SCUDDER, 1890, p. 288 [**D. abductum* SCUDDER, 1890, p. 290; SD CARPENTER, herein]. Similar to *Cixius*, but RS arising near midwing, each of its forks dividing into 2 or 3 distal, curved branches. *Oligo.*, USA (Colorado).
- Eofulgorella** COCKERELL, 1909j, p. 172 [**E. bradburyi*; OD]. Fore wing resembling that in *Oliarius* but elongate and with costal margin concave; crossveins forming a very regular series. [Family assignment doubtful.] *Eoc.*, USA (Colorado).
- Eoliarius** COCKERELL, 1925a, p. 10 [**E. quadri-stictus*; OD]. Similar to *Oliarius*, but RS arising well before the pterostigmal area and giving rise to 4 very oblique branches anteriorly. *Eoc.*, USA (Colorado).
- Hyaesthes** SIGNORET, 1865, p. 128 [**H. obsoletus*; OD]. STATZ, 1950a. *Oligo.*, Europe (Germany)—*Holo.*
- Mesocixiella** BECKER-MIGDISOVA, 1949b, p. 38 [**M. asiatica*; OD]. Fore wing with costal margin only slightly curved; R with a series of parallel branches leading to margin; RS arising before midwing with 3 or 4 terminal branches; M forked beyond midwing. EVANS, 1956. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Kazakh).—FIG. 152,7. **M. asiatica*; fore wing, $\times 6.5$ (Becker-Migdisova, 1962b).
- Mesocixius** TILLYARD, 1919c, p. 876 [**M. trias-sicus*; OD]. Fore wing with RS forking about halfway between origin of RS and wing apex; fork of M less distal. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 152,10. **M. trias-sicus*; fore wing, $\times 5.4$ (Tillyard, 1919c).
- Mundopoides** COCKERELL, 1925g, p. 11 [**M. cisthenaria*; OD]. Similar to *Mundopa* (recent), having nearly straight costal and outer margins, the apex being obliquely truncate; SC terminating at midwing. *Mio.*, USSR (Asian RSFSR).
- Myndus** STÅL, 1862, p. 307. COCKERELL, 1926b. *Oligo.*, England—*Holo.*
- Oeclixius** FENNAH, 1963, p. 43 [**O. amphion*; OD]. Similar to *Oecleus* (recent) but with long, slender tibiae; pterostigma only moderately developed; tegminal veins distinctly granulate. *Mio.*, Mexico (Chiapas).—FIG. 152,5. **O. amphion*; fore wing, $\times 13$ (Fennah, 1963).
- Oliarites** SCUDDER, 1890, p. 293 [**Mnemosyne terrentula* SCUDDER, 1878b, p. 773; OD]. Little-known genus, with head less than half as broad as thorax; veins forming a weak reticulation distally. [Family assignment doubtful.] *Eoc.*, USA (Wyoming).
- Oliarius** STÅL, 1862, p. 306. COCKERELL, 1910b. *Oligo.*, Europe (Baltic)—*Holo.*
- Oligonila** CARPENTER, herein [**O. defectuosa* THÉOBALD, 1937a, p. 258; OD]. Fore wing as in *Anila* (recent) but lacking the oblique vein in the costal area. [The original generic name, *Oligonila*, was a *nomen nudum* (THÉOBALD, 1937a).] *Oligo.*, Europe (France).
- Permcixiella** BECKER-MIGDISOVA, 1961c, p. 361 [**P. venosa*; OD]. Fore wing elongate, costal margin nearly straight; R2 straight; branches of CUA nearly straight. *Perm.*, USSR (Asian RSFSR).—FIG. 152,4. **P. venosa*; fore wing, $\times 5.4$ (Becker-Migdisova, 1961c).
- Protoliarius** COCKERELL, 1920c, p. 243 [**P. hamatus*; OD]. Similar to *Oliarius* but without a stigmatic spot on wings. COCKERELL, 1924a; COCKERELL & LEVEQUE, 1931. *Eoc.*, USA (Colorado).
- Scytocixius** MARTYNOV, 1937b, p. 34 [**S. mendax*; OD]. Fore wing broader distally than basally; costal margin smoothly curved; R2 strongly arched away from margin; RS similarly arched but less strongly; M with 3 distal branches; CUA forking at the level of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 152,1. **S. mendax*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).
- Suriokocixius** BECKER-MIGDISOVA, 1961c, p. 359

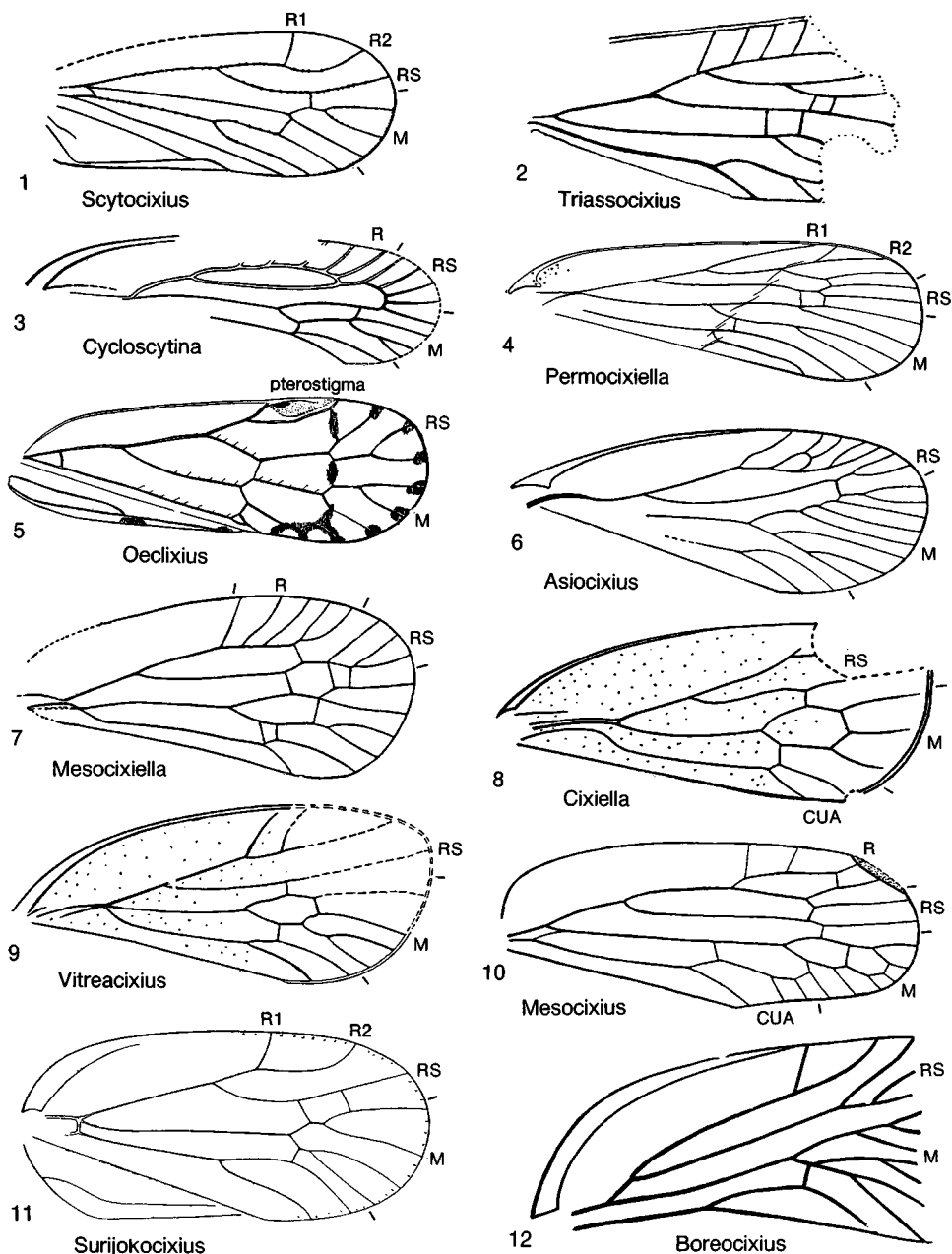


FIG. 152. Cixiidae (p. 236-238).

[**S. tomiensis*; OD]. Fore wing broad, with broadly rounded apex; costal margin thickened; R2 strongly curved; RS unbranched; branches of CUA long and curved. EVANS, 1956. *Perm.*, USSR (Asian RSFSR).—FIG. 152,11. **S. tomiensis*; fore wing, $\times 15$ (Becker-Migdisova, 1961c). **Triassocixius** TILLYARD, 1919c, p. 878 [**T. aus-*

tralicus; OD]. Little-known genus, based on fragment of fore wing; R forked close to the origin of RS; oblique crossveins from R to costal margin. [Family position uncertain.] *Trias.*, Australia (Queensland).—FIG. 152,2. **T. australicus*; fore wing, $\times 5.5$ (Evans, 1956). **Vitreacixius** BECKER-MIGDISOVA, 1962a, p. 99 [**V.*

ellipticus; OD]. Fore wing weakly tegminous; similar to *Cixiella*, but RS arising slightly more basally; M with 4 branches, closed cell smaller than in *Cixiella*. *Trias.*, USSR (Kirghiz).—FIG. 152,9. **V. ellipticus*; fore wing, $\times 6$ (Becker-Migdisova, 1962b).

Family ACHILIDAE Stål, 1866

[Achilidae STÅL, 1866, p. 130]

Head usually small; frons and clypeus large. Hind tibiae elongate; second segment of hind tarsus large. Fore wing well developed, basal two-thirds thickened; veins SC and R united for a short interval basally; SC with 2 or more short branches leading to costal margin, forming stigmatic area; R branched only apically, connected to M by 2 or more crossveins; M with at least 3 branches; clavus short, claval veins united to form claval stem. Hind wing moderately large. *Oligo.*—*Holo.*

Achilus KIRBY, 1819, p. 474. *Holo.*

Elidiptera SPINOLA, 1839, p. 304. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Proteiptera USINGER, 1939, p. 66 [**P. kaweckii*; OD]. Similar to *Eiptera* (recent) but with vertex distinctly in front of eyes; posterior margin of vertex concavely arcuate. *Oligo.*, Europe (Baltic).

Family RICANIIDAE

Amyot & Serville, 1843

[Ricaniidae AMYOT & SERVILLE, 1843, p. 527]

Head usually as wide as the pronotum; vertex short and broad; clypeus much narrower than frons. Fore wing large, broadly triangular; costal margin usually nearly straight; costal area broad with numerous crossveins; basal area of clavus without pustules; venation diverse; veins R, M, and CU typically with numerous branches, with 1 or 2 subapical lines of gradate crossveins. Hind wing smaller than fore wing and with reduced venation. Basal segment of hind tarsus very small, without lateral spines. *Trias.*—*Holo.*

Ricania GERMAR, 1818, p. 221. DALMAN, 1826; GIEBEL, 1862; SCUDDER, 1890. *Eoc.*, Canada (British Columbia); *Oligo.*, Europe (Baltic)—*Holo.* *Cotradechites* FENNAH, 1968, p. 144 [**C. litbinus*; OD]. Similar to *Cotrades* (recent), but tegmen twice as long as broad; costal area broad, with dense venation. *Paleoc.*, USA (North Dakota).

Dilaropsis COCKERELL, 1920c, p. 244 [**D. ornatus*; OD]. Fore wing broad, triangular; costal margin slightly convex; SC ending about two-thirds wing length from base; M diverging abruptly from R near origin of RS. *Eoc.*, USA (Colorado).

Eobladina HAUPT, 1956, p. 13 [**E. antiqua*; OD]. Little-known genus, based on fore wing; costal area wide distally; SC joined to R at base by curved crossvein, forming a very short basal cell; RS arising well before midwing. *Eoc.*, Europe (Germany).—FIG. 153,2. **E. antiqua*; fore wing, $\times 6$ (Haupt, 1956).

Eoricania HENRIKSEN, 1922b, p. 24 [**E. danica*; OD]. Fore wing as in *Ricania* (recent), but 1A and 2A joined proximally beyond wing base. *Eoc.*, Europe (Denmark).—FIG. 153,4. **E. danica*; fore wing, $\times 2.5$ (Henriksen, 1922b).

Hammapteryx SCUDDER, 1890, p. 298 [**H. reticulata*; OD]. Fore wing subtriangular; costal margin arched at base; numerous crossveins from SC to margin; R with at least 2 arcuate branches distally; RS arising well before midwing. COCKERELL, 1920a, 1920b; COCKERELL & SANDHOUSE, 1921; HENRIKSEN, 1922b; PITON, 1940a. *Eoc.*, USA (Colorado, Wyoming), Europe (Denmark, France), England.—FIG. 153,3. *H. paucistriata* HENRIKSEN, Denmark; fore wing, $\times 4$ (Henriksen, 1922b).

Ludibrium BECKER-MIGDISOVA, 1962a, p. 100 [**L. ludus*; OD]. Hind wing little known; RS apparently arising distally as a continuation of stem R; M forked to about midwing. *Trias.*, USSR (Kirghiz).—FIG. 153,5. **L. ludus*; hind wing, $\times 6$ (Becker-Migdisova, 1962a).

Neoricania CARPENTER, 1990, p. 131, *nom. subst. pro Eoricania* HAUPT, 1956, p. 12, *non* HENRIKSEN, 1922b [**Eoricania reticulata* HAUPT; OD]. Fore wing with costal space much narrower than in *Eoricania*; SC much closer to C. *Eoc.*, Europe (Germany).

Scolypopites TILLYARD, 1923a, p. 17 [**S. bryani*; OD]. Fore wing as in *Scolypopa* (recent), but SC shorter, reaching only a little beyond midwing; only one series of gradate veins. *Mio.*, Australia (Queensland).—FIG. 153,6. **S. bryani*; fore wing, $\times 3.5$ (Tillyard, 1923a).

Family NOGODINIDAE

Melichar, 1898

[Nogodinidae MELICHAR, 1898, p. 204]

Head about as wide as pronotum; frons longer than wide. Fore wing large, usually broadest towards apex, coriaceous or hyaline, with numerous veins and crossveins; costal area with several crossveins; basal cell usually large; clavus not punctulate; claval stem reaching apex of fore wing. Hind tibiae with

lateral spines; second segment of hind tarsus small, with a pair of spines distally. *Eoc.*—*Holo.*

Nogodina STÅL, 1859, p. 326. *Holo.*

Detyopsis COCKERELL, 1920c, p. 242 [**D. scuderi*; OD]. Fore wing much as in *Detya* (recent); veinlets from SC to costal margin numerous; RS forking well before midwing. *Eoc.*, USA (Colorado).

Tritophania JACOBI, 1937, p. 188 [**T. patruelis*; OD]. Similar to *Gaetulia* (recent), but frons without a keel; pterostigma absent. *Oligo.*, Europe (Baltic).—FIG. 153, 1. **T. patruelis*; whole insect, $\times 3.4$ (Jacobi, 1937).

Family FULGORIDAE Latreille, 1807

[Fulgoridae LATREILLE, 1807, p. 163]

Head usually large and simple, but often with prominent, cephalic process; postclypeus large, triangular; compound eyes large. Fore wing well developed, with numerous supernumerary veins and crossveins; hind wing with the anal and jugal areas reticulate. *Eoc.*—*Holo.*

Fulgora LINNÉ, 1767, p. 703. *Holo.*

Callospilopteron COCKERELL, 1920c, p. 245 [**C. ocellatum*; OD]. Fore wing broad, with obtuse apex; costal area much reduced; SC short; anterior veinlets from SC and R very oblique; ocelliform spots near outer margin. [Family assignment doubtful.] *Eoc.*, USA (Wyoming).

Eucophora SPINOLA, 1839, p. 200. SCUDDER, 1895b. *Eoc.*, Canada (British Columbia)—*Holo.*

Lystra FABRICIUS, 1803, p. 56. SCUDDER, 1890. [Generic assignment of fossil doubtful.] *Eoc.*, USA (Wyoming)—*Holo.*

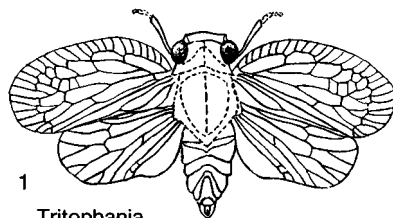
Nyktalos METCALF, 1952, p. 230, *nom. subst. pro Nyctophylax* SCUDDER, 1890, p. 279, *non FITZINGER*, 1860 [**Nyctophylax ubleri* SCUDDER; OD]. Large species of uncertain affinities; head with a stout, recurved process; legs stout; femora and tibiae carinate. *Oligo.*, USA (Colorado).

Poiocera LAPORTE, 1832, p. 221. GERMAR & BERENDT, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

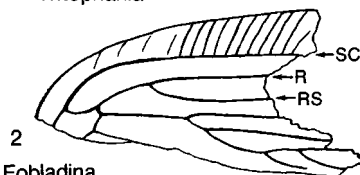
Family FLATIDAE Spinola, 1838

[Flatidae SPINOLA, 1838, p. 205]

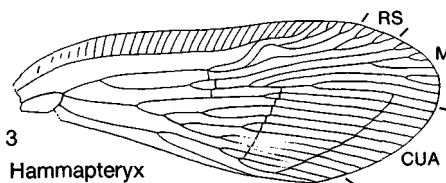
Head narrower than thorax; lateral edges of face not angular. Fore wing with costal area having crossveins; basal area of clavus granulate; clavus often open, claval veins separate or joined apically. Hind tibiae without a movable spur; first hind tarsomere short,



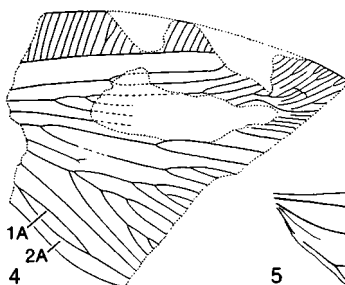
1
Tritophania



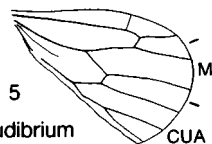
2
Eobladina



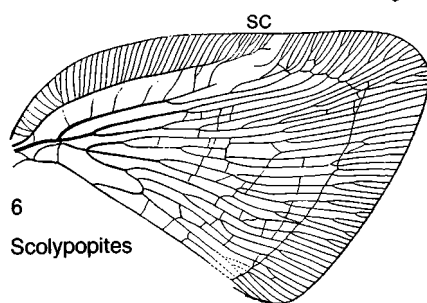
3
Hammapteryx



4
Eoricania



5
Ludibrum



6
Scolyopites

FIG. 153. Ricaniidae and Nogodinidae (p. 238–239).

second one small with a spine on each side. *Eoc.*—*Holo.*

Flata FABRICIUS, 1798, p. 511. *Holo.*

Aphaena GUÉRIN & MÉNEVILLE, 1833, p. 452. SCUDDER, 1890; COCKERELL, 1920c. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado)—*Holo.*

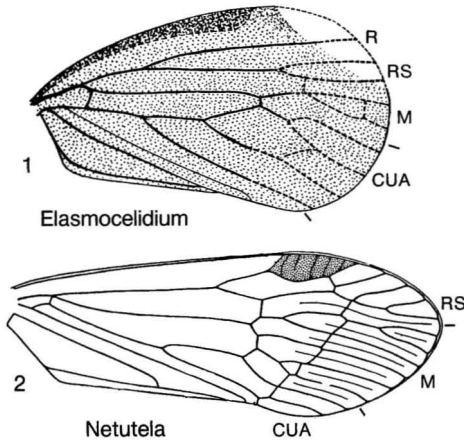


FIG. 154. Issidae and Dictyopharidae (p. 240–241).

Ficarasites SCUDDER, 1890, p. 301 [**F. stigmatiscum*; OD]. Little-known genus; costal area narrow, with oblique veinlets; few crossveins. *Eoc.*, USA (Wyoming).

Giselia HAUPT, 1956, p. 14 [**G. multifurcata*; OD]. Fore wing as in *Uxantis* (recent); SC curved away from margin as it approaches midwing; R and M fused basally, separating early, with RS arising about one-sixth wing length from base; CUA apparently with a deep fork. *Eoc.*, Europe (Germany).

Lechaea STÅL, 1866, p. 236. HENRIKSEN, 1922b. *Eoc.*, Europe (Denmark)—*Holo.*

Ormenis STÅL, 1862, p. 68. COCKERELL, 1926a. *Tert.* (epoch unknown), Argentina. *Holo.*

Poekilloptera LATREILLE, 1796, p. 90. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Thaumastocladus COCKERELL & SANDHOUSE, 1921, p. 456 [**T. simplex*; OD]. Fore wing as in *Gaga* (recent); costal area broad, with numerous oblique veinlets; R branching apically; M and CUA coalesced to about midwing; CUP distinctly forked. [Family position doubtful.] COCKERELL, 1924a. *Eoc.*, USA (Wyoming).

Family ARAEOPIDAE Metcalf, 1938

[*Araeopidae* METCALF, 1938, p. 281]

Head usually small; antennae short, usually not longer than head and thorax combined. Fore wing diverse, ranging from brachypterous, with reduced venation, to fully developed, with normal venation; vein SC typically with 2 branches; R coalesced with SC for about half its length, then coalesced with part of M; M usually with 3 branches; CU with 3 branches. Hind wing usually present, sometimes reduced; SC and R coalesced for more than half their lengths; M

unbranched. Hind femora and tibiae elongate; spur well developed at apex of tibia, either spinelike or much enlarged and complex. *Eoc.*—*Holo.*

Araeopus SPINOLA, 1839, p. 336. COCKERELL, 1924a; STATZ, 1950a. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany)—*Holo.*

Amagua COCKERELL, 1924a, p. 3 [**A. fortis*; OD]. Fore wing as in *Stenocranus* (recent); wing of uniform width, narrow; crossveins m-cu long. *Mio.*, USSR (Asian RSFSR).

Chloriona FIEBER, 1866, p. 519. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Liburnia STÅL, 1866, p. 179. COCKERELL, 1917h. *Mio.*, Burma—*Holo.*

Family ISSIDAE Spinola, 1838

[*Issidae* SPINOLA, 1838, p. 158]

Head usually at least as wide as thorax; lateral margins of thorax not keeled; anterior margin of pronotum rounded and extended. Fore wing usually with reduced venation and often small; costal area small, without crossveins, or absent; base of costal margin not strongly curved; clavus not granulate. Hind tibiae with 2 to 4 spines; second hind tarsomere with a spine on each side. *Jur.*—*Holo.*

Issus FABRICIUS, 1803, p. 99. BERVOETS, 1910. *Oligo.*, Europe (Baltic)—*Holo.*

Elasmocelidium MARTYNOV, 1926b, p. 1355 [**E. rotundatum*; OD]. Fore wing short, much broadened distally; SC nearly parallel to costal margin; costal margin thickened; RS arising well before midwing; RS and M forked distally; anal area extending only to about midwing. BODE, 1953; EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh); Europe (Germany).—FIG. 154, 1. **E. rotundatum*, Kazakh; fore wing, $\times 6.3$ (Becker-Migdisova, 1962b).

Issites HAUPT, 1956, p. 16 [**I. glaber*; OD]. Fore wing as in *Issus* (recent) but without the dense reticulation. *Eoc.*, Europe (Germany).

Mesotubulistrum BECKER-MIGDISOVA, 1949b, p. 35 [**M. asiaticum*; OD]. Similar to *Elasmocelidium*, but RS arising near midwing. *Jur.*, USSR (Kazakh).

Tetragonidium BODE, 1953, p. 194 [**T. paralelogramma*; OD]. Fore wing as in *Elasmocelidium*, but M with more branches. *Jur.*, Europe (Germany).

Family DICTYOPHARIDAE Spinola, 1838

[*Dictyopharidae* SPINOLA, 1838, p. 202]

Head relatively large; structural details of vertex and of frons diverse. Legs usually slender

and elongate; hind tibiae commonly with 3 to 5 stout spines; second hind tarsal segment large, with a row of small spines at apex. Fore wing either normal or reduced; vein SC and R coalesced beyond basal area of wing; R branching irregularly distally; an irregular transverse line commonly formed by series of crossveins in apical third of wing. Hind wing usually large, with irregular venation. EMELJANOV, 1983. *Cret.—Holo.*

Dictyophara GERMAR, 1833, p. 175. [The family assignment of "*Dictyophara scudderi* PITON (1940a), from the Eocene of France, is uncertain.] SCUDDER, 1890; BECKER-MIGDISOVA, 1964; EMELJANOV, 1983. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Chanithus AMYOT, 1847, p. 160. BECKER-MIGDISOVA, 1964; EMELJANOV, 1983. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Florissantia SCUDDER, 1890, p. 293 [**F. elegans*; OD]. Little-known genus, apparently related to *Dictyophara*. [Originally placed in Cixiidae by SCUDDER (1890); transferred to Dictyopharidae by EMELJANOV (1983).] COCKERELL, 1909a. *Oligo.*, USA (Colorado).

Netutela EMELJANOV, 1983, p. 84 [**N. annunciator*; OD]. Similar to *Cladodiptera* (recent), but clavus of fore wing without crossveins; M forking distally of origin of RS. *Cret.*, USSR (Asian RSFSR).—FIG. 154,2. **N. annunciator*; fore wing, $\times 6.5$ (Emeljanov, 1983).

Family ARCHESCYTINIDAE Tillyard, 1926

[Archescytinidae TILLYARD, 1926g, p. 385] [=Permpopsyllidae TILLYARD, 1926g, p. 390; Lithoscytinidae CARPENTER, 1933a, p. 436; Maueriidae ZALESSKY, 1937e, p. 54; Permoscytinopsidae ZALESSKY, 1939, p. 36; Uraloscytinidae ZALESSKY, 1939, p. 40; Maripsoicidae ZALESSKY, 1939, p. 44; Kaltanaphididae SZELEGIEWICZ, 1971, p. 63]

Fore and hind wings membranous, similar in size and almost alike in venation. Fore wing with vein SC very close and parallel to R+M, R, and R1; R forming a pterostigma; RS originating at about midwing; M usually with at least 3 branches; CUA arising from stem CU, then directed towards R+M, which it touches at the point of separation of M; CUA forked; anal area small. Hind wing similar to fore wing except that CUA arises as an independent vein from the wing base and is not directed towards R+M. Head hypognathous; beak long; antennae long, multisegmented; ovipositor prominent in some genera at least. SZELEGIEWICZ & POPOV, 1978. *Perm.*

Archescytina TILLYARD, 1926g, p. 385 [**A. permiana*; OD] [=*Maueria* ZALESSKY, 1937e, p. 54 (type, *M. sylvensis*); *Permoscytinopsis* ZALESSKY, 1939, p. 36 (type, *P. maueriaeformis*)]. Fore wing with costal margin nearly straight except near base; SC close and parallel to R; R+M arched anteriorly; R2 parallel to RS; M usually with 3 branches. Antennae long and slender, with about 25 segments; beak long; forelegs with thickened femora; female with long, retractible ovipositor. CARPENTER, 1931b, 1939; ZALESSKY, 1937e, 1939; BECKER-MIGDISOVA, 1961c, 1961d, 1962b. *Perm.*, USA (Kansas), USSR (European and Asian RSFSR).—FIG. 155,1a. *Archescytina* sp., USSR; lateral view of body, $\times 6$ (Becker-Migdisova, 1961d).—FIG. 155,1b,c. **A. permiana*, Kansas; *b*, fore wing; *c*, hind wing, $\times 6.5$ (Carpenter, 1939).

Bekkerscytina EVANS, 1958, p. 111 [**B. primitiva*; OD]. Similar to *Eoscytina*, but RS arising nearer to origin of *M. Perm.*, Australia (New South Wales).—FIG. 155,10. **B. primitiva*; fore wing, $\times 6.3$ (Evans, 1958).

Eoscytina EVANS, 1958, p. 109 [**E. migdisovae*; OD]. Similar to *Archescytina*, but fork of CUA very deep and broad and stem of CUA, as it leaves CUP, sigmoidally curved. *Perm.*, Australia (New South Wales).—FIG. 155,9. **E. migdisovae*; fore wing, $\times 6$ (Evans, 1958).

Kaltanaphis BECKER-MIGDISOVA, 1959a, p. 107 [**K. permiensis*; OD]. Little-known genus, based on fragment of hind wing. [Originally assigned to Permaphidopseidae; placed in new family, Kaltanaphididae, by SZELEGIEWICZ, 1971; transferred to Archescytinidae by SZELEGIEWICZ & POPOV, 1978.] *Perm.*, USSR (Asian RSFSR).

Kaltanoscytina BECKER-MIGDISOVA, 1959a, p. 105 [**K. nigra*; OD]. Wings as in *Archescytina*, but R longer and straighter in both pairs. BECKER-MIGDISOVA, 1961c; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (Asian RSFSR).—FIG. 155,8. **K. nigra*; fore wing, $\times 7$ (Becker-Migdisova, 1961c).

Maripsozus ZALESSKY, 1939, p. 44 [**M. ambiguus*; OD]. Little-known fore wing; venation as in *Archescytina*, but M apparently with 2 branches. EVANS, 1956. *Perm.*, USSR (European RSFSR).

Paleoscytina CARPENTER, 1931b, p. 118 [**P. brevistigma*; OD]. Similar to *Archescytina*, but CUA of fore wing unbranched. BECKER-MIGDISOVA, 1961c. *Perm.*, USA (Kansas), USSR (Asian RSFSR).—FIG. 155,3. **P. brevistigma*; fore wing, $\times 18$ (Carpenter, 1933a).

Permpopsylla TILLYARD, 1926g, p. 390 [**P. americana*; OD] [=*Lithoscytina* CARPENTER, 1933a, p. 436 (type, *L. cubitalis*)]. Fore wing as in *Archescytina* but relatively broader; costal margin slightly concave at level of origin of *M.* BECKER-MIGDISOVA, 1960, 1961c, 1962b. *Perm.*, USA (Kansas), USSR (European and Asian RSFSR).—FIG. 155,7. **P. americana*; fore wing, $\times 16$ (Carpenter, 1931b)

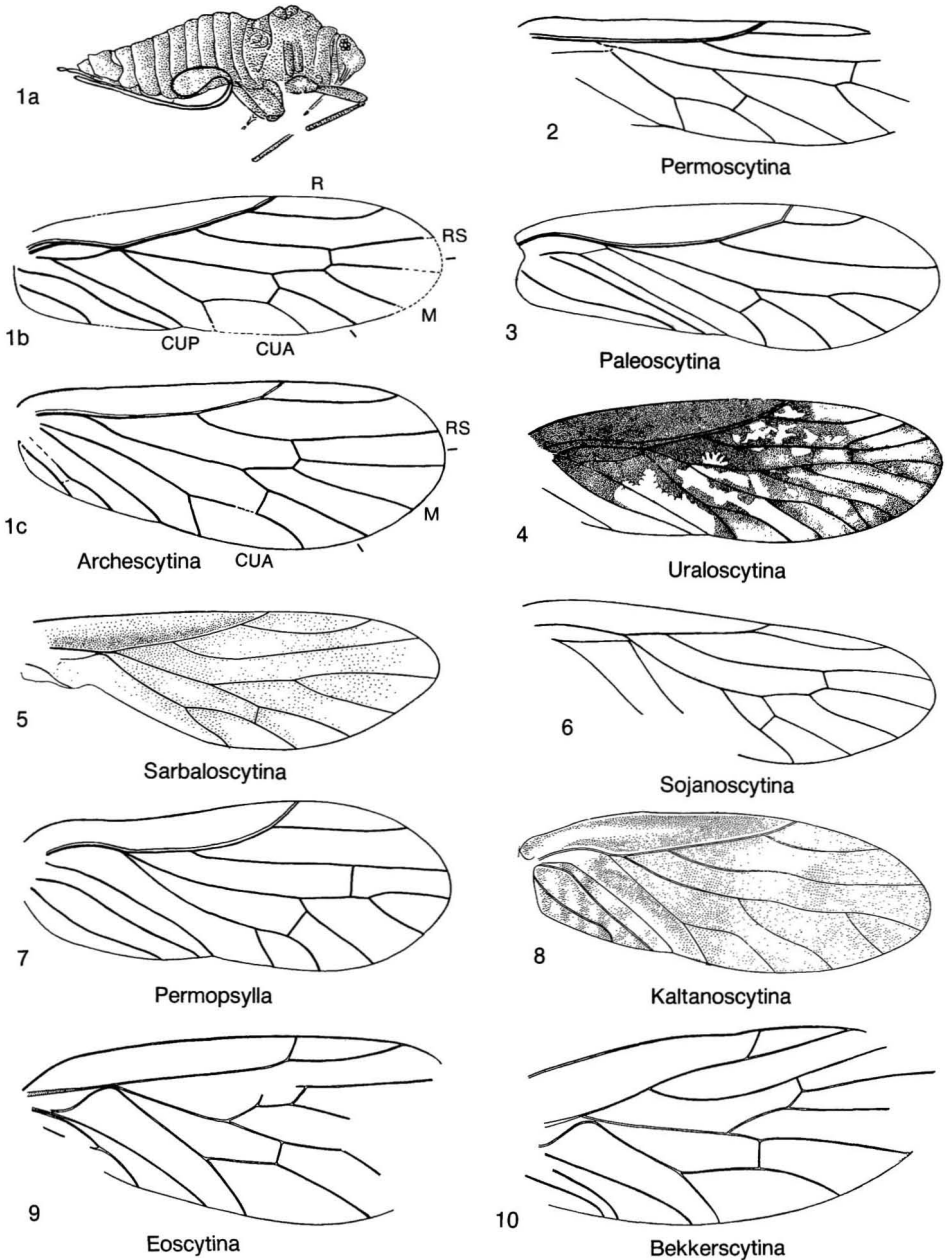


FIG. 155. Archescytinidae (p. 241–243).

Permopsyllopsis ZALESSKY, 1939, p. 38 [**P. rosica*; OD]. Little-known fore wing; venation as in *Archescytina*, but RS straight. BECKER-MIGDISOVA, 1960. *Perm.*, USSR (Asian RSFSR).
Permoscytina TILLYARD, 1926g, p. 387 [**P. kansasensis*; OD]. Similar to *Archescytina*, but SC and R nearly straight basally; proximal branch

of M arising at about level of origin of RS. CARPENTER, 1939. *Perm.*, USA (Kansas). — FIG. 155,2. **P. kansasensis*; fore wing, $\times 4.2$ (Carpenter, 1939).

Sarbaloscytina BECKER-MIGDISOVA, 1959a, p. 104 [**S. angustipennis*; OD]. Similar to *Archescytina*, but stem R+M short and nearly straight.

BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 155,5. **S. angustipennis*; fore wing, $\times 4.5$ (Becker-Migdisova, 1961c).

Sojanoscytina MARTYNOV, 1933c, p. 885 [**S. grandis*; OD] [= *Ivascytina* MARTYNOV, 1933c, p. 888 (type, *I. difficilis*). Fore wing similar to that of *Archescytina*, but M with 4 or more branches. *Perm.*, USSR (European RSFSR).—FIG. 155,6. **S. grandis*; fore wing, $\times 3.4$ (Becker-Migdisova, 1961c).

Tshekardaella BECKER-MIGDISOVA, 1960, p. 59 [**T. tshekardaensis*; OD; = *Tshekardaella tshekardaensis* BECKER-MIGDISOVA, 1948a, p. 130, *nom. nud.*]. Little-known genus, based on wing and body fragments. Fore wing as in *Archescytina* but shorter and more nearly oval. BECKER-MIGDISOVA, 1962b; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (Asian RSFSR).

Uraloscytina ZALESSKY, 1939, p. 40 [**U. prosbolicoides*; OD]. Fore wing as in *Archescytina*, but M more extensively branched and with proximal branch arising about the level of origin of RS. [Type of family Uraloscytinidae ZALESSKY, 1939.] *Perm.*, USSR (Asian RSFSR).—FIG. 155,4. *U. multinervosa* BECKER-MIGDISOVA; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Family BOREOSCYTIDAE
Becker-Migdisova, 1949

[Boreoscytidae BECKER-MIGDISOVA, 1949a, p. 171]

Little-known family. Fore wing much broader distally than basally; vein M with at least 3 branches. Hind wing and body unknown. *Perm.*

Boreoscyta BECKER-MIGDISOVA, 1949a, p. 172 [**B. nefasta*; OD]. Fore wing triangular; RS with pectinate branches directed to costal margin. ROHDENDORF, 1957. *Perm.*, USSR (European RSFSR).—FIG. 156,4. *B. mirabilis* BECKER-MIGDISOVA; fore wing, $\times 6.5$ (Becker-Migdisova, 1949a).

Archescytinopsis BECKER-MIGDISOVA, 1949a, p. 175 [**Sojanoscytina latipennis* MARTYNOV, 1933c, p. 887; OD]. Fore wing not so markedly triangular as in *Boreoscyta*; RS without pectinate branches. *Perm.*, USSR (European RSFSR).—FIG. 156,3. **A. latipennis* (MARTYNOV); fore wing, $\times 6.5$ (Becker-Migdisova, 1949a).

Family PINCOMBEIDAE
Tillyard, 1922

[Pincombeidae TILLYARD, 1922a, p. 282]

Little-known family of uncertain affinities. Fore(?) wing triangular; veins M and CUA originating at same point on R; anal area apparently very narrow. Hind wing appar-

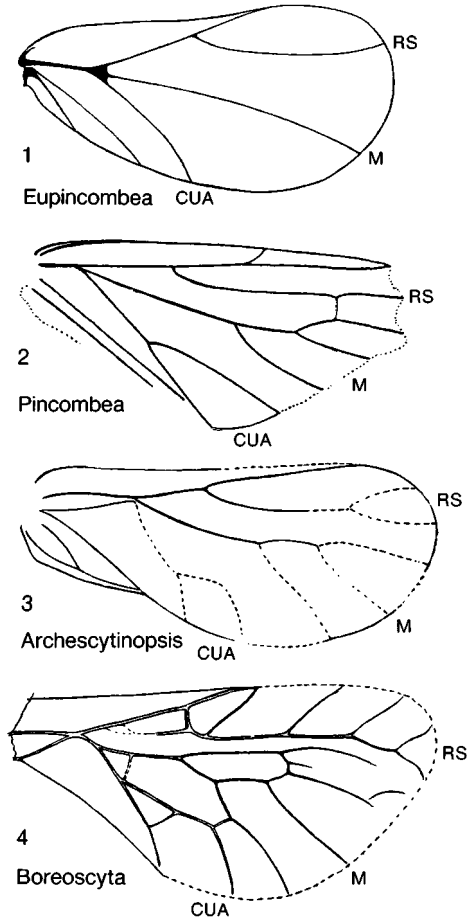


FIG. 156. Boreoscytidae and Pincombeidae (p. 243).

ently smaller than fore; R, M, and CUA diverging from same place. Body unknown. *Perm.*

Pincombea TILLYARD, 1922a, p. 282 [**P. mirabilis*; OD]. Fore(?) wing: M with 3 branches; CUA forked to half its length; one crossvein between M and RS, none between CUA and M. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 156,2. **P. mirabilis*; fore(?) wing, $\times 16$ (Tillyard, 1922a).

Eupincombea DAVIS, 1942, p. 114 [**E. postica*; OD]. Hind wing: RS, M, and CUA unbranched; costal area triangular. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 156,1. **E. postica*; hind wing, $\times 20$ (Davis, 1942).

Protopincombea EVANS, 1943b, p. 193 [**P. obscura*; OD]. Fore wing as in *Pincombea*, but 2 crossveins between RS and M and one between

M and CUA. EVANS, 1956. *Perm.*, Australia (New South Wales).

Family PROTOPSYLLIDIIDAE
Carpenter, 1931

[Protopsyllidiidae CARPENTER, 1931b, p. 119] [=Permaphidopsidae BECKER-MIGDISOVA, 1960, p. 57]

Fore wing variable in shape; vein SC not a distinct vein; RS typically unbranched; stem of M fused with CUA; anal area small but distinct and coriaceous; CUP straight. Hind wing smaller than fore wing. Body structure little known; legs slender. *Perm.-Jur.*

Protopsyllidium TILLYARD, 1926a, p. 26 [**P. australe*; OD]. Fore wing with RS arising well before midwing; M with 2 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157,9. **P. australe*; fore wing, $\times 16$ (Tillyard, 1926a).

Asiopsyllidium BECKER-MIGDISOVA, 1959a, p. 113 [**A. unicum*; OD]. Fore wing much wider distally than basally; RS arising well before midwing; M with 2 branches; CUA with a narrow fork. *Trias.*, USSR (Kirghiz).—FIG. 157,6. **A. unicum*; fore wing, $\times 10$ (Becker-Migdisova, 1959a).

Belpsylla EVANS, 1943b, p. 192 [**B. reticulata*; OD]. Fore wing broad distally; M with 3 straight branches; one crossvein between RS and M1+2 and another between RS and M1; CUA with small fork; anal area with Y-shaped vein. *Perm.*, Australia (New South Wales).—FIG. 157,10. **B. reticulata*; fore wing, $\times 12$ (Evans, 1943b).

Cicadellopsis MARTYNOV, 1937a, p. 107 [**C. incerta*; OD]. Fore wing with costal margin strongly convex; RS arising near wing base; M forked; CUA with small distal fork. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Trias.-Jur.*, USSR (Kirghiz).—FIG. 157,8. **C. incerta*, *Jur.*; fore wing, $\times 13$ (Martynov, 1937a).

Cicadopsyllidium BECKER-MIGDISOVA, 1959a, p. 112 [**C. elongatum*; OD]. Little-known genus. Fore wing narrow; pterostigma apparently absent; RS arising well before midwing; M and CUA apparently fused basally. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).

Clavopsyllidium DAVIS, 1942, p. 117 [**C. minutum*; OD]. Fore wing as in *Protopsyllidium*, but M with 3 branches; CUA1 arched. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).—FIG. 157,7. **C. minutum*; fore wing, $\times 18$ (Davis, 1942).

Permaphidopsis BECKER-MIGDISOVA, 1960, p. 58 [**P. sojanensis*; OD]. Little-known genus, based on hind wing. Wing broad distally; M coalesced

basally with CUA; CUA forked distally with strongly curved CUA1. SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (European RSFSR).

Permapsyllidium TILLYARD, 1926a, p. 27 [**P. mitchelli*; OD]. RS arising near midwing; M with 3 branches. CARPENTER, 1931b. *Perm.*, Australia (New South Wales).—FIG. 157,5. **P. mitchelli*; fore wing, $\times 14$ (Tillyard, 1926a).

Permapsyllidops DAVIS, 1942, p. 116 [**P. stanleyi*; OD]. Fore wing similar to *Protopsyllidium*, but CUP absent or poorly developed; M with 3 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157,1. **P. stanleyi*; fore wing, $\times 15$ (Davis, 1942).

Permapsylloides EVANS, 1943b, p. 193 [**P. insolita*; OD]. Fore wing of uniform width; costal area wide; RS arising before midwing, curved; M apparently with 2 branches; CUA sinuate; anal area with Y-shaped vein. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157,4. **P. insolita*; fore wing, $\times 12$ (Evans, 1943b).

Permothea TILLYARD, 1926a, p. 28 [**P. latipennis*; OD]. Fore wing much as in *Protopsyllidium*, but M with 3 branches. CARPENTER, 1931b; EVANS, 1956. *Perm.*, Australia (New South Wales).

Permotheella DAVIS, 1942, p. 116 [**P. scytinopteroides*; OD]. RS strongly curved; M with 3 branches; anal veins forming Y-shaped vein. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).—FIG. 157,3. **P. scytinopteroides*; fore wing, $\times 14$ (Davis, 1942).

Propatrix BECKER-MIGDISOVA, 1960, p. 55 [**P. psylloides*; OD; =*P. psylloides* BECKER-MIGDISOVA, 1948a, p. 130, *nom. nud.*]. Fore wing with long pterostigmal area. RS arising at midwing; M with 3 branches; CUA with wide fork. BECKER-MIGDISOVA, 1962b; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (European RSFSR).—FIG. 157,2. **P. psylloides*; fore wing and body, $\times 8$ (Becker-Migdisova, 1960).

Psocopsyllidium DAVIS, 1942, p. 115 [**P. media*; OD]. Fore wing as in *Protopsyllidium* but more slender. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).

Psococytina DAVIS, 1942, p. 112 [**P. bifida*; OD]. Similar to *Protopsyllidium*, but M with 3 branches; RS arising at midwing with distal fork. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 158,2. **P. bifida*; fore wing, $\times 12$ (Davis, 1942).

Psyllidella EVANS, 1943b, p. 192 [**P. magna*; OD]. Fore wing with RS arising beyond midwing; M with 3 long branches; costal margin sinuate. *Perm.*, Australia (New South Wales).—FIG. 158,5. **P. magna*; fore wing, $\times 10$ (Evans, 1943b).

Psyllidiana EVANS, 1943b, p. 192 [**P. davisia*; OD] [=*Protopsyllidops* EVANS, 1943b, p. 192 (type, *P. minuta*)]. Fore wing as in *Protopsyllid-*

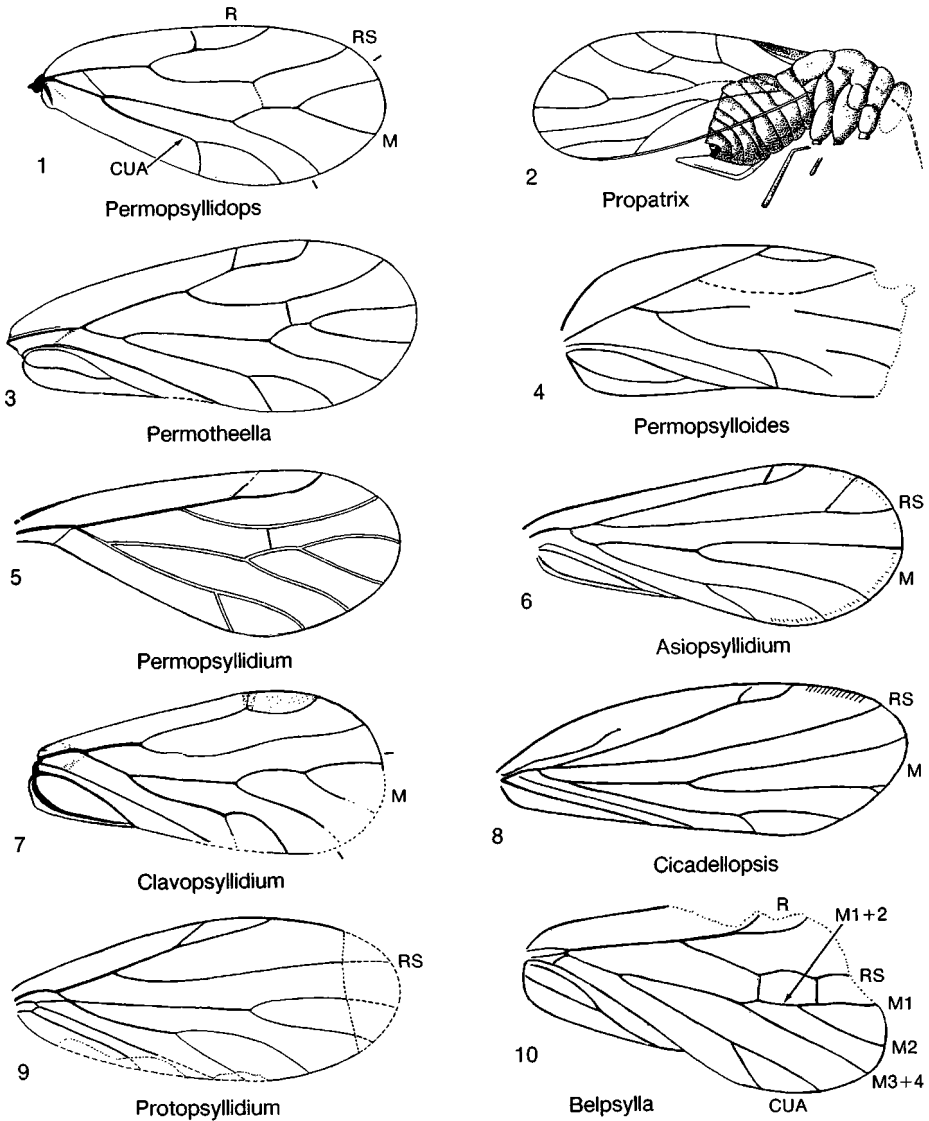


FIG. 157. Protosylliidae (p. 244).

lidium, but RS arising near midwing and very straight; CUA deeply forked. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 158, 1. **P. davisia*; fore wing, $\times 22$ (Evans, 1943b).

Tomiopsyllidium BECKER-MIGDISOVA, 1959a, p. 112 [**T. iljinskiense*; OD]. Fore wing slender, triangular; RS arising just before midwing, curving away from R distally. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 158, 4.

**T. iljinskiense*; fore wing, $\times 22$ (Becker-Migdisova, 1960).

Triassoptylla TILLYARD, 1918b, p. 753 [**T. pleiocoides*; OD]. Little-known genus, based on wing fragment; RS curved; M with 3 branches. EVANS, 1956. *Trias.*, Australia (New South Wales).

Triassothea EVANS, 1956, p. 236 [**T. analis*; OD]. Fore wing as in *Protosyllidium*, but RS arising near wing base; M+CUA very short; M with distal fork. *Trias.*, Australia (Queensland).

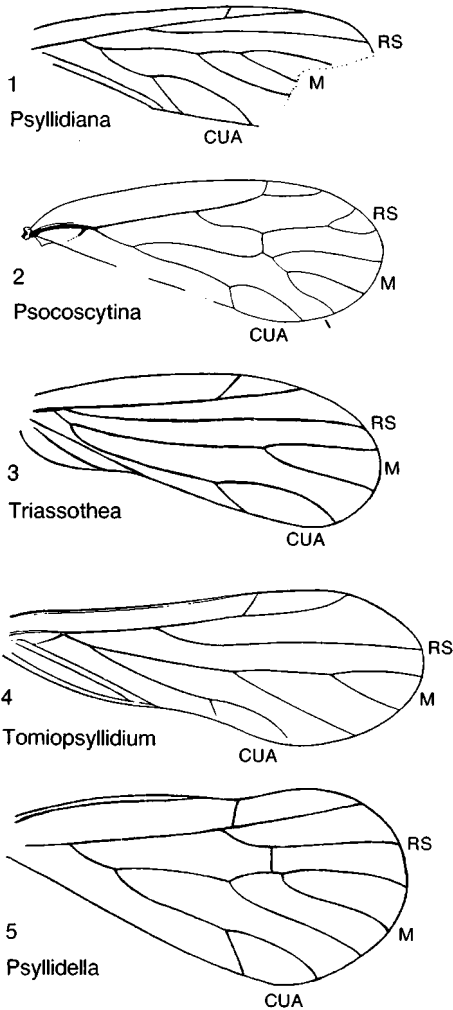


FIG. 158. Protopsyllidiidae (p. 244–246).

— FIG. 158.3. **T. analis*; fore wing, $\times 14$ (Evans, 1956).

Family GENAPHIDIDAE Handlirsch, 1907

[Genaphididae HANDLIRSCH, 1907, p. 643]

Little-known family. Antennae with 7 segments, bearing annular, secondary sense organs (rhinaria). Fore wing with all veins of nearly same thickness; M arising at level of base of pterostigma, with 3 terminal branches; CUA with short base, arising from stem R+M. HEIE, 1967, 1985; SHAPOSHNIKOV, 1979b, 1980. *Jur.*

Genaphis HANDLIRSCH, 1907, p. 643 [**Apbis valdensis*; OD]. Little-known genus. RS arising near middle of pterostigma. HEIE, 1967. *Jur.*, England. — FIG. 159.1. **G. valdensis*; fore wing, $\times 18$ (Heie, 1967).

Juraphis SHAPOSHNIKOV, 1979b, p. 66 [**J. crassipes*; OD]. Fore wing with RS arising slightly distally of middle of pterostigma. Antennae and legs stout. HEIE, 1985. *Jur.*, USSR (Kazakh). — FIG. 159.4. **J. crassipes*; fore and hind wings, $\times 18$ (Shaposhnikov, 1979b).

Family CANADAPHIDIDAE Richards, 1966

[*nom. transl.* KONONOVA, 1976, p. 119, ex Canadaphidinae RICHARDS, 1966, p. 757]

Head dorsoventrally flattened, prolonged anteriorly; antennal bases ventral, in front of compound eyes; antennae with 5 to 6 segments; rostrum apparently very short; tarsi long; ovipositor well developed; siphuncles and cauda apparently not present. Fore wing with vein M with two forks. Hind wing relatively large. *Cret.*

Canadaphis ESSIG in CARPENTER & others, 1937, p. 19 [**C. carpenteri*; OD]. M of fore wing arising near origin of CUA1; CUA1 slightly sinuate; tarsi with 2 segments. HEIE, 1967, 1981; KONONOVA, 1976. [A record of this genus (*C. mordvilko*) KONONOVA, 1976, p. 120] from the Cretaceous of USSR (Asian RSFSR) is very questionable. See KONONOVA, 1976, and HEIE, 1985.] *Cret.*, Canada (Manitoba). — FIG. 159.2. **C. carpenteri*; dorsal view, $\times 35$ (Essig in Carpenter & others, 1937).

Alloambria RICHARDS, 1966, p. 756 [**A. caudata*; OD]. Antennae with at least 5 segments. Fore wing with CUA1 and CUA2 arising independently from stem SC+R+M; CUA1 sinuate. Tarsi with 2 segments. *Cret.*, Canada (Manitoba). — FIG. 159.3. **A. caudata*; dorsal view, $\times 50$ (Richards, 1966).

Pseudambria RICHARDS, 1966, p. 758 [**P. longirostris*; OD]. Antennae with 6 segments. Fore wing with CUA1 sinuate; CUA2 very weakly developed. HEIE, 1981, 1985. *Cret.*, Canada (Manitoba).

Family PALAEOAPHIDIDAE Richards, 1966

[*nom. transl.* KONONOVA, 1976, p. 121, ex Palaeoaphidinae RICHARDS, 1966, p. 750]

Similar to Canadaphididae, but antennae with 7 segments; ovipositor well developed. Fore wing with vein RS arising from proxi-

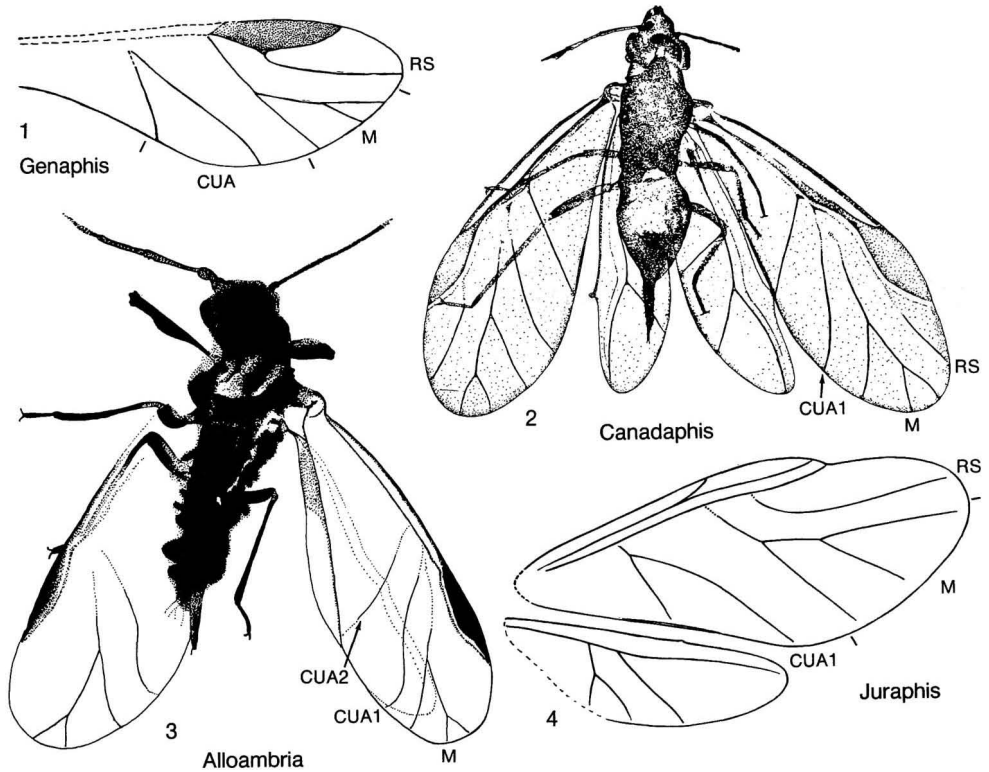


FIG. 159. Genaphididae and Canadaphididae (p. 246).

mal third of pterostigma; hind wing relatively shorter than in Canadaphididae. HEIE, 1985. *Cret.*

Palaeoaphis RICHARDS, 1966, p. 750 [**P. archimedita*; OD]. Little-known genus. Media of fore wing incomplete basally; legs with short hairs. [The assignment of *P. incognata* KONONOVA, 1976, p. 121 (Cretaceous of USSR) to the family Palaeoaphididae is very uncertain.] HEIE, 1985. *Cret.*, Canada (Manitoba).—FIG. 160, I. **P. archimedita*; fore wing, $\times 45$ (Richards, 1966).

Ambaraphis RICHARDS, 1966, p. 752 [**A. costalis*; OD]. Similar to *Palaeoaphis*, but apical tarsal segments with long, conspicuous preapical setae. HEIE, 1985. *Cret.*, Canada (Manitoba).

Family SHAPOSHNIKOVIIDAE Kononova, 1976

[Shaposhnikoviidae KONONOVA, 1976, p. 122]

Little-known family. Antennae with 7 segments, its total length only half that of fore wing. Fore wing: vein M with 3 terminal

branches; CUA1 and CUA2 widely separated basally. HEIE, 1981, 1985. *Cret.*

Shaposhnikovia KONONOVA, 1976, p. 122 [**S. electri*; OD]. Fore wing with M arising from base of pterostigma. Second segment of fore tarsus about one-fourth as long as tibia. HEIE, 1981. *Cret.*, USSR (Asian RSFSR).

Family OVIPARASIPHIDAE Shaposhnikov, 1979

[Oviparasiphidae SHAPOSHNIKOV, 1979b, p. 75]

Antennae with annular, secondary sense organs (rhinaria). Fore wing with vein RS arising from middle of pterostigma; M with 3 branches; CUA1 and CUA2 originating separately from a common stem (SC+R+M). Ovipositor large. *Cret.*

Oviparasiphum SHAPOSHNIKOV, 1979b, p. 75 [**O. jakovlevi*; OD]. Rhinaria on antennae forming convex rings. Femora stout. *Cret.*, Mongolia.

Family TAJMYRAPHIDIDAE

Kononova, 1975

[Tajmyraphididae KONONOVA, 1975, p. 795]

Antennae with 4 to 6 segments. Fore wing broadly rounded distally; pterostigma short, vein RS not connected to it; M with one fork; CUA1 about three times as long as CUA2. HEIE, 1985. *Cret.*

Tajmyraphis KONONOVA, 1975, p. 796 [**T. zberichini*; OD]. Antennae with 5 or 6 segments. *Cret.*, USSR (Asian RSFSR).

Jantardakhia KONONOVA, 1975, p. 804 [**J. electri*; OD]. Antennae with 5 segments. Fore wing with bases of CUA1 and CUA2 widely separated. *Cret.*, USSR (Asian RSFSR).

Khatangaphis KONONOVA, 1975, p. 803 [**K. sibirica*; OD]. Similar to *Tajmyraphis*, but antennae with 4 or 5 segments; pterostigma of fore wing very short. *Cret.*, USSR (Asian RSFSR).

Retinaphis KONONOVA, 1975, p. 801 [**R. glandulosa*; OD]. Similar to *Tajmyraphis*, but antennae longer, with 6 segments. *Cret.*, USSR (Asian RSFSR).

Family MINDARIDAE Tullgren, 1909

[Mindaridae TULLGREN, 1909, p. 58]

Cauda subtriangular. Fore wing with pterostigma narrow, pointed, extending to apex of wing; vein RS arising from the proximal part of pterostigma. *Cret.*—*Holo.*

Mindarus KOCH, 1857, p. 277 [= *Pterostigma* BUCKTON, 1883, p. 178 (type, *P. recurvus*); *Schizoneuroides* BUCKTON, 1883, p. 178 (type, *S. scudderi*); *Sychnobrochus* SCUDDER, 1890, p. 268 (type, *S. reviviscens*)]. BAKER, 1922; HEIE, 1967, 1969b, 1985. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Nordaphis KONONOVA, 1977, p. 593 [**N. sukatchevae*; OD]. Little-known genus. Antennae with 6 segments. Fore wing with pterostigma very elongate; RS straight; M with one fork. Legs long. [Placed in Drepanosiphidae by KONONOVA but transferred to Mindaridae by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).

Family HORMAPHIDIDAE

Mordvilko, 1908

[Hormaphididae MORDVILKO, 1908, p. 364]

Antennae with 3 to 5 segments, much shorter than body; antennae of alate form with narrow, ringlike, secondary rhinaria. Fore wing with veins CUA1 and CUA2 arising from same point on SC+R+M. *Oligo.*—*Holo.*

Hormaphis OSTEN-SACKEN, 1861, p. 422. *Holo.*
Electrocornia HEIE, 1972, p. 249 [**E. antiqua*; OD]. Little-known genus, based on nymph. Antennae with 5 segments; head and pronotum fused; frons with 2 hornlike processes. [Originally placed in Thelaxidae but later transferred to Hormaphididae (HEIE, 1985).] *Oligo.*, Europe (Baltic).

Family ELEKTRAPHIDIDAE

Steffan, 1968

[Elektraphididae STEFFAN, 1968, p. 11]

Antennae with 5 segments. Fore wing with vein RS greatly reduced; M typically without branches; CUA1 and CUA2 arising from stem CUA or originating independently from stem SC+R+M. KONONOVA, 1976. *Cret.*—*Oligo.*

Schizoneurites COCKERELL, 1915, p. 487 [**S. brevirostris*; OD] [= *Antiquaphis* HEIE, 1967, p. 88 (type, *A. robustus*); *Elektraphis* STEFFAN, 1968, p. 11 (type, *E. polykrypta*)]. Fore wing with CUA1 and CUA2 arising from common stem CUA. Antennae with transverse folds. HEIE, 1967, 1976, 1980, 1985; STEFFAN, 1968. *Oligo.*, Europe (Baltic), England.—FIG. 160, *S. robustus* (HEIE), Baltic; fore wing, $\times 34$ (Heie, 1967).

Antonaphis KONONOVA, 1977, p. 589 [**A. brachycera*; OD]. Antennae short, with 5 segments. Fore wing with RS long, slightly curved; M branched once. [Originally placed in Pemphigidae but transferred to *Elektraphididae* by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).

Tajmyrella KONONOVA, 1976, p. 118 [**T. cretacea*; OD]. Similar to *Schizoneurites*, but CUA1 and CUA2 arising independently from stem SC+R+M. HEIE, 1981. *Cret.*, USSR (Asian RSFSR).

Family THELAXIDAE Baker, 1920

[Thelaxidae BAKER, 1920, p. 21]

Antennae with 5 segments. Media of fore wing with 2 terminal branches. Hind wing with two oblique veins. *Oligo.*—*Holo.*

Thelaxes WESTWOOD, 1840, p. 118. *Holo.*
Palaeothelaxes HEIE, 1967, p. 42 [**P. setosa*; OD]. Little-known genus. All body segments of apterous form with very thick, large setae; frons of alate form with similar large setae. *Oligo.*, Europe (Baltic).

Family ANOECIIDAE Tullgren, 1909

[Anoeciidae TULLGREN, 1909, p. 186]

Antennae commonly with 6 segments, and in alate forms with oval or subcircular sec-

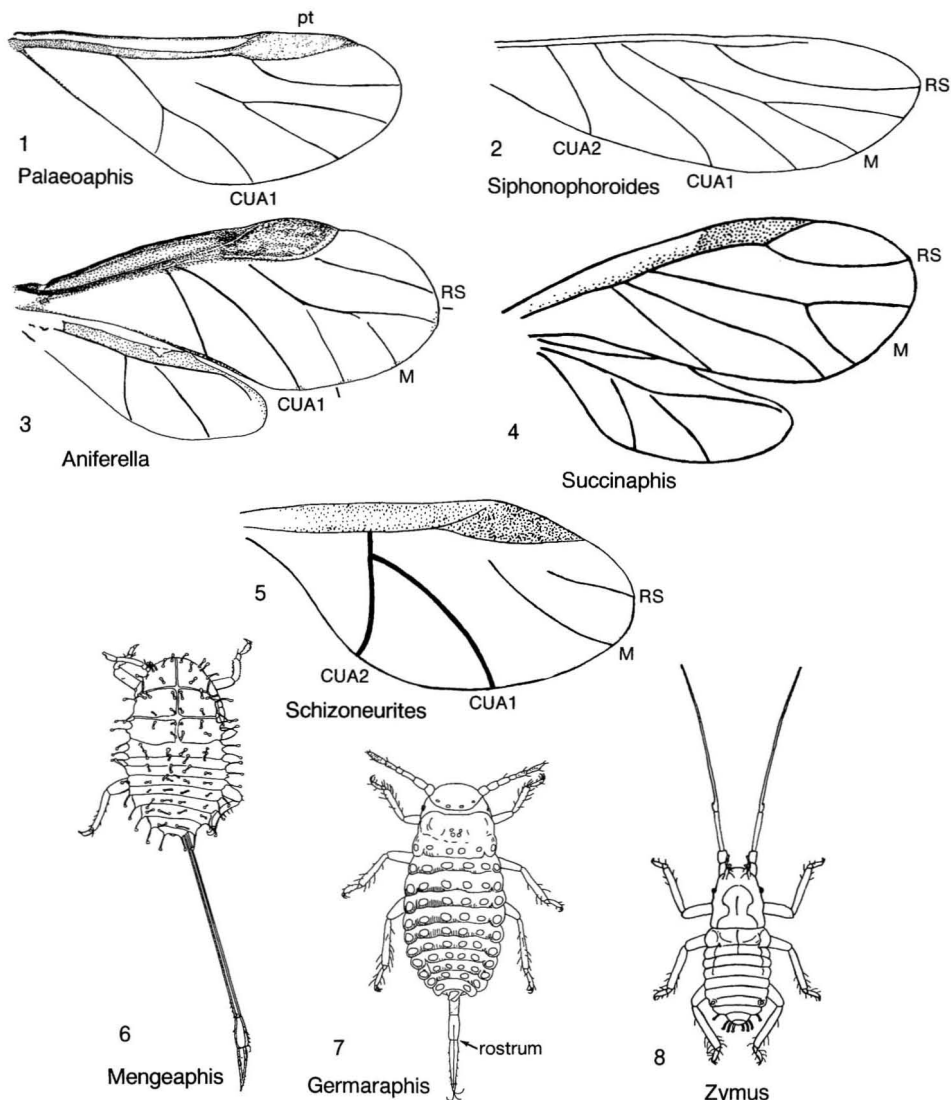


FIG. 160. Palaeoaphididae, Elektraphididae, Pemphigidae, and Drepanosiphidae (p. 247–251).

ondary rhinaria; marginal tubercles present on prothorax and some abdominal segments. Pterostigma of fore wing not more than four times longer than its width. *Oligo.*—*Holo.*

Anoecia KOCH, 1857, p. 275. *Holo.*

Berentaphis HEIE, 1971, p. 262 [**Lachnus cimicoides* GERMAR & BERENDT, 1856, p. 5; OD]. Little-known genus, based on apterous form. Antennae with 6 segments, distal segments conspicuously thickened; head and pronotum not fused. *Oligo.*, Europe (Baltic).

Family PEMPHIGIDAE Koch, 1857

[Pemphigidae KOCH, 1857 p. viii]

Antennae short, usually with 6 segments and with one very short terminal process. Fore wing with vein M unbranched or with one fork. Hind wing with 1 or 2 oblique veins. *Oligo.*—*Holo.*

Pemphigus HARTIG, 1839, p. 645. *Holo.*

Eriosoma LEACH, 1818, p. 60. HEIE, 1968a, 1969a,

- 1969c, 1985. *Mio./Plioc.*, Europe (Germany)—*Holo.*
- Germaraphis** HEIE, 1967, p. 47 [**Lachnus dryoides* GERMAR & BERENDT, 1856, p. 29; OD]. Little-known genus, based mainly on apterous specimens. Antennae with 5 or 6 segments, the second one at least as long as the fourth. [Originally placed in Phloeomyzidae by HEIE (1967) and BECKER-MIGDISOVA (1973) but transferred to Pemphigidae by HILLE RIS LAMBERS (1980) and HEIE (1985).] HEIE, 1969b, 1972, 1985; BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic). — FIG. 160,7. **G. dryoides*; apterous specimen, reconstruction, $\times 30$ (Heie, 1967).
- Succinaphis** HEIE, 1967, p. 173 [**S. flauensgaardii*; OD]. Apparently similar to *Pemphigus* (recent). Media of fore wing branched; wing membrane with fine reticulation. HEIE, 1985. *Oligo.*, Europe (Baltic). — FIG. 160,4. **S. flauensgaardii*; fore and hind wings, $\times 45$ (Heie, 1967).
- Family DREPANOSIPHIDAE**
Koch, 1857
- [Drepanosiphidae Koch, 1857, p. vii]
- Closely allied to the Aphididae. Secondary transverse or circular rhinaria usually present on third antennal segment of alate females. Fore wing: vein M with 2 or 3 terminal branches. Hind wing with 2 or 3 oblique veins. HEIE, 1980, 1982. *Cret.—Holo.*
- Drepanosiphum** KOCH, 1855, p. 201. *Holo.*
- Aixaphis** HEIE, 1970b, p. 115 [**Tetraneura oligocenica* THÉOBALD, 1937a, p. 16; OD]. Antennae about half body length, with 6 segments. Fore wing: M with 3 terminal branches; CUA1 and CUA2 arising independently from stem SC+R+M, their bases relatively remote. [Family assignment doubtful.] HEIE, 1985. *Oligo.*, Europe (France).
- Aniferella** RICHARDS, 1966, p. 759 [**A. bostoni*; OD]. Antennae with 5 segments. Fore wing with well developed pterostigma; RS nearly straight; M with 2 forks; CUA1 and CUA2 arising separately from stem SC+R+M. HEIE, 1981, 1985. *Cret.*, Canada (Alberta). — FIG. 160,3. **A. bostoni*; fore and hind wings, $\times 35$ (Richards, 1966).
- Balticaphis** HEIE, 1967, p. 160 [**B. exsiccata*; OD]. Little-known genus, based on apterous form. Antennae with 5 or 6 segments. Fore femora thickened. HEIE, 1985. *Oligo.*, Europe (Baltic).
- Balticomaraphis** HEIE, 1967, p. 167 [**B. latens*; OD]. Little-known genus, based on cast cuticle of nymph. Antennae with 6 segments; ocular tubercles well developed. *Oligo.*, Europe (Baltic).
- Conicaudus** HEIE, 1972, p. 255 [**C. longipes*; OD]. Little-known genus, based on alate form. Antennae about as long as body. M of fore wing with 3 or 4 terminal branches. Tarsi very long. *Oligo.*, Europe (Baltic).
- Cretacallis** SHAPOSHNIKOV, 1979a, p. 730, footnote [**C. polysensoria*; OD]. Antennae with 6 segments. Fore wing: M with 3 terminal branches; CUA1 and CUA2 originating independently from stem SC+R+M. [Family position doubtful.] *Cret.*, Mongolia.
- Electrocallis** HEIE, 1967, p. 147 [**E. bakeri*; OD] [= *Dimeraphis* BECKER-MIGDISOVA, 1973, p. 87 (type, *D. arnoldii*)]. Antennae of alate form much longer than body and composed of 6 segments. Fore wing with pterostigma short; M with 3 terminal branches; CUA1 and CUA2 arising separately from stem SC+R+M. Fore femora thicker than the others. *Oligo.*, Europe (Baltic).
- Megantennaphis** HEIE, 1967, p. 142 [**M. haurienseis*; OD]. Antennae with 6 segments and much longer than body. Fore wing with pterostigma long, pointed; RS almost straight; M with 3 terminal branches. Fore and hind femora large and strong. BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic).
- Megapodaphis** HEIE, 1967, p. 155 [**M. monstrabilis*; OD]. Antennae with 6 segments and at least as long as body. Fore wing: M with 2 terminal branches. Fore femora strongly thickened. HEIE, 1972, 1985. *Oligo.*, Europe (Baltic).
- Mengeaphis** HEIE, 1967, p. 113 [**Lachnus glandulosus*; OD]. Little-known genus, based on immature nymphs. Antennae with 4 segments; rostrum at least twice the length of body. BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic). — FIG. 160,6. **M. glandulosus*; dorsal view, $\times 85$ (Becker-Migdisova, 1973).
- Oligocallis** HEIE, 1967, p. 133 [**O. larssoni*; OD]. Little-known genus, based on alate form. Similar to *Pterasthenica* (recent), but venation of fore wing less reduced in *Oligocallis*. HEIE, 1972. *Oligo.*, Europe (Baltic).
- Oryctaphis** SCUDDER, 1890, p. 266 [**O. lesueurii*; OD]. Little-known genus, possibly a synonym of *Siphonophoroides*. HEIE, 1985. *Oligo.*, USA (Colorado).
- Palaeophyllaphis** HEIE, 1967, p. 97 [**P. longirostris*; OD]. Antennae with 6 segments. Fore wing: M with 2 or 3 terminal branches; pterostigma slightly pointed but short. GERMAR & BERENDT, 1856; HEIE, 1972, 1985. *Oligo.*, Europe (Baltic).
- Palaeosiphon** HEIE, 1967, p. 119 [**Aphis hirsuta* GERMAR & BERENDT, 1856, p. 6; OD]. Little-known genus. Antennae of apterous form with 5 segments. Fore wing: M with 3 terminal branches. Hind wing with only one oblique vein.

- Head and first two thoracic segments of alate form with long, curved, hornlike projections. HEIE, 1971. *Oligo.*, Europe (Baltic).
- Siphonophoroides** BUCKTON, 1883, p. 176 [**S. antiqua*; OD][=*Archilachus* BUCKTON, 1883, p. 177 (type, *A. pennata*); *Aphantaphis* SCUDDER, 1890, p. 253 (type, *S. exsuca*); *Cataneura* SCUDDER, 1890, p. 245 (type, *C. absens*); *Amalancon* SCUDDER, 1890, p. 270 (type, *A. lutosus*)]. Antennae slender, longer than body. Fore wing with RS very long, relatively straight, arising from proximal half of pterostigma; M with 3 terminal branches. COCKERELL, 1908u, 1909b; HEIE 1967, 1985. *Eoc.*, Europe (Denmark); *Oligo.*, USA (Colorado).—FIG. 160,2. **S. antiqua*; fore wing, $\times 14$ (Heie, 1967).
- Sternaphis** HEIE, 1972, p. 257 [**S. electricola*; OD]. Fore wing with RS short and straight; M with 2 terminal branches. *Oligo.*, Europe (Baltic).
- Succaphis** HEIE, 1967, p. 110 [**S. bolgeri*; OD]. Little-known genus, based on apterous form. Head and pronotum separated; antennae with 4 segments; rostrum longer than body. [Family assignment doubtful.] HEIE, 1985. *Oligo.*, Europe (Baltic).
- Tertiaphis** HEIE, 1969b, p. 144 [**T. haentzscheli*; OD]. Antennae with 6 segments and shorter than body. Fore wing: M with 2 terminal branches; CUA1 and CUA2 arising separately from stem SC+R+M. HEIE, 1985. *Oligo.*, Europe (Baltic).
- Zymus** HEIE, 1972, p. 254 [**Z. succincola*; OD]. Little-known genus, based on nymph. Antennae with 4 segments and with long, filamentous terminal segment; head and pronotum fused; strong bristles on head and posterior part of abdomen. *Oligo.*, Europe (Baltic). — FIG. 160,8. **Z. succincola*; dorsal view of nymph, $\times 24$ (Heie, 1972).

Family APHIDIDAE Latreille, 1802

[Aphididae LATREILLE, 1802a, p. 263]

Compound eyes large in all instars; antennae commonly with 6 segments (rarely with 5), at least half length of body. Fore wing: vein RS with 2 or 3 terminal branches; CUA and CUP arising independently from stem R+M+CU. Hind wing commonly with 2 oblique veins, rarely only one. Wings slanted at rest. *Cret.—Holo.*

Aphis LINNÉ, 1758, p. 451. *Holo.*

Aphidocallis KONONOVA, 1977, p. 595 [**A. caudatus*; OD]. Antennae with 5 segments. Fore wing with pterostigma short, extending only to about level of midwing; M with 3 terminal branches. *Cret.*, USSR (Asian RSFSR).

Baltichaitophorus HEIE, 1967, p. 180 [**B. jurtlandicus*; OD]. Little-known genus, based on apterous forms. Antennae with 6 segments, about as long as body. HEIE, 1980. *Oligo.*, Europe (Baltic).

Diatomyzus HEIE, 1970a, p. 163 [**D. eocaenicus*; OD]. Little-known genus, based on alate specimens. Similar to several existing genera, but RS of fore wing unusually long. *Eoc.*, Europe (Denmark).

Pseudamphorophora HEIE, 1967, p. 175 [**P. succini*; OD]. Little-known genus, based on apterous forms. [Family assignment doubtful.] HEIE, 1971, 1980. *Oligo.*, Europe (Baltic).

Family LACHNIDAE Koch, 1857

[Lachnidae KOCH, 1857, p. vii]

Similar to Anoeciidae, but prothorax and abdominal segments lacking marginal tubercles. Pterostigma of fore wing commonly much longer than 4 times its width. *Mio./Plio.—Holo.*

Lachnus BURMEISTER, 1835, p. 92. *Holo.*

Longistigma WILSON, 1909, p. 385. HEIE & FRIEDRICH, 1971; HEIE, 1985. *Mio./Plio.*, Iceland-*Holo.*

Family ALEYRODIDAE Westwood, 1840

[Aleyrodidae WESTWOOD, 1840, p. 442]

Wings slightly thickened, commonly covered with a powdery wax. Fore wing venation weakly formed, only veins R and M extending to distal part of wing. Antennae with 7 segments; terminal abdominal segment with a large, dorsal opening, associated with storage of honey dew. *Oligo.—Holo.*

Aleyrodes LATREILLE, 1796, p. 93. [Generic assignment of fossil doubtful.] MENGE, 1856; SCHLEE, 1970. *Oligo.*, Europe (Baltic)-*Holo.*

Aleurodicus DOUGLAS, 1892, p. 32. [Generic assignment of fossil doubtful.] COCKERELL, 1919e; SCHLEE, 1970. *Mio.*, Burma-*Holo.*

Family COLEOSCYTIDAE Martynov, 1935

[Coleoscytidae MARTYNOV, 1935c, p. 24]

Fore wing oval, weakly coriaceous, membranous distally; subcostal area abruptly widened at base; costal margin at right angles to wing axis at this point; vein SC marginal;

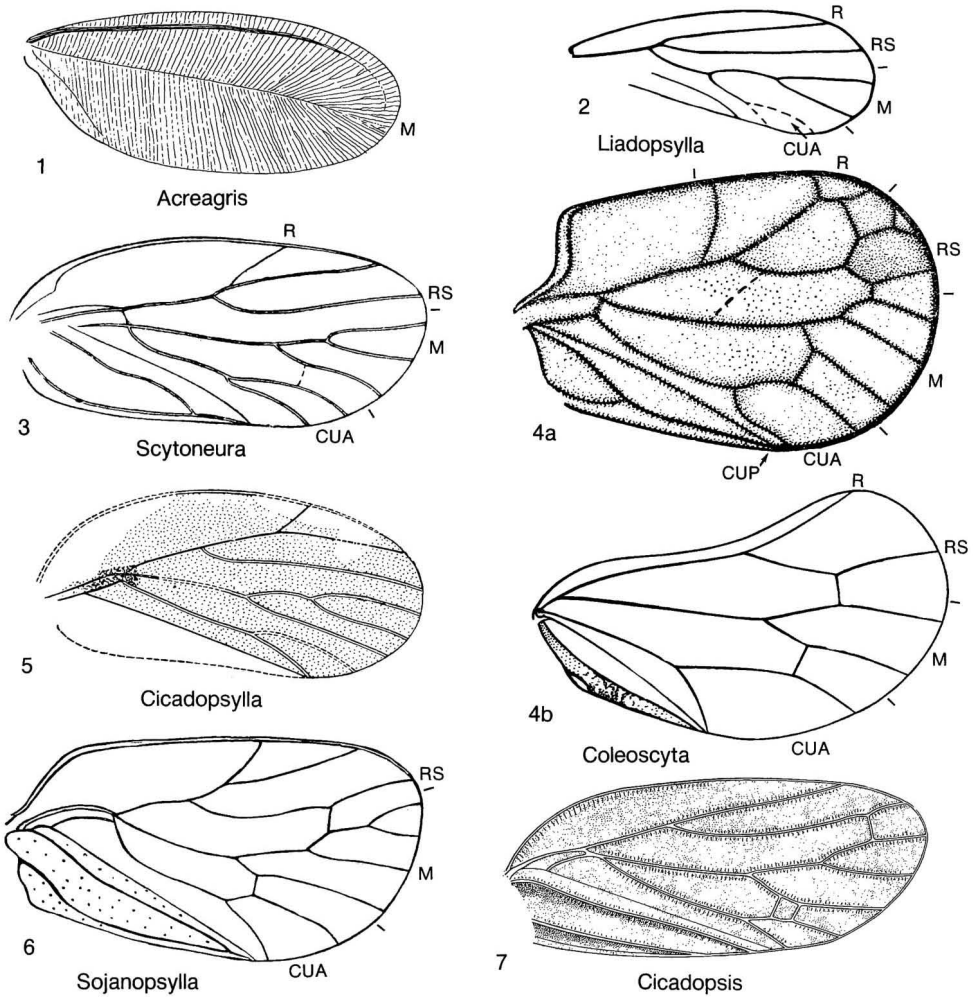


FIG. 161. Coleoscytidae, Cicadopsyllidae, Psyllidae, and Margarodidae (p. 252-254).

R long, with a branch to costal margin near midwing; M and CUA distally branched; CUP straight, unbranched; 1A and 2A with a common stem. Hind wing membranous, widened distally, more slender than fore wing, with concave anterior margin; subcostal area very narrow; M forked, CUA with a very wide fork; anal area narrow. Head hypognathous; eyes not divided. Hind coxae large. *Perm.*

Coleoscyta CARPENTER, herein [**C. rotundata* MARTYNOV, 1935c, p. 24; OD] [= *Coleoscytodes* CARPENTER, herein (type, *C. venosa* MARTYNOV,

1935c, p. 24; OD)]. Fore wing very broad, costal margin thickened; RS with distal fork. [The original generic names, *Coleoscyta* and *Coleoscytodes*, were *nomina nuda* (MARTYNOV, 1935c).] BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (European RSFSR). — FIG. 161,4a. **C. rotundata*; fore wing, $\times 8$. — FIG. 161,4b. *C. venosa* (MARTYNOV); hind wing, $\times 8$ (Becker-Migdisova, 1960).

Sojanopsylla BECKER-MIGDISOVA, 1960, p. 45 [**S. brevipennis*; OD]. Fore wing as in *Coleoscyta*, but subcostal area gradually widened basally and R and RS longer; M with 3 or 4 branches. *Perm.*, USSR (European and Asian RSFSR). — FIG. 161,6. **S. brevipennis*; fore wing, $\times 4.5$ (Becker-Migdisova, 1960).

Family CICADOPSYLLIDAE

Martynov, 1931

[*nom. transl.* MARTYNOV, 1935c, p. 16, ex Cicadopsyllinae MARTYNOV 1931c, p. 172]

Fore wing elongate oval, commonly membranous; subcosta apparently close to costal margin; RS long, ending near wing apex. Hind wing with M apparently arising from stem of R; CUA originating independently of R + M. Head hypognathous, with protuberances on vertex. Hind coxae conical, elongate. BECKER-MIGDISOVA, 1962b. *Perm.*

Cicadopsylla MARTYNOV, 1931c, p. 173 [**C. permiana*; OD]. Fore wing with M forking near level of midwing. *Perm.*, USSR (European RSFSR).—FIG. 161,5. **C. permiana*; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Cicadopsis BECKER-MIGDISOVA, 1959a, p. 110 [**C. rugosipenna*; OD]. Similar to *Cicadopsylla*, but R without distal, anterior branch. *Perm.*, USSR (Asian RSFSR).—FIG. 161,7. **C. rugosipenna*; fore wing, $\times 8$ (Becker-Migdisova, 1962b).

Scytoneura MARTYNOV, 1935c, p. 16 [**S. elliptica*; OD]. Fore wing similar to *Cicadopsylla*, but M dividing more distally. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 161,3. **S. elliptica*; fore wing, $\times 3$ (Becker-Migdisova, 1962b).

Scytoneurella ZALESSKY, 1939, p. 39 [**S. major*; OD]. Fore wing membranous, costal margin slightly convex; M dividing distally of fork of CUA, with 3 short branches. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).

Family PSYLLIDAE Latreille, 1807

[Psyllidae LATREILLE, 1807, p. 168]

Fore wing usually coriaceous; costal area broad; veins M and CUA united to form a basal stem; RS arising from R independently; M and CU usually arising as a common stem; RS unbranched; M and CUA forked. Hind wing smaller and more slender, with R and M unbranched. Antennae with 9 to 10 segments. *Jur.*—*Holo.*

Psylla GEOFFREY, 1762, p. 482. BECKER-MIGDISOVA, 1964. *Oligo.*, England; *Mio.*, USSR (European RSFSR)—*Holo.*

Agonoscena ENDERLEIN, 1914, p. 234. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Catopsylla SCUDDER, 1890, p. 277 [**C. prima*; OD].

Little-known genus. Fore wing as in *Prylla*, but cell of CU much longer. *Oligo.*, USA (Colorado). *Liadopsylla* HANDLIRSCH, 1920, p. 213 [**L. geinitsi*; OD]. Fore wing oval, membranous; R and RS long, parallel; stem of R short; fork of M long. MARTYNOV, 1926b; BECKER-MIGDISOVA, 1949b. *Jur.*, Europe (Germany), USSR (Asian RSFSR).—FIG. 161,2. *L. tenuicornis* MARTYNOV, USSR; fore wing, $\times 20$ (Martynov, 1926b).

Livilla CURTIS, 1836, p. 625. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Necropsylla SCUDDER, 1890, p. 276 [**N. rigida*; OD]. Little-known genus; fore wing as in *Psyllopsis* (recent) but subtriangular. COCKERELL, 1911b, 1915. *Oligo.*, USA (Colorado), England.

Psyllites COCKERELL, 1914f, p. 636 [**P. crawfordi*; OD]. Little-known genus, probably a synonym of *Catopsylla*. *Oligo.*, USA (Colorado).

Retrocizzia HESLOP-HARRISON, 1961, p. 504. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Strophingia ENDERLEIN, 1914, p. 233. *Oligo.*, Europe (Baltic)—*Holo.*

Trioza FÖRSTER, 1848, p. 67. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Family COCCIDAE Fallén, 1814

[Coccidae FALLÉN, 1814, p. 23]

Adults with marked sexual dimorphism. Males with fore wings normally developed; hind wings reduced or halterlike. Females apterous; antennae diverse, commonly much reduced; abdominal spiracles absent. *Oligo.*—*Holo.*

Coccus LINNÉ, 1758, p. 455. MENGE, 1856; COCKERELL, 1906b; BECKER-MIGDISOVA, 1962b. *Oligo.*, Europe (Baltic)—*Holo.*

Family ORTHEZIIDAE

Amyot & Serville, 1843

[Ortheziidae AMYOT & SERVILLE, 1843, p. 619]

Similar to Coccidae. Females with body clearly segmented; antennae with distinct segmentation; abdominal spiracles present. *Oligo.*—*Holo.*

Orthezia BOSC, 1784, p. 173. *Holo.*

Ochyrocoris MENGE, 1856, p. 17 [**O. electrina*; OD]. Little-known genus, probably a synonym of *Orthezia* (recent). COCKERELL, 1906a; BECKER-MIGDISOVA, 1962b. *Oligo.*, Europe (Baltic).

Family MARGARODIDAE

Cockerell, 1899

[Margarodidae COCKERELL, 1899, p. 390]

Males commonly winged, with few unbranched veins. Females with convex body, strongly sclerotized, with clear segmentation; abdomen with an anal tube or a sclerotized ring, lacking setae. *Cret.*—*Holo.*

Margarodes GUILDING, 1829, p. 118. *Holo.*

Acreegris KOCH in KOCH & BERENDT, 1854, p. 123 [**A. crenata*; OD]. Female adult: antennae with 9 segments; body entirely or nearly devoid of setae; tarsi two-segmented. Male adult: compound eyes; wings with a single vein paralleling the costal margin to wing apex; M delicate, bisecting the wing diagonally; hind wing reduced to slender halteres; antennae with at least 8 segments; tarsi one-segmented; abdomen with long threads of wax arising from clusters of dorsal ducts. FERRIS, 1941. *Oligo.*, Europe (Baltic). —FIG. 161, 1. **A. crenata*; fore wing of male, $\times 6$ (Ferris, 1941).

Electrococcus BEARDSLEY, 1969, p. 271 [**E. canadensis*; OD]. Male small; antennae with 10 segments, pedicel conspicuously enlarged; legs long and slender; compound eye reduced to a single row of ommatidia. Fore wing well developed, with R and M distinct. *Cret.*, Canada (Manitoba).

Family PSEUDOCOCCIDAE

Cockerell, 1905

[Pseudococcidae COCKERELL, 1905, p. 193]

Similar to the Coccidae. Females typically covered with a mealy or filamentous, waxy secretion, commonly protruding as short lateral and long anal filaments; legs well developed. Males apterous or winged, typically with two long caudal wax filaments. *Oligo.*—*Holo.*

Pseudococcus WESTWOOD, 1840, p. 118. *Holo.*

Puto SIGNORET, 1875, p. 394. COCKERELL, 1908g. *Oligo.*, Europe (Baltic)—*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the suborder Homoptera, are too poorly known to permit assignment to families.

Anconatus BUCKTON, 1883, p. 177 [**A. dorsuosus*; OD]. Little-known aphidoid of uncertain affinities. HEIE, 1967, 1985. *Oligo.*, USA (Colorado).

Annulaphis SHAPOSHNIKOV, 1979b, p. 73 [**A. ras-*

nitsyni; OD]. Little-known genus, based on incomplete specimens; apparently related to *Ellinaphis*. [Originally placed in Palaeoaphididae, but transferred by HEIE (1985) to family uncertain.] *Cret.*, USSR (Asian RSFSR).

Aphidioides MOTSCHULSKY, 1856, p. 29 [**A. succifera*; OD]. Little-known aphidoid genus, based on apterous form. HEIE, 1967, 1985. *Oligo.*, Europe (Baltic).

Aphidulum HANDLIRSCH, 1939, p. 163 [**A. pusillum*; OD]. Little-known genus. HEIE, 1967. *Jur.*, England.

Archeglyphis MARTYNOV, 1931a, p. 89 [**A. cras-sinervis*; OD]. Little-known wing fragment. BECKER-MIGDISOVA, 1961c; ROHDENDORF & RASNITSYN, 1980. *Perm.*, USSR (Asian RSFSR).

Archipsyche HANDLIRSCH, 1906b, p. 624 [**A. eichstattensis*; OD]. Little-known genus, apparently similar to *Limacodites*. *Jur.*, Europe (Germany).

Austrocystina EVANS, 1943b, p. 181 [**A. imperfecta*; OD]. Little-known wing, possibly related to *Archescytinidae*. *Perm.*, Australia (New South Wales).

Beaconiella EVANS, 1963, p. 21 [**B. fennabi*; OD]. All principal veins of fore and hind wings multibranching; possibly a fulgoroid. RIEK, 1973. *Trias.*, Australia (New South Wales).

Beloptesis HANDLIRSCH, 1906b, p. 625 [**B. oppenbeimi*; OD]. Fore wing markedly triangular, nearly as broad as long; venation apparently as in *Limacodites*. Hind wing small, oval. EVANS, 1956. *Jur.*, Europe (Germany).

Bernaea SCHLEE, 1970, p. 18 [**B. neocomica*; OD]. Female with head wider than pronotum; median ocellus present; antennae with 7 segments, the third segment much longer than distal segments. Veins absent on hind wing, represented by lines of pigment. [Placed by SCHLEE in "Aleyrodina *sensu lato*," without family assignment.] *Cret.*, Lebanon.

Borisrohdendorfia BECKER-MIGDISOVA, 1959b, p. 138 [**B. picturata*; OD]. Based on distal fragment of wing. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).

Cercopidium WESTWOOD, 1854, p. 394 [**C. habni* WESTWOOD, 1854, p. 394; SD CARPENTER, herein]. Little-known genus, based on wing fragment. HEER, 1870a; HENRICKSEN, 1922b. *Jur.*, England; *Eoc.*, Greenland.

Chiliocycla TILLYARD, 1919c, p. 868 [**C. scolopoides*; OD]. Fore wing with strongly thickened costal border; RS present, arising before midwing; closed cell between M1+2 and M3+4; CUA connected to base of M by crossvein. [Type of family Chiliocyclidae EVANS, 1956, p. 209.] EVANS, 1956, 1961. *Trias.*, Australia (Queensland). —FIG. 162, 1. **C. scolopoides*; fore wing, $\times 4.5$ (Evans, 1956).

Cicadellites HEER, 1853a, p. 119 [**C. pallidus* HEER, 1853a, p. 119; SD CARPENTER, herein]. Little-

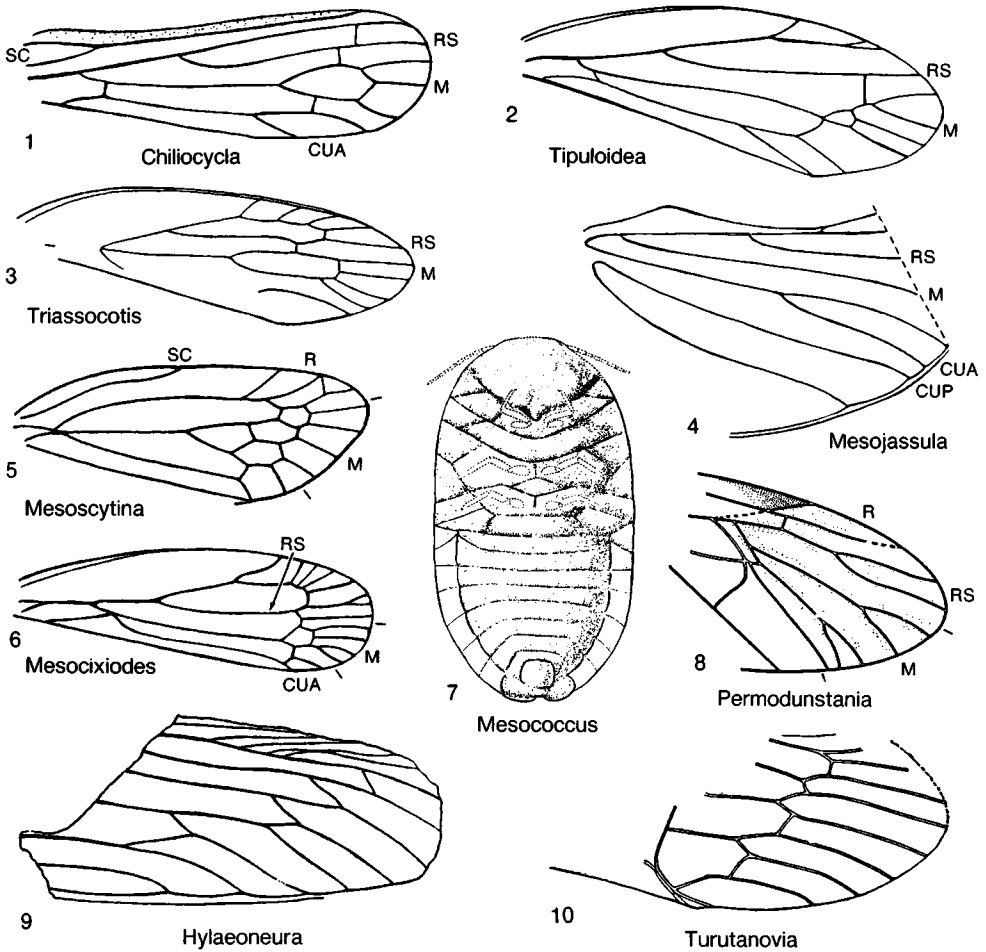


FIG. 162. Uncertain (p. 254–259).

known homopteron, possibly belonging to the Cercopidae. PITON & THÉOBALD, 1935. *Oligo.*, Europe (France); *Mio.*, Europe (Croatia).
Cicadellium WESTWOOD, 1854, p. 394 [**C. dipsas*; SD HANDLIRSCH, 1907, p. 641] [= *Pseudodelphax* HANDLIRSCH, 1907, p. 641 (type, *Delphax pulcher* BRODIE, 1845, p. 33)]. Little-known genus, based on fore wing. EVANS, 1956. *Jur.*, England.
Cixiites HANDLIRSCH, 1906b, p. 498 [**C. liasinus*; OD]. Little-known wing, possibly related to Fulgoridiidae. BECKER-MIGDISOVA, 1962b. *Jur.*, Europe (Germany).
Cixioides HANDLIRSCH, 1906b, p. 640 [**Cixius maculatus* BRODIE, 1845, p. 33; OD]. Little-known fore wing, possibly related to Cixiidae. *Jur.*, England.
Diphtheropsis MARTYNOV, 1937a, p. 110 [**D. incerta*; OD]. Little-known genus, based on incomplete fore wing with nearly straight costal

margin and long R+M. EVANS, 1956. *Jur.*, USSR (Kirghiz).

Dysmorphoscirtella RIEK, 1973, p. 527 [**D. lobata*; OD]. Little-known genus, based on distal fragment of wing. RIEK, 1976a. [Originally placed in Eoscartarellidae.] *Perm.*, South Africa.

Echinaphis COCKERELL, 1913f, p. 229 [**E. rohweri*; OD]. Little-known genus, based on hind wing and body fragments; apparently related to Greenideidae (recent) and Drepanosiphidae. HEIE, 1967, 1970b, 1985. *Oligo.*, USA (Colorado).

Electromyzus HEIE, 1972, p. 250 [**E. acutirostris*; OD]. Fore wing with RS very slightly curved; M with 2 terminal branches, arising close to point of origin of CUA1 and CUA2. HEIE, 1985. *Oligo.*, Europe (Baltic).

Ellinaphis SHAFOSHNIKOV, 1979b, p. 71 [**E. incognita*; OD]. Little-known genus, originally placed

- in Palaeoaphididae but transferred by HEIE (1985) to category of family uncertain. *Cret.*, USSR (Asian RSFSR).
- Eochilicycla** DAVIS, 1942, p. 114 [**E. angusta*; OD]. Little-known genus, based on fore wing; possibly fulgoroid. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Eocicada** OPPENHEIM, 1888, p. 229 [**E. microcephala*; OD]. Little-known genus, based on wing fragment. EVANS, 1956. *Jur.*, Europe (Germany).
- Eopsyllidium** DAVIS, 1942, p. 114 [**E. delicatulum*; OD]. Little-known hind wing, with CUA free from M basally. Possibly related to the Protopsyllidiidae. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Fulgoridiella** BECKER-MIGDISOVA, 1962a, p. 96 [**F. raetica*; OD]. Little-known wing fragment, possibly related to Fulgoridiidae. *Trias.*, USSR (Kirghiz).
- Fulgoropsis** MARTYNOV, 1937a, p. 165 [**F. dubiosa*; OD]. Little-known genus, based on wing fragment, possibly related to Fulgoridiidae. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kirghiz).
- Gerancho** SCUDDER, 1890, p. 248 [**Lacchnus petrorum* SCUDDER, 1877b, p. 279; OD]. Little-known genus, possibly belonging to Aphidoidea. HEIE, 1967, 1985. *Eoc.*, Canada (British Columbia).
- Gryllites** GERMAR, 1842, p. 82 [**G. dubius*; OD]. Little-known genus, originally placed in Orthoptera. HAGEN, 1862; ASSMANN, 1877; POPOV, 1971. *Jur.*, Europe (Germany).
- Hasrites** COCKERELL, 1922f, p. 161 [**H. muiri*; OD]. Little-known genus. Fore wing elongate; R apparently with a short distal branch; M dividing distally, with 3 terminal branches; CUA with 3 terminal branches. *Oligo.*, England.
- Heidea** SCHLEE, 1970, p. 9 [**H. cretatica*; OD]. Male with head about same width as pronotum; median ocellus present; third antennal segment about as long as distal segments. Vein present in hind wing. [Considered by SCHLEE to be related to the existing and Tertiary Aleurodidae but differing markedly in several traits.] *Cret.*, Lebanon.
- Hooley** COCKERELL, 1922f, p. 160 [**H. indecisa*; OD]. Little-known fore wing; costal margin broad; SC apparently separating from R before midwing, and giving rise to a series of short, oblique veinlets to costal margin. *Oligo.*, England.
- Homopterites** HANDLIRSCH, 1906b, p. 499 [**H. anglicus*; OD]. Little-known fore wing. *Jur.*, England.
- Hylaeoneura** LAMEERE & SEVERIN, 1897, p. 37 [**H. lignei*; OD]. Little-known genus, based on distal fragment of fore wing. R with several long, pectinate branches to costal margin; M with 3 branches. *Cret.*, Europe (Belgium). — FIG. 162,9. **H. lignei*; fore wing, $\times 2.5$ (Handlirsch, 1907).
- Hypocixius** COCKERELL, 1926a, p. 501 [**H. oblitescens*; OD]. Little-known genus, based on incomplete fore wing. Possibly related to Cixiidae. *Tert. (epoch unknown)*, Argentina (Jujuy).
- Jurocallis** SHAPOSHNIKOV, 1979b, p. 68 [**J. longipes*; OD]. Antennae tapering from base to apex; RS arising from distal part of prerostigmal area; M arising from base of pterostigma and with 3 terminal branches. [Originally placed in Drepanosiphidae.] HEIE, 1985. *Cret.*, USSR (Asian RSFSR).
- Kaltanocicada** BECKER-MIGDISOVA, 1961c, p. 291 [**K. dunstanoides*; OD]. Little-known hind wing, with broadly rounded apex and wide concavity of front wing margin; CUA with long fork. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).
- Kaltanoscyta** BECKER-MIGDISOVA, 1959a, p. 110 [**K. reticulata*; OD]. Little-known fragment of fore wing, strongly coriaceous and with dense reticulation over wing. Possibly related to Coleoscytidae. *Perm.*, USSR (Asian RSFSR).
- Karabasia** MARTYNOV, 1926b, p. 1356 [**K. paucineris*; OD]. Little-known insect, possibly related to Jassidae. *Jur.*, USSR (Kazakh).
- Karajassus** MARTYNOV, 1926b, p. 1352 [**K. crassineris*; OD]. Little-known insect, possibly close to Cicadellidae. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh).
- Kisylia** MARTYNOV, 1937a, p. 109 [**K. pylloides*; OD]. Little-known genus, based on fore wing. Nodus and nodal line absent; stem of R slightly shorter than R + M; CUA not coalesced with M. *Jur.*, USSR (Kirghiz). — FIG. 163,4. **K. pylloides*; fore wing, $\times 3$ (Becker-Migdisova, 1962b).
- Larssonaphis** HEIE, 1967, p. 168 [**L. obnubila*; OD]. Little-known aphidoid genus. HEIE, 1985. *Oligo.*, Europe (Baltic).
- Liassocicada** BODE, 1953, p. 201 [**L. antecedens*; OD]. Little-known genus, based mainly on body structure. Rostrum elongate, extending at least to middle of abdomen. [Liassocicada was redefined by WHALLEY (1983) and provisionally placed in the Cicadidae. However, I doubt that our very slight knowledge of the body structures of these Jurassic and Triassic specimens justifies the extension of the range of the Cicadidae to another 150 million years before the Paleocene. Accordingly, the genus *Liassocicada* is herein provisionally placed in the Homoptera, family uncertain.] WHALLEY, 1983. *Trias.*, England; *Jur.*, Europe (Germany).
- Limacodites** HANDLIRSCH, 1906b, p. 622 [**L. mesozoicus*; OD]. Little-known genus, based on wing fragments. Probably related to *Eocicada*. *Jur.*, Europe (Germany).
- Lithecphora** SCUDDER, 1890, p. 329 [**L. unicolor* SCUDDER, 1890, p. 329; SD CARPENTER, herein]. Little-known insect, with slender fore wing. *Oligo.*, USA (Colorado).

Lithopsis SCUDDER, 1878b, p. 773 [**L. fimbriata*; OD]. Body stout; head not produced between the eyes. Tegmina extending well beyond abdomen. SCUDDER, 1890; COCKERELL, 1921b; PONGRÁČZ, 1935; PITON, 1940a. *Eoc.*, USA (Wyoming), Europe (France, Germany).

Locrites SCUDDER, 1890, p. 323 [**L. copei* SCUDDER, 1890, p. 323; SD CARPENTER, herein]. Little-known homopteron; head large, protuberant; scutellum equiangular. HEER, 1853a. *Oligo.*, USA (Colorado); *Mio.*, Europe (Croatia).

Margaroptilon HANDLIRSCH, 1906b, p. 499 [**M. woodwardi* HANDLIRSCH, 1906b, p. 499; SD CARPENTER, herein]. Little-known wings, with numerous small maculations; possibly a fulgoroïd. BODE, 1953; EVANS, 1956. *Jur.*, England, Europe (Germany).

Mesaleuropsis MARTYNOV, 1937a, p. 108 [**M. venosa*; OD]. Little-known wings. Fore wing rounded distally; pterostigma absent; M with 2 branches; CUA apparently unbranched. Hind wing about half as long as fore wing, with unbranched RS and M. *Jur.*, USSR (Tadzhik).

Meshemipteron COCKERELL, 1915, p. 476 [**M. incertum*; OD]. Little-known genus, based on small fragment of wing. *Jur.*, England.

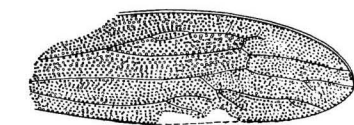
Mesocicadella EVANS, 1956, p. 193 [**M. venosa*; OD]. Little-known genus, based on fragment of fore wing. Several parallel, oblique veins between R and wing margin; M with numerous branches. [Originally placed in the Scytinopteridae but moved to family uncertain by EVANS in 1961.] *Trias.*, Australia (Queensland).—FIG. 163,2. **M. venosa*; fore wing, $\times 3.5$ (Evans, 1956).

Mesocixiodes TILLYARD, 1922b, p. 462 [**M. termioneura*; OD]. Fore wing with SC very close to costal margin; RS present; M forking in distal part of wing, with a small, closed cell between forks. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 162,6. **M. termioneura*; fore wing, $\times 5.2$ (Evans, 1956).

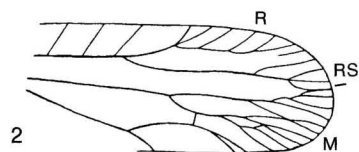
Mesococcus BECKER-MIGDISOVA, 1959a, p. 110 [**M. asiaticus*; OD]. Based on wingless form (female?); body oval; legs greatly reduced; abdomen with 9 visible segments. BECKER-MIGDISOVA, 1962b. *Trias.*, USSR (Kirghiz).—FIG. 162,7. **M. asiaticus*; whole insect, $\times 24$ (Becker-Migdisova, 1959a).

Mesodiphthera TILLYARD, 1919c, p. 873 [**M. grandis*; OD]. Little-known genus, based on small fragment of fore wing. CUA anastomosed with M basally. [Placed in Tropiduchidae by TILLYARD (1922b) and in Homoptera, family uncertain, by EVANS (1956).] *Trias.*, Australia (Queensland).—FIG. 163,3. **M. grandis*; fore wing, $\times 3.5$ (Tillyard, 1919c).

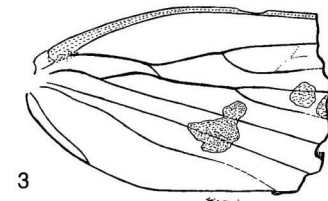
Mesojassula EVANS, 1956, p. 203 [**M. marginata*; OD]. Hind wing with costal margin with marked medial depression; M unbranched; CUA with 2 equal branches; marginal vein present. *Trias.*,



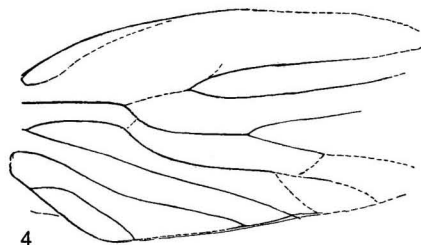
1 Tychitcola



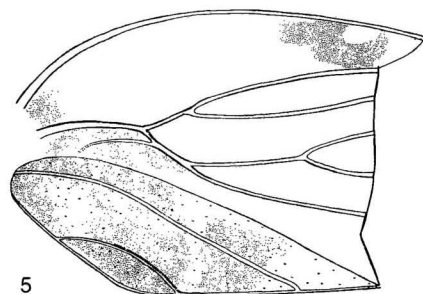
2 Mesocicadella



3 Mesodiphthera



4 Kisylia



5 Shuraboprosbole

FIG. 163. Uncertain (p. 256–259).

Australia (Queensland).—FIG. 162,4. **M. marginata*; hind wing, $\times 4.5$ (Evans, 1956).
Mesoledra EVANS, 1956, p. 211, *nom. subst. pro Mesojassus* HANDLIRSCH, 1939, p. 145, *non* TILLYARD, 1916 [**Mesojassus pachyneurus* HANDLIRSCH, 1939, p. 145; OD]. Little-known

- genus, based on incomplete wing; possibly related to Cicadellidae. *Jur.*, Europe (Germany).
- Mesoscytina** TILLYARD, 1919c, p. 871 [**M. australis*; OD]. Fore wing with SC distinct, long; RS apparently arising in very distal part of wing; M dividing at midwing and forming a closed cell at fork. Possibly related to Scytinopteridae. EVANS, 1956. *Trias.*, Australia (Queensland). —FIG. 162,5. **M. australis*; fore wing, $\times 5.2$ (Evans, 1956).
- Meuniera** PITON, 1936c, p. 1 [**M. haupti*; OD]. Little-known genus, based on fragment of fore wing. RS arising well before midwing; basal stem of M free from R. COOPER, 1941. *Eoc.*, Europe (France).
- Pachypsyche** HANDLIRSCH, 1906b, p. 623 [**Palaontina vidale* MEUNIER, 1902e, p. 9; OD]. Little-known genus. Fore wing rectangular; anterior margin straight, without nodal break; venation as in *Limacodites*. *Jur.*, Europe (Spain).
- Palaeoforda** KONONOVA, 1977, p. 588 [**P. tajmyrensis*; OD]. Little-known genus. Antennae with 6 segments. Fore wing with RS arising from distal part of pterostigma; M unbranched. Legs short. [Placed in Pemphigidae by KONONOVA but transferred to family uncertain by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).
- Parafulgoridium** HANDLIRSCH, 1939, p. 138 [**Fulgoridium simplex* GEINITZ, 1880, p. 528; OD]. Little-known genus, based on poorly preserved fore wing. *Jur.*, Europe (Germany).
- Parajassus** BODE, 1953, p. 200 [**P. hattorfensis*; OD]. Little-known wing. BECKER-MIGDISOVA, 1962b. *Jur.*, Europe (Germany).
- Perissovena** RIEK, 1976a, p. 775 [**P. heidiae*; OD]. Little-known genus, based on hind wing. *Perm.*, South Africa.
- Permocapitus** EVANS, 1943b, p. 195 [**P. globulus*; OD]. Little-known genus, based on head. Head oval, eyes globular; transverse ridge between eyes. *Perm.*, Australia (New South Wales).
- Permocephalus** EVANS, 1943a, p. 8 [**P. knighti*; OD]. Little-known insects, known only by fragments of head. *Perm.*, Australia (New South Wales).
- Permodunstantia** BECKER-MIGDISOVA, 1961c, p. 290 [**P. proboloides*; OD]. Distal fragment of fore wing; RS forked; M4 free from M3 distally. *Perm.*, USSR (Asian RSFSR). —FIG. 162,8. **P. proboloides*; fore wing, $\times 2.7$ (Becker-Migdisova, 1961c).
- Petroperon** COCKERELL, 1912b, p. 94 [**P. mirandum*; OD]. Little-known genus, based on wing fragment; possibly a fulgoroid. *Cret.*, USA (Colorado).
- Phragmatoecicossus** BECKER-MIGDISOVA, 1949b, p. 11 [**P. shurabensis*; OD]. Little-known genus, based on fragment of fore wing. Probably related to Paleontinidae. *Jur.*, USSR (Asian RSFSR).
- Plecopterus** COCKERELL, 1917h, p. 327 [**P. nebulosus*; OD]. Little-known genus, based on wing and fragments of body. [Originally placed in Trichoptera, but transferred to Homoptera, family uncertain, by BOTOSANEANU, 1981.] *Mio.*, Burma.
- Prolystra** OPPENHEIM, 1888, p. 228 [**P. lithographica*; OD]. Little-known genus, probably close to *Limacodites*. EVANS, 1956. *Jur.*, Europe (Germany).
- Prosbolopsis** MARTYNOV, 1935c, p. 19 [**P. ovalis*; OD]. Little-known insect, with reduced venation in tegmen. [Type of family Prosbolopseidae BECKER-MIGDISOVA, 1946.] EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (European RSFSR).
- Protopsyche** HANDLIRSCH, 1906b, p. 623 [**P. braueri*; OD]. Little-known genus, similar to *Limacodites*. *Jur.*, Europe (Germany).
- Reticulocicada** BECKER-MIGDISOVA, 1961c, p. 362 [**R. brachyptera*; OD]. Little-known tegmen, with coarse reticulation; possibly a fulgoroid. *Perm.*, USSR (Asian RSFSR).
- Sbenaphis** SCUDDER, 1890, p. 250 [**S. quesneli*; OD]. Little-known aphidoid genus. HEIE, 1967, 1985. *Eoc.*, Canada (British Columbia).
- Shuraboprosbole** BECKER-MIGDISOVA, 1949b, p. 23 [**S. plachutai*; OD]. Little-known genus, based on wing fragment. Basal stem of R only about half as long as R+M; RS arising well before midwing; CUA anastomosed with M for a short distance. *Jur.*, USSR (Tadzhik). —FIG. 163,5. **S. plachutai*; fore wing as preserved, $\times 2.5$ (Becker-Migdisova, 1949b).
- Stenoglyphis** EVANS, 1947b, p. 432 [**S. kimblensis*; OD]. Little-known genus, possibly related to Scytinopteridae. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Tingiopsis** BECKER-MIGDISOVA, 1953c, p. 461 [**T. reticulata*; OD]. Little-known genus, based on incomplete fore wing with fine reticulation. [Originally placed in Tingidae (Heteroptera) but transferred to Homoptera, probably Cercopidae, by EVANS (1957).] *Trias.*, USSR (Tadzhik).
- Tipuloidea** WIELAND, 1925, p. 23 [**T. rhaetica*; OD]. Little-known genus, based on fore wing. Costal margin arched; SC apparently absent; RS arising before midwing; closed median cell very small. [Originally placed in order Diptera.] EVANS, 1956. *Trias.*, Argentina. —FIG. 162,2. **T. rhaetica*; fore wing, $\times 2$ (Evans, 1956).
- Triassoaphis** EVANS, 1956, p. 238 [**T. cubitus*; OD]. Little-known genus, based on wing fragment. [Originally placed in Aphididae but transferred to Aphidoidea, family uncertain, by BECKER-MIGDISOVA & AIZENBERG (1962).] RICHARDS, 1966; HEIE, 1967, 1981; SHAPOSHNIKOV, 1979a. *Trias.*, Australia (Queensland).
- Triassocotis** EVANS, 1956, p. 194 [**T. australis*; OD]. Little-known genus, based on distal half of tegmen. Tegmen narrow; R with 4 branches;

RS unbranched; M with 4 branches and a cell included between M1+2 and M3+4. [Originally placed in Scytinopteridae but transferred to family uncertain by EVANS (1961).] *Trias.*, Australia (Queensland). — FIG. 162,3. **T. australis*; fore wing, $\times 4.5$ (Evans, 1956).

Triassojassus TILLYARD, 1919c, p. 887 [**T. proavittus*; OD]. Little-known genus, based on incomplete tegmen. Costal margin unusually convex; RS unbranched; M with 5 branches. [Originally placed in the Jassidae, but EVANS transferred first (1956) to the Chilocyclidae and later (1961) to family uncertain.] *Trias.*, Australia (New South Wales).

Turatanovia BECKER-MIGDISOVA, 1949b, p. 21 [**T. karatavia*; OD]. Little-known genus, based on distal fragment of fore wing. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh). — FIG. 162,10. **T. karatavia*; fore wing as preserved, $\times 2$ (Becker-Migdisova, 1962b).

Tychicola BECKER-MIGDISOVA, 1952, p. 181 [**T. longipenna*; OD]. Little-known genus, based on incomplete fore wing. Wing apparently long and narrow; RS long and parallel to R2. *Perm.*, USSR (Asian RSFSR). — FIG. 163,1. **T. longipenna*; fore wing, $\times 5$ (Becker-Migdisova, 1962b).

Suborder HETEROPTERA

Latreille, 1810

[Heteroptera LATREILLE, 1810, p. 433]

Fore wing typically with the proximal part strongly coriaceous and the distal part membranous, forming a hemelytron; wings usually held flat over abdomen at rest. *Perm.*—*Holo.*

Family PROGONOCIMICIDAE

Handlirsch, 1906

[Progonocimicidae HANDLIRSCH, 1906b, p. 493] [=Eocimicidae HANDLIRSCH, 1906b, p. 494; Actinocytinidae EVANS, 1956, p. 244; Cicadocoridae BECKER-MIGDISOVA, 1958, p. 60]

Small species, dorsoventrally flattened; pronotum distinctly broader than long; fore wing apparently of uniform texture; veins RS and M coalesced basally; SC apparently coalesced with stem of R basally, diverging toward costal margin near midwing; M with 2 to 4 branches; CUA with 2 to 3 branches. [Placed by POPOV (1980a) in suborder Peloridiina, along with the Peloridiidae (recent).] *Perm.*—*Jur.*

Progonocimex HANDLIRSCH, 1906b, p. 494 [**P. jurassicus*; OD] [=Eocimex HANDLIRSCH, 1906b,

p. 494 (type, *E. liasinus*)]. Fore wing with rounded apex; clavus broad, nearly triangular; M with 3 branches. BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 164,8. *Progonocimex*; a, **P. jurassicus*, dorsal view; b, *P. liasinus* (HANDLIRSCH), fore wing, both $\times 9$ (Popov & Wootton, 1977).

Actinoscytina TILLYARD, 1926a, p. 18 [**A. belmontensis*; OD] [=Pseudiprivia HANDLIRSCH, 1939, p. 17 (type, *P. ala*)]. Little-known genus. Tegmen similar to that of *Progonocimex*, but more slender, anterior margin less curved; SC curving directly toward anterior margin of wing. EVANS, 1956; POPOV & WOOTTON, 1977. *Perm.*, Australia (New South Wales). — FIG. 164,5. **A. belmontensis*; tegmen, $\times 8$ (Evans, 1956).

Archicercopis HANDLIRSCH, 1939, p. 142 [**A. falcata*; OD]. Anterior margin of fore wing strongly convex basally; precostal area broad; wing apex pointed and directed anteriorly. EVANS, 1956; BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 164,6. **A. falcata*; fore wing, $\times 13$ (Popov & Wootton, 1977).

Cicadocoris BECKER-MIGDISOVA, 1958, p. 62 [**C. kuliki*; OD]. Tegmen with smoothly curved anterior margin; M with 3 branches; M3+4 unbranched. EVANS, 1961; POPOV, 1982. *Trias.*, USSR (Kirghiz). — FIG. 164,9. **C. kuliki*; restoration, $\times 10$ (Becker-Migdisova, 1958).

Eocercopis HANDLIRSCH, 1939, p. 142 [**E. ancyloptera*; OD] [=Cercoprisca HANDLIRSCH, 1939, p. 143 (type, *C. similis*); *Cercopinus* HANDLIRSCH, 1939, p. 143 (type, *C. ovalis*)]. Fore wing with very convex and thickened costal margin; apex pointed; clavus broad and nearly triangular. EVANS, 1956; BECKER-MIGDISOVA, 1958; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 164,7. **E. ancyloptera*; fore wing, $\times 13$ (Popov & Wootton, 1977).

Heterojassus EVANS, 1961, p. 23 [**H. membranaceus*; OD]. Tegmen oval; SC and R terminating on costal margin near level of midwing. *Trias.*, Australia (Queensland). — FIG. 164,4. **H. membranaceus*; fore wing, $\times 19$ (Evans, 1961).

Heteroscytina EVANS, 1956, p. 245 [**H. tillyardi*; OD]. Fore wing narrowed apically, much as in *Actinoscytina*, but costal area narrower and crossveins forming a more nearly complete transverse series. WOOTTON, 1963. *Trias.*, Australia (Queensland).

Hexascytina WOOTTON, 1963, p. 250 [**H. transecta*; OD]. Little-known genus, apparently similar to *Progonocimex*, based on incomplete tegmen. SC diverging from stem R near midwing at almost a 90° angle; anterior margin of tegmen distinctly convex. *Trias.*, Australia (Queensland).

Microscytinella WOOTTON, 1963, p. 251 [**M. radians*; OD]. Little-known genus, based on small

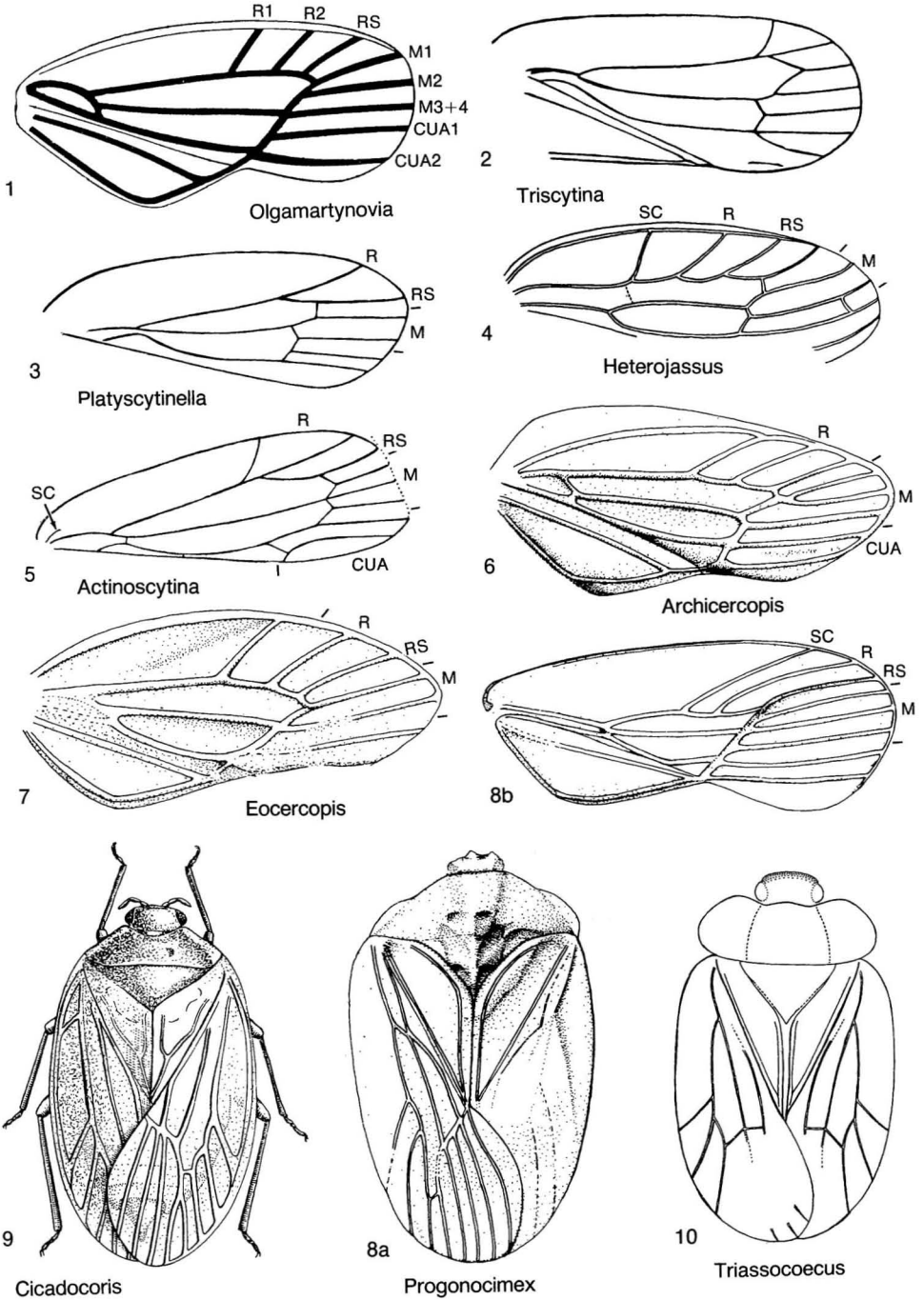


FIG. 164. Progonocimicidae (p. 259–260).

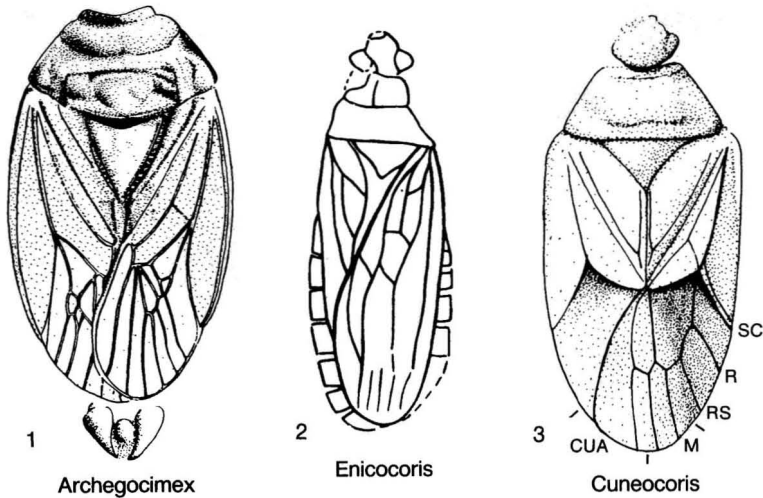


FIG. 165. Archegocimicidae, Enicocoridae, and Cuneocoridae (p. 261–262).

fragment of tegmen. *Trias.*, Australia (Queensland).

Olgamartynovia BECKER-MIGDISOVA, 1958, p. 63 [*O. turanica*; OD]. Tegmen as in *Cicadocoris*, but fork of M1+2 longer. POPOV, 1982. *Trias.*, USSR (Kirghiz).—FIG. 164,1. *O. complexa* POPOV; tegmen, $\times 14$ (Popov, 1982).

Platyscytinella EVANS, 1956, p. 245 [**P. paradoxa*; OD]. Tegmen shaped as in *Actinoscytina*; SC absent; M1 continuing the nearly straight line of stem M; clavus unknown. WOOTTON, 1963. *Trias.*, Australia (New South Wales).—FIG. 164,3. **P. paradoxa*; fore wing, $\times 15$ (Wootton, 1963).

Triassocoecus EVANS, 1963, p. 22 [**T. chinai*; OD]. Little-known genus. Tegmen broader than in *Actinoscytina*; pronotum with large lateral lobes. *Trias.*, Australia (New South Wales).—FIG. 164,10. **T. chinai*; dorsal view, $\times 10$ (Evans, 1963).

Triscytina EVANS, 1956, p. 246 [**T. rotundata*; OD]. Similar to *Actinoscytina* but tegmen much broader; costal margin nearly straight; apex evenly rounded. *Trias.*, Australia (New South Wales).—FIG. 164,2. **T. rotundata*; tegmen, $\times 16$ (Evans, 1956).

Family ARCHEGOCIMICIDAE Handlirsch, 1906

[Archegocimicidae HANDLIRSCH, 1906b, p. 493] [=Eonabidae HANDLIRSCH, 1920, p. 207; Diatillidae HANDLIRSCH, 1920, p. 210]

Small Heteroptera of uncertain relationships. Body dorsoventrally flattened; pronotum coarsely warty. Fore wing with apex rounded; clavus narrow; costal margin

strongly sclerotized; veins SC, R, and M coalesced for about two-fifths length of wing. *Jur.*

Archegocimex HANDLIRSCH, 1906b, p. 493 [**A. geinitzi*; OD] [=Eonabis HANDLIRSCH, 1920, p. 207 (type, *E. primitiva*); *Archegocoris* HANDLIRSCH, 1939, p. 114 (type, *A. liadis*)]. Radial complex of fore wing (R and RS) with 3 branches terminating on anterior margin of wing. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).—FIG. 165,1. **A. geinitzi*; dorsal view, $\times 14$ (Popov & Wootton, 1977).

Anosmus HANDLIRSCH, 1939, p. 115 [**A. spilopteris*; OD]. Costal area of fore wing narrow; radial complex branched. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Corynecoris BODE, 1953, p. 132 [**C. semigranulatus*; OD]. Little-known genus, based on poorly preserved specimen. [Family assignment doubtful.] POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Diatillus HANDLIRSCH, 1920, p. 210 [**D. debilis*; OD]. Little-known genus with archegocimicid venation. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Ensphingocoris BODE, 1953, p. 139 [**E. praerotundatus*; OD]. Little-known genus, based on poorly preserved specimen lacking wings; body apparently that of a large archegocimicid. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Entomecoris BODE, 1953, p. 134 [**A. minor*; OD]. Fore wing with common stem of SC, R, and M curving away from costal margin; wing differentiated into corium and membrane. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Eurynotis BODE, 1953, p. 134 [**E. incisus*; OD].

Similar to *Somatocoris*, but radial complex with 2 branches. BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Macropterocoris BODE, 1953, p. 138 [**M. obtusus*; OD]. Little-known genus; head and thorax resembling those of the Archegocimicidae. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Progonocoris HANDLIRSCH, 1939, p. 115 [**P. pictus*; OD]. Similar to *Anosmus*, but radial complex of fore wing apparently unbranched; costal area long. BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Somatocoris BODE, 1953, p. 141 [**S. conservatus*; OD]. Similar to *Archegocimex* but smaller; radial complex (R and RS) with 3 branches. BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Family ENICOCEPHALIDAE Stål, 1858

[Enicocephalidae STÅL, 1858, p. 81]

Similar to the Reduviidae, but head constricted behind eyes; rostrum with 4 segments; fore wings entirely membranous, with longitudinal veins but few crossveins. *Mio.*—*Holo.*

Enicocephalus WESTWOOD, 1838, p. 22. *Holo.*

Disphaerocephalus COCKERELL, 1917g, p. 361 [**D. constrictus*; OD]. Little-known genus of small, elongate species, with long, thin legs and antennae; body with long, fine pubescence; hind legs long and narrow; tarsi 1-2-2; wings unknown. [Genus based on nymph and adult male.] ŠTYS, 1969. *Mio.*, Burma.

Paenicotechys ŠTYS, 1969, p. 353 [**Enicocephalus fossilis* COCKERELL, 1916a, p. 135; OD]. Similar to *Aenictopachys* (recent), but posterior margin of pronotum excised; eyes contiguous dorsally; middle tarsi with 2 segments. ŠTYS, 1969. *Mio.*, Burma.

Family ENICOCORIDAE Popov, 1980

[Enicocoridae POPOV, 1980a, p. 50]

Apparently related to the Enicocephalidae. Head short, rostrum thick, curved. Tegmen entirely membranous, clavus and corium not differentiated; radial-medial and cubital-anal sectors of veins widely separated at base; veins nearly parallel distally. Legs thin, cursorial. *Cret.*

Enicocoris POPOV, 1980a, p. 50 [**E. manlaicus*; OD]. Head prognathous; pronotum transverse; scutellum much narrower than pronotum; subcostal area of tegmen wide. *Cret.*, Mongolia. —FIG. 165,2 **E. manlaicus*; dorsal view, ×9 (Popov, 1980a).

Family DIPSOCORIDAE Dohrn, 1859

[Dipsocoridae DOHRN, 1859, p. 36]

Similar to the Saldidae, but third antennal segment not thickened at base. *Mio.*—*Holo.*

Dipsocoris HALIDAY, 1855, fig. 61. *Holo.*

Ceratocombus SIGNORET, 1852, p. 542. WYGODZINSKY, 1959. *Mio.*, Mexico (Chiapas)—*Holo.*

Family CUNEOCORIDAE Handlirsch, 1920

[Cuneocoridae HANDLIRSCH, 1920, p. 208]

Small insects. Fore wings reaching end of abdomen and overlapped distally; pronotum wider than long; scutellum triangular. Fore wing not clearly differentiated into corium and membrane; veins M and CU branched. *Jur.*

Cuneocoris HANDLIRSCH, 1920, p. 208 [**C. geinitzi*; OD]. M and CU each with 2 branches. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 165,3. **C. geinitzi*; dorsal view, ×22 (Popov & Wootton, 1977).

Family GERRIDAE Leach, 1815

[Gerridae LEACH, 1815, p. 123]

Body slender; rostrum with 4 segments; fore wings without differentiation of corium, membrane, or clavus; posterior femora extending well beyond end of abdomen; claws ante-apical. Semiaquatic. ANDERSEN, 1982b. *Eoc.*—*Holo.*

Gerris FABRICIUS, 1794, p. 187. COCKERELL, 1909j; HANDLIRSCH, 1910b; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Canada (British Columbia), Europe (France)—*Holo.*

Metrobates UHLER, 1871, p. 108. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Telmatrechus SCUDDER, 1890, p. 351 [**Hygrotrechus stali* SCUDDER, 1879a, p. 183b; SD CARPENTER, herein]. Eyes not prominent; first antennal segment only a little longer than second; thorax relatively short; legs very long, with the tibiae equal in length to femora of same leg. *Eoc.*, USA (Wyoming); *Mio.*, Canada (British Columbia).

Family HYDROMETRIDAE Stephens, 1829

[Hydrometridae STEPHENS, 1829, p. 352]

Very slender species; head long and narrow but widened distally; antennae with 4 (rarely 5) segments; legs very long and slender, claws

apical; rostrum with 3 segments; tegmen with corium and membrane. *Eoc.*—*Holo.*

Hydrometra LATREILLE, 1796, p. 86. *Holo.*

Eocenometra ANDERSEN, 1982a, p. 91 [**E. danica*; OD]. Similar to *Bacillometra* (recent) and *Hydrometra* (recent), but first antennal segment much longer than second; thorax relatively short and robust. ANDERSEN, 1982b. *Eoc.*, Europe (Denmark).

Family VELIIDAE

Amyot & Serville, 1843

[Velidae AMYOT & SERVILLE, 1843, p. 418]

Similar to the Gerridae, but rostrum with 3 segments; posterior femora shorter, extending very little beyond end of abdomen at most. *Oligo.*—*Holo.*

Velia LATREILLE, 1804, p. 270. MEUNIER, 1914a. *Oligo.*, Europe (France)—*Holo.*

Palaeovelina SCUDDER, 1890, p. 349 [**P. spinosa*; OD]. Similar to *Microvelia* (recent). Head small, recessed to level of eyes in emarginate prothorax; hind legs very short, reaching only tip of abdomen; femora and tibiae of equal lengths; hind tibiae with long spines distally. *Oligo.*, USA (Colorado).

Stenovelina SCUDDER, 1890, p. 349 [**S. nigra*; OD]. Similar to *Palaeovelina*, but hind tibiae without long spines distally. *Oligo.*, USA (Colorado).

Family NOTONECTIDAE

Latreille, 1802

[Notonectidae LATREILLE, 1802a, p. 253]

Aquatic species, similar to the Naucoridae, but forelegs raptorial, and hind tarsi without claws. *Jur.*—*Holo.*

Notonecta LINNÉ, 1758, p. 439. PITON, 1942; LAUCK, 1960; POPOV, 1964; MARTINI, 1971. *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (France)—*Holo.*

Anisops SPINOLA, 1837, p. 58. DEICHMÜLLER, 1881; STYS & RIHA, 1975a. *Oligo.*, Europe (Czechoslovakia)—*Holo.*

Asionecta POPOV in BECKER-MIGDISOVA & POPOV, 1963, p. 78 [**A. curtipes*; OD]. Similar to *Notonecta* but with first segment of front and middle legs very short. *Jur.*, USSR (Kazakh). —FIG. 166.2. **A. curtipes*; ventral view, $\times 5$ (Popov in Becker-Migdisova & Popov, 1963).

Clematina POPOV, 1964, p. 66 [**Notonecta primaeva* HEYDEN, 1859a, p. 11; OD]. Little-known genus, apparently related to *Clypostemma*. POPOV, 1971; STYS, 1973. *Oligo.*, Europe (Germany).

Clypostemma POPOV, 1964, p. 64 [**C. xyphiale*; OD]. Species of moderate size and of uncertain

relationship within the family. Rostrum with 4 segments; tarsi of all legs with 2 segments. POPOV, 1971; STYS, 1973. *Cret.*, USSR (Asian RSFSR).

Enithares SPINOLA, 1837, p. 60. A nymph is only fossil record. [Generic assignment uncertain.] STYS & RIHA, 1975a. *Oligo./Mio.*, Europe (Czechoslovakia)—*Holo.*

Liadonecta POPOV, 1971, p. 172 [**L. tomiensis*; OD]. Little-known genus, based on nymph. Body elongate-oval, head transverse; hind tibiae and tarsi of uniform width. *Jur.*, USSR (Asian RSFSR). —FIG. 166.3. **L. tomiensis*; dorso-ventral view, $\times 14$ (Popov, 1971).

Nepidium WESTWOOD, 1854, p. 396 [**N. stolonae*; OD]. Little-known genus, based on poorly preserved specimen. [Put in Naucoridae by HANDLIRSCH (1906b) and in Notonectidae by POPOV (1971).] *Jur.*, England.

Notonectites HANDLIRSCH, 1906b, p. 639 [**Notonecta elterleini* DEICHMÜLLER, 1886, p. 64; OD]. Little-known genus, apparently close to *Notonecta* and *Anisops* (recent). POPOV, 1964, 1971; STYS & RIHA, 1975a. *Jur.*, Europe (Germany).

Pelonecta POPOV, 1971, p. 170 [**P. solnhofeni*; OD]. Body elongate-oval, widest near base of abdomen; hind tibiae shorter than femora or tarsi; femora thickened, strongly developed. *Jur.*, Europe (Germany). —FIG. 166.1. **P. solnhofeni*; ventral view, $\times 2.2$ (Popov, 1971).

Soevenia STATZ, 1950b, p. 63 [**Notonecta beydeni* DEICHMÜLLER, 1881, p. 328; OD]. Similar to *Anisops*; clypeus fused to frons. Body structure little known. *Oligo.*, Europe (Germany, Czechoslovakia).

Family SCAPHOCORIDAE

Popov, 1968

[Scaphocoridae POPOV, 1968, p. 106]

Body oval; head hypognathous; pronotum large, covering scutellum; tegmen with membrane; hind legs relatively short; tarsi with a single segment and dense hairs. Probably related to the Naucoridae. *Jur.*

Scaphocoris POPOV, 1968, p. 106 [**S. notatus*; OD]. Head strongly transverse from above; scutellum very small, triangular; clavus with distinct anal veins; membrane present; hind tarsi shorter than tibiae. *Jur.*, USSR (Kazakh).

Family NAUCORIDAE Leach, 1815

[Naucoridae LEACH, 1815, p. 123] [=Aphlebororidae HANDLIRSCH, 1906b, p. 494; Apopnidae HANDLIRSCH, 1920, p. 209]

Antennae four-segmented, shorter than head; fore wing membrane without veins; forelegs raptorial; tarsi with more than one segment; hind tarsi with claws. *Jur.*—*Holo.*

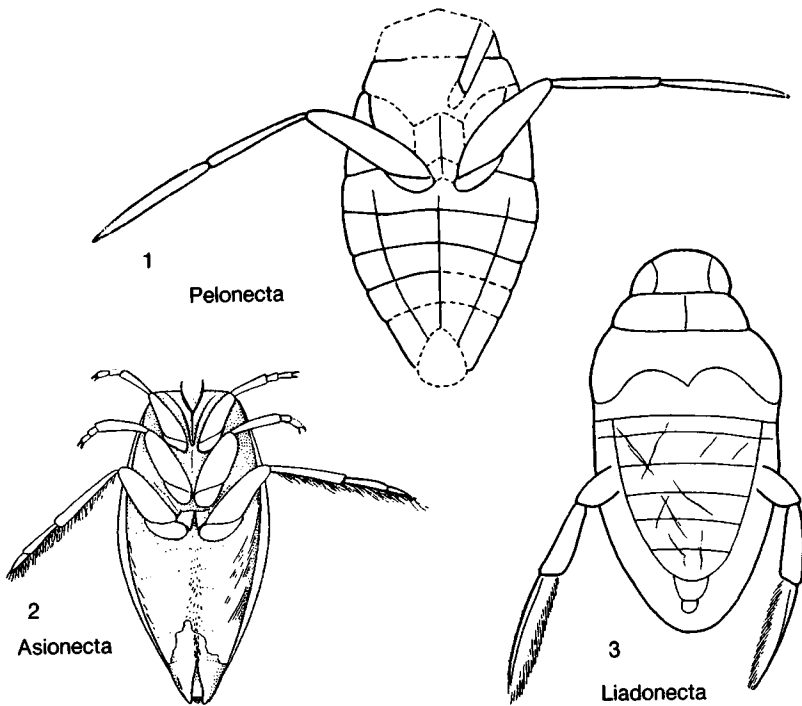


FIG. 166. Notonectidae (p. 263).

- Naucoris** GEOFFROY, 1762, p. 473. HEER, 1853a; PITON & THÉOBALD, 1937; STATZ, 1950b. *Oligo.*, Europe (Germany); *Mio.*, Europe (France, Croatia)—*Holo.*
- Aidium** POPOV, 1968, p. 103 [**A. pleurale*; OD]. Anterior margin of pronotum concave; scutellum very large; tegmen, except for clavus, without venation; embolium absent; clavus narrow, hind legs relatively short. POPOV, 1971. *Jur.*, USSR (Kazakh).
- Angaronecta** POPOV, 1971, p. 146 [**A. longirostris*; OD]. Rostrum very long, reaching hind margin of prothorax; forelegs short; femora of all legs thickened; hind tarsi with single segment. *Jur.*, USSR (Asian RSFSR). — FIG. 167,3. **A. longirostris*; ventral view, $\times 3.7$ (Popov, 1971).
- Aphlebocoris** HANDLIRSCH, 1906b, p. 495 [**A. nana*; OD]. Fore wing not differentiated into corium and membrane; clavus narrow, nearly quadrilateral. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 167,6. *A. punctata* HANDLIRSCH; fore wing, $\times 11$ (Popov & Wootton, 1977).
- Apopnus** HANDLIRSCH, 1920, p. 209 [**A. magniclavus*; OD]. Little-known genus. Fore wing differentiated into corium and membrane; costal margin convex; clavus broad and triangular. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).
- Diplonychus** LAPORTE, 1832, p. 18. HEER, 1853a. *Mio.*, Europe (Croatia)—*Holo.*
- Heleonaucoris** POPOV, 1971, p. 149 [**H. maculipennis*; OD]. Clavus of moderate size; embolium narrow and developed only at base of tegmen; border between corium and membrane indistinct; corium spotted. *Jur.*, USSR (Kirghiz). — FIG. 167,1. **H. maculipennis*; tegmen, $\times 4.2$ (Popov, 1971).
- Liadonaucoris** POPOV, 1971, p. 144 [**L. robdendorfi*; OD]. Tegmen longer than abdomen; clavus longer than scutellum; vein R present on tegmen. *Jur.*, USSR (Kirghiz). — FIG. 167,2. **L. robdendorfi*; $\times 5.5$ (Popov, 1971).
- Nectodes** POPOV, 1968, p. 105 [**N. maculatus*; OD]. Little-known genus, based on tegmen. Clavus large and broad; embolium distinct, extending for half length of corium; membrane large. *Jur.*, USSR (Kazakh).
- Nectonaucoris** POPOV, 1968, p. 104 [**N. lariversi*; OD]. Anterior margin of pronotum straight; tegmen without veins; embolium absent; clavus narrow; hind legs relatively short. *Jur.*, USSR (Kazakh).
- Sphaerodemopsis** HANDLIRSCH, 1906b, p. 543 [**Sphaerodema jurassicum* OPPENHEIM, 1888, p. 235; OD]. Tegmen strongly sclerotized; clavus usually long and heavily sclerotized. POPOV, 1971. *Jur.*, Europe (Germany). — FIG. 167,5. **S. jurassica*; dorsal view, $\times 2.5$ (Popov, 1971).

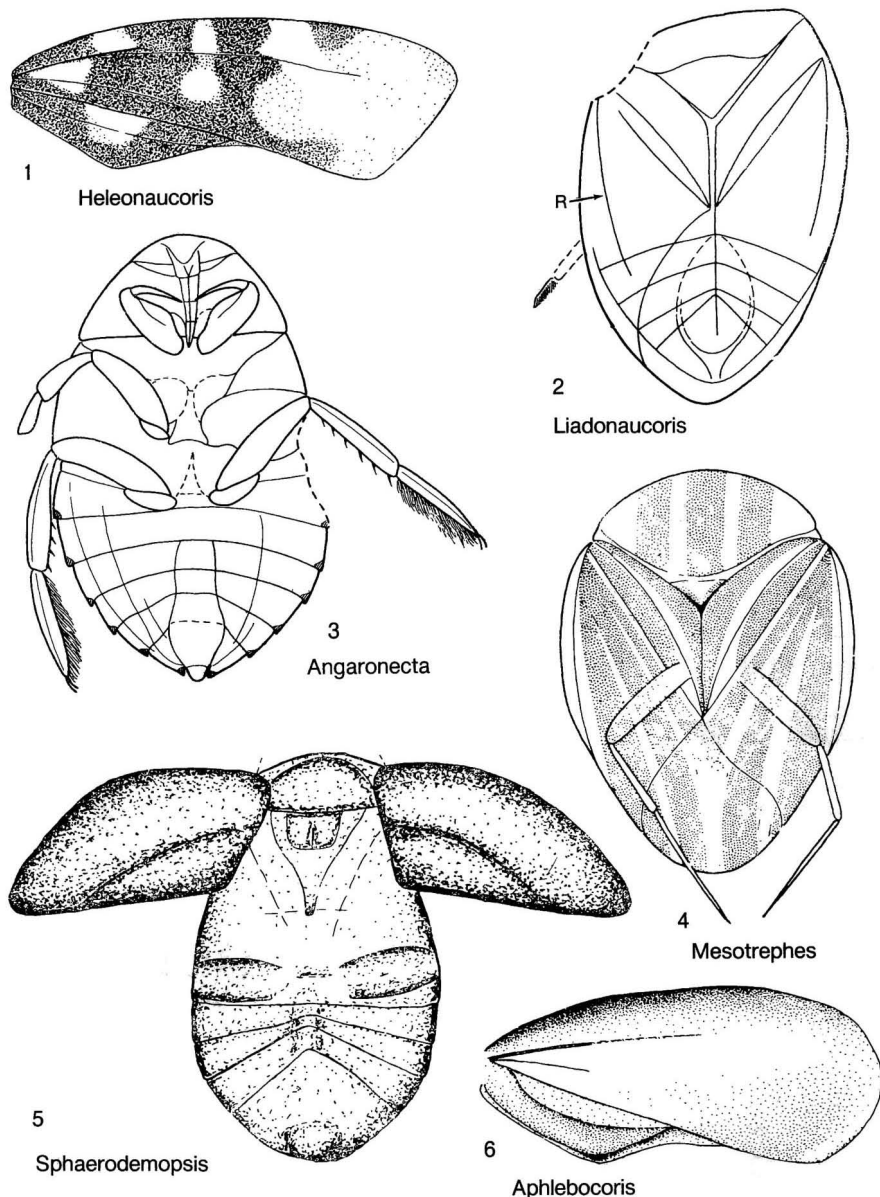


FIG. 167. Naucoridae and Mesotrepidae (p. 264–265).

Family MESOTREPHIDAE
Popov, 1971

[Mesotrepidae POPOV, 1971, p. 160]

Small species, related to the Scaphocoridae. Pronotum transverse, convex, elliptical, completely covering head from above. *Cret.*

Mesotrepes POPOV, 1971, p. 160 [**M. striata*; OD]. Scutellum very small; tegmen with only one vein, extending along most of costal margin.

Hind legs relatively short; tibiae and tarsi thin. *Cret.*, USSR (Kazakh). — FIG. 167, 4. **M. striata*; dorsoventral view, $\times 20$ (Popov, 1971).

Family BELOSTOMATIDAE
Leach, 1815

[Belostomatidae LEACH, 1815, p. 123]

Similar to the Nepidae, but antennae with 4 segments; posterior legs adapted for swimming, the tibiae flattened; aquatic. *Jur.-Hol.*

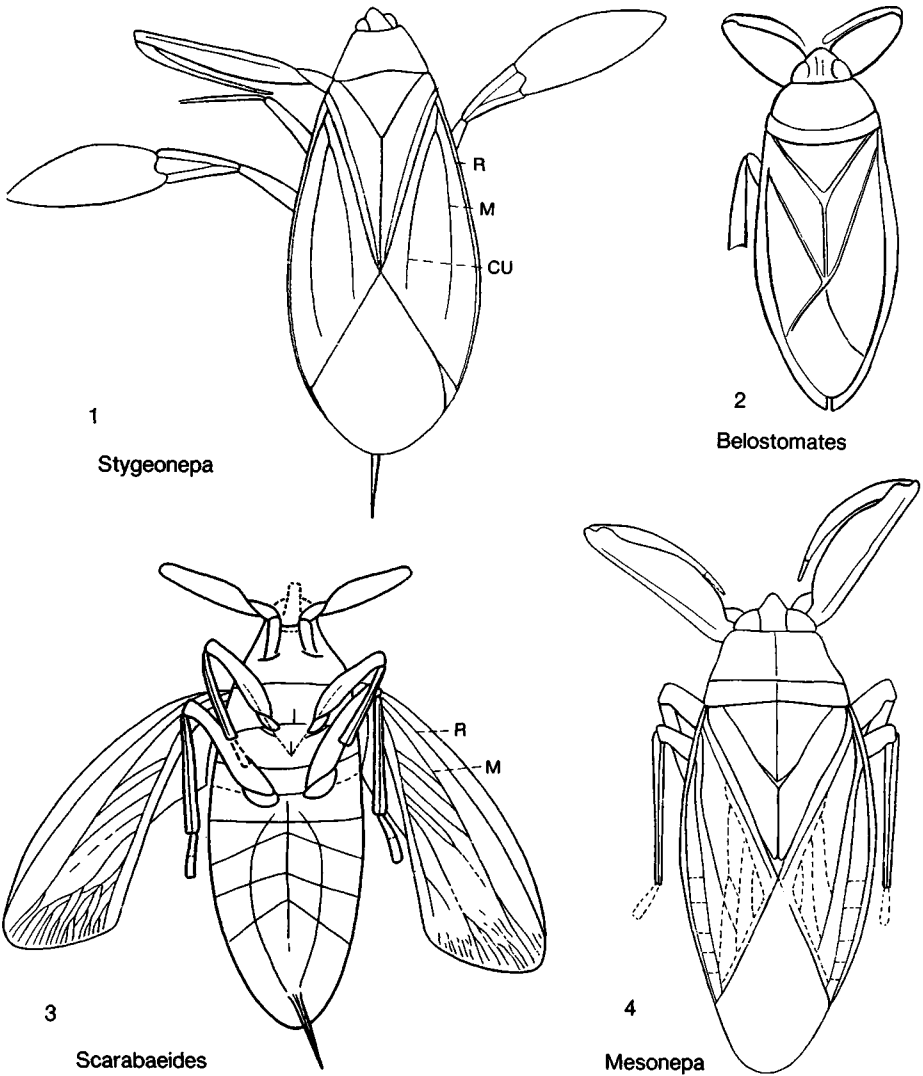


FIG. 168. Belostomatidae (p. 266–267).

Belostoma LATREILLE, 1807, p. 144. GERMAR, 1837. *Oligo.*, Europe (Germany)—*Holo.*

Belostomates SCHÖBERLIN, 1888, p. 61 [**Belostomum speciosa* HEER, 1865, p. 303; OD]. Little-known genus, with very broad front femora. HEER, 1865. *Mio.*, Europe (Germany).—FIG. 168.2. **B. speciosa*; dorsal view, $\times 0.6$ (Heer, 1865).

Lethocerus MAYR, 1853, p. 17. ŘIHA & KUKALOVÁ, 1967; POPOV, 1971. *Oligo.*, USSR (Asian RSFSR); *Mio.*, Europe (Czechoslovakia)—*Holo.*

Mesonepa HANDLIRSCH, 1906b, p. 637 [**Nepa primordialis* GERMAR, 1839, p. 206; SD POPOV, 1971, p. 116]. Similar to *Belostoma*, but fore

wing with much larger membranous area; fore tarsi with one segment. POPOV, 1971. *Jur.*, Europe (Germany).—FIG. 168.4. **M. primordialis*; dorsal view, $\times 2$ (Popov, 1971).

Scarabaeides GERMAR, 1839, p. 218 [**S. deperditus*; OD] [= *Mesobelostomum* HAASE, 1890a, p. 21, obj. J. Similar to *Lethocerus* (recent), but fore wing with M and R widely separated and remote from costal margin; membranous area of wing without venation. OPPENHEIM, 1888; POPOV, 1971. *Jur.*, Europe (Germany).—FIG. 168.3. **S. deperditus*; ventral view, $\times 1.2$ (Popov, 1971).

Stygonepa POPOV, 1971, p. 119 [**S. foersteri*; OD].

Related to *Belostoma*, but pronotum more transverse; fore wing with vestiges of R, M, and CU; hind tibiae and one-segmented tarsi forming broad lobes. *Jur.*, Europe (Germany).—FIG. 168,1. **S. foersteri*; dorsal view, $\times 2$ (Popov, 1971).

Family NEPIDAE Latreille, 1802

[Nepidae LATREILLE, 1802a, p. 252]

Antennae with 3 segments, shorter than head; membrane of fore wings reticulate; hind legs adapted for walking; tibiae not flattened; aquatic. *Oligo.*—*Holo.*

Nepa LINNÉ, 1758, p. 440. HEER, 1853a; HUNGERFORD, 1932. *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany)—*Holo.*

Family SHURABELLIDAE

Popov, 1971

[Shurabellidae POPOV, 1971, p. 121]

Small species, related to the Corixidae. Pronotum transverse, sculptured; tegmen broad; hind legs relatively slender. *Jur.*

Shurabella BECKER-MIGDISOVA, 1949b, p. 28 [**S. lepyroniopsis*; OD] [= *Coleopteropsis* BECKER-MIGDISOVA, 1949b, p. 31 (type, *C. dolichoptera*)]. Pronotum about three times as wide as long; tegmen strongly sclerotized; vestiges of SC, R, and M present on tegmen. *Jur.*, USSR (Kirghiz).—FIG. 169,4. **S. lepyroniopsis*; dorsoventral view, $\times 10$ (Popov, 1971).

Family CORIXIDAE Leach, 1815

[Corixidae LEACH, 1815, p. 124]

Head not inserted into prothorax; antennae shorter than head; fore tarsi consisting of only one spatulate segment. *Jur.*—*Holo.*

Corixa GEOFFROY, 1762, p. 477. HEER, 1853a; SCUDDER, 1890; SCHLECHTENDAL, 1894. *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany)—*Holo.*

Archaeorixa POPOV, 1968, p. 101 [**A. lata*; OD]. Pronotum transverse; corium of tegmen with distinct venation; SC coalesced with R, M, and CU for varying lengths, finally terminating on costal margin; embolium absent. POPOV, 1971. *Jur.*, USSR (Kazakh).

Baisocorixa POPOV, 1966, p. 99 [**B. jaczewskii*; OD]. Similar to *Corixa*, but veins R, M, and CU more strongly developed; head narrow; eyes small; eighth abdominal tergite well developed. *Jur./Cret.*, USSR (Asian RSFSR).

Diacorixa POPOV, 1971, p. 137 [**D. miocaenica*;

OD]. Similar to *Sigara* (recent) but with deep furrow along entire length of pronotum; vein CU weakly formed. *Mio.*, USSR (Kirghiz).

Diapherinus POPOV, 1966, p. 97 [**D. ornatipennis*; OD]. Little-known genus, based on tegmen. SC, R, M, and CU visible on corium; anal veins clear on clavus; embolium weakly developed. *Jur./Cret.*, USSR (Asian RSFSR).—FIG. 169,2. **D. ornatipennis*; tegmen, $\times 5$ (Popov, 1966).

Gazimuria POPOV, 1971, p. 130 [**G. scutellata*; OD]. Elongate species. Antennae with 4 segments; pronotum not more than three times wider than its length; tegmen with veins R, M, and CU; hind legs densely covered with hairs. *Jur.*, USSR (Asian RSFSR).—FIG. 169,5. **G. scutellata*; dorsoventral view, $\times 6$ (Popov, 1971).

Ijanecta POPOV, 1971, p. 132 [**I. angarica*; OD]. Pronotum well developed; scutellum small; fore margin of wing with wide embolium; all veins apparently absent. *Jur.*, USSR (Asian RSFSR).—FIG. 169,1. **I. angarica*; dorsal view, $\times 1$ (Popov, 1971).

Karataviella BECKER-MIGDISOVA, 1949b, p. 25 [**K. brachyptera*; OD]. Pronotum twice as wide as long; only vein 1A on clavus. *Jur.*, USSR (Kazakh).—FIG. 169,3. **K. brachyptera*; dorsal view, $\times 7$ (Popov, 1971).

Mesosigara POPOV, 1971, p. 129 [**M. kryshstofovichi*; OD]. Similar to *Baisocorixa*, but fore wing with R coalesced with SC for its entire length; M fused at base with CU. *Cret.*, USSR (Asian RSFSR).—FIG. 169,7. **M. kryshstofovichi*; lateral view, $\times 12$ (Popov, 1971).

Sigaretta POPOV, 1971, p. 136 [**Corixa florissantiella* COCKERELL, 1906e, p. 209; OD]. Pronotum large but covering only part of the scutellum; tegmen with well-developed embolium rim; anal vein present on clavus. *Oligo.*, USA (Colorado).—FIG. 169,6. **S. florissantiella* (COCKERELL); dorsal view, $\times 9$ (Popov, 1971).

Family ARADIDAE Brullé, 1835

[Aradidae BRULLÉ, 1835, p. 326]

Body strongly flattened; head porrect; antennae and rostrum with 4 segments; clavus narrowed apically; wing membrane with few or no veins; abdomen broader than wings; tarsi with 2 segments. *Oligo.*—*Holo.*

Aradus FABRICIUS, 1803, p. 116. GERMAR & BERENDT, 1856; USINGER, 1941; POPOV, 1978. *Oligo.*, Europe (Baltic); *Mio.*, Europe (Croatia)—*Holo.*

Calisius STÅL, 1858, p. 67. USINGER, 1941. *Oligo.*, Europe (Baltic)—*Holo.*

Mezira AMYOT & SERVILE, 1843, p. 305. USINGER, 1941. *Oligo.*, Europe (Baltic); *Mio.*, Europe (Croatia)—*Holo.*

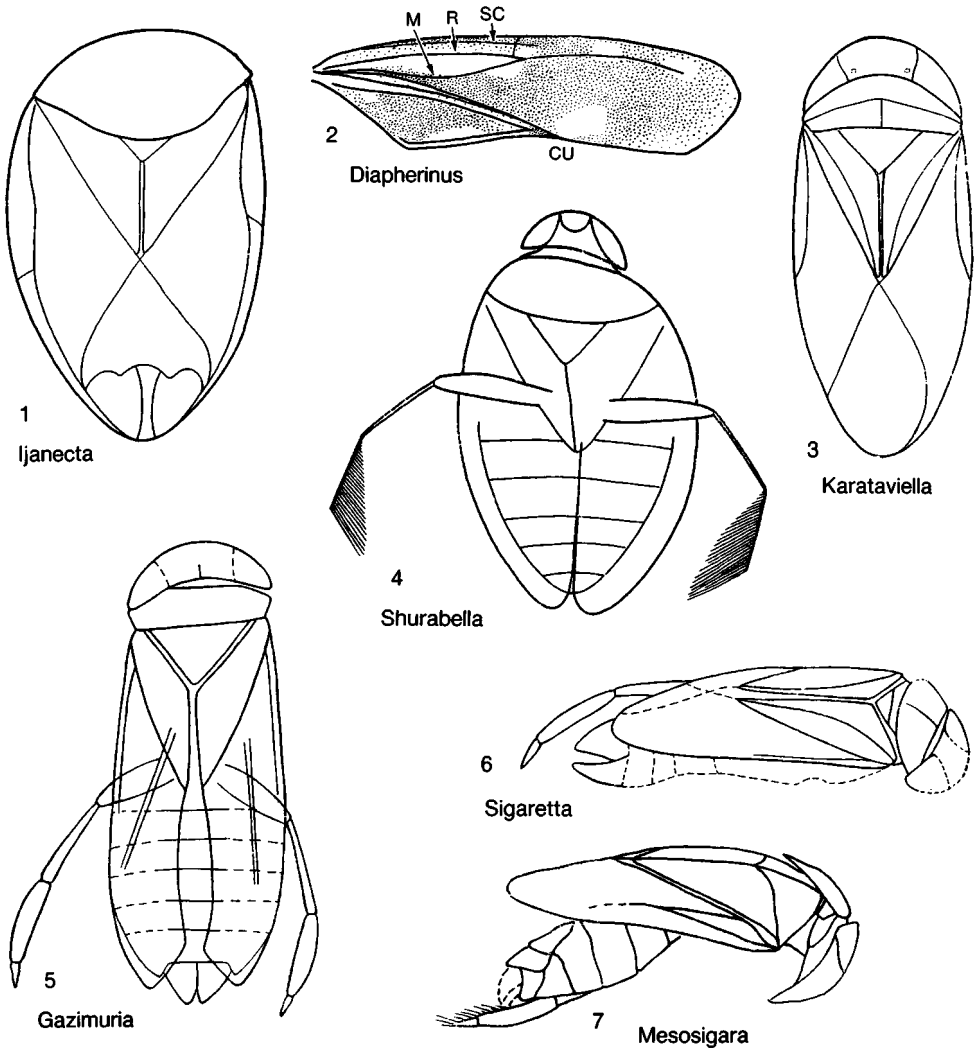


FIG. 169. Shurabellidae and Corixidae (p. 267).

Family SALDIDAE
Amyot & Serville, 1843

[Saldidae AMYOT & SERVILLE, 1843, p. xlix]

Head shorter than thorax and scutellum; antennae four-segmented, longer than head; third antennal segment thickened at base; rostrum three-segmented; fore wings without reticulate cells, but with 4 or 5 long, closed cells; corium with an embolium; forelegs not raptorial. *Jur.*—*Holo.*

Salda FABRICIUS, 1803, p. 113. GERMAR & BERENDT, 1856. *Oligo.*, Europe (Baltic)—*Holo.*
Oligosaldina CARPENTER, herein [**O. rottensis* STATZ

& WAGNER, 1950, p. 101; OD]. Fore wing similar to *Chiloxanthus* (recent) but with cells of membrane nearly the same length. [The original generic name, *Oligosaldina*, was a *nomen nudum* (STAZ & WAGNER, 1950).] *Oligo.*, Europe (Germany).

Saldonia POPOV, 1973, p. 704 [**S. rasnitsyni*; OD]. Pronotum transverse; RS close to front margin of tegmen; membrane not present on tegmen; scutellum small, shorter than claval suture. *Jur.*, USSR (Asian RSFSR).

Family COREIDAE Leach, 1815

[Coreidae LEACH, 1815, p. 121]

Head much narrower and shorter than prothorax; antennae longer than head, with

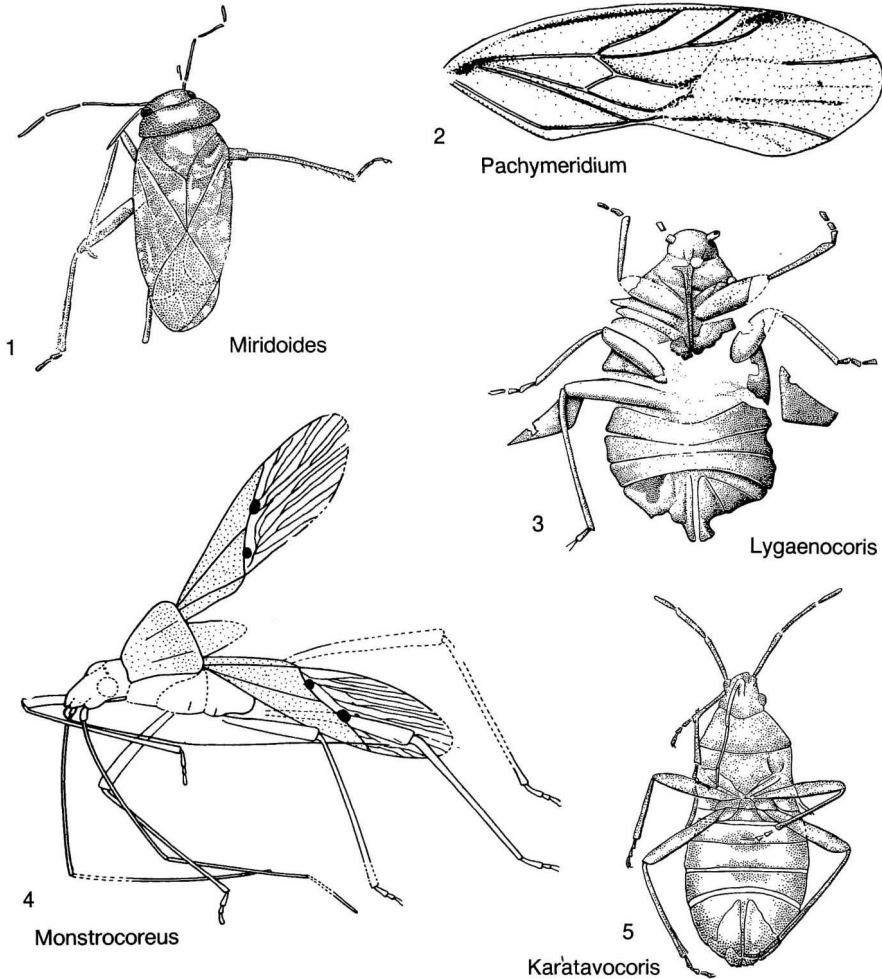


FIG. 170. Coreidae, Alydidae, Lygaeidae, Pachymeridiidae, and Miridae (p. 269–275).

4 segments; fore wing not reticulate, its membrane with many longitudinal veins, often uniting; body stout, legs thick. *Jur.*—*Holo.*

Coreus FABRICIUS, 1794, p. 120. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Achrestocoris SCUDDER, 1890, p. 413 [**A. cinerarius*; OD]. Tegmen with large rhomboidal cell at apex of corium. *Oligo.*, USA (Colorado).

Anasa AMYOT & SERVILLE, 1843, p. 209. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Berytopsis HEER, 1853a, p. 54 [**B. femoralis*; OD]. Little-known coreid, apparently related to *Berytus* (recent). *Mio.*, Europe (Germany).

Corizus FALLÉN, 1814, p. 8. SCUDDER, 1890; COCKERELL, 1926a. *Oligo.*, USA (Colorado); *Tert.* (epoch unknown), Argentina—*Holo.*

Harmostites HEER, 1853a, p. 49 [**H. oeningensis*;

OD]. Little-known genus, based on poorly preserved specimen. *Mio.*, Europe (Germany).

Heeria SCUDDER, 1890, p. 430 [**H. gulosa*; SD HANDLIRSCH, 1907, p. 1049]. Similar to *Arenocoris* (recent) but with second and third antennal segments unequal. *Oligo.*, USA (Colorado).

Hypselonotus HAHN, 1833, p. 186. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Jadera STÅL, 1860, p. 59. COCKERELL, 1909j. *Eoc.*, USA (Colorado)—*Holo.*

Karatavocoris BECKER-MIGDISOVA, 1962b, p. 222 [**K. asiatica*; OD]. Head much narrower than pronotum; first antennal segment short, not extending beyond apex of head; femora without spines. *Jur.*, USSR (Kazakh). — FIG. 170, 5. **K. asiatica*; ventral view, $\times 6$ (Becker-Migdisova, 1962b).

Leptoscelis LAPORTE, 1832, p. 31. HEYDEN, 1858.

- Palaeocoris** HEER, 1853a, p. 46 [**P. spectabilis*; OD]. Little-known genus, apparently related to *Acanthosoma* (recent). *Mio.*, Europe (Croatia).
- Phthinocoris** SCUDDER, 1890, p. 414 [**P. colligatus*; SD HANDLIRSCH, 1907, p. 1049]. Similar to *Achrestocoris*, but thorax much longer. *Oligo.*, USA (Colorado).
- Piezocoris** SCUDDER, 1890, p. 416 [**P. peritus* SCUDDER, 1890, p. 416; SD CARPENTER, herein]. Similar to *Phthinocoris*, but head large, one-half to two-thirds width of thorax. *Oligo.*, USA (Colorado).
- Spartocera** LAPORTE, 1832, p. 42. HEER, 1853a. *Mio.*, Europe (Croatia)—*Holo.*
- Syromastes** LATREILLE, 1829, p. 196. HEER, 1853a; STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany)—*Holo.*

Family ALYDIDAE Stål, 1872

[Alydidae STÅL, 1872, p. 53]

Similar to Coreidae, but head nearly as broad and as long as the prothorax, broader than anterior margin of pronotum; body and legs elongate. ŠTYS & RIHA, 1977. *Jur.*—*Holo.*

- Alydus** FABRICIUS, 1803, p. 248. *Holo.*
- Cydamus** STÅL, 1858, p. 33. [Generic assignment of fossil doubtful.] SCUDDER, 1890; ŠTYS & RIHA, 1975b, 1977. *Oligo.*, USA (Colorado)—*Holo.*
- Daclera** SIGNORET, 1862, p. 27. [Generic assignment of fossil doubtful.] THÉOBALD, 1937a; ŠTYS & RIHA, 1977. *Oligo.*, Europe (France)—*Holo.*
- Heeralydus** ŠTYS & RIHA, 1975b, p. 190 [**H. bucculatus*; OD]. Similar to *Alydus* (recent), but head relatively short and having long bucculae reaching proximally between insertion of antennae and anterior margins of eyes. ŠTYS & RIHA, 1977. *Oligo.*, Europe (Germany).
- Monstrococcus** POPOV, 1968, p. 109 [**M. quadrimaculatus*; OD]. Antennae thin and long, nearly as long as body; rostrum also very long; tegmen long, with only one distinct vein; legs long and thin, femora about as long as tibiae and much broader; tarsi with 3 segments. ŠTYS & RIHA, 1977. *Jur.*, USSR (Kazakh).—FIG. 170.4. **M. quadrimaculatus*; lateral view, $\times 3$ (Popov, 1968).
- Orthricorisa** SCUDDER, 1890, p. 429 [**O. longipes*; OD]. Little-known genus, similar to *Leptocoris* (recent). ŠTYS & RIHA, 1977. *Oligo.*, USA (Colorado).
- Protenor** STÅL, 1867, p. 543. [Generic assignment of fossil doubtful.] SCUDDER, 1890; ŠTYS & RIHA, 1977. *Oligo.*, USA (Colorado)—*Holo.*
- Sulcalydus** ŠTYS & RIHA, 1975b, p. 186 [**S. kalabisi*; OD]. Similar to *Alydus* (recent), but membrane of tegmen with more veins and apical part of corium longer. *Oligo.*, Europe (Czechoslovakia).

Family MESOPENTACORIDAE

Popov, 1968

[Mesopentacoridae Popov, 1968, p. 112]

Pronotum transverse, anterior corners projecting; anterior margins of tegmen thickened, forming a ridge along entire length of corium; venation vestigial. Tegmina and pronotum coarsely punctate. [Apparently related to the Urostylidae (recent).] *Jur.*

- Mesopentacoris** POPOV, 1968, p. 112 [**M. costalis*; OD]. Head narrower than pronotum; second antennal segment longest; corium with one vein; tibiae very slender. *Jur.*, USSR (Kazakh).

Family LYGAEIDAE

Schilling, 1829

[Lygaeidae SCHILLING, 1829, p. 85]

Head shorter than thorax and scutellum; antennae straight, not elbowed; four to five veins in membrane of fore wing, not forming ante-apical cells. SLATER, 1964. *Jur.*—*Holo.*

- Lygaeus** FABRICIUS, 1794, p. 133. HEER, 1853a; SCUDDER, 1890; PITON & THÉOBALD, 1935; THÉOBALD, 1937b; SLATER, 1964. *Oligo.*, USA (Colorado), Europe (France, Germany); *Mio.*, Europe (France, Germany, Croatia)—*Holo.*
- Aphanus** LAPORTE, 1832, p. 35. THÉOBALD, 1937a; SLATER, 1964. *Oligo.*, Europe (Germany, France)—*Holo.*
- Catopamera** SCUDDER, 1890, p. 387 [**C. augheyi*; SD SLATER, 1964, p. 1519]. Related to *Myodochina* (recent); head subtriangular, slightly broader than long; antennae slender, no longer than the head and thorax together. SLATER, 1964. *Oligo.*, USA (Colorado).
- Cephalocoris** HEER, 1853a, p. 61 [**C. pilosus*; OD]. Similar to *Cymus* (recent). SLATER, 1964. *Mio.*, Europe (Germany).
- Chilacis** FIEBER, 1864, p. 72. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
- Cholula** DISTANT, 1882, p. 210. SLATER, 1964. *Eoc.*, USA (Wyoming)—*Holo.*
- Cophocoris** SCUDDER, 1890, p. 391 [**C. tenebricosus*; OD]. Little-known genus; probably close to *Catopamera*, but head rounded; antennae only half as long as body. SLATER, 1964. *Oligo.*, USA (Colorado).
- Coptochromus** SCUDDER, 1890, p. 405 [**C. manium*; OD]. Little-known genus; head fully as long as broad and as broad as apex of thorax. SLATER, 1964. *Oligo.*, USA (Colorado).
- Cryptochromus** SCUDDER, 1890, p. 409 [**C. letatus*; OD]. Related to *Coptochromus*; head large,

- much broader than long. SLATER, 1964. *Oligo.*, USA (Colorado).
- Ctereacoris** SCUDDER, 1890, p. 394 [**C. primigenus*; OD]. Little-known genus; probably related to *Catopamera* but with much shorter middle femora. SLATER, 1964. *Oligo.*, USA (Colorado).
- Diniella** BERGOTH, 1893, p. 202. SLATER, 1964. *Oligo.*, Europe (France, Germany)—*Holo.*
- Drymus** FIEBER, 1860, p. 178. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
- Eucorites** SCUDDER, 1890, p. 392 [**E. serescens*; OD]. Little-known genus; probably related to *Catopamera* but with more rounded head; antennae longer than head and thorax. SLATER, 1964. *Oligo.*, USA (Colorado).
- Exitelus** SCUDDER, 1890, p. 408 [**E. exsanguis*; OD]. Similar to *Cryptochromus*, but head only a little broader than long. SLATER, 1964. *Oligo.*, USA (Colorado).
- Geocoris** FALLÉN, 1814, p. 10. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
- Heterogaster** SCHILLING, 1829, p. 37. HEER, 1853a; SLATER, 1964. *Oligo.*, Europe (France); *Mio.*, Europe (Germany, Croatia)—*Holo.*
- Ischnodemus** FIEBER, 1837, p. 337. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
- Ligyrocoris** STÅL, 1872, p. 51. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
- Linnaea** SCUDDER, 1890, p. 396 [**L. carcerata*; SD SLATER, 1964, p. 1523]. Little-known lygaeid; head small; antennae as long as combined head and thorax; thorax very broad. *Oligo.*, USA (Colorado).
- Lithochromus** SCUDDER, 1890, p. 402 [**L. gardneri*; SD SLATER, 1964, p. 1524]. Little-known lygaeid; head as broad as long; antennae about half as long as body. *Oligo.*, USA (Colorado).
- Lithocoris** SCUDDER, 1890, p. 390 [**L. evulsus*; OD]. Little-known genus, apparently related to *Myodochina* (recent); head large, subrotund. SLATER, 1964. *Oligo.*, USA (Colorado).
- Lygaenocoris** POPOV, 1961, p. 1211 [**L. prynadai*; OD]. Eighth abdominal segment strongly developed, covering the ninth. *Jur.*, USSR (Kazakh). —FIG. 170,3. **L. prynadai*; whole insect, $\times 6.5$ (Popov, 1961).
- Lygaeosoma** SPINOLA, 1837, p. 254. SLATER, 1964. *Oligo.*, Europe (Germany)—*Holo.*
- Mesolygaeus** PING, 1928, p. 43 [**M. laiyangensis*; OD]. Similar to *Lygaeus*, but veins of fore wing membrane more prominent. SLATER, 1964. *Cret.*, China (Shantung).
- Miognates** SAILER & CARVALHO in A. R. PALMER, 1957, p. 256 [**M. subimpunctatus*; OD]. Similar to *Lethaeus* and other recent lethaeini but with a smoother integument than is characteristic of the related genera. *Mio.*, USA (California).
- Necrochromus** SCUDDER, 1890, p. 406 [**N. cockerelli*; SD SLATER, 1964, p. 1525]. Body regularly oval; head as broad as apex of thorax. *Oligo.*, USA (Colorado).
- Phrudopamera** SCUDDER, 1890, p. 388 [**P. wilsoni*; SD SLATER, 1964, p. 1521]. Similar to *Catopamera*, but antennae much longer than combined head and thorax. *Oligo.*, USA (Colorado).
- Pionosomus** FIEBER, 1860, p. 48. SLATER, 1964. *Oligo.*, Europe (Germany)—*Holo.*
- Praenotochilus** THÉOBALD, 1937a, p. 289 [**P. parallelus*; OD]. Similar to *Aphanus*, but body more cylindrical and first antennal segment much longer. *Oligo.*, Europe (France).
- Procoris** SCUDDER, 1890, p. 392 [**P. bechleri*; SD SLATER, 1964, p. 1521]. Little-known genus; probably similar to *Eucorites*, but posterior margin of thorax more truncate. *Oligo.*, USA (Colorado).
- Procrophius** SCUDDER, 1890, p. 382 [**P. communis*; SD SLATER, 1964, p. 1512]. Similar to *Crophius* (recent) but with shorter antennae. *Oligo.*, USA (Colorado).
- Procympophyes** SAILER & CARVALHO in A. R. PALMER, 1957, p. 255 [**P. lithax*; OD]. Similar to *Cymophyes* (recent), but eyes well removed from anterior margin of pronotum. *Mio.*, USA (California).
- Procyms** USINGER, 1940, p. 79 [**P. cockerelli*; OD]. Similar to *Cymus* (recent), but body short, broad, and covered with cymine punctures. SLATER, 1964. *Oligo.*, USA (Colorado).
- Prolygaeus** SCUDDER, 1890, p. 405 [**P. inundatus*; OD]. Body very regularly oval. Antennae as long as head and thorax, the first segment not extending beyond frons, the last two segments longer than first two. *Oligo.*, USA (Colorado).
- Raglius** STÅL, 1872, p. 57. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
- Rhyparochromus** HAHN, 1826, p. 17. [Most extinct species included here have uncertain generic positions; they were originally put in *Pachymerus* LEPELETIER & SERVILLE, 1825, which is now placed on the Official Index of Rejected and Invalid Names in Zoology (Op. 676, 1963, ICZN).] SLATER, 1964. *Eoc.*, USA (Wyoming); *Oligo.*, Europe (Germany, Baltic, France), USA (Colorado); *Mio.*, USA (Colorado), Europe (Germany, Croatia)—*Holo.*
- Scolopostethus** FIEBER, 1860, p. 188. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
- Stenopamera** SCUDDER, 1890, p. 385 [**S. senebrosa*; SD SLATER, 1964, p. 1521]. Little-known genus, related to *Catopamera*. *Oligo.*, USA (Colorado).
- Tiromerus** SCUDDER, 1890, p. 401 [**T. torpefactus*; OD]. Little-known genus, similar to *Rhyparochromus*; second segment of antennae much longer than third or fourth. *Oligo.*, USA (Colorado).
- Trapezonotus** FIEBER, 1860, p. 50. SCUDDER, 1890; STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany), USA (Colorado)—*Holo.*

Family BERYTIDAE Fieber, 1851

[Berytidae FIEBER, 1851, p. 9]

Body very slender; head conical, porrect; antennae and rostrum four-segmented; pronotum much longer than wide; scutellum armed; legs very slender; tarsi three-segmented. *Oligo.-Holo.*

Berytus FABRICIUS, 1803, p. 264. *Holo.*

Megalomerium FIEBER, 1859, p. 208. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Family PYRRHOCORIDAE
Fieber, 1860

[Pyrrhocoridae FIEBER, 1860, p. 43]

Body elongate-oval; antennae and beak four-segmented; ocelli absent; membrane with 2 large basal cells, giving rise to several (about 8) branching veins; tarsi three-segmented. *Oligo.-Holo.*

Pyrrhocoris FALLÉN, 1814, p. 9. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Dysdercus AMYOT & SERVILLE, 1843, p. 272. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Family CYDNIDAE Billberg, 1820

[Cydniidae BILLBERG, 1820, p. 7]

Similar to the Pentatomidae, but forelegs fossorial; tibiae strongly spinose, veins of fore wing membrane radiating from base. *Eoc.-Holo.*

Cydnus FABRICIUS, 1803, p. 184. HEER, 1853a; FÖRSTER, 1891; THÉOBALD, 1937a; STATZ, 1950a. *Oligo.*, Europe (Germany, France)—*Holo.*

Crocistethus FIEBER, 1860, p. 84. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Cyrtomenus AMYOT & SERVILLE, 1843, p. 90. SCUDDER, 1890. *Eoc.*, USA (Wyoming)—*Holo.*

Necroclydnus SCUDDER, 1890, p. 443 [**N. amyzonus* SCUDDER, 1890, p. 443; SD CARPENTER, herein]. Head only slightly sunk into prothorax; anterior-lateral angles of thorax rounded. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado).

Procydnus SCUDDER, 1890, p. 438 [**P. quietus* SCUDDER, 1890, p. 438; SD CARPENTER, herein].

Very similar to *Stenopelta*, but body less than twice as long as broad. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado).

Sehirus AMYOT & SERVILLE, 1843, p. 96. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Stenopelta SCUDDER, 1890, p. 437 [**Aethus punctulatus* SCUDDER, 1878b, p. 769; OD]. Scutellum triangular, as broad as long; head sunk deeply

into prothorax, the depth of the thoracic emargination being about half its width; body more than twice as long as broad. *Eoc.*, USA (Wyoming).

Teleocydnus HENRIKSEN, 1922b, p. 32 [**T. transitorius*; OD]. Similar to *Cydnus* (recent) but with a long, slender scutellum, reaching about to abdominal apex. *Eoc.*, Europe (Denmark).

Thlibomenus SCUDDER, 1890, p. 448 [**T. petreus*; OD]. Similar to *Necroclydnus*, but head even more prominent; anterior emargination of prothorax slight or absent. *Oligo.*, USA (Colorado).

Family SCUTELLERIDAE Leach, 1815

[Scutelleridae LEACH, 1815, p. 121]

Body oval, usually strongly convex; head triangular; 2 ocelli; rostrum four-segmented; scutellum very large, U-shaped; tarsi three-segmented. *Eoc.-Holo.*

Scutellera LAMARCK, 1801, p. 293. *Holo.*

Coptosoma LAPORTE, 1832, p. 73. PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*

Poecilocoris DALLAS, 1848, p. 100. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Tectocoris HAHN, 1834, p. 33. HENRIKSEN, 1922b. *Eoc.*, Europe (Denmark)—*Holo.*

Family PACHYMERIDIIDAE
Handlirsch, 1906

[Pachymeridiidae HANDLIRSCH, 1906b, p. 495] [=Sisyrochoridae HANDLIRSCH, 1920, p. 210; Psychochoridae HANDLIRSCH, 1920, p. 298; Hypocimicidae HANDLIRSCH, 1939, p. 119]

Fore wing differentiated into corium and membrane; venation of membrane indistinct; clavus broad and nearly half as long as wing; vein SC separating from R + M near division of R and M. POPOV & WOOTTON, 1977. *Jur.*

Pachymeridium GEINITZ, 1880, p. 529 [**P. dubium*; OD]. Fore wing with SC, R, and M separating at a single point; R branched. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany). — FIG. 170,2. **P. dubium*; fore wing, X9 (Popov & Wootton, 1977).

Apsicoria HANDLIRSCH, 1939, p. 121 [**A. semideleta*; OD]. Similar to *Sisyrocoris*, but R branched; corium relatively smooth. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Cathalus HANDLIRSCH, 1939, p. 121 [**C. alutaceus*; OD]. Little-known genus, based on wing fragment; apparently similar to *Sisyrocoris*, but R and M very close together in fore wing; corium less punctate. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).

Hypocimex HANDLIRSCH, 1939, p. 119 [**H. membranaceus*; OD]. Little-known genus, based on

- poorly preserved specimen; family position doubtful. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).
- Psychrocoris** HANDLIRSCH, 1920, p. 208 [**P. cuneifera*; OD]. Little-known genus, apparently similar to *Sisyrocoris*. Fore wing slender; corium including more than three-fourths of wing surface. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).
- Sisyrocoris** HANDLIRSCH, 1920, p. 210 [**S. rudis*; OD]. Little-known genus. Fore wing coarsely punctate; R unbranched. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).
- Family PENTATOMIDAE Leach, 1815**
[Pentatomidae LEACH, 1815, p. 121]
- Body oval; head triangular, porrect, much narrower than thorax; antennae five-segmented; rostrum four-segmented; ocelli present; scutellum extending beyond middle of abdomen, narrowed posteriorly to form triangle; membrane with numerous veins; tarsi two- or three-segmented. *Eoc.*—*Holo.*
- Pentatoma** OLIVIER, 1789, p. 25. HEER, 1853a; HEYDEN & HEYDEN, 1865; FÖRSTER, 1891; HANDLIRSCH, 1906b. *Eoc.*, Europe (Greenland); *Oligo.*, Europe (Germany, Baltic); *Mio.*, Europe (Croatia, Germany)—*Holo.*
- Acanthosoma** CURTIS, 1824, p. 28. HEER, 1853a; FÖRSTER, 1891; PITON & THÉOBALD, 1935. *Oligo.*, Europe (Germany); *Mio.*, Europe (Croatia, France)—*Holo.*
- Arma** HAHN, 1832, p. 91. FÖRSTER, 1891. *Oligo.*, Europe (Germany)—*Holo.*
- Asopus** BURMEISTER, 1834, p. 19. PITON, 1940b. *Eoc.*, Europe (France)—*Holo.*
- Brachypelta** AMYOT & SERVILLE, 1843, p. 89. NOVÁK, 1877. *Oligo.*, Europe (Germany, Czechoslovakia)—*Holo.*
- Cacoschistus** SCUDDER, 1890, p. 459 [**C. maceratus*; OD]. Similar to *Mataeoschistus* (recent) but with broader head and less prominent frontal area. *Oligo.*, USA (Colorado).
- Carpocoris** KOLENATI, 1846, p. 45. KUKALOVÁ & ŘIHA, 1957. *Mio.*, Europe (Czechoslovakia)—*Holo.*
- Deryeuma** PITON, 1940a, p. 159 [**D. primordialis*; OD]. Pronotum narrowed in front, notched in region of head; antennae five-segmented, the first segment very short, the second very long; tarsi three-segmented. *Eoc.*, Europe (France).
- Dinidorites** COCKERELL, 1921e, p. 34 [**D. marginiformis*; OD]. Body narrow; pronotum and scutellum with numerous, dark punctures. *Eoc.*, USA (Colorado).
- Doryderes** AMYOT & SERVILLE, 1843, p. 121. PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*
- Eurydema** LAPORTE, 1832, p. 61. HEER, 1853a; PITON & THÉOBALD, 1935; THÉOBALD, 1937a. *Mio.*, Europe (Germany); *Mio./Plio.*, Europe (France)—*Holo.*
- Eurygaster** LAPORTE, 1832, p. 68. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Eysarcoris** HAHN, 1834, p. 66. HEER, 1853a; NAORA, 1933b; THÉOBALD, 1937a. *Oligo.*, Europe (France); *Mio.*, Europe (Germany); *Tert. (epoch unknown)*, Japan—*Holo.*
- Halys** FABRICIUS, 1803, p. 180. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*
- Latahcoris** COCKERELL, 1931b, p. 312 [**L. spectatus*; OD]. Head less than one-third width of pronotum; pronotum coarsely punctate, more than twice as long as wide; scutellum with straight sides. *Mio.*, USA (Washington).
- Manevalia** PITON, 1940a, p. 159 [**M. pachyliformis*; OD]. Little-known genus, apparently related to *Pachylis* (recent). *Oligo.*, Europe (France).
- Mesohalys** BEIER, 1952, p. 134 [**M. muezzenbergiana*; OD]. Pronotum and mesonotum very coarsely punctate; abdominal tergites finely punctate; front margin of pronotum notched. *Mio.*, Europe (Germany).
- Neurocoris** HEER, 1853a, p. 23 [**N. rotundatus* HEER, 1853a, p. 23; SD CARPENTER, herein]. Little-known genus; pronotum very broad; tegmen very short and broad. SCUDDER, 1885b. *Mio.*, Europe (Croatia).
- Nezara** AMYOT & SERVILLE, 1843, p. 143. THÉOBALD, 1937a. *Oligo.*, Europe (France); *Mio./Plio.*, Europe (France).
- Pachycoris** BURMEISTER, 1835, p. 391. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*
- Palomena** MULSANT & REY, 1866, p. 277. MEUNIER, 1915a. *Mio.*, Europe (France)—*Holo.*
- Pentatomites** SCUDDER, 1890, p. 461 [**P. foliarum*; OD]. Similar to *Polioschistus* but with sides of thorax convex in front of lateral prominences. VERHOEFF, 1917; COCKERELL, 1927d. *Oligo.*, England, USA (Colorado); *Tert. (epoch unknown)*, USSR (Asian RSFSR).
- Phloeocoris** BURMEISTER, 1835, p. 371. HEER, 1853a. *Mio.*, Europe (Croatia)—*Holo.*
- Poliocoris** KIRKALDY, 1910, p. 130 [**P. amnesis*; OD]. Allied to *Teleoschistus*. Body oval; head longer than wide between eyes; scutellum extending halfway to apex of abdomen and rounded posteriorly. *Oligo.*, USA (Colorado).
- Polioschistus** SCUDDER, 1890, p. 460 [**P. ligatus* SCUDDER, 1890, p. 460; SD CARPENTER, herein]. General form as in *Euschistus* (recent); head in front of eyes subquadrate; thorax very short, about 4 times as broad as long. *Oligo.*, USA (Colorado).
- Poteschistus** SCUDDER, 1890, p. 458 [**P. obnubilus*; OD]. Little-known genus, with body regularly ovate. *Oligo.*, USA (Colorado).
- Pycanum** AMYOT & SERVILLE, 1843, p. 171. PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*

Teleocoris KIRKALDY, 1910, p. 129 [**T. pothetias*; OD]. Head prominent, longer than its width between the eyes; pronotum more than 3 times as wide as base of head; scutellum regularly triangular, half the length of abdomen. *Oligo.*, USA (Colorado).

Teleschistus SCUDDER, 1890, p. 454 [**T. antiquus*; SD COCKERELL, 1909b, p. 74]. Head nearly half as broad as thorax and broader than long; apical border of prothorax emarginate; scutellum about as long as wide, reaching less than halfway to end of abdomen. COCKERELL, 1909b; HENRIKSEN, 1922b. *Eoc.*, Europe (Denmark); *Oligo.*, USA (Colorado).

Teryra FABRICIUS, 1803, p. 128. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Thnetoschistus SCUDDER, 1890, p. 457 [**T. revulsus*; OD] [= *Mataeoschistus* SCUDDER, 1890, p. 459 (type, *M. limigenus* SCUDDER), obj.; the two species are based on counterparts of the same fossil]. Similar to *Euschistus* (recent) but more elongate. *Oligo.*, USA (Colorado).

Tiroschistus SCUDDER, 1890, p. 462 [**T. indurescens*; OD]. Head rounded, with very little extension in front of eyes; antennae 2 times as long as head and thorax together. *Oligo.*, USA (Colorado).

Family ANTHOCORIDAE

Amyot & Serville, 1843

[Anthocoridae AMYOT & SERVILLE, 1843, p. xxxvii]

Similar to the Saldidae, but fore wing membrane without long, closed cells; corium with an embolium. *Oligo.*—*Holo.*

Anthocoris FALLÉN, 1814, p. 9. *Holo.*

Temnostethus FIEBER, 1860, p. 263. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Family NABIDAE Costa, 1852

[Nabidae COSTA, 1852, p. 66]

Similar to the Reduviidae but more slender; rostrum with 4 segments; membrane of fore wings with distinctly branched veins or with a few longitudinal veins emitting radiating veins. *Jur.*—*Holo.*

Nabis LATREILLE, 1802, p. 248. HEER, 1853a, 1865; THÉOBALD, 1937a; JORDAN, 1952. *Oligo.*, Europe (Baltic, France); *Mio.*, Europe (Croatia)—*Holo.*

Karanabis BECKER-MIGDISOVA, 1962b, p. 219 [**K. kiritschenko*; OD]. Antennae with 4 segments; pronotum conical, strongly narrowed anteriorly; legs long. *Jur.*, USSR (Kazakh).

Family REDUVIIDAE Latreille, 1807

[Reduviidae LATREILLE, 1807, p. 126]

Head shorter than thorax and scutellum, not constricted behind eyes; antennae four-segmented; rostrum three-segmented; fore wings not reticulate; forelegs raptorial. *Oligo.*—*Holo.*

Reduvius FABRICIUS, 1775, p. 729. *Holo.*

Eothes SCUDDER, 1890, p. 355 [**E. elegans*; OD].

Related to *Opsicoetus* (recent), but body more slender and terminal antennal segments stout. *Oligo.*, USA (Colorado).

Evagoras BURMEISTER, 1843, p. 368. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Harpactor LAPORTE, 1832, p. 8. HEER, 1853a. *Mio.*, Europe (Germany, Croatia)—*Holo.*

Limnaci GERMAR, 1856, p. 19. HEER, 1853a. *Oligo.*, Europe (Baltic)—*Holo.*

Miocoris COCKERELL, 1927e, p. 591 [**M. fagi*; OD]. Anterior femora stout; first antennal segment not as long as head. *Oligo.*, USA (Colorado).

Pirates BURMEISTER, 1835, p. 222. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Poliosphageus KIRKALDY, 1910, p. 130 [**P. psychrus*; OD]. Similar to *Repipta* (recent) but with first antennal segment scarcely longer than head; second segment much longer than first. *Oligo.*, USA (Colorado).

Propilocerus WASMANN, 1933, p. 1 [**P. dolosus*; OD]. Similar to *Ptilocerus* (recent) but with second antennal segment and the 2 terminal segments longer and thicker. *Oligo.*, Europe (Baltic).

Prostemma LAPORTE, 1832, p. 12. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Rhinocoris HAHN, 1833, p. 20. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*

Stenopoda LAPORTE, 1832, p. 26. HEER, 1853a. *Mio.*, Europe (Germany)—*Holo.*

Tagalodes SCUDDER, 1890, p. 356 [**T. inermis*; OD]. Similar to *Taglis* (recent) but with shorter thorax and without spines on fore femora. *Oligo.*, USA (Colorado).

Family TINGIDAE Laporte, 1833

[Tingidae LAPORTE, 1833, p. 47]

Head shorter than thorax; antennae shorter than head, with 4 segments; fore wings lace-like, entirely reticulate. *Oligo.*—*Holo.*

Tingis FABRICIUS, 1803, p. 124. DRAKE & RUHOFF, 1960. *Oligo.*, USA (Colorado); *Mio.*, Europe (Croatia)—*Holo.*

Cantacader AMYOT & SERVILLE, 1843, p. 299. DRAKE, 1950; DRAKE & RUHOFF, 1960. *Oligo.*, Europe (Baltic)—*Holo.*

Celantia DISTANT, 1903, p. 137. COCKERELL, 1921f; DRAKE & RUHOFF, 1960. *Oligo.*, Europe (England)—*Holo.*
Diclyla STÅL, 1874, p. 57. SCUDDER, 1890; DRAKE & RUHOFF, 1960. *Oligo.*, USA (Colorado), Europe (Czechoslovakia); *Mio.*, Europe (Germany)—*Holo.*
Eotingis SCUDDER, 1890, p. 359 [**E. antennata*; OD]. Similar to *Tingis*; pronotum smooth; costal area of fore wing enlarged apically. DRAKE & RUHOFF, 1960. *Oligo.*, USA (Colorado).
Phatnoma FIEBER, 1844, p. 57. DRAKE, 1950; DRAKE & RUHOFF, 1960. *Oligo.*, Europe (Baltic)—*Holo.*

Family MIRIDAE Hahn, 1831

[Miridae HAHN, 1831, p. 234]

Head porrect; eyes large; ocelli absent; antennae and beak with 4 segments, beak not held in a groove; scutellum distinct; membrane of tegmen usually with 2 basal cells, veins otherwise absent from membrane; tarsi two-segmented. *Jur.*—*Holo.*

Miris FABRICIUS, 1794, p. 183. *Holo.*
Aporema SCUDDER, 1890, p. 369 [**A. praestricum*; OD]. Little-known genus, probably close to *Phytocoris*; scutellum large, equiangular, with straight sides. *Oligo.*, USA (Colorado).
Calocoris FIEBER, 1858, p. 305. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
Capsus FABRICIUS, 1803, p. 241. [Generic assignment of species doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Carmelus DISTANT, 1884, p. 297. [Generic assignment of species doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Closterocoris UHLER, 1890, p. 76. [Generic assignment of species doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Fulvius STÅL, 1862, p. 322 [= *Oligocoris* JORDAN, 1944a, p. 8 (type, *O. bidentata*)]. CARVALHO, 1954. *Oligo.*, Europe (Baltic)—*Holo.*
Fuscus DISTANT, 1884, p. 299. [Generic assignment of species doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Hadronema UHLER, 1872, p. 412. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Jordanofulvius CARVALHO, 1954, p. 188, *nom. subt. pro Electrocoris* JORDAN, 1944b, p. 133, *non* USINGER, 1942 [**Electrocoris fuscus* JORDAN, 1944b, p. 133; OD]. Little-known genus, apparently belonging to recent tribe Cylapinae. *Oligo.*, Europe (Baltic).
Lygus HAHN, 1831, p. 28. STATZ & WAGNER, 1950. *Oligo.*, Europe (Germany)—*Holo.*
Miomonalonion SAILER & CARVALHO in PALMER, 1957, p. 257 [**M. conoidifrons*; OD]. Related to *Monalonion* (recent), but frons conately pro-

duced between antennae; first antennal segment very thick. PALMER, 1957. *Mio.*, USA (California).

Miridoides BECKER-MIGDISOVA, 1962b, p. 217 [**M. mesozoicus*; OD]. Antennae shorter than body; tegmen reaching to end of abdomen with front margin convex and only 2 veins in corium. *Jur.*, USSR (Kazakh).—FIG. 170, I. **M. mesozoicus*; ×10 (Becker-Migdisova, 1962b).
Phytocoris FALLÉN, 1814, p. 10. GERMAR & BERENDT, 1856; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)—*Holo.*
Poecilocapsus REUTER, 1875, p. 73. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Scutellifer POPOV, 1968, p. 108 [**S. karataunicus*; OD]. Antennae longer than body, its first segment longer than pronotum; scutellum very large; membrane of tegmen without spots; fore femora long, slightly flattened; hind legs very long. *Jur.*, USSR (Kazakh).

Family UNCERTAIN

The following genera, apparently belonging to the suborder Heteroptera, are too poorly known to permit assignment to families.

Cacalydus SCUDDER, 1890, p. 419 [**C. exstertatus*; SD ŠTYS & ŘIHA, 1977, p. 180]. Little-known genus; probably a coreid. *Oligo.*, USA (Colorado).
Copidopus HANDLIRSCH, 1906b, p. 635 [**C. jurasicus*; OD]. Little-known genus. Large species; antennae with 5 segments; hind legs with thickened femora. *Jur.*, Europe (Germany).
Coreites HEER, 1853a, p. 56 [**C. crassus* HEER, 1853a, p. 56; SD CARPENTER, herein]. Little-known heteropteron, possibly belonging to Coreidae. PITON & THÉOBALD, 1935. *Oligo.*, Europe (France); *Mio.*, Europe (Croatia).
Cydnopsis HEER, 1853a, p. 13 [**C. haidingeri* HEER, 1853a, p. 13; SD CARPENTER, herein]. Little-known genus; legs without spines. COCKERELL, 1909j; HANDSCHIN, 1937; PITON & RUDEL, 1936. *Eoc.*, USA (Colorado); *Oligo.*, Europe (France)—*Mio.*, Europe (Croatia, Germany).
Deraiocoris BODE, 1953, p. 128 [**D. insculptus*; OD]. Little-known heteropteron; head and thorax punctate. *Jur.*, Europe (Germany).
Dichaspis BODE, 1953, p. 137 [**D. laesa*; OD]. Little-known heteropteron, with small head; wings and venation virtually unknown. *Jur.*, Europe (Germany).
Electrocoris USINGER, 1942, p. 43 [**E. brunneus*; OD]. Cimicoid genus, with ocelli present; 4 free, longitudinal veins in membrane of tegmen; abdominal trichobothria absent. *Oligo.*, Europe (Baltic).

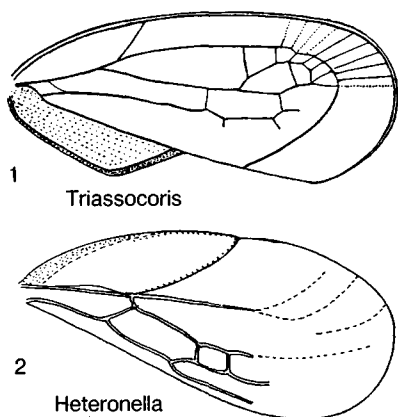


FIG. 171. Uncertain (p. 276–277).

- Engerrophorus** BODE, 1953, p. 144 [**E. nitidus*; OD]. Little-known heteropteron, with small head. *Jur.*, Europe (Germany).
- Engynabis** BODE, 1953, p. 130 [**E. tenuis*; OD]. Little-known genus, based on incomplete wings and body; probably related to Gerridae. POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).
- Eogerridium** BODE, 1953, p. 131 [**E. gracile*; OD]. Little-known genus, based on fragment of body; legs long and slender. *Jur.*, Europe (Germany).
- Etirocoris** SCUDDER, 1890, p. 425 [**E. infernalis*; OD]. Little-known genus; head elongate, slender, prolonged between antennae. ŠTYS & RIHA, 1977. *Oligo.*, USA (Colorado).
- Euraspidium** BODE, 1953, p. 137 [**E. granulosum*; OD]. Little-known heteropteron, with punctations on thorax. *Jur.*, Europe (Germany).
- Hadrocoris** HANDLIRSCH, 1939, p. 117 [**H. oculatellaris*; OD]. Little-known heteropteron, with a large scutellum and punctate head and thorax. [Type of family Hadrocoridae HANDLIRSCH, 1939, p. 116.] *Jur.*, Europe (Germany).
- Heteronella** EVANS, 1961, p. 22 [**H. marksei*; OD]. Little-known genus. Tegmen with suggestion of costal fracture; venation distinct in basal half of tegmen only. *Trias.*, Australia (Queensland).—FIG. 171.2. **H. marksei*; fore wing, $\times 14$ (Evans, 1961).
- Ischnocoris** BODE, 1953, p. 136 [**I. bitoratus*; OD]. Little-known genus, with broad head. *Jur.*, Europe (Germany).
- Leptoserinetha** THÉOBALD, 1937a, p. 362 [**L. navicularis*; OD]. Little-known genus, based on poorly preserved specimen. ŠTYS & RIHA, 1977. *Oligo.*, Europe (France).
- Liasocoris** WENDT, 1940, p. 19 [**L. hainmulleri*; OD]. Little-known genus, with prominent scutellum. *Jur.*, Europe (Germany).
- Megalocoris** BODE, 1953, p. 127 [**M. laticlavus*;

OD]. Little-known heteropteron; body large, oval in form; venation unknown. *Jur.*, Europe (Germany).

- Ophthalmocoris** BODE, 1953, p. 126 [**O. liasscus*; OD]. Little-known insect; fore wings apparently membranous. Ordinal assignment doubtful. *Jur.*, Europe (Germany).

Palaeonepidoideus MEUNIER, 1900, p. 13 [**P. carinata*; OD]. Little-known heteropteron, possibly belonging to the Nepidae. *Jur.*, Europe (Germany).

- Pricecoris** PINTO & ORNELLAS, 1974b, p. 296 [**P. beckeras*; OD]. Little-known genus, based on poorly preserved specimen; venation not preserved. [Type of family Pricecoridae PINTO & ORNELLAS.] *Cret.*, Brazil (Maranhão).

Probascanion HANDLIRSCH, 1939, p. 118 [**P. megacephalum*; OD]. Little-known heteropteron, with relatively large head; venation unknown. [Type of family Probascanionidae HANDLIRSCH, 1939.] *Jur.*, Europe (Germany).

- Pronabis** BODE, 1953, p. 129 [**P. utroquelaesus*; OD]. Little-known genus; fore wing without distinct membranous area. *Jur.*, Europe (Germany).

Protocoris HEER, 1852, p. 15 [**P. planus*; OD]. Little-known genus; fore wing with distinct membranous area. [Type of family Protocoridae HANDLIRSCH, 1906b, p. 495.] *Jur.*, Europe (Germany).

Rhepocoris SCUDDER, 1890, p. 426 [**R. praetectus*; SD ŠTYS & RIHA, 1977, p. 182] [= *Parodarmistus* SCUDDER, 1890, p. 421 (type, *P. collisus* SCUDDER; SD ŠTYS & RIHA, 1977)]. Little-known genus, possibly related to family Pyrrhocoridae. *Oligo.*, USA (Colorado).

Stiphroschema BODE, 1953, p. 143 [**S. longealatum*; OD]. Little-known heteropteron, with small head and broad thorax; fore wing apparently very thin. *Jur.*, Europe (Germany).

Strobilocoris BODE, 1953, p. 138 [**S. mediocordatus*; OD]. Little-known heteropteron; thorax quadrate, with coarse sculpturing; venation unknown. *Jur.*, Europe (Germany).

Tenor SCUDDER, 1890, p. 425 [**C. speluncaae*; OD]. Little-known genus, based on poorly preserved specimen. ŠTYS & RIHA, 1977. *Oligo.*, USA (Colorado).

Trachycoris BODE, 1953, p. 142 [**T. abbreviatus*; OD]. Little-known heteropteron; similar to *Strobilocoris* but with broader wings; venation unknown. *Jur.*, Europe (Germany).

Triassocoris TILLYARD, 1922b, p. 466 [**T. myersi*; OD]. Tegmen with corium present in central part of wing; membrane submarginal, separated from corium by impressed line; M and CU arising independently from stem R; radiating veins extending from M to distal margin; clavus sharply defined, short. [Type of family Triassocoridae

TILLYARD.] EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 171, 1. **T. myersi*; tegmen, $\times 8$ (Tillyard, 1922b).

Suborder UNCERTAIN

The following genera, apparently belonging to the Hemiptera, are too poorly known to permit assignment to suborders.

Family PARAKNIGHTIIDAE

Evans, 1950

[Paraknightiidae EVANS, 1950, p. 250]

Paranotal lobes well developed. Tegmen with costal fracture in basal third of wing. Female with well-developed ovipositor. *Perm.*

Paraknightia EVANS, 1943b, p. 185 [**P. magnifica*; OD]. Tegmen with costal margin thickened; R + M dividing about one-fifth wing length from base. [Originally placed in Homoptera but transferred to Heteroptera by EVANS (1950); moved to a different suborder, Peloridiina, by POPOV (1980b) along with the existing family Peloridiidae.] EVANS, 1950; BECKER-MIGDISOVA & POPOV, 1962. *Perm.*, Australia (New South Wales).—FIG. 172. **P. magnifica*; a, dorsal view, $\times 3$ (Becker-Migdisova & Popov, 1962); b, tegmen, $\times 4.6$ (Evans, 1950).

Family UNCERTAIN

Docimus SCUDDER, 1890, p. 314 [**D. psylloides*; OD]. Little-known genus, based on fragment. HANDLIRSCH, 1907. *Oligo.*, USA (Colorado).

Prosigara SCUDDER, 1890, p. 343 [**P. flabellum*; OD]. Little-known genus, based on poorly preserved specimen. HANDLIRSCH, 1907. *Oligo.*, USA (Colorado).

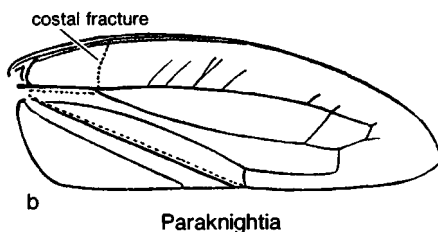
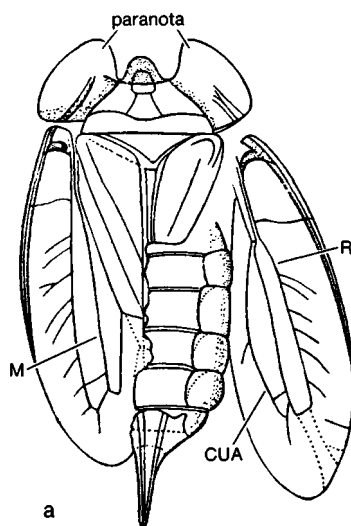


FIG. 172. Paraknightiidae (p. 277).

TREATISE ON INVERTEBRATE PALEONTOLOGY

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Part R ARTHROPODA 4

Volume 4: Superclass Hexapoda

By F. M. CARPENTER

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Division ENDOPTERYGOTA

Sharp, 1899

[Endopterygota SHARP, 1899, p. 248]

Immature stages (larvae) very different in form from the adults, typically living in equally different environments (except for social species), and feeding on distinctly different foods. Wings developing in an inactive pupal stage. *Perm.—Holo.*

Nine orders are usually recognized in this division, comprising nearly 88% of the existing species of insects. The relationships between certain of the orders (Hymenoptera, Trichoptera, Lepidoptera, Mecoptera, Siphonaptera, and Diptera) seem to be clear, but those of the remaining orders are uncertain (see Fig. 10). Only one extinct order, Glosselytrodea, is included in the Endopterygota.

Order COLEOPTERA

Linné, 1758

[Coleoptera LINNÉ, 1758, p. 339]

Minute to large insects. Head strongly sclerotized and rigid, frequently recessed beneath pronotum. Antennal structure diverse, commonly with 11 segments, but ranging from 1 to 30 throughout the order; antennae frequently filiform, although all types (for example, geniculate, pectinate, clavate) occur; sexual dimorphism of antennae common. Mouthparts mandibulate, with few modifications except for sexual dimorphism of mandibles and rare fusion of labrum with clypeus. Prothorax well developed and usually freely movable (not rigidly attached to the mesothorax); pronotum diversely formed, commonly extending anteriorly over base of head, and usually with a marginal lateral carina.

In the more generalized suborders, Archostemata and Adephaga, the pronotum is clearly separated from the propleura by notopleural sutures, but in the Polyphaga those sutures are not visible. The prosternum is separated from the rest of the prothorax in the Archostemata, Adephaga, and most

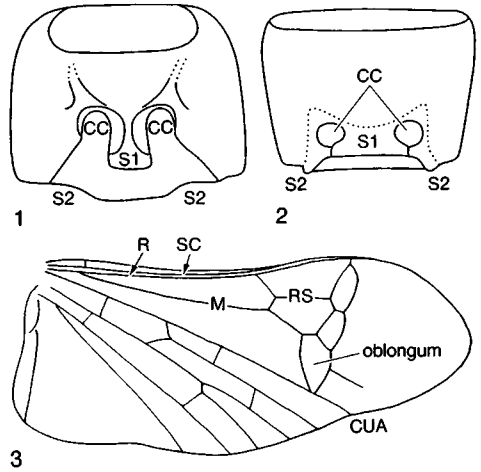


FIG. 173. Coleoptera; the open and closed coxal cavities and the hind wing (S1, prosternum; S2, mesosternum; CC, coxal cavity).—1. Diagram of a prosternum of *Thortus* sp., Cryptophagidae, with open coxal cavities (courtesy of Richard Leschen).—2. Diagram of a prosternum of *Loemophloeus* sp., Loemophloidae, with closed coxal cavities (courtesy of Richard Leschen).—3. Diagram of hind wing of *Priacma serrata* LE CONTE, Archostemata, Cupedidae (after Atkins, 1958).

of the Polyphaga by the prosternal sutures. The structural relationship between the coxal cavities of the prothorax and the prosternum is variable. In some species the prothoracic sclerites extend around the coxae and posteriorly to them; in these species the coxal cavities are considered to be closed (Fig. 173,2). In other species the prothoracic sclerites do not extend so far posteriorly, and the sternites behind the coxae are mesothoracic; in these species the coxal cavities are considered to be open (Fig. 173,1). The mesothorax and metathorax are not visible from above, except for the mesoscutellum, a small sclerite just posterior to the pronotum.

Legs typically cursorial, but sometimes fossorial and usually modified for swimming in aquatic species; coxae usually globose, but commonly elongate laterally; in some species, hind coxae are broad, flat plates that may cover part of femora; trochanters usually small; femora and tibiae of all legs usually similar in cursorial species; tarsi normally with

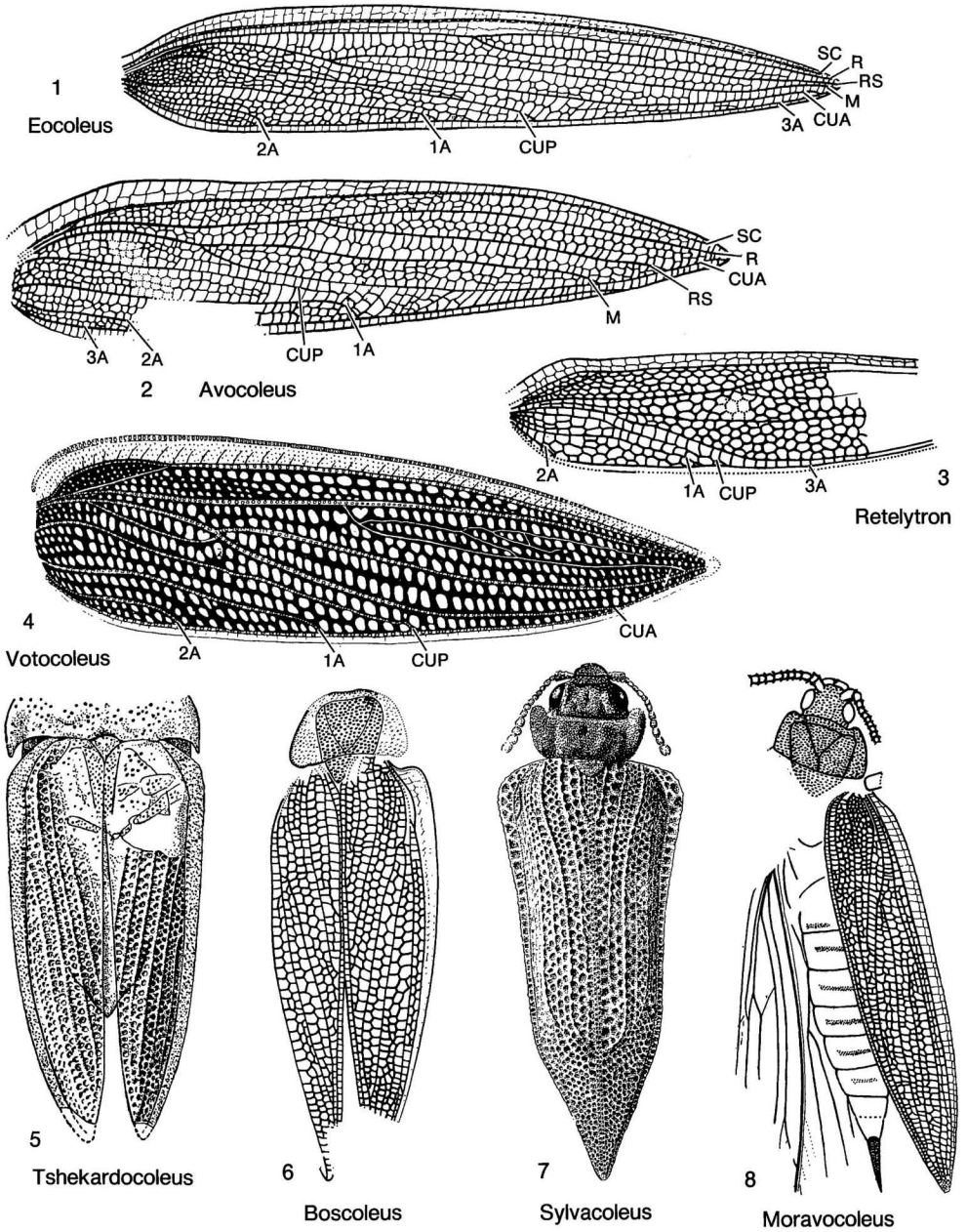


FIG. 174. Tshekardocoleidae (p. 283).

5 segments, but with 4 or less on one or more pairs of legs in a few families. Fore wings modified to rigid or semirigid elytra that fit over abdomen at rest, the sutural edges commonly meeting along medial line of body.

Elytra of the Archostemata, especially of

Permian species, have a definite venational pattern, the veins apparently being homologous with those of other insects (Fig. 174, 1). Elytra of the Adephaga and Polyphaga commonly have distinct longitudinal striae, some of which appear to correspond to the veins

of the Archostemata. Hind wings are membranous and at rest are usually folded both transversely and longitudinally beneath the elytra. The venational pattern in the hind wings has obviously been modified in relation to the folding, but the veins can apparently be homologized with those of other insects (Fig. 173,3). Veins C, SC, and R are close to the costal margin; CUA is well developed, along with several anal veins; M is commonly present, though weak (PONOMARENKO, 1969b). Ten abdominal segments are usually present, but segments 9 and 10 and the sternites of segments 1 and 2 are commonly modified and much reduced.

Most coleopterous larvae have a well-developed and heavily sclerotized head, 3 distinct thoracic segments, and usually 10 abdominal segments. The most generalized larvae, such as those of the Adephaga, are campodeiform and have a prognathous head, well-developed thoracic legs, and a pair of long, segmented processes (urogomphi) at the end of the abdomen. The eruciform, scarabaeiform, and apodous larvae among the Polyphaga clearly represent adaptations to the diverse environments in which development takes place. Pupae are commonly exarate and usually occur in soil or wood.

Environments and food of beetles are very diverse. Most larvae of the existing Archostemata and Polyphaga are phytophagous or saprophagous; those of the Adephaga are chiefly predaceous. *Perm.—Holo.*

Coleoptera comprise not only the largest order of the Insecta but the largest order within the animal kingdom. Estimates of the number of described species now existing exceed 300,000, comprising about 40 percent of the known insect fauna. The geological record indicates that they have held that dominant position in the Insecta since the early Jurassic (PONOMARENKO, 1969b; LAURENTIAUX, 1953).

Division of the order into three suborders, Archostemata, Adephaga, and Polyphaga, has been generally accepted since about the beginning of the present century. A fourth suborder, Myxophaga, tentatively proposed

by CROWSON (1967) for 4 small families, consists of species having a combination of certain features of the Adephaga and Archostemata; it has no geological record. In the recent fauna the Archostemata is the smallest suborder, including only 3 or possibly 4 families; the Adephaga is a larger and more diverse group, consisting of 11 families; the Polyphaga, by far the largest suborder, includes well over 100 families, which are usually grouped into 6 infraorders or series and about 20 superfamilies (CROWSON, 1981; LAWRENCE & NEWTON, 1982). The positions of many families within this hierarchy of the Polyphaga are by no means agreed upon by all students of the Coleoptera, and the placement of the extinct families of Polyphaga is even more uncertain. In the present treatment of the fossil Coleoptera the infraorders and superfamilies are omitted, and the sequence of families follows that of BRITTON (1970).

The most obvious and characteristic feature of the Coleoptera is the modification of the fore wing to a thick elytron. In the Archostemata, especially in Permian forms, the elytra show a distinct venational pattern, but in the Adephaga and Polyphaga no venation, at least as such, exists. For most of the Coleoptera, therefore, the main source of characters present in nearly all other fossil insects is eliminated (DARLINGTON, 1929, 1969). The classification of Coleoptera into suborders and families is based mainly on the presence and positions of certain sutures between sclerites and on details of such structures as antennae, mouthparts, coxae, and tarsi—details that are not usually preserved in fossil insects, except those in amber. Most fossil Coleoptera consist of isolated elytra or parts of elytra combined with crushed portions of the head and thorax. Nearly all beetles described from Mesozoic and Tertiary beds of Europe during the last century are very poorly preserved, and, with some exceptions, all were placed in recent genera that seemed to have similar body form. HANDLIRSCH (1906b, 1907, 1908a) made new generic names for the Mesozoic species,

although he was not able to assign them to families. These genera are cited below in the category Suborders and Families Uncertain.

A similar situation exists regarding the Tertiary Coleoptera described from North America in the early part of this century. SCUDDER and COCKERELL, who were excellent entomologists but not specialists in the Coleoptera, described many Tertiary species and assigned most of them to recent genera. WICKHAM, who was in fact a coleopterist and who described more fossil Coleoptera than all others combined, attempted to make the generic determinations within all families of the order. Subsequent examination of the type specimens by individuals specializing in the recent families concerned, however, indicates that on the average fully 90 percent of these extinct species either do not belong to the genera in which they have been placed or could equally well be assigned to several other genera. The very dubious records of such recent genera are cited below in the category Recent Genera of Coleoptera with Doubtfully Assigned Species.

In spite of the problems due to poor preservation of the fossils, the geological history of the Coleoptera is probably as extensive as that of such other large orders of insects as the Hymenoptera and Diptera. This is mainly due to the very large collections of pre-Tertiary beetles obtained by the staff of the Paleontological Institute of the Academy of Sciences in the Soviet Union and in particular to the monographs based on these collections by A. G. PONOMARENKO.

The archaic nature of the Archostemata is clearly supported by the geological records. The oldest known Coleoptera are from Permian beds, and all of these belong or could belong to the Archostemata: thirty genera in five families, all extinct. The known Triassic Coleoptera are mostly Archostemata also, some belonging to the existing family Cupedidae. In the Early Jurassic the Archostemata continued to be diverse, though less so; the family Cupedidae is represented by many genera, including the recent *Omma* and

Tetraphalerus. By the Late Jurassic the Archostemata comprised only about 10 percent of the Coleoptera and were well on the way to becoming the relict fauna they now are.

The Adephaga are first found in the Triassic, in which they are represented by many aquatic forms. Their diversity increased greatly by the early Jurassic, with at least the recent families Carabidae and Trachypachidae being present. In the Middle Jurassic they were the dominant group of the Coleoptera, but they lost that status in the Late Jurassic and now hold a very secondary position.

The Polyphaga are first known from the Early Jurassic, in which they have small representation, including elateroids. By the middle of the Jurassic the diversity was much greater, including some staphylinoids; by the later Jurassic they were clearly the dominant suborder, a position they still hold. The Early Cretaceous forms were essentially like Cenozoic and modern species.

The presence of several families of Coleoptera in the Middle and Upper Permian suggests that the order arose in the very Early Permian at least, quite possibly in the Late Carboniferous, and in any case before the origin of the Hymenoptera and Diptera. However, the ancestral stock is unknown. The generally accepted hypothesis is that they were derived from primitive endopterygotes, possibly related to the sialoid Neuroptera, but at present there is no fossil evidence to support or to refute that view.

Suborder ARCHOSTEMATA Kolbe, 1908

[Archostemata KOLBE, 1908, p. 246]

Prothorax with distinct notopleural sutures; hind coxae attached to metasternum, slightly movable, not dividing first visible abdominal sternite; all tarsi with 5 segments; antennae filiform; hind wing with a closed cell (oblongum) between veins M and CUA distally, and at resting position with distal part spi-

rally rolled. Larvae eruciform, with a distinct labrum and 5-segmented legs; wood boring. *Perm.—Holo.*

Family TSHEKARDOCOLEIDAE Rohdendorf, 1944

[Tshekardocoleidae ROHDENDORF, 1944, p. 252] [=Uralocoleidae ZALESSKY, 1947, p. 857]

Small to medium-sized beetles. Antennae with 13 moniliform segments and at most only slightly longer than head and pronotum combined; fore coxae small, rounded, widely separated; mesothorax almost as long as metathorax; abdomen with 5 visible sternites; elytra usually much longer than abdomen; all main veins usually present, including R; RS with 1 or 2 branches directed posteriorly; hind wing little known; SC and R close together; folds present between M and CUA and between CUA and CUP. *Perm.*

Tshekardocoleus ROHDENDORF, 1944, p. 252 [**T. magnus*; OD]. Elytron with M and CUA without common stem, or at most with very short stem; RS with 2 posterior branches; CUP extending to margin of elytron. PONOMARENKO, 1963a, 1977a. *Perm.*, USSR (Asian RSFSR).—FIG. 174.5. **T. magnus*; elytra and pronotum, $\times 3.8$ (Rohdendorf, 1944).

Avocoleus PONOMARENKO, 1969b, p. 51 [**Moravocoleus fractus* KUKALOVÁ, 1969a, p. 145; OD]. Elytron slender with small cells; area between R and RS with 3 rows of cells. *Perm.*, Europe (Czechoslovakia).—FIG. 174.2. **A. fractus* (KUKALOVÁ); elytron, $\times 16$ (Kukalová, 1969a).

Boscoleus KUKALOVÁ, 1969a, p. 149 [**B. blandus*; OD]. Elytron with coarsely reticulate venation; 2 rows of cells above distal half of RS; stem M+CUA short; CUP distinct only for length of common stem of M+CUA. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).—FIG. 174.6. **B. blandus*; elytra and pronotum, $\times 5.5$ (Kukalová, 1969a).

Ecocoleus KUKALOVÁ, 1969a, p. 147 [**E. scaber*; OD]. Elytron with stem M+CUA long; CUP extending to sutural ridge. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).—FIG. 174.1. **E. scaber*; elytron, $\times 6$ (Kukalová, 1969a).

Moravocoleus KUKALOVÁ, 1969a, p. 141 [**M. permianus*; OD]. Elytron with stem M+CUA long and strongly curved; CUA and 2A convergent distally, separated by only 1 row of cells. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).—FIG. 174.8. **M. permianus*; elytron and body, $\times 9$ (Kukalová, 1969a).

Prosperocoleus KUKALOVÁ, 1969a, p. 152 [**P. prosperus*; OD]. Elytron with similar to that of *Retelytron*, but M with a distinct posterior branch; CUP obsolete. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).

Retelytron KUKALOVÁ, 1965, p. 78 [**R. conopeum*; OD]. Elytron with area between R and M broad; M without a distinct posterior branch; area between M and CUA broad near mid-elytron; 2A short. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).—FIG. 174.3. **R. conopeum*; elytron, $\times 10$ (Kukalová, 1969a).

Sylvacoleodes PONOMARENKO, 1969b, p. 56 [**S. admirandus*; OD]. Elytron similar to that of *Sylvacoleus*, but CUA curved along sutural edge. *Perm.*, USSR (European RSFSR).

Sylvacoleus PONOMARENKO, 1963a, p. 73 [**S. richteri*; OD]. Elytron with M and CUA without common stem; RS unbranched; 3 or less rows of cells between RS and M; CUA bent abruptly toward sutural edge of elytron. *Perm.*, USSR (European RSFSR).—FIG. 174.7. *S. sharovi*; elytron and body, $\times 7.2$ (Ponomarenko, 1969b).

Umoricoleus KUKALOVÁ, 1969a, p. 148 [**U. perplexa*; OD]. Elytron little known; RS area apparently narrow; stem M+CUA very long. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).

Uralocoleus ZALESSKY, 1947, p. 858 [**U. splendens*; OD]. Little-known genus. Main veins of elytron apparently parallel to longitudinal axis of elytron. [Family assignment doubtful.] PONOMARENKO, 1963b, 1969b. *Perm.*, USSR (European RSFSR).

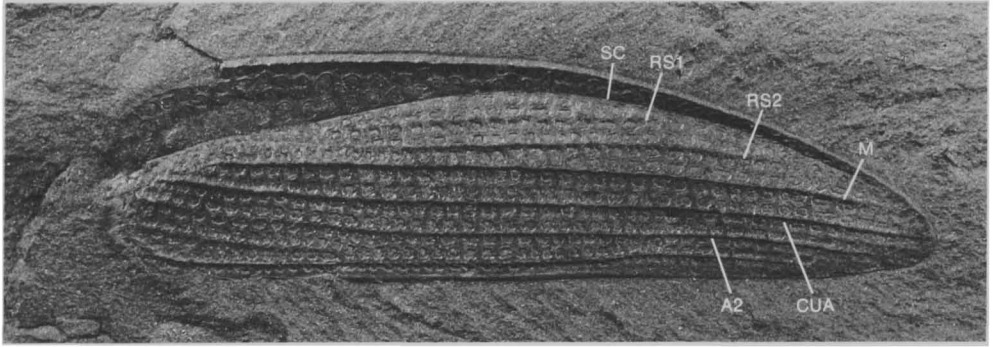
Votocoleus KUKALOVÁ, 1969a, p. 151 [**V. submissus*; OD]. Similar to *Tshekardocoleus*, but CUP not extending to distal margin. PONOMARENKO, 1969b. *Perm.*, Europe (Czechoslovakia).—FIG. 174.4. **V. submissus*; elytron, $\times 8$ (Kukalová, 1969a).

Family LABRADOROCOLEIDAE Ponomarenko, 1969

[Labradorocoleidae PONOMARENKO, 1969a, p. 307]

Similar to the Tshekardocoleidae, but vein CUP absent; all veins parallel to posterior elytral margin. *Cret.*

Labradorocoleus PONOMARENKO, 1969a, p. 309 [**L. carpenteri*; OD]. Costal area narrowing to apex of elytron; 3A more than one-fourth length of elytron. *Cret.*, Canada (Labrador).—FIG. 175. **L. carpenteri*; elytron, $\times 9$ (Ponomarenko, 1969a).



Labradorocoleus

FIG. 175. Labradorocoleidae (p. 283).

Family OBOROCOLEIDAE

Kukalová, 1969

[Oborocoleidae KUKALOVÁ, 1969a, p. 155]

Similar to the Tshekardocoleidae, but veins CUA and M reduced; 1A long. *Perm.*

Oborocoleus KUKALOVÁ, 1969a, p. 155 [**O. rohdendorfi*; OD]. Elytron broad; costal margin strongly convex; CUA apparently absent. *Perm.*, Europe (Czechoslovakia).

Liberocoleus KUKALOVÁ, 1969a, p. 157 [**L. intactus*; OD]. Similar to *Oborocoleus*, but elytron narrow and costal margin nearly straight. *Perm.*, Europe (Czechoslovakia).

Family PERMOCUPEDIDAE

Martynov, 1933

[*nom. correct.* PONOMARENKO, 1963a, p. 72, *pro* Permocupidae MARTYNOV, 1933b, p. 85] [=Kaltanocoleidae ROHDENDORF, 1961b, p. 397]

Small to medium-sized beetles; usually elongate and flattened; elytron reticulate; most main veins clearly distinguishable, but RS absent; CUA arising independently of M; CUP usually present, sometimes indistinct; at least 4 rows of cells at base of cubital area between CU and R. *Perm.*

Permocupes MARTYNOV, 1933b, p. 85 [**P. semenovii*; OD] [=Permocupoides MARTYNOV, 1933b, p. 86 (type, *P. distinctus*)]. Elytron with R and M ending before apex; CUA and 2A coalesced before apex. PONOMARENKO, 1963b. *Perm.*, USSR (European RSFSR). — FIG. 176,6. *P. sojanensis* PONOMARENKO; elytron and body, $\times 5$ (Ponomarenko, 1969b).

Archicupes ROHDENDORF, 1961b, p. 401 [**A. jacobsoni*; OD] [=Palaeocupes ROHDENDORF, 1961b, p. 404 (type, *P. kaltanicus*)]. Elytron

with 2A very short, running obliquely to sutural margin; CUP distinct. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Cytocupes ROHDENDORF, 1961b, p. 405 [**C. angustus*; OD]. Elytron with 3 rows of polygonal cells in subcostal area; R and M coalescing before apex; 6 rows of cells between CUA and 2A. *Perm.*, USSR (Asian RSFSR). — FIG. 176,3. **C. angustus*; elytron, $\times 11$ (Ponomarenko, 1969b). **Cytocupoides** PONOMARENKO, 1969b, p. 59 [**C. elongatus*; OD]. Similar to *Cytocupes*, but 2A long and parallel to hind margin of elytron. *Perm.*, USSR (Asian RSFSR).

Eocupes ROHDENDORF, 1961b, p. 400 [**E. lukjanoviitshi*; OD]. Elytron with 2 rows of cells in subcostal area; 2A longer than in *Archicupes*. *Perm.*, USSR (Asian RSFSR). — FIG. 176,2. **E. lukjanoviitshi*; elytron, $\times 12$ (Ponomarenko, 1969b).

Ichthyocupes ROHDENDORF, 1961b, p. 415 [**I. tyzbnovi*; OD]. Elytron with 2A very short, less than half length of elytron. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR, Kazakh).

Kaltanicupes ROHDENDORF, 1961b, p. 402 [**K. richteri*; OD]. Little-known genus; elytron similar to that of *Archicupes* but having 3 rows of cells in subcostal area. PONOMARENKO, 1963b, 1969b. *Perm.*, USSR (Asian and European RSFSR).

Kaltanocoleus ROHDENDORF, 1961b, p. 397 [**K. pospelovi*; OD]. Little-known genus, similar to *Kaltanicupes*. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Protocupes ROHDENDORF, 1961b, p. 406 [**P. martynovi*; OD]. Little-known genus, similar to *Kaltanicupes*. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Protocupoides ROHDENDORF, 1961b, p. 408 [**P. plavilstshikovii*; OD] [=Tomocupes ROHDENDORF, 1961b, p. 409 (type, *T. carinatus*); *Tricupes* ROHDENDORF, 1961b, p. 410 (type, *T. acer*)]. Elytron much as in *Ichthyocupes*, but 2A extending to its apex. *Perm.*, USSR (Asian

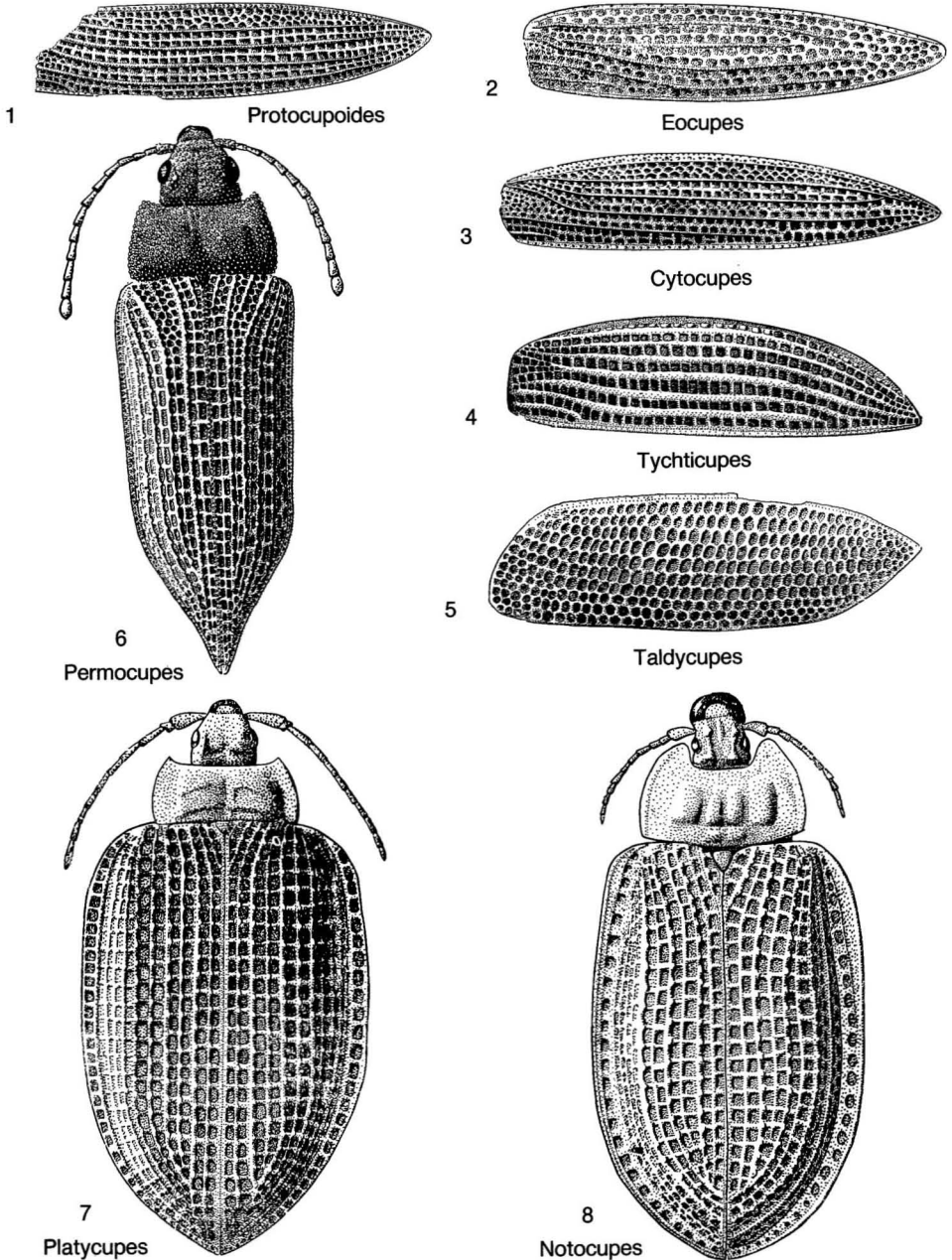


FIG. 176. Permocupedidae, Cupedidae, and Taldycupidae (p. 284–287).

RSFSR). — FIG. 176, 1. **P. plavilstshikovi*; elytron, $\times 10$ (Ponomarenko, 1969b).

Uralocupes PONOMARENKO, 1969b, p. 60 [**Kaltanocupes major* PONOMARENKO, 1963a, p. 78; OD]. Elytron with 3 rows of cells in medial area. PONOMARENKO, 1963b. *Perm.*, USSR (European RSFSR).

Family CUPEDIDAE Lacordaire, 1857

[Cupedidae LACORDAIRE, 1857, p. 505]

Small to large beetles, usually elongate and flattened or cylindrical; antennae with 11 segments of diverse form and length; abdomen with 5 distinct sternites. Elytra with

- distinct venation, all main veins present except CUP and 1A; rows of cells present between main veins. *Trias.*—*Holo.*
- Cupes** FABRICIUS, 1801, p. 66. DE PEYERIMHOFF, 1909; IABLOKOV-KHNZORIAN, 1960b; PONOMARENKO, 1969b; GERSDORF, 1976. *Oligo.*, Europe (Baltic); *Plio.*, Europe (Germany)—*Holo.*
- Anaglyphites** PONOMARENKO, 1964, p. 55 [**A. clavatus*; OD]. Head broad at level of eyes, abruptly narrowed anteriorly; third antennal segment much longer than second. PONOMARENKO, 1966b, 1968b, 1969b. *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).
- Asimma** PONOMARENKO, 1966a, p. 58 [**A. rara*; OD]. Little-known genus; prothorax narrow, without lateral lobes. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Cupesia** PONOMARENKO, 1966a, p. 57 [**C. monilicornia*; OD]. Antennae short, not extending beyond base of prothorax; main veins not fused distally. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Cupidium** PONOMARENKO, 1968b, p. 126 [**C. abavum*; OD]. Second and third antennal segments about equal in length. PONOMARENKO, 1969b. *Jur.*, USSR (Kazakh).
- Cupoides** MOTSCHULSKY, 1856, p. 27 [**C. tessellatus*; OD]. Very similar to *Priacma* (recent) but with eyes smaller and anterior angles of pronotum more acute. DE PEYERIMHOFF, 1909. *Oligo.*, Europe (Baltic).
- Eurydictyon** PONOMARENKO, 1969b, p. 96 [**E. conspicuum*; OD]. Large beetles, with very large cells along sutural ridge of elytron; radial area of elytron reduced. *Jur.*, USSR (Kazakh).
- Kirghizocupes** PONOMARENKO, 1966a, p. 59 [**K. cellulosus*; OD]. Little-known genus. Teeth of mandibles projecting vertically, not in plane of mandibles. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Lithocupes** PONOMARENKO, 1966a, p. 65 [**L. incertus*; OD]. Little-known genus. Length and width of head subequal; first antennal segment swollen, third longest. PONOMARENKO, 1969b. *Trias.*—*Jur.*, USSR (Kirghiz).
- Mesocupes** MARTYNOV, 1926a, p. 6 [**M. primitivus*; OD]. Similar to *Mesocupoides*, but pronotum without paranotal extensions. PONOMARENKO, 1964, 1968b, 1969b. *Jur.*, USSR (Kazakh).
- Mesocupoides** PONOMARENKO, 1969b, p. 106 [**M. proporeius*; OD]. Head with vertex flat; tubercles on occiput and bases of antennae; antennae with last segment broad. Elytra with small cells; pronotum rectangular and with paranotal extensions. *Trias.*, USSR (Kirghiz).
- Mesothoris** TILLYARD in TILLYARD & DUNSTAN, 1916, p. 23 [**M. clathrata*; OD]. Little-known genus; elytron only. [Family assignment doubtful.] DUNSTAN, 1923; PONOMARENKO, 1969b. *Trias.*, Australia (Queensland).
- Miocupes** PONOMARENKO, 1973c, p. 102 [**M. ribai*; OD]. Similar to *Priacma* (recent), but head with prominent occipital lobes. *Mio.*, Europe (Czechoslovakia).
- Moltenocupes** ZEUNER, 1961, p. 304 [**M. townrowi*; OD]. Little-known genus. Last abdominal sternite short; mandibles large. PONOMARENKO, 1969b. *Trias.*, South Africa.
- Notocupes** PONOMARENKO, 1964, p. 61 [**N. picturatus*; OD]. Posterior veins of elytron coalesced distally before reaching posterior edge of elytron; second and third antennal segments equal; mandibles very large. PONOMARENKO, 1966a, 1966b, 1968b, 1969b, 1971b. *Trias.*, USSR (Kirghiz); *Jur.*, Europe (Germany), USSR (Asian RSFSR, Kazakh); *Cret.*, USSR (Asian RSFSR).—FIG. 176.8. *N. nigrimonticola* PONOMARENKO, *Jur.*, Kazakh; elytra and body, $\times 3$ (Ponomarenko, 1969b).
- Notocupoides** PONOMARENKO, 1966a, p. 63 [**N. triassicus*; OD]. Antennae setiform, segments being smaller distally; ridges over eyes. DEICHMÜLLER, 1886; PONOMARENKO, 1969b, 1971b. *Trias.*, USSR (Kirghiz).
- Omma** NEWMAN, 1839, p. 303 [= *Procarabus* OPPENHEIM, 1888, p. 236 (type, *P. zitteli*, SD PONOMARENKO, 1971b, p. 68); *Ommamima* PONOMARENKO, 1964, p. 50 (type, *O. pilosum*)]. CROWSON, 1962; PONOMARENKO, 1968a, 1969b. *Jur.*, England, Europe (Germany), USSR (Kazakh); *Cret.*, USSR (Asian RSFSR)—*Holo.*
- Platycupes** PONOMARENKO, 1966a, p. 48 [**P. dolichoцерus*; OD]. Head short, generally transverse; antennae filiform, extending beyond base of pronotum; mandibles small. Posterior veins of elytron as in *Notocupes*. *Trias.*, USSR (Kirghiz).—FIG. 176.7. **P. dolichoцерus*; elytra and body, $\times 9$ (Ponomarenko, 1969b).
- Priacmopsis** PONOMARENKO, 1966b, p. 142 [**P. adumbrata*; OD]. Similar to *Priacma* (recent), but prothorax about twice as wide as long. PONOMARENKO, 1969b. *Cret.*, USSR (Asian RSFSR).
- Procupes** PONOMARENKO, 1966a, p. 57 [**P. mandibularis*; OD]. Head about twice as long as wide; mandibles large, apical tooth much longer than others. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Pterocupes** PONOMARENKO, 1966a, p. 55 [**P. antennatus*; OD]. Antennae with second and third segments equal. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Rhabdocupes** PONOMARENKO, 1966a, p. 60 [**R. longus*; OD]. Antennae with third segment twice as long as second. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).
- Sinocupes** LIN, 1976, p. 111 [**S. validus*; OD]. Little-known genus. *Jur.*, China (Liaoning).
- Tetraphalerus** WATERHOUSE, 1901, p. 520 [= *Tetraphalerites* CROWSON, 1962, p. 154 (type, *T. oligocenicus*)]. PONOMARENKO, 1964, 1968a,

1969b. *Jur.*, USSR (Kazakh), England; *Cret.*, USSR (Asian RSFSR)—*Holo.*

Triadocupes PONOMARENKO, 1966a, p. 51 [**T. ferganensis*; OD]. Head about as wide as long; antennae setiform. CUA and 2A not joined distally. PONOMARENKO, 1969b. *Trias.*, USSR (Kirghiz).

Family TALDYCUPIDAE Rohdendorf, 1961

[Taldycupidae ROHDENDORF, 1961b, p. 412]

Small, elongate, flattened beetles. Elytron with reticulate venation consisting of 9 thick, complete veins separated on each side by a row of cells, with a few additional cells basally. Head prognathous; antennae very slightly thickened apically; prothorax with small paranotals. *Perm.*—*Trias.*

Taldycupes ROHDENDORF, 1961b, p. 421 [**T. khalfini*; OD] [= *Taldycupidium* ROHDENDORF, 1961b, p. 424 (type, *T. bergi*); *Cryptocupes* ROHDENDORF, 1961b, p. 425 (type, *C. rjabini*)]. Elytron wide, nearly flat; longitudinal veins nearly straight; M terminating at apex of elytron; 2A terminating directly on sutural margin. *Perm.*, USSR (Asian RSFSR, Kazakh). — FIG. 176, 5. **T. khalfini*; elytron, $\times 18$ (Ponomarenko, 1969b).

Simmondsia DUNSTAN, 1923, p. 35 [**S. subpyriformis*; OD]. Similar to *Tecticipes* but with only 2 rows of cells at base of cubital area. ROHDENDORF, 1961b; PONOMARENKO, 1969b. *Perm.*, USSR (European RSFSR); *Trias.*, Australia (Queensland).

Tecticipes ROHDENDORF, 1961b, p. 417 [**T. beckeri*; OD] [= *Stegocupes* ROHDENDORF, 1961b, p. 418 (type, *S. efremovi*)]. Base of cubital area of elytron with 3 rows of cells. PONOMARENKO, 1969b. *Perm.*, USSR (European RSFSR).

Tychtipes ROHDENDORF, 1961b, p. 426 [**T. radtschenkoi*; OD]. Vein 3A terminating on sutural edge of elytron without merging with another vein. *Perm.*, USSR (European RSFSR). — FIG. 176, 4. **T. radtschenkoi*; elytron, $\times 22$ (Ponomarenko, 1969b).

Tychtipoides ROHDENDORF, 1961b, p. 430 [**T. grjasevi*; OD]. Little-known genus. Elytron with 3 posterior veins merging distally to form a composite vein. PONOMARENKO, 1969b. *Perm.*, USSR (European RSFSR).

Family ADEMOSYNIDAE Ponomarenko, 1968

[Ademosynidae PONOMARENKO, 1968b, p. 128]

Small beetles. Body oval or elongate-oval; mandibles small; antennae filiform, usually

thin; prothorax broader than long, paranotal extensions small or absent. Elytra with 9 or 10 punctate grooves. Hind wings unknown. Front coxal cavities opening posteriorly. [Assignment of these genera to the Archostemata is doubtful since the structure of their hind wings and of their larvae is unknown.] *Trias.*—*Cret.*

Ademosyne HANDLIIRSCH, 1906b, p. 402 [**A. major*; SD PONOMARENKO, 1969b, p. 132]. Head orthognathous; prothorax narrowed anteriorly; hind coxae transverse. DUNSTAN, 1923. *Trias.*, Australia (Queensland), USSR (Kirghiz).

Ademosynoides DUNSTAN, 1923, p. 25 [**Ademosyne minor* HANDLIIRSCH, 1906b, p. 403; OD]. Little-known genus; small species, known by elytra only. MARTYNOV, 1936; ZEUNER, 1959b; FUJIYAMA, 1973. *Trias.*, Australia (Queensland, New South Wales), Antarctica (Graham Land), USSR (Asian RSFSR), Japan.

Cephalosyne PONOMARENKO, 1969b, p. 134 [**C. capitata*; OD]. Head orthognathous, large, much broader than long. *Trias.*, USSR (Kirghiz).

Dolichosyne PONOMARENKO, 1969b, p. 126 [**D. confragosa*; OD]. Head prognathous; mandibles large; hind coxae large; anterior part of thorax narrowed. *Trias.*, USSR (Kirghiz).

Gnathosyne PONOMARENKO, 1969b, p. 129 [**G. akkolensis*; OD]. Head prognathous; prothorax slightly narrowed anteriorly. *Jur.*, USSR (Kazakh).

Grammositus DUNSTAN, 1923, p. 37 [**Grammositum bilineatus*; OD]. Similar to *Ademosyne* but with apex of elytra distinctly blunt. *Trias.*, Australia (Queensland).

Petrosyne PONOMARENKO, 1969b, p. 135 [**P. liasica*; OD]. Elytron as in *Ademosyne*, but metasternum rectangular, not narrowed anteriorly. *Jur.*, USSR (Kirghiz).

Platycrossos DUNSTAN, 1923, p. 32 [**Ademosyne tumida* TILLYARD in TILLYARD & DUNSTAN, 1916, p. 21; OD]. Similar to *Ademosyne*, but elytra with more pronounced lateral or humeral borders. *Trias.*, Australia (Queensland).

Polysitum DUNSTAN, 1923, p. 40 [**Polysitum punctatus*; OD]. Similar to *Ademosyne*, but elytra uniformly granulate. *Trias.*, Australia (Queensland).

Ranis PONOMARENKO, 1968b, p. 129 [**R. ovalis*; OD]. Head prognathous, transverse; body broadly oval. *Jur.*, USSR (Kirghiz, Kazakh). — FIG. 177, 3. **R. ovalis*; elytra and body, $\times 9$ (Ponomarenko, 1969b).

Shepherdia DUNSTAN, 1923, p. 38 [**S. quadrivittata*; OD]. Similar to *Ademosyne*, but elytron with strigose sculpturing. *Trias.*, Australia (Queensland).

Sphaerosyne PONOMARENKO, 1969b, p. 135 [**S. globosa*; OD]. Body broadly oval, strongly con-

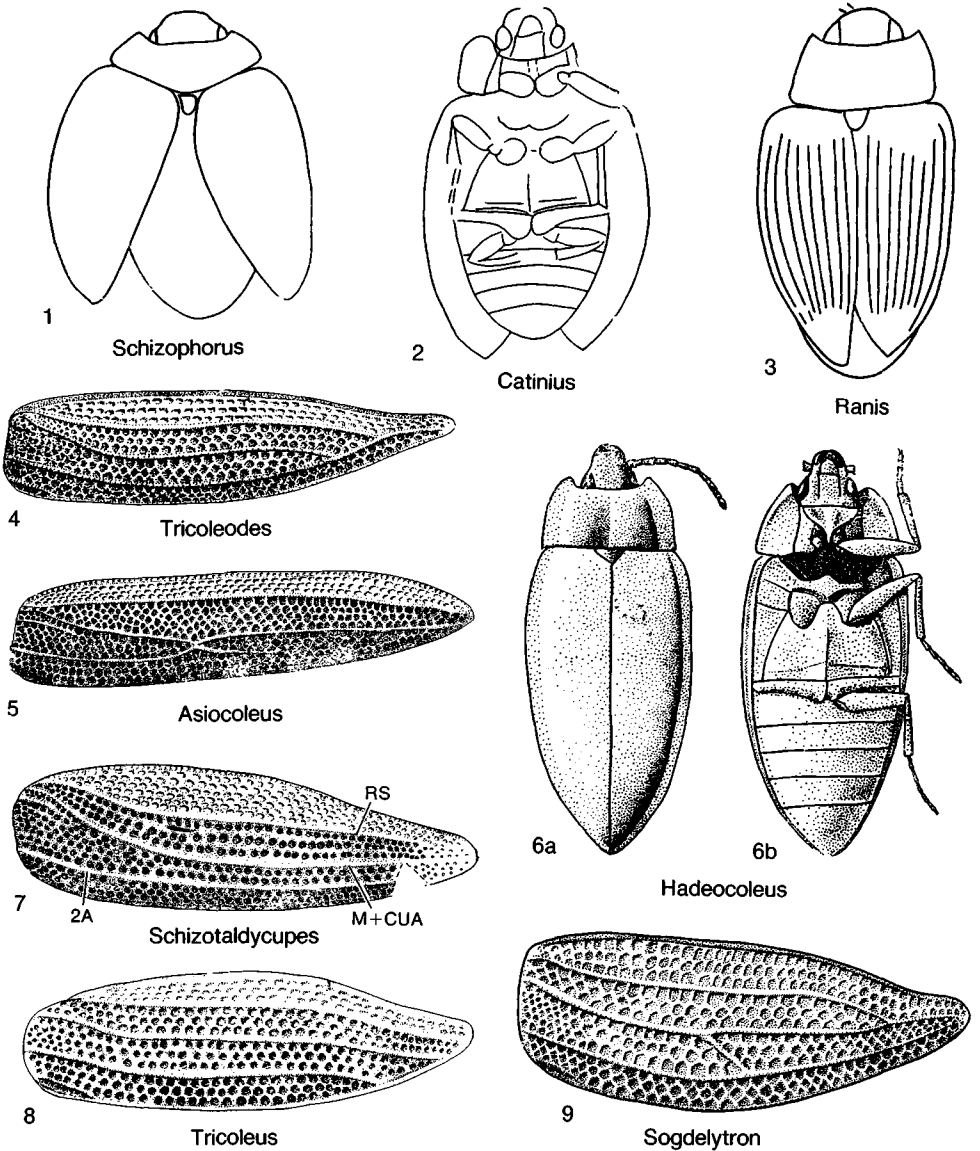


FIG. 177. Ademosynidae, Tricoleidae, Asiocolaeidae, Rhombocoleidae, Schizophoridae, and Catiniidae (p. 287–290).

vex; head prognathous. *Cret.*, USSR (Asian RSFSR).

Family TRICOLEIDAE
Ponomarenko, 1969

[Tricoleidae Ponomarenko, 1969b, p. 138]

Elytron reticulate; 3 distinct main veins, RS, M+CUA, and 2A, each separated for

almost their entire lengths by 3 rows of cells. *Trias.-Jur.*

Tricoleus Ponomarenko, 1969b, p. 139 [*T. punctatus*; OD]. Elytron with RS terminating at apex. *Jur.*, USSR (Kazakh).—FIG. 177, 8. **T. punctatus*; elytron, ×12 (Ponomarenko, 1969b).

Sogdelytron Ponomarenko, 1969b, p. 141 [*S. latum*; OD]. Elytron broad; RS terminating on

M just before apex; CUA ending on 2A near midwing. *Trias.*, USSR (Kirghiz). — FIG. 177,9. **S. latum*; elytron, $\times 7$ (Ponomarenko, 1969b).

Tricoleodes PONOMARENKO, 1969b, p. 140 [**T. acutus*; OD]. Elytron acute distally; RS and M+CUA terminating on 2A distally. *Trias.*, USSR (Kirghiz). — FIG. 177,4. **T. acutus*; elytron, $\times 5.5$ (Ponomarenko, 1969b).

Willcoxia DUNSTAN, 1923, p. 62 [**W. magnopunctata*; OD]. Little-known genus. Elytral cells weakly developed. [Family assignment doubtful.] PONOMARENKO, 1969b. *Trias.*, Australia (Queensland).

Family ASIUCOLEIDAE Rohdendorf, 1961

[Asiucoleidae ROHDENDORF, 1961b, p. 396]

Elytron with veins SC, RS, and associated interstitial veins close together along anterior margin; stem M+CUA long, extending nearly to midwing and directed obliquely toward posterior margin; CUA directed toward sutural margin; 2A parallel to sutural margin basally, then merging with CUA at its separation from M. Body unknown. *Perm.*

Asiucoleus ROHDENDORF, 1961b, p. 396 [**A. novojilovi*; OD]. Elytron with M terminating nearly at apex. *Perm.*, USSR (Asian RSFSR). — FIG. 177,5. **A. novojilovi*; elytron, $\times 7.5$ (Ponomarenko, 1969b).

Family RHOMBOCOLEIDAE Rohdendorf, 1961

[Rhombocoleidae ROHDENDORF, 1961b, p. 432]

Elytron with main veins distinct or replaced by punctate grooves; in most genera main veins not distinguished from interstitial veins; anterior part of elytron with 4 to 6 rows of cells. Body not definitely known. *Perm.*

Rhombocoleus ROHDENDORF, 1961b, p. 432 [**R. andreae*; OD]. Little-known genus. Anterior area of elytron with 5 rows of cells. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Erunakicipes ROHDENDORF, 1961b, p. 433 [**E. kryshrovichii*; OD] [= *Schizocupes* ROHDENDORF, 1961b, p. 450 (type, *S. obrutshchevi*)]. Elytron with 3 rows of punctations in anterior area and 4 rows at base of middle area. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Karakanocoleus ROHDENDORF, 1961b, p. 451 [**K. lebedevi*; OD; probably = *Erunakicipes venjukovi* ROHDENDORF, 1961b] [= *Karakanocoleodes* ROHDENDORF, 1961b, p. 455 (type, *K. latissi-*

mus)]. Elytron with 4 rows of cells in anterior area and 6 rows at base of middle area. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Rhombocoleites PONOMARENKO, 1969b, p. 147 [**R. adumbratus*; OD]. Only head and thorax known. [Family assignment doubtful.] *Perm.*, USSR (European RSFSR).

Rossocoleus ROHDENDORF, 1961b, p. 456, *nom. subst. pro Curculiopsis* MARTYNOV, 1937b, p. 39, *non* HANDLIRSCH, 1907 [**Curculiopsis ellipticus* MARTYNOV, 1937b, p. 39; OD]. Little-known genus. Elytron apparently without rows of cells and punctate grooves. PONOMARENKO, 1969b. *Perm.*, USSR (Asian RSFSR).

Schizotaldycupes ROHDENDORF, 1961b, p. 414 [**S. ananjevi*; OD] [= *Carinicipes* ROHDENDORF, 1961b, p. 416 (type, *C. beckermigdisovae*)]. Elytron with RS, M+CUA, and 2A distinct; 10 rows of cells at base between M+CUA and 2A. *Perm.*, USSR (Asian RSFSR). — FIG. 177,7. **S. ananjevi*; elytron, $\times 7.4$ (Ponomarenko, 1969b).

Family SCHIZOPHORIDAE Ponomarenko, 1968

[Schizophoridae PONOMARENKO, 1968b, p. 130]

Body flattened, oval; head usually hypognathous, rarely prognathous; antennae filiform, with 11 homonomous segments; eyes large, mostly lateral; mandibles usually three-toothed, small; pronotum transverse, with flat paranotals; abdomen with 5 visible sternites. Elytron without veins or cells; hind wings well developed. Body covered with dense tubercles. *Trias.*—*Jur.*

Schizophorus PONOMARENKO, 1968b, p. 130 [**S. crassus*; OD]. Body broadly oval; head retracted under pronotum; propleura very wide. *Jur.*, USSR (Kirghiz). — FIG. 177,1. **S. crassus*; elytra and body, $\times 6$ (Ponomarenko, 1969b).

Catabrycus PONOMARENKO, 1969b, p. 176 [**C. hoptitus*; OD]. Large beetles, with large head and projecting mandibles. *Trias.*, USSR (Kirghiz).

Hadeocoleodes PONOMARENKO, 1969b, p. 153 [**H. calus*; OD]. Similar to *Hadocoleus* but with intercoxal process extending only as far as middle of front coxae. *Jur.*, USSR (Kazakh).

Hadeocoleus PONOMARENKO, 1969b, p. 150 [**H. gigas*; OD]. Body convex; head and prothorax directed slightly downward; antennae thin; prothorax with anteriorly extended paranotals; fore coxae small, protruding posteriorly. *Trias.*, USSR (Kirghiz). — FIG. 177,6. **H. gigas*; a, dorsal view, b, ventral view, $\times 1.4$ (Ponomarenko, 1969b).

- Lethocoleus** PONOMARENKO, 1969b, p. 165 [**L. sternalis*; OD]. Body slender; mesosternum long; head shorter than pronotum. *Trias.*, USSR (Kirghiz).
- Malmelater** HANDLIRSCH, 1906b, p. 541 [**Elaterites priscus* OPPENHEIM, 1888, p. 241; SD PONOMARENKO, 1971b, p. 72]. Similar to *Schizophorinus* but with prominent, flat carina on prosternum; terminal abdominal sternite short. *Jur.*, Europe (Germany).
- Parathnesidius** PONOMARENKO, 1969b, p. 175 [**P. oculatus*; OD]. Head long, prognathous; eyes displaced to dorsal surface; prothorax transverse, narrowed anteriorly, with narrow pronotals and low, flat keel; fore coxae round. *Jur.*, USSR (Kirghiz).
- Pesus** PONOMARENKO, 1969b, p. 155 [**P. prognathus*; OD]. Little-known genus. Prothorax with narrow paranotals extending anteriorly and tapered; fore coxae large and transverse; head prognathous. *Trias.*, USSR (Kirghiz).
- Praesagus** PONOMARENKO, 1969b, p. 171 [**P. capitatus*; OD]. Mandibles short, not projecting; head and thorax wide. *Trias.*, USSR (Kirghiz).
- Salebrocoleus** PONOMARENKO, 1969b, p. 161 [**S. megacephalus*; OD]. Similar to *Praesagus*, but metasternum narrowed abruptly anteriorly; body with large tubercles. *Jur.*, USSR (Kirghiz).
- Salebroferus** PONOMARENKO, 1969b, p. 159 [**S. confragosus*; OD]. Similar to *Triassocoleus*, but first antennal segment shorter than third. *Trias.*, USSR (Kirghiz).
- Schizophorinus** PONOMARENKO, 1969b, p. 167 [**S. punctatus*; OD]. Pronotum with anterior edge straight; first abdominal sternite longer than others. *Trias.*, USSR (Kirghiz).
- Schizophoroides** PONOMARENKO, 1969b, p. 169 [**S. tuberculatus*; OD]. Body convex, slightly elongate; head and pronotum directed obliquely forward and down; paranotals almost absent; fore coxae not protruding backward; fore femora much thickened. *Trias.*, USSR (Kirghiz).
- Tersoides** PONOMARENKO, 1968b, p. 134 [**T. capitatus*; OD]. Similar to *Tersus*, but head longer and eyes more nearly lateral; femora thickened. PONOMARENKO, 1969b. *Jur.*, USSR (Kazakh, Kirghiz).
- Tersus** MARTYNOV, 1926a, p. 11 [**T. crassicornis*; OD]. Paranotals wide, projecting anteriorly; metasternum very narrow; eyes displaced dorsally. PONOMARENKO, 1969b. *Jur.*, USSR (Kazakh).
- Thnesidius** PONOMARENKO, 1969b, p. 172 [**T. xyphoborus*; OD]. Head almost prognathous; mandibles small, not projecting; basal segment of antennae slightly thickened, second segment very small, third segment largest; prosternum in form of flat keel without elevations on sides. *Trias.*, USSR (Kirghiz).
- Triassocoleus** PONOMARENKO, 1969b, p. 136 [**T. sulcatus*; OD]. First antennal segment shorter than second and third together; sides of prothorax with a double notch. *Trias.*, USSR (Kirghiz).
- Xyphosternum** PONOMARENKO, 1968b, p. 134 [**S. punctatum*; OD]. Head prognathous, not longer than wide and shorter than prothorax; sides of prosternum contiguous with keel, having flat, round, elevated areas. PONOMARENKO, 1969b. *Jur.*, USSR (Kazakh).

Family CATINIIDAE Ponomarenko, 1968

[Catiniidae PONOMARENKO, 1968b, p. 137]

Body flattened, oval; head and pronotum directed slightly downward; head strongly retracted under pronotum; eyes lateral; paranotals with sides extending anteriorly; prosternum without a process extending between fore coxae. Elytra as in Schizophoridae. *Trias.—Jur.*

Catinus PONOMARENKO, 1968b, p. 137 [**C. pelta*; OD]. Small beetles, broadly oval. Head strongly transverse; prosternum with pronounced longitudinal keel, having small extensions between fore coxae. *Jur.*, USSR (Kazakh).—FIG. 177, 2. **C. pelta*; body and elytra, ventral view, $\times 5$ (Ponomarenko, 1969b).

Avocatinus PONOMARENKO, 1969b, p. 178 [**A. elongatus*; OD]. Small, elongate beetles, lacking keel on prosternum. *Trias.*, USSR (Kirghiz).

Catinoides PONOMARENKO, 1969b, p. 179 [**C. rotundatus*; OD]. Small, broad beetles, without longitudinal keel. *Trias.*, USSR (Kirghiz).

Macrocatinius PONOMARENKO, 1969b, p. 180 [**M. brachycephalus*; OD]. Large, elongate beetles; posterior edge of prosternum triangular, about twice as long in middle as on sides; propleura triangular. *Trias.*, USSR (Kirghiz).

Triassocatinus PONOMARENKO, 1969b, p. 182 [**T. glabratus*; OD]. Similar to *Macrocatinius*, but propleura widened posteriorly. *Trias.*, USSR (Kirghiz).

Family MICROMALTHIDAE Barber, 1913

[Micromalthidae BARBER, 1913, p. 185]

Very small beetles of uncertain affinities. Antennae with 11 segments, slightly moniliform; pronotum much smaller than head, not margined laterally; all tarsi with 5 segments; hind wings with distal half spirally rolled and with reduced venation. Larvae

diversely formed in the several instars. Adults and larvae occurring in decaying wood. *Oligo./Mio.—Holo.*

Micromalthus LE CONTE, 1878, p. 613. [Larvae of *M. debilis* LE CONTE, a recent species.] PONOMARENKO, 1969b; ROZEN, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Suborder ADEPHAGA

Emery, 1886

[Adephaga EMERY, 1886, p. 653]

Prothorax with distinct notopleural sutures, separating pronotum from propleura; hind coxae fused to metasternum, completely dividing first visible abdominal sternite; all tarsi with 5 segments; hind wing commonly with a closed cell between M and CUA distally; 6 abdominal sternites commonly visible, abdominal segments 2, 3, and 4 at least partly fused. Larvae lacking labrum; legs with 5 segments. Adults and larvae mostly predaceous. *Trias.—Holo.*

Family CARABIDAE Latreille, 1802

[Carabidae LATREILLE, 1802a, p. 80]

Head prognathous; antennae with 10 or commonly 11 filiform or flattened segments, inserted under a frontal ridge between eyes and mandibles; mandibles and maxillae well developed; prothorax usually with conspicuous, inflexed lateral margins; legs cursorial; elytra striate, with setiferous punctures; abdomen with 6 visible sternites. Larvae usually campaniform and mostly predaceous. Adults and larvae occurring on ground, in trees, or near ponds and streams. *Trias.—Holo.*

Carabus LINNÉ, 1758, p. 413. *Holo.*

Agatoides MOTSCHULSKY, 1856, p. 26 [**A. carinulatus*; OD]. Similar to *Agatus* (recent) but with elytra distinctly ribbed. *Oligo.*, Europe (Baltic).

Arthropterillus Wasmann, 1926b, p. 229 [**Arthropterus helmi* Stein, 1877, p. 28; OD]. Similar to *Arthropterus*, but body apparently longer. Wasmann, 1929a; Darlington, 1950. *Oligo.*, Europe (Baltic).

Arthropterites Wasmann, 1926a, p. 28 [**A. klebsi*; OD]. Little-known genus, possibly related to *Pentaplatarthrus* (recent); at least 9 antennal seg-

ments present. Wasmann, 1929a; Darlington, 1950. *Oligo.*, Europe (Baltic).

Arthropterus M'Leay, 1838, p. 75. Wasmann, 1926b, 1929a; Darlington, 1950; Statz, 1952. *Oligo.*, Europe (Baltic)—*Holo.*

Carabites Heer, 1852, p. 12 [collective group]. Isolated elytra resembling those of carabids. Heer, 1862a, 1868, 1870a; Scudder, 1892; Meunier, 1898c; Handlirsch, 1906b, 1907, 1908a; Cockerell, 1908a, 1920b, 1920c, 1920d, 1928a, 1936; Fiori, 1932; Zeuner, 1941a. *Jur.*, Europe (Switzerland); *Cret.*, USA (South Dakota); *Eoc.*, USA (Colorado, Wyoming), Greenland (Grinnell Land); *Oligo.*, Europe (France); *Mio.*, Iceland, Europe (Norway); *Paleoc.—Plio.*, Europe (Italy), Argentina (Jujuy).

Carabopteron Martynov, 1926a, p. 2 [**C. punctatolineatum*; OD]. Little-known genus. Outer elytral margins nearly straight and parallel to inner ones; 4 main tuberculate ridges usually present. [Family assignment doubtful.] *Jur.*, USSR (Kazakh).

Cerapterites Wasmann, 1926a, p. 27 [**C. primaeus*; OD]. Similar to *Protocerapterus*, but body very broad, about 2.5 times as long as wide. Wasmann, 1929a; Darlington, 1950. *Oligo.*, Europe (Baltic).

Conjunctia Ponomarenko, 1977b, p. 87 [**C. prodroma*; OD]. Similar to *Mesorabus*, but mandibles not so long. *Cret.*, USSR (Asian RSFSR).

Cordorabus Ponomarenko, 1977b, p. 78 [**C. notatus*; OD]. Similar to *Protorabus*, but abdomen more pointed; tegmen smooth. *Jur.*, USSR (Kazakh).

Cretorabus Ponomarenko, 1977b, p. 83 [**C. capitatus*; OD]. Head large, strongly transverse; prothorax also transverse, widest before center; metepisternum narrowed posteriorly; apex of abdomen rounded. *Cret.*, USSR (Asian RSFSR).

Elaphrotites Haupt, 1956, p. 37 [**E. densus*; OD]. Little-known genus, based on elytral fragment, possibly related to *Elaphrus* (recent). [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Eodromeus Ponomarenko, herein [**E. dissectus* Ponomarenko, 1977b, p. 69; OD]. Mandibles shorter than head, triangular; antennae short, barely reaching pronotum, their segments thick; pronotum rectangular, weakly incised anteriorly. [In the original description of the genus, the name of the type species was given as *E. fasciatus*. However, Dr. Ponomarenko has informed me that the name *fasciatus* was a printing error, there being no species of that name in his account of the genus. In order to validate the generic name, he has accordingly requested permission to designate in the present publication his species *dissectus* as the type of his genus, as originally intended.] *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).—FIG. 178, 5. *E. antiquus*, *Jur.*,

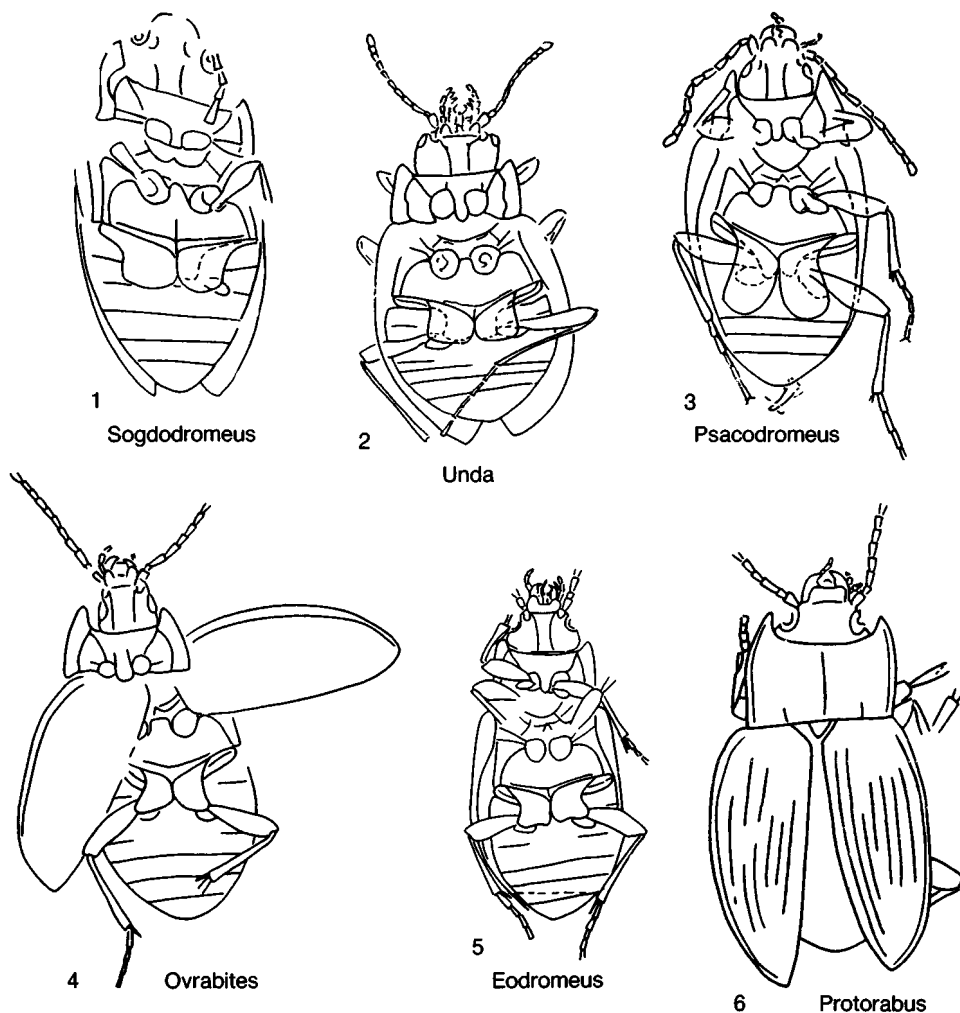


FIG. 178. Carabidae (p. 291–293).

- Kazakh; ventral view, $\times 7$ (Ponomarenko, 1977b).
- Eopaussus** Wasmann, 1926a, p. 29 [*E. balticus*; OD]. Little-known genus, apparently lacking transverse prothoracic suture; prosternal process separating fore coxae apparently present. Wasmann, 1929a; Darlington, 1950. *Oligo.*, Europe (Baltic).
- Karadromeus** Ponomarenko, 1977b, p. 62 [*K. rostratus*; OD]. Pronotum slightly narrowed anteriorly; legs not elongate. *Jur.*, USSR (Kazakh).
- Karatoma** Ponomarenko, 1977b, p. 59 [*K. agilis*; OD]. Pronotum almost rectangular; legs long. *Jur.*, USSR (Kazakh).
- Lithorabus** Ponomarenko, 1977b, p. 82 [*L. incertus*; OD]. Small, flat beetles; similar to *Cretorabus*, but posterior end of metepisternum blunt. *Jur.*, USSR (Kirghiz).
- Mesorabus** Ponomarenko, 1977b, p. 85 [*M. elongatus*; OD]. Mandibles large and protruding; both spurs of fore tibiae apical; hind margin of metathorax almost straight. *Jur.*, USSR (Kazakh).
- Neothanes** Scudder, 1890, p. 535 [*Cychnus testeus* Scudder, 1878b, p. 758; OD]. Little-known genus, possibly related to *Carabus. Eoc.*, USA (Wyoming).
- Ovrabites** Ponomarenko, 1977b, p. 76 [*O. ovalis*; OD]. Small, oval, flat beetles; prothorax transverse, but widest posteriorly, evenly narrowed anteriorly. *Jur.*, USSR (Kazakh).—FIG. 178.4. *O. ovalis*; elytra and body, ventral view, $\times 7$ (Ponomarenko, 1977b).
- Paussoides** Motschulsky, 1856, p. 26 [*P. mengei*; OD]. Similar to *Pausus* (recent), but antennae with 7 segments. Wasmann, 1926a, 1929a; Bolow, 1940; Darlington, 1950. *Oligo.*, Europe (Baltic).

Platycoxa PONOMARENKO, 1977b, p. 47 [**P. armata*; OD]. Small, flat beetles; antennae long and thick; pronotum transverse, slightly narrowed anteriorly. *Jur.*, USSR (Kirghiz, Kazakh).

Protocerapterus Wasmann, 1926a, p. 27 [**P. primigenius*; OD]. Similar to *Cerapterus* (recent), but tibiae very broad; body not as broad as in *Cerapterites*. Wasmann, 1929a; Darlington, 1950. *Oligo.*, Europe (Baltic).

Protorabus PONOMARENKO, 1977b, p. 72 [**P. planus*; OD]. Clypeus not reaching base of antennae; fore coxal cavities open; metepisternum forming part of wall of middle coxal cavities; abdomen short, its apex blunt; last abdominal sternite only slightly narrower than base of abdomen. *Jur.*, USSR (Kazakh).—FIG. 178.6. **P. planus*; dorsal view, $\times 3.5$ (Ponomarenko, 1977b).

Protoscalidion Schaufuss, 1888, p. 266 [**P. rugiae*; OD]. Similar to *Scalidion* (recent), but antennae filiform, their second segment minute; prothorax quadrate; first 4 tarsal segments bilobed. *Oligo.*, Europe (Baltic).

Psacodromeus PONOMARENKO, 1977b, p. 53 [**P. gutta*; OD]. Body streamlined, lateral outlines forming even curve from head to ends of elytra. *Jur.*, USSR (Kazakh).—FIG. 178.3. **P. gutta*; ventral view, $\times 4.5$ (Ponomarenko, 1977b).

Sinis Heer, 1862a, p. 31 [**S. brevicollis*; OD]. Little-known genus. Heer, 1862b. *Mio.*, Europe (Germany).

Sogdodromeus PONOMARENKO, 1977b, p. 46 [**S. altus*; OD]. Small, flat beetles; antennae long and thick; clypeus not reaching antennal bases; pronotum transverse, broadened anteriorly. *Trias.*, USSR (Kirghiz).—FIG. 178.1. **S. altus*; ventral view, $\times 5$ (Ponomarenko, 1977b).

Tauredon Handlirsch, 1910a, p. 23 [**T. borni*; OD]. Little-known genus. Pronotum transverse, nearly twice as wide as long, lateral edges projecting anteriorly, anterior margin with a slight median bulge. *Jur.*, Europe (Germany).

Trechinites Heer, 1862a, p. 34 [**T. clairvillei* Heer, 1862a, p. 34; SD Carpenter, herein]. Little-known genus. Heer, 1862b. *Mio.*, Europe (Germany).

Trechoides Motschulsky, 1856, p. 26 [**T. fasciatus*; OD]. Similar to *Trechus* (recent), but elytra distinctly truncate. *Oligo.*, Europe (Baltic).

Unda PONOMARENKO, 1977b, p. 49 [**U. microplata*; OD]. Antennae long and thin; pronotum transverse, narrowed anteriorly. *Cret.*, USSR (Asian RSFSR).—FIG. 178.2. *U. cursoria*; ventral view, $\times 7$ (Ponomarenko, 1977b).

Family TRIAPLIDAE

Ponomarenko, 1977

[Triaplidae Ponomarenko, 1977b, p. 17]

Large, elongate beetles. Head orthognathous or opisthognathous; antennae appar-

ently thin; fore coxae not divided; hind coxae long, dividing metanotum; abdomen with 6 visible sternites. *Trias.*

Triaplus PONOMARENKO, 1977b, p. 17 [**T. macroplatus*; OD]. Head strongly bent under pronotum; pronotum transverse; hind coxae slightly shorter than wide; body punctate. *Trias.*, USSR (Kirghiz).—FIG. 179.3. **T. macroplatus*; a, dorsal view, b, ventral view, $\times 6$ (Ponomarenko, 1977b).

Family DYTISCIDAE Leach, 1815

[Dytiscidae Leach, 1815, p. 84]

Aquatic beetles, small to large; body smooth, streamlined; head prognathous; antennae with 11 filiform segments, inserted under frontal ridge; compound eyes reniform; pronotum with explanate lateral margins; hind coxae very large; hind legs modified to varying degrees for swimming, tarsi flattened and bearing flat hairs; abdomen with 6 visible sternites. Larvae elongate, head prognathous; aquatic and predaceous. *Jur.*—*Holo.*

Dytiscus LINNÉ, 1758, p. 411. *Holo.*

Agabus LEACH, 1817, p. 72. ŘIHA, 1960. *Mio.*, Europe (Czechoslovakia)—*Holo.*

Angaragabus PONOMARENKO, 1963b, p. 128 [**A. jurassicus*; OD]. Larva with head flat; mandibles twice as long as basal width; fourth antennal segment without processes; legs lacking swimming hairs; urogomphi short; eighth abdominal segment not elongate. *Jur.*, USSR (Asian RSFSR).—FIG. 179.2. **A. jurassicus*; larva, $\times 7$ (Ponomarenko, 1963b).

Colymbetes SCHELLENBERG, 1806, p. 188. ŘIHA, 1974. *Mio.*, USSR (European RSFSR)—*Holo.*

Copelatus ERICHSON, 1832, p. 38. ŘIHA, 1974. *Mio.*, USSR (European RSFSR)—*Holo.*

Cretodytes PONOMARENKO, 1977b, p. 40 [**C. latipes*; OD]. Little-known genus. Hind tibiae much shorter than femora. [Family assignment doubtful.] *Cret.*, USSR (Kazakh).

Cybister CURTIS, 1827, p. 151. ŘIHA, 1974. *Mio.*, USSR (European and Asian RSFSR)—*Holo.*

Graphoderus DEJEAN, 1833, p. 54. ŘIHA, 1974. *Mio.*, USSR (European RSFSR)—*Holo.*

Hydroporus SCHELLENBERG, 1806, p. 182. ŘIHA, 1974. *Mio.*, USSR (European RSFSR)—*Holo.*

Methles SHARP, 1882, p. 489. ŘIHA, 1974. *Mio.*, USSR (European RSFSR)—*Holo.*

Miodytiscus WICKHAM, 1911, p. 54 [**M. hirtipes*; OD]. Similar to *Dytiscus* (recent); elytra with 9 striae, those near outer margin with fine punctation. *Oligo.*, USA (Colorado).

Palaeogyrinus SCHLECHTENDAL, 1894, p. 200 [**P.*

strigatus; OD]. Mesosternum apparently long; elytra short, not reaching end of abdomen; antennae with 11 segments. HATCH, 1927a; DARLINGTON, 1929; STATZ, 1939–1940. *Oligo.*, Europe (Germany).—FIG. 179, 1. **P. strigatus*; ventral view, $\times 10$ (Statz, 1939–1940).

Procoelambus THÉOBALD, 1937a, p. 389 [**P. macrocephalus*; OD]. Little-known genus. [Family assignment doubtful.] *Oligo.*, Europe (France). *Schistomerus* PALMER, 1957, p. 259 [**S. californense*; OD]. Larva similar to that of *Deronectes* (recent) but with distinct sternal plate on seventh abdominal segment. Adult unknown. *Mio.*, USA (California).

Family GYRINIDAE Latreille, 1810

[Gyrinidae LATREILLE, 1810, p. 141]

Aquatic beetles, mainly surface swimmers, with streamlined body; head large, prognathous; antennae with 8 segments, first 2 segments very short, remainder forming a short club; compound eyes divided, an upper pair near dorsal surface of head, the lower pair smaller and ventral; middle and hind legs modified for swimming, broad and flat. Larvae elongate, aquatic, predaceous; adults scavengers. *Jur.*—*Holo.*

Gyrinus GEOFFROY, 1762, p. 193. *Holo.*

Anagyrius HANDLIRSCH, 1906b, p. 447 [**Gyrinus atavus* HEER, 1865, p. 64; OD]. Little-known genus. HATCH, 1927a; STATZ, 1952. *Jur.*, Europe (Germany, Switzerland).

Angarogyrus PONOMARENKO, 1977b, p. 44 [**A. minimus*; OD]. Similar to *Mesodineutes*, but mesothorax longer. *Jur.*, USSR (Asian RSFSR).

Avitortor PONOMARENKO, 1977b, p. 42 [**A. primitivus*; OD]. Metathorax long and middle coxae narrow. *Cret.*, USSR (Asian RSFSR).

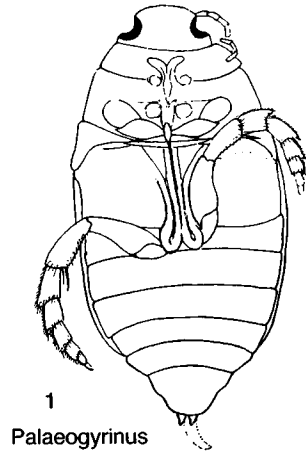
Bassogyrus PONOMARENKO, 1973b, p. 66 [**B. savilovi*; OD]. Hind coxae transverse; tibiae long. PONOMARENKO, 1977b. *Cret.*, USSR (Asian RSFSR).

Cretortor PONOMARENKO, 1973b, p. 67 [**C. zberichini*; OD]. Elytron with 9 prominent furrows and a sutural margin. PONOMARENKO, 1977b. *Cret.*, USSR (Kazakh).

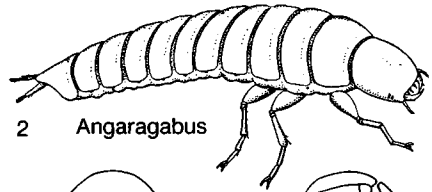
Gyrinoides MOTSCHULSKY, 1856, p. 26 [**G. limbatus*; OD]. Similar to *Gyrinus* (recent), but elytra without striae. HATCH, 1925, 1927a. *Oligo.*, Europe (Baltic).

Mesodineutes PONOMARENKO, 1977b, p. 43 [**M. amurensis*; OD]. Body smooth; hind coxae short and transverse; mesothorax wider than long; abdomen short and broad. *Cret.*, USSR (Asian RSFSR).

Mesogyrus PONOMARENKO, 1973b, p. 63 [**M. striatus*; OD]. Hind coxae short; middle and hind femora and tibiae slightly dilated apically.



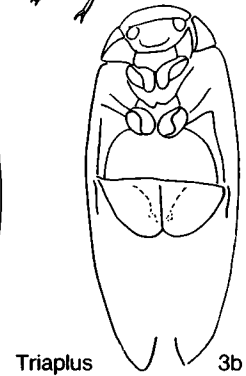
1
Palaeogyrius



2
Angaragyrius



3a



3b

FIG. 179. Triaplidae and Dytiscidae (p. 293–294).

Jur., USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).

Miodineutes HATCH, 1927a, p. 91 [**M. oeningensis*; OD]. Similar to *Enhydus* (recent), but body less broadly oval and with most elytral striae obsolete. *Mio.*, Europe (Germany).

Protogyrius HATCH, 1927a, p. 92 [**Gyrinus confinis* SCUDDER, 1900, p. 80; OD]. Similar to *Gyrinus* (recent), but elytral striae extending independently nearly to apex, present as rows of punctures. *Pleist.*, Canada (Ontario).

Family PARAHYGROBIIDAE Ponomarenko, 1977

[Parahygrobiidae PONOMARENKO, 1977b, p. 19]

Aquatic beetles, known only by larva; swimming legs; antennae with 4 segments;

mandibles strongly curved, inner margins with a small tooth; prothorax longer than other 2 thoracic segments combined; abdomen with prominent urogomphi. *Jur.*

Parahydrobia PONOMARENKO, 1977b, p. 20 [**P. natans*; OD]. Urogomphi slightly shorter than abdomen. *Jur.*, USSR (Asian RSFSR).—FIG. 180,4. **P. natans*; ventral view of larva, $\times 9$ (Ponomarenko, 1977b).

Family COPTOCLAVIDAE Ponomarenko, 1961

[Coptoclavidae PONOMARENKO, 1961, p. 68]

Medium-sized to large aquatic beetles. Adults with flat body; compound eyes divided; metepisternum not reaching middle coxae; hind coxae not widened anteriorly; middle and hind legs at least slightly modified for swimming. Larvae active swimmers; body cylindrical; urogomphi long; mandibles each with at least 1 prominent tooth; forelegs raptorial, slender, with numerous setae; middle and hind legs flattened; abdomen with 8 segments; spiracles metapneustic. PONOMARENKO, 1975b. *Jur.—Cret.*

Coptoclava PING, 1928, p. 39 [**C. longipoda*; OD]. Middle and hind tibiae and tarsi very broad. ROHDENDORF, 1962a; PONOMARENKO, 1961, 1975b. *Jur.*, USSR (Asian RSFSR); *Cret.*, China (Shandong). — FIG. 180,1. **C. longipoda*, restorations; *a, b*, adult, dorsal and ventral views, *c*, larva, all $\times 1.5$ (Ponomarenko, 1961).

Charonoscapha PONOMARENKO, 1977b, p. 32 [**C. grossa*; OD]. Large beetles with flat bodies; head transverse; middle and hind tibiae flattened; anterior margin of pronotum strongly emarginate. *Jur.*, USSR (Kazakh). — FIG. 180,2. **C. grossa*; ventral view, $\times 2.3$ (Ponomarenko, 1977b).

Charonoscaphidia PONOMARENKO, 1977b, p. 35 [**C. elongata*; OD]. Similar to *Charonoscapha*, but pronotum not markedly emarginate. *Jur.*, USSR (Kazakh).

Exedia PONOMARENKO, 1977b, p. 28 [**E. plana*; OD]. Similar to *Necronectes*, but pronotum broadened basally. *Jur.*, USSR (Kazakh).

Necronectes PONOMARENKO, 1977b, p. 22 [**N. aquaticus*; OD]. Large, elongate beetles; pronotum extending anteriorly along sides of head; hind tarsi of adults long and thin. Larvae with single tooth on cutting edge of mandibles. *Jur.*, USSR (Asian RSFSR, Kazakh, Kirghiz); *Cret.*, Algeria (Sayda).

Pseudohydrophilus DEICHMÜLLER, 1886, p. 67 [**P. longispinosus*; OD; = *Blabera avita* HEYDEN, 1847, p. 100] [= *Prodytiscus* OPPENHEIM, 1888, p. 237,

obj.]. Little-known genus, similar to *Necronectes*, with middle segments of fore tarsi not indented apically. PONOMARENKO, 1971b, 1977b. *Jur.*, Europe (Germany).

Stygeonectes PONOMARENKO, 1977b, p. 29 [**S. jurassicus*; OD]. Larvae similar to that of *Coptoclava*, but forelegs shorter. *Jur.*, USSR (Asian RSFSR).

Family LIADYTIDAE Ponomarenko, 1977

[Liadytidae PONOMARENKO, 1977b, p. 38]

Small aquatic beetles; head withdrawn into prothorax; metathorax with a longitudinal keel; hind coxae not widened anteriorly; legs slender and long; tibiae and tarsi with swimming hairs. *Jur.*

Liadytes PONOMARENKO, 1963b, p. 129 [**L. avus*; OD]. Pronotum not covering scutellum. PONOMARENKO, 1977b. *Jur.*, USSR (Asian RSFSR). — FIG. 180,3. **L. avus*; dorsal view, $\times 8$ (Ponomarenko, 1963b).

Suborder POLYPHAGA Emery, 1886

[Polyphaga EMERY, 1886, p. 655]

Prothorax without notopleural sutures; hind coxae only rarely fused to metasternum, not dividing first visible abdominal sternite; tarsal segmentation diverse; hind wing without a closed cell between veins M and CU distally; abdomen with 3 to 7 visible sternites. Larval legs with 4 segments. Adult and larvae with diverse feeding habits. *Trias.—Holo.*

Family HYDROPHILIDAE Latreille, 1802

[Hydrophilidae LATREILLE, 1802a, p. 136]

Very small to large beetles. Adults usually aquatic, with smooth, oval form; maxillary palpi at least as long as antennae, usually longer; antennal club with fine hydrofuge pubescence; scape curved; each pair of coxae close together; all tarsi with 5 segments; abdomen typically with 5 visible sternites. Adults phytophagous. Larvae campodeiform, usually aquatic, and predaceous; pupae formed in mud cells near water. *Jur.—Holo.*

Hydrophilus GEOFFROY, 1762, p. 180. *Holo.*
Creniphilites WICKHAM, 1913c, p. 8 [**C. orpheus*;

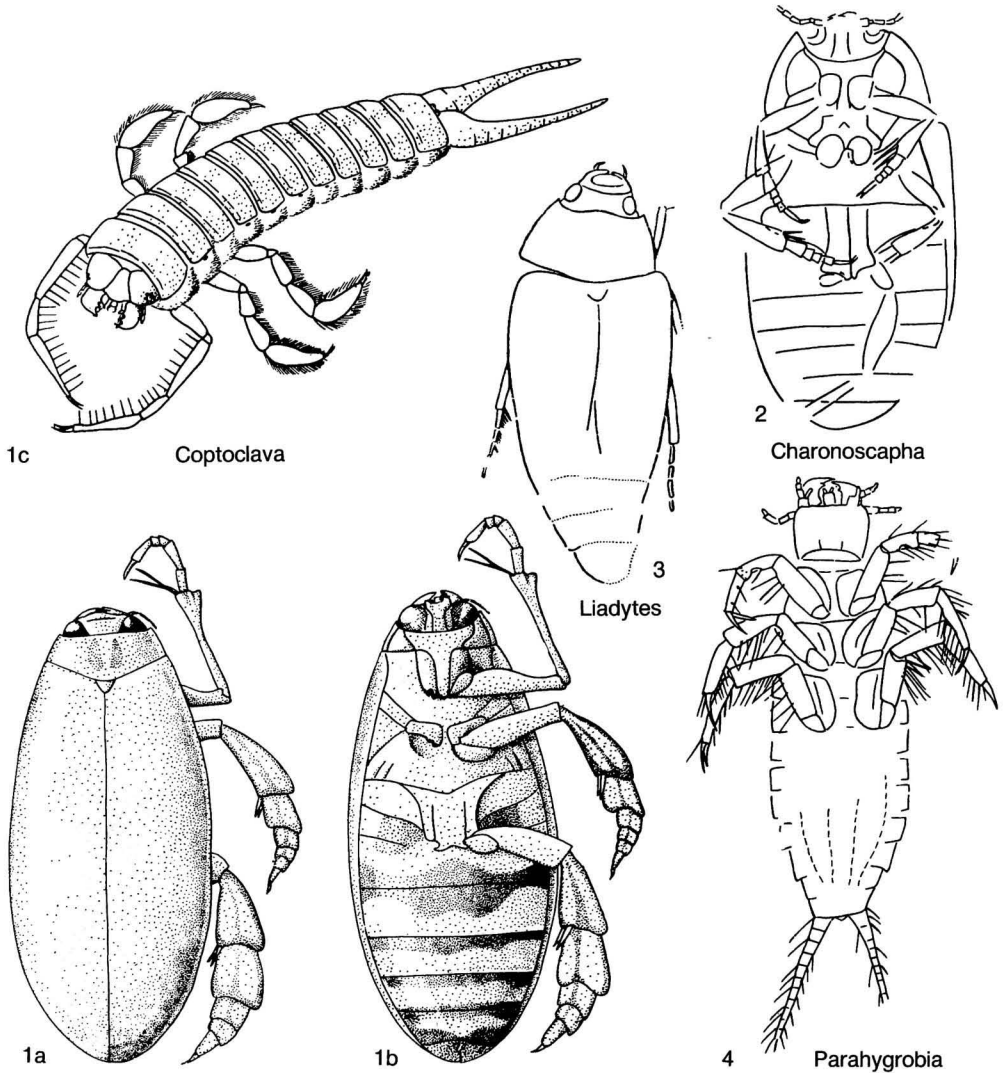


FIG. 180. Parahygrobiiidae, Coptoclavidae, and Liadytidae (p. 294–295).

OD]. Similar to *Creniphilus* (recent), but metasternum more elongate; antennal club consisting of 4 segments, first and fourth smaller than second and third. *Oligo.*, USA (Colorado).
Escheria HEER, 1847, p. 57 [**E. ovalis*; OD]. Little-known genus. HEER, 1862a; FÖRSTER, 1891. *Oligo.*–*Mio.*, Europe (Germany).
Hydrophilopsis HEER, 1862a, p. 69 [**H. elongata*; OD]. Little-known genus. OUSTALET, 1874. *Oligo.*, Europe (France); *Mio.*, Europe (Germany).
Mesochelophorus PONOMARENKO, 1977c, p. 113 [**M. sibiricus*; OD]. Similar to *Helophorus* (recent), but pronotum with straight sides and angular corners. *Cret.*, USSR (Asian RSFSR).

Mesosperchus PONOMARENKO, 1977c, p. 108 [**M. tarsalis*; OD]. Small, flat beetles; pronotum transverse; antennal scrobes on prothorax; last tarsal segment much longer than others combined. *Cret.*, USSR (Asian RSFSR). — FIG. 181. **M. tarsalis*; *a*, dorsal and *b*, ventral views, ×12 (Ponomarenko, 1977c).

Mesydra PONOMARENKO, 1977c, p. 111 [**M. elongata*; OD]. Small, elongate beetles; antennae with a short, 3-segmented club; abdomen with 6 visible sternites; legs short. *Cret.*, USSR (Asian RSFSR).

Paraspercheus PONOMARENKO, 1977c, p. 114 [**P. asiaticus*; OD]. Large, flat beetles, with 5 visible

abdominal segments; integument coarsely punctate. *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).

Family SCYDMAENIDAE Leach, 1815

[Scydmaenidae LEACH, 1815, p. 92]

Small beetles; body generally with heavy pubescence; marked constriction between thorax and abdomen; penultimate segment of maxillary palpi much larger than terminal segment; elytra usually entire; all tarsi with 5 segments; basal 4 abdominal tergites membranous. Adults and larvae carnivorous, occurring in leaf mold, moss, and other damp places. *Oligo.*—*Holo.*

Scydmaenus LATREILLE, 1802, p. 116. *Holo.*

Clidicus LAPORTE, 1833, p. 396. SCHAUFUSS, 1896.

Oligo., Europe (Baltic)—*Holo.*

Cryptodiodon SCHAUFUSS, 1890c, p. 564 [**C. corticaroides*; OD]. Antennae straight, with 11 segments and with a club distally; prothorax subquadrate; third segment of maxillary palpi short and oval, fourth short and awl-shaped; hind coxae flattened. *Oligo.*, Europe (Baltic).

Cyrtoscydmus MOTSCHULSKY, 1869, p. 260.

SCHAUFUSS, 1890c. *Oligo.*, Europe (Baltic)—*Holo.*

Electrosydmaenus SCHAUFUSS, 1890c, p. 584 [**E. pterostichoides*; OD]. Similar to *Heuretus*, but coalesced third and fourth segments of maxillary palpi much shorter and drop-shaped; prothorax subcordate, margined laterally. *Oligo.*, Europe (Baltic).

Euconnus THOMSON, 1859, p. 87. FIORI, 1932. *Mio.*, Europe (Sicily)—*Holo.*

Hetereuthia SCHAUFUSS, 1890c, p. 579 [**H. elegans*; OD]. Similar to *Palaeomastigus*, but coalesced third and fourth segments of maxillary palpi forming an oval club. *Oligo.*, Europe (Baltic).

Heuretus SCHAUFUSS, 1890c, p. 583 [**H. coriaceus*; OD]. Similar to *Palaeothia*, but coalesced third and fourth segments of maxillary palpi forming a long, cylindrical club. *Oligo.*, Europe (Baltic).

Palaeomastigus SCHAUFUSS, 1890c, p. 575 [**P. helmi*; OD]. Related to *Clidicus* (recent). Antennae geniculate, with 11 segments; third and fourth segments of maxillary palpi coalesced, forming a wedge-shaped club; elytra striate; tarsi with first segment elongate. *Oligo.*, Europe (Baltic).

Palaeothia SCHAUFUSS, 1890c, p. 581 [**P. tenuitarsis*; OD]. Antennae straight, terminating in a club; third and fourth segments of maxillary palpi forming a short, oval club; prothorax margined laterally; elytra short. *Oligo.*, Europe (Baltic).

Scydmaenoides MOTSCHULSKY, 1856, p. 27 [**S.*



Mesosperchus

FIG. 181. Hydrophilidae (p. 296).

nigrescens; OD]. Similar to *Scydmaenus* (recent), but antennae with a club composed of 4 segments. *Oligo.*, Europe (Baltic).

Semnodioceras SCHAUFUSS, 1890c, p. 573 [**S. balticaeforme*; OD]. Similar to *Cryptodiodon*, but hind coxae elevated; fourth segment of maxillary palpi oval and pointed. *Oligo.*, Europe (Baltic).

Family PTILIIDAE Heer, 1843

[Ptiliidae HEER, 1843, p. 60]

Minute beetles, body and elytra pubescent. Antennae with 11 segments, the 3 distal ones forming a weak club; each antennal segment with a whorl of long setae; fore coxae globular, contiguous; all tarsi with 3 segments, the 2 basal ones very small; elytra usually entire but commonly truncate; hind wing very narrow, with fringe of long hairs; abdomen with 6 or 7 visible sternites. Larvae

elongate, with well-developed thoracic legs; adults and larvae apparently fungivorous, usually occurring in decaying vegetation or dung. *Oligo.*—*Holo.*

- Ptilium* GYLLENHAL, 1827, p. 292. *Holo.*
Microptilium MATTHEWS, 1872, p. 107. DYBAS, 1961. *Oligo.*, Europe (Baltic)—*Holo.*
Ptinella MOTSCHULSKY, 1844, p. 820. PARSONS, 1939. *Oligo.*, Europe (Baltic)—*Holo.*

Family SILPHIDAE Latreille, 1807

[Silphidae LATREILLE, 1807, p. 1]

Beetles of small to moderate size, body usually flattened; antennae with 10 or 11 segments, terminal 3 to 4 segments forming a pubescent club; pronotum large, transverse, lateral borders margined; elytra usually entire; all tarsi with 5 segments; abdomen with 5 to 6 visible sternites. Larvae campodeiform. Adults and larvae carrion feeders. *Jur.*—*Holo.*

- Silpha* LINNÉ, 1758, p. 359. *Holo.*
Eosilphites HAUPT, 1950, p. 53 [**E. decoratus*; OD]. Little-known genus; pronotum transverse, with curved lateral margins. [Family assignment doubtful.] *Eoc.*, Europe (Germany).
Mesecanus NEWTON, 1982, p. 335, *nom. subst. pro Mesagyrtes* PONOMARENKO, 1977c, p. 117, *non* BROUN, 1895 [**Mesagyrtes communis* PONOMARENKO, 1977c, p. 117; OD]. Antennae with weakly formed club; elytra with punctate grooves. *Jur.*, USSR (Asian RSFSR).
Miosilpha WICKHAM, 1912a, p. 9 [**M. necrophiloides*; OD]. Similar to *Silpha* (recent), but middle coxae contiguous or at least closely approximate. *Oligo.*, USA (Colorado).
Palaeosilpha FLACH, 1890, p. 107 [**P. fraasii*; OD]. Similar to *Ptomascopus* (recent), but thorax emarginate laterally. *Oligo.*, Europe (Baltic).
Ptomaphagus ILLIGER, 1798, p. 84. SCHLECHTENDAL, 1888. *Oligo.*, Europe (Baltic)—*Holo.*
Ptomascopus KRAATZ, 1877, p. 102. FLACH, 1890. *Oligo.*, Europe (France)—*Holo.*

Family STAPHYLINIDAE Latreille, 1802

[Staphylinidae LATREILLE, 1802a, p. 124]

Small to large beetles, with long body and very short elytra; antennae usually with 11 segments, ordinarily filiform or moniliform; exposed abdominal tergites heavily sclerotized; hind wings usually well developed; 6 or 7 abdominal sternites visible. Adults usu-

ally feeding on carrion or decaying vegetation. Larvae campodeiform and usually carrion feeders, though some are predaceous. *Jur.*—*Holo.*

- Staphylinus* LINNÉ, 1758, p. 421. *Holo.*
Abolescus TIKHOMIROVA, 1968, p. 139 [**A. glabratus*; OD]. Similar to *Piestus* (recent), but elytron longer and abdomen narrowed distally. *Jur.*, USSR (Kazakh).
Abscondus TIKHOMIROVA, 1968, p. 151 [**A. regularis*; OD]. Similar to *Mesotachinus* but with lateral margins of pronotum curved ventrally, and with longer antennae. *Jur.*, USSR (Kazakh).
Aleocharopsis WICKHAM, 1913b, p. 286 [**A. caseyi*; OD]. Similar to *Maseochara* (recent) but with shorter antennae; pronotum with long setae. *Oligo.*, USA (Colorado).
Archodromus TIKHOMIROVA, 1968, p. 143 [**A. comptus*; OD]. Similar to *Porrbodromus*, but head larger, broader behind middle, and not markedly narrowed posteriorly; elytra with parallel sides. *Jur.*, USSR (Kazakh).
Bembicidiodes SCHAUFUSS, 1888, p. 267 [**B. inaequicollis*; OD]. Similar to *Holisus* (recent), but head shorter. *Oligo.*, Europe (Baltic).
Globoides TIKHOMIROVA, 1968, p. 144 [**G. oculatus*; OD]. Similar to *Porrbodromus*, but head strongly transverse; pronotum with rounded corners. *Jur.*, USSR (Kazakh).
Laasbium SCUDDER, 1900, p. 49 [**L. agasizi* SCUDDER, 1900, p. 49; SD CARPENTER, herein]. Little-known genus, resembling *Lathrobium* (recent), but head broadly sessile upon thorax. *Oligo.*, USA (Colorado).
Lathrobium GRAVENHORST, 1802, p. 53. ABDULLAH, 1968. *Oligo.*, Europe (Baltic)—*Holo.*
Lithoplanes SCUDDER, 1886a, p. 81, *nom. subst. pro Erinnyis* OUSTALET, 1874, p. 145, *non* SHRANK, 1801 [**Erinnyis elongata* OUSTALET, 1874, p. 145; SD CARPENTER, herein]. Little-known genus. [Family position doubtful.] *Oligo.*, Europe (France).
Mesotachinus TIKHOMIROVA, 1968, p. 148 [**M. major*; OD]. Similar to *Tachinus* (recent), but hind margin of sixth visible abdominal sternite without indentations and teeth. *Jur.*, USSR (Kazakh).
Mesozytelus TIKHOMIROVA, 1968, p. 146 [**T. parvus*; OD]. Very similar to *Oxytelus* (recent), but elytra longer and tibiae without spines. *Jur.*, USSR (Kazakh).
Micropeplus LATREILLE, 1809, p. 377. MATTHEWS, 1970. *Plio.*, USA (Alaska)—*Holo.*
Miolithocharis WICKHAM, 1913b, p. 289 [**M. lithographicus*; OD]. Similar to *Lithocharis* (recent) but with more rounded head and lack of long setae on posterior margin of head. *Oligo.*, USA (Colorado).
Oxypoda MANNERHEIM, 1831, p. 483. SEEVERS, 1971. *Oligo.* (*Mio.*, Mexico (Chiapas)—*Holo.*

- Palaeopsenius** SEEVERS, 1971, p. 78 [**P. mexicanus*; OD]. Similar to *Termitopsenius* (recent) and *Neocapritermes* (recent) but without pronotal and elytral setae; pronotal sculpturing reticulate; maxillary palpi long. *Mio.*, Mexico (Chiapas).
- Paracyptus** SEEVERS, 1971, p. 82 [**P. minutissima*; OD]. Similar to *Anacyptus* (recent), but antennae with 11 segments; mandibles long and hook-shaped. *Mio.*, Mexico (Chiapas).
- Porrhodromus** ТИХОМИРОВА, 1968, p. 141 [**P. communis*; OD]. Similar to *Porrhodites* (recent) but with the second antennal segment shorter. *Jur.*, USSR (Kazakh).
- Protractus** HEER, 1847, p. 28 [**P. erichsoni*; OD]. Little-known genus. [Family assignment uncertain.] *Mio.*, Europe (Germany).
- Protostaphylinus** LIN, 1976, p. 114 [**P. mirus*; OD]. Little-known genus. *Jur.*, China (Liaoning).
- Pseudolesteva** SCHAUFUSS, 1890b, p. 69 [**P. insinuans*; OD]. Similar to *Lesteva* (recent) but smaller; penultimate antennal segment lenticular, the last segment thick. *Oligo.*, Europe (Baltic).
- Seniaulus** HEYDEN & HEYDEN, 1866, p. 137 [**S. scaphioides*; OD]. Little-known genus. [Family position doubtful.] *Oligo.*, Europe (Germany).
- Subcelytrinus** ТИХОМИРОВА, 1968, p. 153 [**S. antiquus*; OD]. Apparently related to *Staphylinus* (recent) but with deep sculpturing on elytra. *Jur.*, USSR (Kazakh).
- Tachyporoidea** ТИХОМИРОВА, 1968, p. 150 [**T. villosus*; OD]. Similar to *Mesotachinus*, but elytra shorter and with a dense hair cover. *Jur.*, USSR (Kazakh).
- Trigites** HANDLIRSCH, 1907, p. 731, *nom. subst. pro Triga* SCUDDER, 1900, p. 78, *non* FAUVAL, 1878 [**Triga coeni* SCUDDER, 1900, p. 78; OD]. Little-known genus. *Oligo.*, USA (Colorado).
- Tunicopterus** ТИХОМИРОВА, 1968, p. 153 [**T. sigara*; OD]. Similar to *Staphylinus*, but elytra with broadly rounded posterolateral corners, inner margins being much longer than lateral margins. *Jur.*, USSR (Kazakh).

Family PSELAPHIDAE Latreille, 1802

[Pselaphidae LATREILLE, 1802a, p. 239]

Small beetles, with very short elytra; body relatively short, abdomen oval and stout; antennae usually with 11 segments; maxillary palpi diversely developed. Adults and larvae mostly carnivorous, occurring in decaying vegetation, under bark, and even in nests of ants and termites. *Oligo.*—*Holo.*

Pselaphus HERBST, 1792, p. 106. *Holo.*

Barybryaxis SCHAUFUSS, 1890a, p. 121 [**B. lata*; OD]. Similar to *Bryaxis* (recent), but maxillary palpi smaller; antennae with 11 segments, filiform, barely clavate. *Oligo.*, Europe (Baltic).

Batrissus AUBÉ, 1833, p. 45. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Bryaxis KUGELANN, 1794, p. 580. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Bythinus LEACH, 1817, p. 80. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Ctenistodes SCHAUFUSS, 1890a, p. 142 [**C. claviger*; OD]. Similar to *Ctenistes* (recent). Maxillary palpi with second segment elongate, clavate, its base petiolate; antennae with segments 3 to 8 very small, segments 9 to 11 elongate. *Oligo.*, Europe (Baltic).

Cymbalizon SCHAUFUSS, 1890a, p. 138 [**C. tyroides*; OD]. Little-known genus. Antennae geniculate, with 11 segments; maxillary palpi with third segment very slender, slightly clavate. *Oligo.*, Europe (Baltic).

Dantiscanus SCHAUFUSS, 1890a, p. 143 [**D. castalis*; OD]. Resembling *Aphodea* (recent), but maxillary palpi lacking stalked penultimate segment; hind coxae not globose. *Oligo.*, Europe (Baltic).

Deuterotyrrus SCHAUFUSS, 1890a, p. 131 [**D. redivivus*; OD]. Similar to *Tyrrus* (recent); maxillary palpi with 3 distinct segments, the first elongate, curved, and slightly enlarged distally. *Oligo.*, Europe (Baltic).

Euplectus LEACH, 1817, p. 80. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Eupsinoides MOTSCHULSKY, 1856, p. 26 [**E. glabrellus*; OD]. Similar to *Eupsinus* (recent); antennal club composed of 6 distal segments. *Oligo.*, Europe (Baltic)—*Holo.*

Faronus AUBÉ, 1844, p. 157. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Greys SCHAUFUSS, 1890a, p. 113 [**G. conciliator*; OD]. Similar to *Goniacerus* (recent), but antennae not geniculate and elytra ecarinate. *Oligo.*, Europe (Baltic).

Hagnometopias SCHAUFUSS, 1890a, p. 134 [**H. pater*; OD]. Similar to *Metopias* (recent); maxillary palpus elongate, its second segment long, third broadly oval; antennae with 11 segments, geniculate. *Oligo.*, Europe (Baltic).

Heteroeuplectus SCHAUFUSS, 1890a, p. 156 [**H. retrorsus*; OD]. Similar to *Euplectus* (recent), but pronotum smooth; first segment of maxillary palpus slender; antennae with 11 segments. *Oligo.*, Europe (Baltic).

Monyx SCHAUFUSS, 1890a, p. 129 [**M. spiculatus*; OD]. Little-known genus. Maxillary palpus with last segment conical; antennae with 11 segments. *Oligo.*, Europe (Baltic).

Nugaculus SCHAUFUSS, 1890a, p. 148 [**M. calcitrans*; OD]. Similar to *Faronus* (recent), but antennal club composed of 3 segments; angles of pronotum very prominent. *Oligo.*, Europe (Baltic).

Nugator SCHAUFUSS, 1890a, p. 149 [**N. stricticollis*; OD]. Similar to *Nugaculus*, but thorax cordate dorsally, not angular. *Oligo.*, Europe (Baltic).

Pammiges SCHAUFUSS, 1890a, p. 144 [**P. spectrum*; OD]. Little-known genus. Antennae with 11 segments, slightly clavate; second segment of maxillary palpus elongate, third and fourth transverse. *Oligo.*, Europe (Baltic).

Pantobatriscus SCHAUFUSS, 1890a, p. 145 [**P. censor*; OD]. Little-known genus. Body elongate, cylindrical; antennae inserted in lateral fossae and with 11 segments. FLACH, 1890. *Oligo.*, Europe (Baltic).

Tmesiphoroides MOTSCHULSKY, 1856, p. 26 [**T. cariniger*; OD]. Similar to *Tmesiphorus* (recent), but antennae with club composed of 3 very large segments, other segments strongly serrate. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic).

Tychus LEACH, 1817, p. 81. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Tyrus AUBÉ, 1833, p. 15. SCHAUFUSS, 1890a. *Oligo.*, Europe (Baltic)—*Holo.*

Family LUCANIDAE Latreille, 1806

[Lucanidae LATREILLE, 1806, p. 241]

Medium-sized to large beetles, with conspicuously lamellate antennal clubs, the lamellae thick; head small but mandibles often large, with marked sexual dimorphism; scutellum conspicuous; abdomen with 5 visible sternites. Larvae developing in decaying wood. *Oligo.*—*Holo.*

Lucanus SCOPOLI, 1763, p. 1. *Holo.*

Ceruchites STATZ, 1952, p. 5 [**C. habnei*; OD]. Little-known genus, similar to *Ceruchus* (recent). *Oligo.*, Europe (Germany).

Dorcasoides MOTSCHULSKY, 1856, p. 27 [**D. bilobus*; OD]. Similar to *Dorcas* (recent), but head strongly bilobed. SCUDDER, 1885b. *Oligo.*, Europe (Baltic).

Paleognathus WAGA, 1883, p. 191 [**P. succini*; OD]. Similar to *Lamprima* (recent) and *Sphenognathus* (recent) but with antennae, mandibles, and legs less modified. HANDLIRSCH, 1908b, 1920. *Oligo.*, Europe (Baltic).—FIG. 182, 1. **P. succini*; dorsal view, $\times 1.4$ (Waga, 1883).

Family ACANTHOCNEMIDAE Crowson, 1964

[Acanthocnemidae CROWSON, 1964, p. 317]

Antennae with a club of 3 segments; prothorax with large pits on edges of sternopleuron; claws simple; tibiae with short, stout spines. *Cret.*—*Holo.*

Acanthocnemus PERRIS, 1866, p. 187. *Holo.*

Acanthocnemoides ZHERIKHIN, 1977a, p. 135 [**A. sukatshevae*; OD]. Body flat; antennal segments

4 through 8 elongate. *Cret.*, USSR (Asian RSFSR).—FIG. 182, 6. **A. sukatshevae*; a, dorsal and b, ventral views, $\times 25$ (Zherikhin, 1977a).

Family PASSALIDAE Leach, 1815

[Passalidae LEACH, 1815, p. 100]

Body flat, sides parallel; head prognathous; antennae with 10 segments, the last 3 free but forming a loose club; mandibles large, toothed, blunt; pronotum much broader than head; elytra with well-developed longitudinal striae; abdomen with 5 visible sternites. Larvae active; first 2 pairs of legs long, hind pair much reduced and forming a stridulatory structure. Adults and larvae in decaying logs and stumps. *Oligo.*—*Holo.*

Passalus FABRICIUS 1792, p. 240. REYES-CASTILLO, 1977. *Oligo.*, USA (Oregon)—*Holo.*

Family SCARABAEIDAE Latreille, 1802

[Scarabaeidae LATREILLE, 1802a, p. 144]

Medium-sized to large beetles. Antennae with a lamellate club, lamellae very thin; mandibles small and thin, adapted for feeding on soft or liquid food; head and pronotum often showing sexual dimorphism; abdomen usually with 6 visible sternites. Larvae usually in soil, feeding on plant roots, decaying vegetation, or dung. *Jur.*—*Holo.*

Scarabaeus LINNÉ, 1758, p. 345. *Holo.*

Anomalites FRITZSCH, 1884b, p. 163 [**A. fugitivus*; OD]. Little-known genus. *Paleoc.*—*Plio.*, Europe (Germany).

Ateuchites MEUNIER, 1898c, p. 114 [**A. grandis*; OD]. Little-known genus. *Oligo.*, Europe (France).

Geotrupoides HANDLIRSCH, 1906b, p. 545 [**Geotrupes lithographicus* DEICHMÜLLER, 1886, p. 69; OD]. Little-known genus. Flat beetles; labrum and mandibles projecting far beyond clypeus; pronotum transverse, sides curved; elytra with punctate grooves. PONOMARENKO, 1977c. *Jur.*, Europe (Germany); *Cret.*, USSR (Asian RSFSR).

Heliocopris HOPE, 1837, p. 23. FUJIYAMA, 1968b. *Mio.*, Japan—*Holo.*

Holcoribeus NIKRITIN, 1977, p. 127 [**H. vittatus*; OD]. Little-known genus. Mandibles projecting well beyond clypeus; hind tibiae with terminal spurs. [Family assignment doubtful.] *Cret.*, USSR

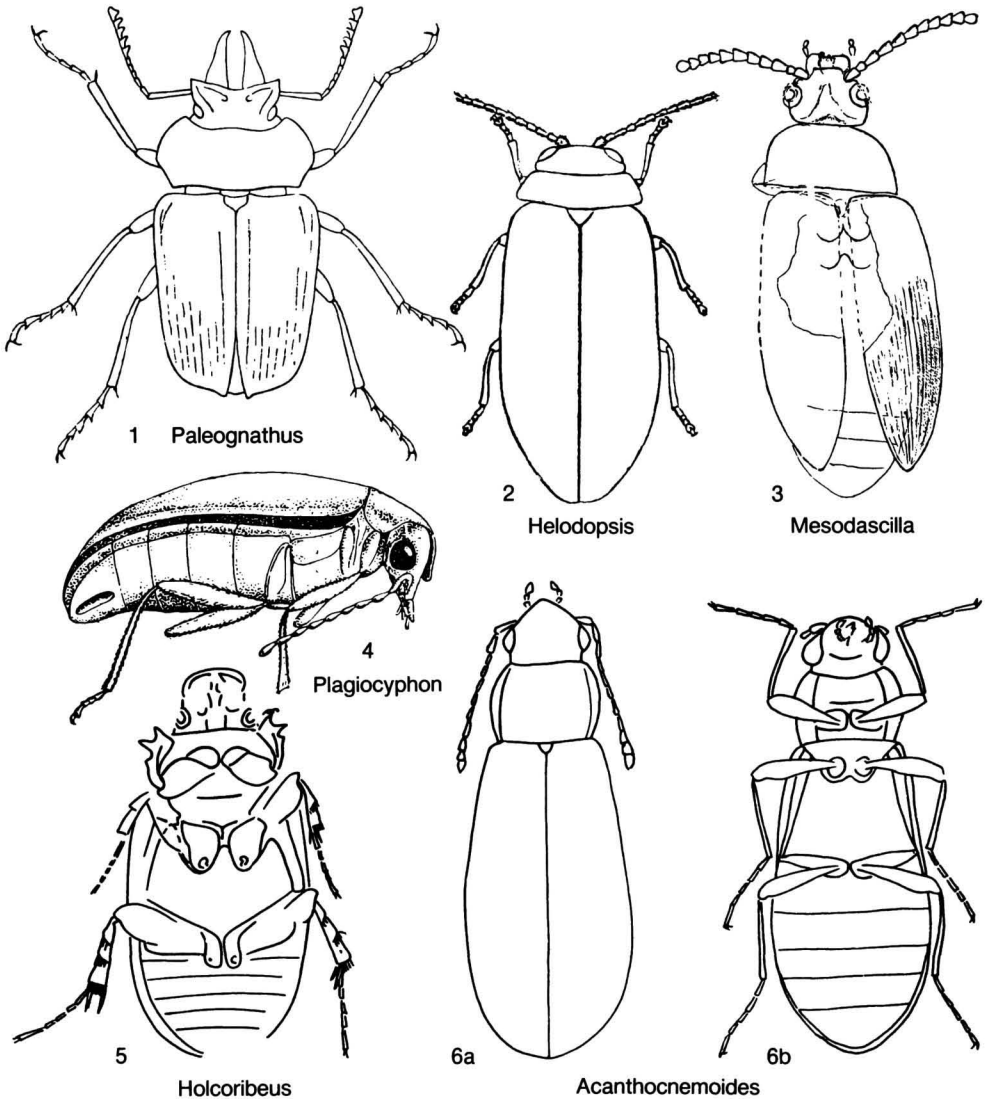


FIG. 182. Lucanidae, Acanthocnemidae, Scarabaeidae, Helodidae, and Dascillidae (p. 300–302).

(Asian RSFSR). — FIG. 182, 5. **H. vittatus*; ventral view, $\times 4.5$ (Nikritin, 1977).

Miolachnosterna WICKHAM, 1914a, p. 458 [**M. tristoides*; OD]. Similar to *Lachnosterna* (recent), but hind tarsi with simple claws. *Oligo.*, USA (Colorado).

Pelidnortes COCKERELL, 1920b, p. 462 [**P. atavus*; OD]. Little-known genus, apparently related to *Pelidonta* (recent). STRAND, 1936. *Eoc.*, England.

Proteroscarabeus GRABAU, 1923, p. 175 [**P. yeni*; OD]. Little-known genus, apparently related to *Geotrupes* (recent). PONOMARENKO, 1977c. *Cret.*, China (Shandong), USSR (Asian RSFSR).

Family HELODIDAE Le Conte, 1861

[Helodidae LE CONTE, 1861 in LE CONTE, 1861–1862, p. 179]

Small, convex beetles, with slender, fili-form antennae consisting of 11 segments; pronotum very broad and short; fore coxal cavities opening posteriorly; all tarsi with 5 segments, only fourth bilobed. Adults occurring in damp places. Larvae aquatic, cam-podeiform, with multisegmented antennae and rectal tracheal gills. *Oligo.*—*Holo.*

Helodes LATREILLE, 1796, p. 44. KLAUSNITZER, 1976. *Oligo.*, Europe (Baltic)—*Holo.*

Brachelodes IABLOKOV-KHNZORIAN, 1961c, p. 109 [**B. motschulskyi*; OD]. Similar to *Microcara* (recent) but with shorter tarsal claws, broader tarsal segments, and without femoral grooves. *Oligo.*, Europe (Baltic).

Cyphon PAYKULL, 1799, p. 117. IABLOKOV-KHNZORIAN, 1961a. *Oligo.*, Europe (Baltic)—*Holo.*

Cyphonogenius IABLOKOV-KHNZORIAN, 1961c, p. 112 [**C. zakhratkini*; OD]. Similar to *Helodopsis*, but fore coxae contiguous. *Oligo.*, Europe (Baltic).

Helodopsis IABLOKOV-KHNZORIAN, 1961c, p. 110 [**H. solskyi*; OD]. Head weakly indented ventrally and not completely recessed within prothorax; fore coxae separated. *Oligo.*, Europe (Baltic). —FIG. 182,2. **H. solskyi*; dorsal view, $\times 15$ (Iablokov-Khnzorian, 1961c).

Miocyphon WICKHAM, 1914a, p. 436 [**M. punctulatus*; OD]. Little-known genus. *Oligo.*, USA (Colorado).

Plagiocyphon IABLOKOV-KHNZORIAN, 1961c, p. 113 [**P. plavilshchikovi*; OD]. Similar to *Cyphon* (recent), but fore coxae contiguous; body broad. *Oligo.*, Europe (Baltic). —FIG. 182,4. **P. plavilshchikovi*; lateral view, $\times 23$ (Iablokov-Khnzorian, 1961c).

Family DASCILLIDAE Guérin-Méneville, 1823

[Dascillidae GUÉRIN-MÉNEVILLE, 1823, p. 121]

Similar to Helodidae, but body more slender and elongate; antennae slightly serrate; all tarsi with 5 segments, second, third, and fourth bilobed. Adults on foliage near water; larvae in soil. *Jur.*—*Holo.*

Dascillus LATREILLE, 1796, p. 43. *Holo.*

Mesodascilla MARTYNOV, 1926a, p. 9 [**M. jacobsoni*; OD]. Similar to *Dascilla* (recent); elytra long, convex, densely clothed with short hairs, indistinctly striped. *Jur.*, USSR (Kazakh). —FIG. 182,3. **M. jacobsoni*; dorsal view, $\times 7$ (Martynov, 1926a).

Protacnaeus WICKHAM, 1914a, p. 435 [**P. tenuicornis*; OD]. Little-known genus; head large; antennae filiform; fore coxae contiguous. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Family PTILODACTYLIDAE Le Conte, 1861

[Ptilodactylidae LE CONTE, 1861 IN LE CONTE, 1861–1862, p. 179]

Small beetles, body covered with fine pubescence; antennae long and pectinate; hind margin of pronotum crenulate; all tarsi with

5 segments; abdomen with 5 visible sternites. Adults on vegetation, near water. Larvae aquatic, with prominent setae and tufts of tracheal gills on several abdominal segments. *Oligo.*—*Holo.*

Ptilodactyla ILLIGER, 1807, p. 342. *Holo.*

Ptilodactyloides MOTSCHULSKY, 1856, p. 26 [**P. stipulicornis*; OD]. Similar to *Ptilodactyla*, but antennae longer than body and with a vertical process on each of its segments. *Oligo.*, Europe (Baltic).

Family DRYOPIDAE Erichson, 1848

[Dryopidae ERICHSON, 1848, p. 509]

Elongate-oval beetles; body usually covered with water-repelling hairs; head retracted into prothorax; antennae short, pectinate, with 6 terminal segments forming a loose, laminate club; fore coxae transverse; pronotum larger than head; all tarsi with 5 segments. Adults and larvae mostly aquatic, a few terrestrial. *Eoc.*—*Holo.*

Dryops OLIVIER, 1791, p. 297. *Holo.*

Lutrochites WICKHAM, 1912a, p. 16 [**L. lecontei*; OD]. Little-known genus, perhaps similar to *Lutrochus* (recent), but head with strong, longitudinal striations. *Oligo.*, USA (Colorado).

Palaeorhohelmis BOLLOWS, 1940, p. 117 [**P. samlandica*; OD]. Similar to *Lathelmis* (recent), but body more slender. *Oligo.*, Europe (Baltic).

Potamophilites HAUPT, 1956, p. 49 [**P. angustifrons*; OD]. Little-known genus. *Eoc.*, Europe (Germany).

Family ARTEMATOPIDAE Lacordaire, 1857

[Artematopidae LACORDAIRE, 1857, p. 260]

Small beetles; antennae moniliform or filiform, rarely pectinate; fore coxae transverse or projecting slightly, with cavities open posteriorly; apex of elytra with a tongue-shaped lobe ventrally; tarsal segments 3 and 4 with membranous lobes ventrally; empodia absent or small. Adults and larvae apparently occurring under lichens. *Oligo.*—*Holo.*

Artematopus PERTY, 1832, p. 115. *Holo.*

Electricrus CROWSON, 1973, p. 231 [**E. oligocenicus*; OD]. Similar to *Ctesibius* (recent), but pronotum with deep, oblique impressions near hind angles; labrum small, exposed. *Oligo.*, Europe (Baltic).

Protartematopus CROWSON, 1973, p. 233 [**P. elec-*

tricus; OD]. Similar to *Carcinognathus* (recent), but mandibles not prominent and antennae somewhat moniliform, not serrate. SLEEPER, 1969. *Oligo.*, Europe (Baltic).

Family ELECTRAPATIDAE Iablokov-Khnzorian, 1962

[Electrapatidae IABLOKOV-KHNZORIAN, 1962, p. 87]

Apparently related to Arrematopidae. All coxae flat, elongate; second through fourth tarsi bilobed; abdomen with 6 visible sternites. *Oligo.*

Electrapate IABLOKOV-KHNZORIAN, 1962, p. 87 [**E. martynovi*; OD]. All tibiae flattened. *Oligo.*, Europe (Baltic).

Family BUPRESTIDAE Leach, 1815

[Buprestidae LEACH, 1815, p. 85]

Small to large species, usually elongate and heavily sclerotized. Head hypognathous, retracted into prothorax; antennae usually serrate, with 11 segments; pronotum slightly broader than head; elytra usually strongly striate; fore coxal cavities open posteriorly; abdomen with 5 visible sternites, the basal 2 being fused. Adults on foliage. Larvae apodous, with soft bodies and with prothorax very broad and usually flattened; mostly wood borers. *Trias.—Holo.*

Buprestis LINNÉ, 1758, p. 408. *Holo.*

Archelater CARPENTER, herein [**A. major* PONGRÁČZ, 1935, p. 549; OD]. Little-known genus (elytron only). [Family assignment doubtful. The original generic name, *Archelater*, was a *nomen nudum* (PONGRÁČZ, 1935).] *Eoc.*, Europe (Germany).

Brachyspathus WICKHAM, 1917, p. 466 [**B. curiosus*; OD]. Little-known genus. Prosternal process spatulate and emarginate; prothorax and head with rough punctations. *Oligo.*, USA (Colorado).

Chlorodema HAUPT, 1950, p. 70 [**Iridotaenia primordialis* PONGRÁČZ, 1935, p. 559; OD]. Little-known genus, possibly related to *Evides* (recent). OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Eoanthaxites HAUPT, 1950, p. 66 [**Coroebus carniolicus* PONGRÁČZ, 1935, p. 565; OD]. Little-known genus. HAUPT, 1956; OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Eochalophora HAUPT, 1950, p. 94 [**E. abbreviata*; OD]. Little-known genus, possibly related to *Gyascutus* (recent). *Eoc.*, Europe (Germany).

Eolampetis PONGRÁČZ, 1935, p. 561 [**E. weigelti*; OD]. Little-known genus, based mainly on elytron. HAUPT, 1950; OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Fuesslinia HEER, 1847, p. 123 [**F. amoena*; OD]. Little-known genus. [Family assignment doubtful.] *Mio.*, Europe (Germany).

Glaphyroptera HEER, 1852, p. 13 [**G. insignis*; SD HANDLIRSCH, 1906b, p. 452]. Little-known genus. [Family assignment doubtful.] *Jur.*, Europe (Switzerland).

Mesostigmodera ETHERIDGE & OLLIFF, 1890, p. 9 [**M. typica*; OD]. Little-known genus apparently related to *Stigmodera* (recent). TILLYARD & DUNSTAN, 1916; HAUPT, 1950. *Trias.*, Australia (Queensland).

Microjulodis HAUPT, 1950, p. 64 [**M. auratus*; OD]. Little-known genus, possibly related to *Sponsor* (recent). OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Protogenia HEER, 1847, p. 118 [**P. escheri*; OD]. Little-known genus. *Mio.*, Europe (Germany).

Rhabdoglyptus HAUPT, 1950, p. 74 [**R. viridistriatus*; OD]. Little-known genus, possibly related to *Evides* (recent). OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Stizonotus HAUPT, 1950, p. 77 [**Ancylocheira acroptera* PONGRÁČZ, 1935, p. 556; OD]. Little-known genus, possibly related to *Psiloptera* (recent). HAUPT, 1956; OBENBERGER, 1957. *Eoc.*, Europe (Germany).

Taenionotus HAUPT, 1950, p. 84 [**T. fasciatus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).

Family PRAELATERIIDAE Dolin, 1973

[Praelateriidae DOLIN, 1973, p. 78]

Body elongate, shaped as in the Elateridae; head short; pronotum with well-developed but relatively broad projections on posterior corners; mesoepisterna exceptionally narrow; elytron with 9 rows of pits. *Jur.*

Praelaterium DOLIN, 1973, p. 78 [**P. prolematicum*; OD]. Head very small; pronotum broadest at middle. *Jur.*, USSR (Kirghiz).

Elaterocoleus DOLIN, 1973, p. 79 [**E. oculatus*; OD]. Similar to *Praelaterium*, but head much broader; pronotum broadest posteriorly, narrowed anteriorly. *Jur.*, USSR (Kirghiz).

Family ELATERIDAE Leach, 1815

[Elateridae LEACH, 1815, p. 85]

Small to large, elongate beetles, body usually slightly flattened. Antennae usually serrate, less commonly filiform or pectinate; pronotum large with a pronotal process fitting into a cavity (click mechanism) on mesosternum; hind angles of pronotum acute

and projecting posteriorly; fore coxal cavities open posteriorly; all tarsi with 5 segments; abdomen with 5 visible sternites. Adults on foliage; larvae mainly phytophagous on roots, some carnivorous. *Jur.*—*Holo.*

Elater LINNÉ, 1758, p. 404. *Holo.*

Abrotus DOLIN, 1980, p. 62 [**A. sepultus*; OD].

Similar to *Hypnomorphus*, but prothorax bell-shaped, much narrower anteriorly, and indented before posterior corners; antennae filiform, first segment well developed. *Jur.*, USSR (Kazakh).

Adiagnostus DOLIN, 1980, p. 44 [**A. cardiophorinus*; OD].

Body narrow, elongate; antennae filiform, segments homonomous; pronotum narrow; scutellum narrow, cordate; hind coxal plates very broad. *Jur.*, USSR (Kazakh).

Adocetus SCUDDER, 1900, p. 97 [**A. buprestoides*; OD].

Little-known genus, apparently related to *Scaptolenus* (recent) but with apical segments of antennae less enlarged. *Eoc.*, USA (Wyoming).

Ageratus DOLIN, 1980, p. 72 [**A. ponomarenkoi*; OD].

Similar to *Composferus*, but prothorax longer than broad; antennal segments elongate, nearly filiform. *Jur.*, USSR (Kazakh).

Agriotes ESCHSCHOLTZ, 1829, p. 34. BECKER, 1963.

Oligo./Mio., Mexico (Chiapas)—*Holo.*

Alaodima DOLIN, 1980, p. 74 [**A. grandis*; OD].

Similar to *Cryptocardius*, but prothorax shorter, wider than long. *Jur.*, USSR (Kazakh).

Archeonus DOLIN, 1980, p. 20 [**A. abbreviatus*; OD].

Related to *Protagrypnus*, but elytra short. *Jur.*, USSR (Kazakh).

Codemus DOLIN, 1980, p. 35 [**C. synaptoides*; OD].

Similar to *Adiagnostus*, but scutellum suboval. *Jur.*, USSR (Kazakh).

Composferus DOLIN, 1980, p. 71 [**C. priscus*; OD].

Anterior corners of prothorax extending anteriorly; femoral plates of hind coxae wide. *Jur.*, USSR (Kazakh).

Crioraphes IABLOKOV-KHNZORIAN, 1961a, p. 93 [**C. robdendorphi*; OD].

Similar to *Paracardiophorus* (recent) but with propleura extending further medially. *Oligo.*, Europe (Baltic).

Cryptagriotes WICKHAM, 1916a, p. 512 [**C. minisculus*; OD].

Similar to *Cryptobypnus* (recent), but prosternum short and with a small subtruncate lobe. *Oligo.*, USA (colorado).

Cryptocardius DOLIN, 1980, p. 74 [**C. mirabilis*; OD].

Antennae short, nearly filiform, first 5 segments elongate, the rest shorter; first segment longest and thickest. *Jur.*, USSR (Kazakh).

Desmatus DOLIN, 1975, p. 60 [**D. lapidarius*; OD].

Similar to *Protagrypnus*, but femoral plates of hind coxae much larger and triangular. DOLIN, 1980. *Jur.*, USSR (Kazakh).

Diaraphes IABLOKOV-KHNZORIAN, 1961a, p. 89 [**D. kozhantshikovi*; OD].

Similar to *Elastrus* (recent),

but first tarsal segment longer. *Oligo.*, Europe (Baltic).

Elateridium TILLYARD, 1918b, p. 751, *nom. subst.*

pro Elaterites TILLYARD in TILLYARD & DUNSTAN, 1916, p. 41, *non* HEER, 1847 [**Elaterites wianamitensis*; OD]. Little-known genus; elytron elongate-oval, apparently without sculpturing. MARTYNOVA, 1954. *Jur.*, Australia (New South Wales).

Elaterophanes HANDLIRSCH, 1906b, p. 436 [**Elater*

socius GIEBEL, 1856, p. 91; SD CARPENTER, herein]. Little-known genus, apparently related to *Protagrypnus*. COCKERELL, 1915; HAUPT, 1956; DOLIN, 1973. *Jur.*, England.

Elatron IABLOKOV-KHNZORIAN, 1961a, p. 90 [**E. semenovi*; OD].

Similar to *Elater*, but hairs on pronotum directed forward. *Oligo.*, Europe (Baltic).

Eopyrophorus HAUPT, 1950, p. 101 [**E. mixtus*; OD].

Little-known genus, apparently similar to *Pyrophorus* (recent). HAUPT, 1956. *Eoc.*, Europe (Germany).

Ganestrius DOLIN, 1976, p. 69 [**G. stibicki*; OD].

Similar to *Protoquasimus*, but prothorax not wider than long; elytra with thin, long furrows. DOLIN, 1980. *Jur.*, USSR (Kazakh).

Glyphonyx CANDÈZE, 1863, p. 451. BECKER, 1963.

Oligo./Mio., Mexico (Chiapas)—*Holo.*

Graciolacón DOLIN, 1980, p. 61 [**G. aeternus*; OD].

Similar to *Idiomorphus*, but body more elongate; femoral plates of hind coxae transverse, triangular, and narrowed anteriorly. *Jur.*, USSR (Kazakh).

Holopeurus IABLOKOV-KHNZORIAN, 1961a, p. 86

[**H. succineus*; OD]. Little-known genus. Antennae serrate beyond third segment; pronotum with lateral margins entire. *Oligo.*, Europe (Baltic).

Hypnomorphoides DOLIN, 1980, p. 54 [**H. catachtonius*; OD].

Prothorax transverse; middle part of pronotum strongly broadened anteriorly; body short, oval. *Jur.*, USSR (Kazakh).

Hypnomorphus DOLIN, 1975, p. 54 [**H. robdendorfi*; OD].

Similar to *Protagrypnus*, but prosternal sutures closed; pronotum with parallel, longitudinal furrows. DOLIN, 1980. *Jur.*, USSR (Kazakh).

Idiomerus DOLIN, 1980, p. 47 [**I. inflatus*; OD].

Pronotum with curved lateral margins and very short posterior projections. *Jur.*, USSR (Kazakh).

Idiomorphus DOLIN, 1980, p. 60 [**I. singularis*; OD].

Prothorax transverse, with strongly convex lateral margins and sharp, diverging, posterolateral projections. *Jur.*, USSR (Kazakh).

Lapidiconides DOLIN, 1980, p. 43 [**L. excellens*; OD].

Similar to *Hypnomorphus*, but prothorax narrowed anteriorly and femoral plates of hind coxa slender. *Jur.*, USSR (Kazakh).

Lapidostenus DOLIN, 1980, p. 30 [**L. infossus*;

- OD]. Similar to *Hypnomorphus*, but fourth and fifth antennal segments the largest. *Jur.*, USSR (Kazakh).
- Lithocoelus** DOLIN, 1975, p. 53 [**L. detrusus*; OD]. Prosternum divided into 3 sclerites by longitudinal grooves; mesosternum divided by transverse suture into pre- and post-episternum; femoral plates of hind coxae short; prothorax prominent and transverse. DOLIN, 1980. *Jur.*, USSR (Kazakh).
- Litholacon** DOLIN, 1980, p. 67 [**L. derumpens*; OD]. Body elongate-oval; prothorax transverse, fore corners not projecting anteriorly; distal antennal segment widened. *Jur.*, USSR (Kazakh).
- Lithomerus** DOLIN, 1980, p. 23 [**L. cockerelli*; OD]. Similar to *Lithocoelus*, but prosternal sutures entirely open. *Jur.*, USSR (Kazakh).
- Lithoptychus** DOLIN, 1980, p. 57 [**L. handlirschi*; OD]. Similar to *Idiomorus* but with longer metanotum; pronotum weakly narrowed anteriorly, sides almost straight; body slender. *Jur.*, USSR (Kazakh).
- Lithosomus** DOLIN, 1980, p. 46 [**L. erosus*; OD]. Middle coxal cavities closed; posterior pronotal projections unusually strong. *Jur.*, USSR (Kazakh).
- Ludiophanes** WICKHAM, 1916a, 522 [**L. hayden*; OD]. Similar to *Megapenthes* (recent), but coxal plates narrow, with little distal dilation; punctuation of pronotum close and deep. *Oligo.*, USA (Colorado).
- Micragrypnites** DOLIN, 1973, p. 76 [**G. issykiensis*; OD]. Similar to *Protagrypnus*, but pronotum almost square, its posterior corners only slightly extended. *Jur.*, USSR (Kirghiz).
- Mionelater** BECKER, 1963, p. 125 [**M. planatus*; OD]. Similar to *Horistonotus* (recent), but frons strongly margined, pronotum emarginate basally, and last segment of maxillary palpus acutely pointed. *Oligo./Mio.*, Mexico (Chiapas).
- Necrocelus** DOLIN, 1980, p. 58 [**N. aselloides*; OD]. Similar to *Idiomorphus* but with posterolateral projections of pronotum more strongly developed; hind coxae short. *Jur.*, USSR (Kazakh).
- Negastrioides** DOLIN, 1980, p. 52 [**N. tenuis*; OD]. Similar to *Hypnomorphus*, but antennae serrate, long; middle coxal cavities closed by articulation of meso- and metathorax. *Jur.*, USSR (Kazakh).
- Orthoraphes** IABLOKOV-KHNZORIAN, 1961a, p. 86 [**O. reichardti*; OD]. Similar to *Ischnodes* (recent), but third antennal segment simple; metathorax without oblique suture. *Oligo.*, Europe (Baltic).
- Paragrypnites** DOLIN, 1980, p. 22 [**P. jagemanni*; OD]. Similar to *Lithocoelus* but with short pronotum. *Jur.*, USSR (Kazakh).
- Parahypnomorphus** DOLIN, 1980, p. 33 [**P. jurasicus*; OD]. Similar to *Hypnomorphus*; antennal segments nearly homonomous, but second segment slightly broadened. *Jur.*, USSR (Kazakh).
- Plagiographes** IABLOKOV-KHNZORIAN, 1961a, p. 84 [**P. fasciatus*; OD]. Similar to *Alaeotypus* (recent), but frons flat, without indentations; first antennal segment short and straight; first segment of hind tarsus short. *Oligo.*, Europe (Baltic).
- Platyelata** DOLIN, 1980, p. 40 [**P. reflexicollis*; OD]. Femoral plates of hind coxae strongly developed along entire width of coxae. *Jur.*, USSR (Kazakh).
- Plesiorhaphes** DOLIN, 1980, p. 65 [**P. scabei*; OD]. Similar to *Desmatus*, but distal antennal segment not broadened. *Jur.*, USSR (Kazakh).
- Protagrypnus** DOLIN, 1973, p. 75 [**P. exoletus*; OD]. Small species, with slender, convex body; head strongly transverse; mesosternum divided by a suture; pronotum broadly conical, narrowed anteriorly, its posterior corners extended as narrow projections. *Jur.*, USSR (Kirghiz).
- Protocardiophorus** DOLIN, 1976, p. 71 [**P. ancestralis*; OD]. Prothorax strongly transverse, broadened basally; mid-coxae oval. DOLIN, 1980. *Jur.*, USSR (Kazakh).
- Protoquasimus** DOLIN, 1976, p. 69 [**P. brevicollis*; OD]. Similar to *Quasimus* (recent), but prothorax short, about twice as wide as long; elytra with long furrows. DOLIN, 1980. *Jur.*, USSR (Kazakh).
- Pseudocardiophorites** DOLIN, 1976, p. 73 [**P. fragilis*; OD]. Prothorax about as long as wide, not broadened basally; middle coxae nearly circular. DOLIN, 1980. *Jur.*, USSR (Kazakh).
- Sinoelaterium** PING, 1928, p. 22 [**S. melanovolor*; OD]. Little-known genus. Head triangular; antennae serrate; elytra narrow. [Family assignment doubtful.] *Cret.*, China (Liaoning).
- Tetraraphes** IABLOKOV-KHNZORIAN, 1961a, p. 95 [**T. ebersini*; OD]. Little-known genus. Elytra without furrows or pitted rows, but covered with dense hairs; lateral border of pronotum entire. *Oligo.*, Europe (Baltic).

Family EUCNEMIDAE Latreille, 1824

[Eucnemidae LATREILLE, 1824, p. 426]

Elongate beetles of moderate size, resembling the Elateridae. Head strongly deflexed, resting on prosternum; labrum absent; prosternum without median lobe; antennae with 11 segments, moniliform, filiform, or serrate; all tarsi with 5 slender segments; abdomen with 5 visible sternites. Larvae slender, subcylindrical, apparently predaceous, occurring with adults under bark in wood infested with borers. *Eoc.—Holo.*

Eucnemis AHRENS, 1812, p. 38. *Holo.*

Potergites BRITTON, 1960, p. 34 [**P. senectus*; OD].

Related to *Epipleurus* (recent); lateral margins of pronotum broadly rounded, posterior angles acute; scutellum transverse, quadrate; elytra with 9 longitudinal striae. *Eoc.*, England.

Family CEROPHYTIDAE

Latreille, 1834

[Cerophytidae LATREILLE, 1834, p. 119]

Small beetles, body elongate and slightly depressed; antennae with 11 segments, pectinate or serrate; labrum short, concealed; pronotum transverse; hind coxae transverse; femoral plate absent; hind trochanters very long, all tarsi with 5 segments. Adults and larvae in rotting wood. *Cret.*—*Holo.*

Cerophytum LATREILLE, 1809, p. 375. *Holo.*

Aphytocerus ZHERIKHIN, 1977a, p. 131 [**A. communis*; OD]. Antennae of male weakly serrate; first segment very large; head withdrawn into prothorax, almost invisible from above. *Cret.*, USSR (Asian RSFSR).

Family CANTHARIDAE

Latreille, 1802

[Cantharidae LATREILLE, 1802a, p. 185]

Elongate beetles of small to moderate size; body weakly sclerotized, with fine though dense pubescence; antennae filiform, typically with 11 segments; pronotum oval or nearly quadrate and flat; fourth tarsal segment bilobed. Adults omnivorous feeders, commonly found on flowers and foliage; larvae campodeiform, mostly predaceous. *Oligo.*—*Holo.*

Cantharis LINNÉ, 1758, p. 400. *Holo.*

Cacomorphocerus SCHAUFUSS, 1892, p. 58 [**C. cerambyx*; OD]. Apparently related to *Dysmorphocerus* (recent). Antennae long, with 12 segments, first segment elongate, cylindrical, second very short, third very large; elytra elongate. KORSCHESKY, 1939. *Oligo.*, Europe (Baltic).

Family LYCIDAE Castelnau, 1840

[Lycidae CASTELNAU, 1840, p. 261]

Elongate beetles of moderate size; body soft; head partly concealed from above by pronotum; antennae long, thick, usually serrate, with 11 segments; pronotum broader than head; elytra very long and slender, usu-

ally broadened distally; all tarsi with 5 segments; abdomen with 7 or 8 visible sternites. Larvae elongate, usually occurring under bark; adults and larvae predaceous. *Oligo.*—*Holo.*

Lycus FABRICIUS, 1787, p. 163. *Holo.*

Miocaenia WICKHAM, 1914a, p. 443 [**M. pectinicornis*; OD]. Similar to *Caeniella* (recent) but with antennae pectinate distally. *Oligo.*, USA (Colorado).

Pseudoplatopterus KLEINE, 1940, p. 179 [**P. scheelei*; OD]. Similar to *Dictyopterus* (recent), but elytra with 8 distinct ridges, those in basal half strong, with distinct sculpturing between them. *Oligo.*, Europe (Baltic).

Family TRIXAGIDAE Seidlitz, 1888

[Trixagidae SEIDLITZ, 1888, p. xlv]

Small, oval beetles, with fine pubescence; head retracted into pronotum; antennae with 11 segments, serrate or with last 3 segments forming weak club; pronotum transverse, narrowed anteriorly, posterior angles projecting; all tarsi with 5 segments; prothorax fused with metathorax. Adults on flowers; larvae in decaying vegetation. *Oligo.*—*Holo.*

Trixagus KUGELANN, 1794, p. 534. *Holo.*

Palaeothroscus IABLOKOV-KHNZORIAN, 1962, p. 83 [**P. sosnovskiyi*; OD]. Antennal pits large; furrows of metathorax reaching only to its center; lateral margins of hind coxae parallel basally; antennae clubbed. *Oligo.*, Europe (Baltic).

Throscites IABLOKOV-KHNZORIAN, 1962, p. 84 [**T. tschitscherini*; OD]. Furrows of metathorax reaching its apical margin; hind corners of pronotum with sharp projections. *Oligo.*, Europe (Baltic).

Throscogenius IABLOKOV-KHNZORIAN, 1962, p. 81 [**T. takhtajani*; OD]. Prothorax without antennal grooves; antennae with 11 thick segments, the first very long, the second very short; elytra without rows of pits or furrows. *Oligo.*, Europe (Baltic).

Family MELYRIDAE Leach, 1815

[Melyridae LEACH, 1815, p. 87]

Small beetles, with slender, flattened bodies; antennae with 11 or 12 segments; pronotum quadrate; fore coxae prominent, almost contiguous; all tarsi with 5 segments; abdomen with 5 or 6 visible sternites. Larvae elongate, subcylindrical. Adults and larvae usually carnivorous. *Oligo.*—*Holo.*

Melyris FABRICIUS, 1775, p. 58. *Holo.*

Eudasytites WICKHAM, 1912a, p. 19 [collective group]. Dasytine species, with slender body and coarse sculpturing. *Oligo.*, USA (Colorado).

Family DERMESTIDAE Latreille, 1807

[Dermestidae LATREILLE, 1807, p. 3]

Small, ovoid species; body usually with dense covering of fine hairs; antennae with 5 to 11 segments, having loose club of 3 to 8 segments; pronotum narrowed anteriorly; hind coxae usually grooved to receive femora; all tarsi with 5 segments. Adults commonly on flowers. Larvae subcylindrical, with dense cover of long setae; mostly scavengers, commonly feeding on dried animal tissue. *Oligo.*—*Holo.*

Dermestes LINNÉ, 1758, p. 354. *Holo.*

Cryptorhopalum GUÉRIN-MÉNEVILLE, 1838, p. 42. BEAL, 1972. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Micryptorhopalum PIERCE, 1960, p. 46 [**M. kirkbyae*; OD]. Little-known genus (larva only); apparently related to *Cryptorhopalum*. *Mio.*, USA (California).

Family ANOBIIDAE Westwood, 1838

[Anobiidae WESTWOOD, 1838, p. 44]

Small ovoid species, body covered with fine setae; head strongly deflexed; antennae with 9 to 11 segments, 3 terminal segments long; fore coxal cavities open posteriorly; hind coxae with concavity for femora; all tarsi with 5 segments; abdomen with 5 visible sternites. Adults commonly occurring in wooded regions. Larvae with curved body, anterior and posterior portions larger than central region; phytophagous, on dried wood. *Eoc.*—*Holo.*

Anobium FABRICIUS, 1775, p. 62. *Holo.*

Eucrada LE CONTE, 1861, p. 202 [= *Crichtonia* ABDULLAH & ABDULLAH, 1967, p. 23 (type, *C. macheani*)]. WHITE, 1969. *Oligo.*, Europe (Baltic)—*Holo.*

Gastrallanobium WICKHAM, 1914b, p. 261 [**G. subconfusum*; OD]. Similar to *Gastrallus* (recent); prothorax strongly projecting over head with side margins less oblique than in *Gastrallus* (recent). *Oligo.*, USA (Colorado).

Stichtoptychus FALL, 1905, p. 258. SPILMAN, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Venablesia BRITTON, 1960, p. 31 [**V. colluvium*; OD]. Similar to *Stagetus* (recent), but pronotum

with a shallow emargination at junction of lateral and posterior margins. *Eoc.*, England.

Xyletinites HEYDEN & HEYDEN, 1866, p. 142 [**X. tumbicolus*; OD]. Little-known genus. [Family assignment uncertain.] *Oligo.*, Europe (Germany).

Family BOSTRYCHIDAE Latreille, 1802

[Bostrychidae LATREILLE, 1802a, p. 202]

Cylindrical species, with heavy sclerotization. Head small, deflexed, not visible from above; antennae with 8 to 10 segments, having a loose club of 3 to 4 segments; fore coxae projecting, the cavities opening posteriorly; hind coxae with concavity for femora; elytra usually having apical spines; all tarsi with 5 segments. Adults commonly found in wooded areas; larvae curved, with head small; all wood boring. *Oligo.*—*Holo.*

Bostrychus GEOFFROY, 1762, p. 301. *Holo.*

Protapate WICKHAM, 1912a, p. 20 [**P. contorta*; OD]. Similar to *Apatides* (recent), but eyes from above much larger; prothorax without recurved processes. *Oligo.*, USA (Colorado).

Family TROGOSSITIDAE Latreille, 1802

[Trogossitidae LATREILLE, 1802a, p. 159]

Ovoid beetles, small to moderate-sized. Head prognathous; antennae with 10 or 11 segments, including a club of 1 to 3 segments; fore coxae transverse; all tarsi with 5 segments, first segment much shorter than second; abdomen with 5 visible segments. Adults and larvae occurring under bark, in fungi growing on wood, and in stored vegetable products. *Jur.*—*Holo.*

Trogossita OLIVIER, 1790, no. 19. *Holo.*

Lithostoma MARTYNOV, 1926a, p. 13 [**L. expansum*; OD]. Similar to *Ostoma* (recent), but without a distinct antennal club. *Jur.*, USSR (Kazakh).

Family CLERIDAE Klug, 1842

[Cleridae KLUG, 1842 in KLUG, 1840–1842, p. 259]

Body elongate, convex; head strongly deflexed; antennae with 8 to 11 segments and diverse in form but usually clubbed or capitate; pronotum not broader than head; femora slightly swollen; tarsi with 5 segments; abdomen with 5 or 6 visible sternites.

Larvae elongate; head usually prognathous; antennae with 3 segments. Adults and larvae predaceous, usually occurring under bark, in tunnels in wood, or on foliage. *Oligo.*—*Holo.*

Clerus GEOFFROY, 1762, p. 303. *Holo.*

Orthrius GORHAM, 1876, p. 74. MENIER, 1983. *Oligo.*, Europe (Baltic)—*Holo.*

Family NITIDULIDAE Latreille, 1802

[Nitidulidae LATREILLE, 1802a, p. 131]

Small, flat species; head prognathous; antennae with 11 segments, the last 3 forming a large club; pronotum strongly transverse; fore coxal cavities closed posteriorly; tarsi usually with 5 segments, the 3 basal segments usually broad; abdomen with 5 visible sternites. Adults and larvae omnivorous, feeding mostly on vegetable products, pollen, and fungi. *Jur.*—*Holo.*

Nitidula FABRICIUS, 1775, p. 77. *Holo.*

Cychramites WICKHAM, 1913c, p. 14 [**C. birtus*; OD]. Similar to *Cychramus* (recent), but scutellum smaller; terminal segment of abdomen closely punctate dorsally. *Oligo.*, USA (Colorado).

Epanurea SCUDDER, 1900, p. 86 [**E. ingenita*; OD]. Related to *Epuraea* (recent), but head larger and antennae shorter than width of body; antennae with 10 segments beyond scape, the first 5 segments forming short, slender stem for the club. SCUDDER, 1893a. *Oligo.*, USA (Colorado).

Meligethiella MEDVEDEV, 1969, p. 119 [**M. soroniformis*; OD]. Related to *Nitidula* (recent), but with oblique grooves along sides of metathorax; antennae with a conspicuous club consisting of 3 segments. *Cret.*, USSR (Asian RSFSR).

Miophenolia WICKHAM, 1916b, p. 7 [**M. cilipes*; OD]. Similar to *Phenolia* (recent), but legs stouter; middle tibiae strongly curved along posterior margins. *Oligo.*, USA (Colorado).

Nitidulina MARTYNOV, 1926a, p. 15 [**N. eclavata*; OD]. Similar to *Nitidula* (recent), but antennal club weakly formed. *Jur.*, USSR (Kazakh).

Omositoidea SCHAUFUSS, 1892, p. 55 [**O. gigantea*; OD]. Little-known genus, apparently related to *Omosita* (recent). KORSCHESKY, 1939. *Oligo.*, Europe (Baltic).

Procarpophilus DE JONG, 1953, p. 44 [**P. macgillavryi*; OD]. Similar to *Carpophilus* (recent) but with relatively longer elytra and more attenuate scutellum; lateral margins of pronotum apparently entire. *Paleoc.*—*Plio.*, Sumatra.

Family CUCUJIDAE Latreille, 1802

[Cucujidae LATREILLE, 1802a, p. 210]

Moderate-sized to small beetles, with prognathous head and very flat body; anten-

nae with 11 segments, filiform or nearly moniliform, inserted near base of mandibles; all tarsi usually with 5 segments, rarely with 4 on some pairs of legs; pronotum margined, often serrate; abdomen with 5 visible sternites. Adults and larvae with diverse feeding habits, occurring under bark, in decaying vegetation, or in dried cereals. *Oligo.*—*Holo.*

Cucujus FABRICIUS, 1775, p. 204. *Holo.*

Lithocoryne SCUDDER, 1900, p. 83 [**L. gravis*; OD]. Similar to *Lathropus* (recent), but head narrower; antennae about as long as head and half of thorax combined, first segment large and stout, segments 9 to 11 forming a distinct club. *Oligo.*, USA (Colorado).

Family CRYPTOPHAGIDAE Erichson, 1848

[Cryptophagidae ERICHSON, 1848, p. 341]

Very small beetles. Head prognathous; antennae moniliform, with 11 segments, the 3 terminal ones forming a conspicuous club; fore coxae globular, coxal cavities open posteriorly; tarsi with 5 segments. Adults and larvae mainly fungivorous, occurring in such diverse environments as flowering plants, stored food products, and nests of social insects. *Cret.*—*Holo.*

Cryptophagus HERBST, 1792, p. 172. *Holo.*

Nganasania ZHERIKHIN, 1977a, p. 138 [**N. rheticca*; OD]. Similar to *Ootypus* (recent), but body with conspicuous hair covering. *Cret.*, USSR (Asian RSFSR).

Family ENDOMYCHIDAE Leach, 1815

[Endomychidae LEACH, 1815, p. 116]

Beetles of moderate size and convex form. Antennae with conspicuous club composed of 3 terminal segments; head recessed into cavity of pronotum; fore coxal cavities open posteriorly; all tarsi with 4 segments, third very small, concealed in second; 5 visible abdominal sternites. Larvae and adults fungivorous, occurring in dung, under bark, or in decaying vegetation. *Oligo.*—*Holo.*

Endomychus PANZER, 1795, p. 175. *Holo.*

Phymaphoroides MOTSCHULSKY, 1856, p. 27 [**P. antennatus*; OD]. Similar to *Phymaphorus* (recent), but ninth antennal segment abruptly enlarged. *Oligo.*—*Europe* (Baltic).

Family LATHRIDIIDAE
Redtenbacher, 1845

[Lathridiidae REDTENBACHER, 1845, p. 123]

Very small beetles. Antennae with 8 to 11 segments, last 2 or 3 forming club; pronotum commonly narrower than combined width of elytra at base; elytra commonly coarsely ribbed; all tarsi commonly with 3 simple segments; abdomen with 5 or 6 visible sternites. Adults and larvae fungivorous, living in vegetable debris. *Cret.—Holo.*

Lathridius [BECK], 1817, p. 14, *nom. subst. pro Latridius* HERBST, 1793, p. 3. *Holo.*

Succinimontia ZHERIKHIN, 1977a, p. 140 [**S. inflata*; OD]. Similar to *Corticarkna* (recent), but elytra without distinct hair cover; 5 visible abdominal sternites. *Cret.*, USSR (Asian RSFSR).

Family MYCETOPHAGIDAE
Leach, 1815

[Mycetophagidae LEACH, 1815, p. 110]

Small, oval beetles, with pubescent body; antennae with 11 segments and with a club of 2 or 3 segments; fore coxae with cavities open posteriorly; fore tarsi with 3 (males) or 4 segments; mid- and hind tarsi with 4 segments; abdomen with 5 visible sternites. Adults and larvae fungivorous. *Oligo.—Holo.*

Mycetophagus HELLWIG, 1792, p. 394. *Holo.*

Crowsonium ABDULLAH, 1964, p. 334 [**C. succinum*; OD]. Antennal club with 3 segments, the last tapering; eyes entire; lateral margins of pronotum and elytra bordered by spinelike hairs; elytral punctures arranged in at least 10 long rows. *Oligo.*, Europe (Baltic).

Family CIRCAEIDAE
Iablokov-Khnzorian, 1961

[Circaeidae IABLOKOV-KHNZORIAN, 1961b, p. 209]

Related to Mycetophagidae. All tarsi with 4 segments; first 3 segments of fore tarsi transverse and nearly identical; first segment of middle tarsi very long, third bilobed; first segment of hind tarsi much larger than other 3 segments combined, second bilobed, third very small. *Oligo.*

Circaeus IABLOKOV-KHNZORIAN, 1961b, p. 209 [**I. borisjaki*; OD]. Antennae with 11 segments, with 5 distal segments forming a club; first 4 club segments transverse, and fifth large and long. *Oligo.*, Europe (Baltic).

Family COLYDIIDAE Erichson, 1848

[Colydiidae ERICHSON, 1848, p. 251]

Small to medium-sized beetles; body cylindrical or flattened, with coarse sculpturing or ridges; antennae with a short club formed by 2 or 3 terminal segments; fore coxal cavities closed posteriorly; all tarsi with 4 segments. Adults mostly phytophagous or fungivorous; larvae little known, but some ectoparasites on other Coleoptera. *Oligo.—Holo.*

Colydium FABRICIUS, 1792, p. 495. *Holo.*

Rhagoderidea WICKHAM, 1914a, p. 430 [**R. striata*; OD]. Similar to *Rhagodera* (recent), but side margins of pronotum entire or nearly so; elytral striae weak. *Oligo.*, Europe (Colorado).

Family TENEBRIONIDAE
Latreille, 1802

[Tenebrionidae LATREILLE, 1802a, p. 165]

Small to large beetles, with body form diverse but strongly sclerotized, the head prognathous; antennae stout, usually moniliform but rarely clubbed; fore coxal cavities closed posteriorly; elytra entire, often curving over sides of abdomen; fore and middle tarsi with 5 segments, hind pair with 4 segments; claws simple; abdomen with 5 visible sternites, the 3 basal segments fused. Adults commonly on ground, under bark, or in rotting wood. Larvae elongate and strongly sclerotized, with short legs. Adults and larvae mainly scavengers. *Trias.—Holo.*

Tenebrio LINNÉ, 1758, p. 417. *Holo.*

Anthracohelops HAUPT, 1950, p. 128 [**A. gigas*; OD]. Little-known genus. [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Miostenosis WICKHAM, 1913b, p. 297 [**M. lacordairei*; OD]. Similar to *Stenosis* (recent), but anterior and middle coxae closely approximate; hind coxae meeting on median line. *Oligo.*, Europe (Colorado).

Proteleates WICKHAM, 1914b, p. 267 [**P. centralis*; OD]. Similar to *Eleates* (recent), but fore coxae round; third and fourth ventral segments of abdomen short, their combined lengths not longer than second. *Oligo.*, USA (Colorado).

Protoplaticera WICKHAM, 1914a, p. 484 [**P. laticornis*; OD]. Little-known genus. Antennae with basal 2 or 3 segments slender, the rest broad and flat. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Pyrochalcaspis HAUPT, 1950, p. 115 [**P. giselta-*

lensis; OD]. Little-known genus. [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Tenebrionites COCKERELL, 1920d, p. 67 [collective group]. Isolated elytra resembling those of tenebrionids. COCKERELL, 1925f, 1927e. *Eoc.*, England; *Oligo.*, USA (Colorado); *Paleoc.-Plio.*, Argentina (Jujuy).

Ulomites TILLYARD in TILLYARD & DUNSTAN, 1916, p. 22 [**U. willcoxi*; OD]. Elytron similar to that of *Uloa* (recent). [Family assignment doubtful.] DUNSTAN, 1923. *Trias.*, Australia (Queensland).

Family SALPINGIDAE Leach, 1815

[Salpingidae LEACH, 1815, p. 106]

Small, elongate beetles, sides nearly parallel; head prognathous; antennae filiform, with 11 segments; pronotum quadrate, not margined laterally; fore coxal cavities open posteriorly; fore and middle tarsi with 5 segments, hind tarsi with 4 segments; abdomen with 5 visible sternites. Adults and larvae occurring under bark. *Oligo.-Holo.*

Salpingus ILLIGER, 1812, p. 301. *Holo.*

Neopolypria ABDULLAH, 1964, p. 336 [**N. nigra*; OD]. Similar to *Polypria* (recent). Antennae slightly serrate; eyes large, hairy, slightly emarginate near antennal insertion; pronotum slightly wider than long, coarsely punctate toward lateral margins. *Oligo.*, Europe (Baltic).

Family PYTHIDAE Mulsant, 1856

[Pythidae MULSANT, 1856, p. 26]

Elongate beetles of moderate size; head prognathous; antennae with 11 segments, segments gradually thickened toward distal end of antennae; fore coxae projecting and contiguous, cavities opening posteriorly; fore and middle tarsi with 5 segments, hind tarsi with 4; abdomen with 5 visible sternites. Larvae elongate; larvae and adults carnivorous. *Oligo.-Holo.*

Pytho LATREILLE, 1796, p. 23. *Holo.*

Pythoceroopsis WICKHAM, 1913c, p. 20 [**P. singularis*; OD]. Similar to *Lecontia* (recent), but antennae more slender, their lengths about 1.3 times head width. *Oligo.*, USA (Colorado).

Family ALLECULIDAE Seidlitz, 1891

[Alleculidae SEIDLITZ, 1891, p. xlix]

Slender beetles of moderate size; head subprognathous; antennae long, filiform, with 11 segments; pronotum strongly margined;

fore and middle tarsi with 5 segments, hind pair with 4; claws pectinate; abdomen with 5 visible sternites. Adults occurring on flowers and foliage, feeding chiefly on pollen; larvae in plant debris. *Jur.-Holo.*

Allecula FABRICIUS, 1801, p. 21. *Holo.*

Hymenorus MULSANT, 1851, p. 201. WICKHAM, 1914a; CAMPBELL, 1964. *Oligo.*, USA (Colorado); *Oligo./Mio.*, Mexico (Chiapas)-*Holo.*

Isomira MULSANT, 1856, p. 52. SEIDLITZ, 1896. *Oligo.*, Europe (Baltic)-*Holo.*

Jurallecula MEDVEDEV, 1969, p. 123 [**J. grossa*; OD]. Head elongate; eyes large, reniform; fore coxal cavities closed; fore and middle tarsi with first and fifth segments long. *Jur.*, USSR (Kazakh).

Mycetocharoides SCHAUFUSS, 1888, p. 269 [**M. baumeisteri*; OD]. Similar to *Mycetochares* (recent), but antennae and legs more slender; pronotum not margined; antennae with first, third, and fourth segments longest. *Oligo.*, Europe (Baltic).

Family PYROCHROIDAE

Latreille, 1807

[Pyrochroidae LATREILLE, 1807, p. 201]

Head strongly constricted behind eyes, forming prominent neck; antennae serrate, pectinate, or plumose; pronotum much narrower than width across elytral bases; fore coxae with cavities opening posteriorly; fore and middle tarsi with 5 segments, hind tarsi with 4; abdomen with 5 visible sternites. Adults occurring on flowers and foliage; larvae predaceous, usually found under bark of trees. *Oligo.-Holo.*

Pyrochroa GEOFFROY, 1762, p. 338. *Holo.*

Palaeopyrochroa ABDULLAH, 1965, p. 40 [**P. crowsoni*; OD]. Similar to *Techmessa* (recent) and *Exocalopus* (recent) with appendiculate tarsal claws. *Oligo.*, Europe (Baltic).

Family MELANDRYIDAE Leach, 1815

[Melandryidae LEACH, 1815, p. 104]

Elongate beetles of small to moderate size; head strongly deflexed, not constricted behind eyes; antennae usually with 11 filiform segments, a small club sometimes present; pronotum strongly arched anteriorly; fore coxae projecting, contiguous, cavities closed posteriorly; fore and middle tarsi with 5 segments, hind tarsi with 4, second segment longest. Adults and larvae occurring in

decaying wood, mostly carnivorous. *Cret.*—*Holo.*

Melandrya FABRICIUS, 1801, p. 163. *Holo.*

Abderina SEIDLITZ, 1898, p. 576 [**A. belmsi*; OD].

Similar to *Serropalpus* (recent), but antennae long and penultimate tarsal segment simple; elytra densely punctate. *Oligo.*, Europe (Baltic).

Archaeoxylita NIKITSKY, 1977, p. 141 [**A. zberichini*; OD]. Similar to *Rushia* (recent), but fourth to seventh antennal segments not broadened and third segment of hind tarsus relatively longer. *Cret.*, USSR (Asian RSFSR).

Cicindelopsis COCKERELL, 1920c, p. 254 [**C. eopbilus*; OD]. Little-known genus (elytron only), apparently related to *Prothalpia* (recent). COCKERELL, 1924a. *Eoc.*, USA (Colorado).

Pseudohallomenus NIKITSKY, 1977, p. 142 [**P. cretaceous*; OD]. Similar to *Hallomenus* (recent), but scutellum rectangular. *Cret.*, USSR (Asian RSFSR).

Family SCRAPTIIDAE Latreille, 1807

[Scaptiidae LATREILLE, 1807, p. 199]

Small, elongate-oval beetles; body pubescent. Head deflexed, constricted behind eyes; antennae filiform, usually with 11 segments; fore coxae long, projecting, the bases widely separated and cavities closed posteriorly; legs very long; fore and middle tarsi with 5 segments; hind tarsi with 4, basal segments very long. Adults commonly on flowers, larvae in decaying wood. *Cret.*—*Holo.*

Scaptia LATREILLE, 1807, p. 199. ERMISCH, 1941. *Oligo.*, Europe (Baltic)—*Holo.*

Anaspis GEOFFROY, 1762, p. 315. ABDULLAH, 1964. *Oligo.*, Europe (Baltic)—*Holo.*

Archescaptia ABDULLAH, 1964, p. 340 [**A. emarginata*; OD]. Similar to *Palaescaptia*, but pronotum only slightly wider than long. *Oligo.*, Europe (Baltic).

Palaescaptia ABDULLAH, 1964, p. 339 [**P. elongata*; OD]. Related to *Scaptia* (recent), but pronotum more transverse and eyes lacking setae. *Oligo.*, Europe (Baltic).

Scaptiomima MEDVEDEV, 1969, p. 121 [**S. brachycornis*; OD]. Antennae short, segments broader than long; tibiae with long spines, especially long on hind legs. *Cret.*, USSR (Asian RSFSR).

Family MORDELLIDAE Latreille, 1802

[Mordellidae LATREILLE, 1802a, p. 103]

Small to moderate-sized beetles. Head and prothorax strongly deflexed, head covering fore coxae; antennae with 11 segments, distal

segments frequently forming a serrate club; fore and middle tarsi with 5 segments, hind tarsi with 4; claws serrate; terminal abdominal segment produced to form a stout spine; abdomen with 5 or 6 visible sternites. Adults phytophagous, on flowers; larvae phytophagous, predaceous, or parasitic. *Jur.*—*Holo.*

Mordella LINNÉ, 1758, p. 420 [= *Mordellina* GERMAR, 1813, p. 14 (type, *M. inclusa*)]. SCHLECTENDAL, 1888. *Oligo.*, Europe (Baltic)—*Holo.*

Praemordella SHCHEGOLEVA-BAROVSKAYA, 1929, p. 27 [**P. martynovi*; OD]. Abdomen with at least 7 distinct segments; hind tarsi as long as tibiae; pygidium pointed. *Jur.*, USSR (Kazakh).

Family OEDEMERIDAE Latreille, 1810

[Oedemeridae LATREILLE, 1810, p. 216]

Slender beetles of moderate size, the integument soft and finely pubescent. Head small, narrower than prothorax; antennae with 11 segments, long, filiform; fore coxae projecting, contiguous, cavities open posteriorly; legs long and slender; fore and middle tarsi with 5 segments, hind tarsi with 4; 5 visible abdominal sternites. Larvae elongate, weakly sclerotized; mandibles unusually long. Adults phytophagous, on flowers; larvae developing in timber, especially in driftwood along coasts. *Jur.*—*Holo.*

Oedemera OLIVIER, 1789, p. 31. *Holo.*

Eumecoleus HAUPT, 1950, p. 109 [**E. tenuis*; OD]. Little-known genus. [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Necromera MARTYNOV, 1926a, p. 18 [**N. baeckmanni*; OD]. Similar to *Ischnomera* (recent) but with shorter and thicker antennae. *Jur.*, USSR (Kazakh).

Paloedemera WICKHAM, 1914a, p. 487 [**P. cresipes*; OD]. Little-known genus. Legs stout, hind femora strongly thickened and toothed. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Family ANTHICIDAE Latreille, 1825

[Anthicidae LATREILLE, 1825, p. 383]

Slender beetles, small to moderate in size; head strongly deflexed and constricted behind eyes; antennae filiform or moniliform, slightly broadened distally; fore coxae elongate, cavities usually open posteriorly; pronotum narrow; fore and middle tarsi with 5 segments, hind tarsi with 4; abdomen with 5 visible sternites. Larvae elongate, subcylindrical.

Adults on flowers and foliage; larvae in vegetable debris. *Oligo.*—*Holo.*

Anthicus PAYKULL, 1798, p. 253. *Holo.*

Lithomacratia WICKHAM, 1914a, p. 490 [**L. mirabilis*; OD]. Little-known genus. Similar to *Protomacratia* and *Macratia* but the 3 apical antennal segments much longer than the rest; pronotum short, transverse. WICKHAM, 1920. *Oligo.*, USA (Colorado).

Macratia NEWMAN, 1838, p. 377. ABDULLAH, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Protomacratia ABDULLAH, 1964, p. 332 [**P. appendiculata*; OD]. Similar to *Macratia* but lacking pubescence on tibial spurs. *Oligo.*, Europe (Baltic).

Family CERAMBYCIDAE Latreille, 1802

[Cerambycidae LATREILLE, 1802a, p. 211]

Small to large, flat beetles; antennae long, usually at least as long as body and inserted on frontal prominences; fore coxal cavities open or narrowly closed posteriorly; all tarsi with 5 segments, fourth segment often minute; abdomen with 5 visible sternites. Larvae diverse in form, elongate or robust; legs very minute or short. Adults phytophagous, on stems, roots, leaves, or pollen; larvae borers in wood or roots. *Eoc.*—*Holo.*

Cerambyx LINNÉ, 1758, p. 388. *Holo.*

Aenictosoma SCHAUFUSS, 1892, p. 58 [**A. doenitzi*; OD]. Little-known genus. KORSCHESKY, 1939. *Oligo.*, Europe (Baltic).

Anelaphus LINSLEY, 1936, p. 464. WICKHAM, 1914a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Arhopalus SERVILLE, 1834, p. 77. COCKERELL, 1927d; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Callidiopsis WICKHAM, 1913a, p. 363 [**C. grandiceps*; OD]. Similar to *Callidium* (recent), but head much larger; mesosternum between middle coxae much narrower. *Oligo.*, USA (Colorado).

Callimoxys KRAATZ, 1863, p. 105. COCKERELL, 1911b; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Dorcadionoides MOTSCHULSKY, 1856, p. 27 [**D. subaeneus*; OD]. Similar to *Dorcadion* (recent), but elytra and body metallic, with a green pubescence; antennae a little longer than body. *Oligo.*, Europe (Baltic).

Eocallidium HAUPT, 1950, p. 143 [**E. rugulosum*; OD]. Little-known genus (elytron only). [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Grammoptera SERVILLE, 1835, p. 215. WICKHAM, 1914a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Hylurgops LE CONTE, 1876, p. 389 [= *Myelophilites* SCHEDL, 1947, p. 39 (type, *M. dubius*; Baltic amber)]. HAGEDORN, 1906. *Oligo.*, Europe (Baltic)—*Holo.*

Megacyllene CASEY, 1912, p. 351. WICKHAM, 1914a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Mesosites DEICHMÜLLER, 1881, p. 319 [**M. macrophthalmus*; OD]. Little-known genus. *Mio.*, Europe (Czechoslovakia).

Palaeossemum ABDULLAH, 1967, p. 148 [**P. crowsoni*; OD]. Similar to *Megasemum* (recent), but pronotum nearly rectangular and constricted at base. *Oligo.*, Europe (Baltic).

Palaeoncoderes PITON & THÉOBALD, 1937, p. 84 [**P. eocenicus*; OD]. Little-known genus, apparently belonging to subfamily Lamiinae. PITON, 1940a. *Eoc.*, Europe (France).

Palaeosmodicum WICKHAM, 1914b, p. 264 [**P. hamiltoni*; OD]. Similar to *Smodicum* (recent), but front coxal cavities meeting. *Oligo.*, USA (Colorado).

Parmenops SCHAUFUSS, 1892, p. 60 [**P. longicornis*; OD]. Little-known genus. KORSCHESKY, 1939. *Oligo.*, Europe (Baltic).

Phymatodes MULSANT, 1839, p. 47. COCKERELL, 1908p; WICKHAM, 1914a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Pidonia MULSANT, 1863, p. 186. WICKHAM, 1913a, 1914a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Prolamioides PITON & THÉOBALD, 1937, p. 85 [**P. bituminosus*; OD]. Similar to *Palaeoncoderes*, but last antennal segment less swollen. PITON, 1940a. *Eoc.*, Europe (France).

Protipochus WICKHAM, 1914a, p. 467 [**P. vandykei*; OD]. Similar to *Ipochus* (recent), but antennal segments 3 to 5 not abruptly decreasing in length. LINSLEY, 1942. *Oligo.*, USA (Colorado).

Protoncideres WICKHAM, 1913c, p. 18 [**P. primus*; OD]. Similar to *Oncideres* (recent). Antennae of male about 2.5 times body length; forelegs not elongate. *Oligo.*, Europe (Colorado).

Protospondylis LINSLEY, 1942, p. 19 [**Spondylis florissantensis* WICKHAM, 1920, p. 359; OD; *nom. subst. pro Spondylis tertiaris* WICKHAM, 1917, p. 469, *non* GERMAR, 1849, p. 58]. Similar to *Scaphinus* (recent), but tibiae longitudinally carinate and pronotum with straight sides. HAUPT, 1956. *Oligo.*, USA (Colorado).

Psapharochrus THOMSON, 1864, p. 18. WICKHAM, 1914b; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Saperda FABRICIUS, 1775, p. 184. SCUDDER, 1900; COCKERELL, 1916c; WICKHAM, 1916b, 1920; STATZ, 1938a; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Scaptolenopsis WICKHAM, 1914b, p. 263 [**S. wilmatiae*; OD]. Antennae with 12 segments, slightly serrate, second segment very short; elytra

closely striate. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Semanotus MULSANT, 1839, p. 54. WICKHAM, 1914b; LINSLEY, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Family CHRYSOMELIDAE

Latreille, 1802

[Chrysomelidae LATREILLE, 1802a, p. 220]

Small to moderate in size, usually robust, with much structural diversity; very similar in most respects to the Cerambycidae. Head hypognathous; antennae filiform, relatively short, not more than half length of body, inserted on front of head, not on a prominence. Larvae also very diverse in form. Larvae and adults phytophagous. *Trias.*—*Holo.*

Chrysomela LINNÉ, 1758, p. 368. *Holo.*

Acassidites HAUPT, 1950, p. 155 [**A. separandus*; OD]. Little-known genus (elytron only). *Eoc.*, Europe (Germany).

Airaphilus REDTENBACHER, 1858, p. 999. ERMISCH, 1942. *Oligo.*, Europe (Baltic)—*Holo.*

Cerambyomina MEDVEDEV, 1968, p. 160 [**C. longipennis*; OD]. Similar to *Protoscelis*, but antennae very long, the individual segments much enlarged distally. *Jur.*, USSR (Kazakh).

Chrysomelites HEER, 1865, p. 89 [collective group]. Elytra resembling those of Chrysomelidae. [Family assignment doubtful.] HEER, 1868, 1869, 1870a, 1870b, 1877; OPPENHEIM, 1888; COCKERELL, 1920d, 1926b; STRAND, 1936. *Trias.*, Europe (Switzerland); *Jur.*, Europe (Germany, Switzerland); *Eoc.*, USA (Alaska), England; *Mio.*, Europe (Norway), Greenland; *Paleoc.*—*Plio.*, Argentina (Jujuy).

Clythrina PITON, 1940a, p. 211 [**C. eocenica*; OD]. Little-known genus, possibly related to *Clythra* (recent). [Family assignment doubtful.] *Eoc.*, Europe (France).

Crepidodera (Chevrolat MS.) DEJEAN, 1835, p. 391. GRESSITT, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Crioceridea WICKHAM, 1912a, p. 27 [**C. dubia*; OD]. Similar to *Crioceris* (recent) but with fine elytral sculpturing and a longer second antennal segment. *Oligo.*, USA (Colorado).

Electrolema SCHAUFUSS, 1892, p. 63 [**E. baltica*; OD]. Little-known genus. KORSCHESKY, 1939. *Oligo.*, Europe (Baltic).

Eochrysomela HAUPT, 1950, p. 151 [**E. ornata*; OD]. Little-known genus, possibly similar to *Chrysomela* (recent). HAUPT, 1956. *Eoc.*, Europe (Germany).

Eodonacia HAUPT, 1956, p. 54 [**E. goeckei*; OD]. Little-known genus (elytral fragments). *Eoc.*, Europe (Germany).

Eoemolpinus HAUPT, 1950, p. 149 [**E. azureovirdis*; OD]. Little-known genus, apparently similar to *Eomolpinus* (recent). *Eoc.*, Europe (Germany).

Eosagra CARPENTER, herein [**E. subparallela* HAUPT, 1950, p. 144; OD]. Little-known genus, apparently similar to *Sagra* (recent), but hind femora more enlarged. [The original generic name, *Eosagra*, was a *nomen nudum* (HAUPT, 1950).] *Eoc.*, Europe (Germany).

Gonocelis HAUPT, 1950, p. 152 [**G. natatus*; OD]. Little-known genus (elytra only). [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Oligocassida THÉOBALD, 1937a, p. 121 [**O. melaena*; OD]. Similar to *Laccoptera* (recent) but with elytra less rugose and apex of scutellum rounded. *Oligo.*, Europe (France).

Oposispa UHMANN, 1939, p. 21 [**O. schleeli*; OD]. Similar to *Wallaceana* (recent). Antennae filiform, the 2 basal segments short, the rest longer and cylindrical and with numerous hairs; prothorax subquadrate. *Oligo.*, Europe (Baltic).

Paracassida HAUPT, 1956, p. 76 [**P. punctillata*; OD]. Little-known genus (elytron only). [Family assignment doubtful.] *Eoc.*, Europe (Germany).

Phloeonemites WICKHAM, 1912a, p. 14 [**P. miocenius*; OD]. Similar to *Phloeonemus* (recent) but with antennal club not so abruptly formed; prothorax without sharp, raised lines. *Oligo.*, USA (Colorado).

Plectrotetrophanes WICKHAM, 1914a, p. 477 [**P. hageni*; OD]. Little-known genus. Similar to *Plectrotetra* (recent) but with shorter antennae and prosternum. *Oligo.*, USA (Colorado).

Profidia GRESSITT, 1963, p. 108 [**P. nitida*; OD]. Similar to *Fidia* (recent) but flatter dorsally; pronotum smooth, not ridged; femora toothed. *Oligo./Mio.*, Mexico (Chiapas).

Protanisodera QUELÉ, 1910, p. 50 [**P. glaesi*; OD]. Similar to *Anisodera* (recent), but antennae only a little longer than prothorax and legs short. *Oligo.*, Europe (Baltic).

Protoscelis MEDVEDEV, 1968, p. 156 [**P. jurassicus*; OD]. Body elongate; head prognathous; eyes oval; antennae attached to lateral margins of head between lower edges of eyes and base of mandibles; flagellum slender, with distal part of the segments only moderately enlarged; elytra covering entire abdomen; abdomen with 5 visible sternites. *Jur.*, USSR (Kazakh).

Protosceloides MEDVEDEV, 1968, p. 159 [**P. nitidicornis*; OD]. Similar to *Pseudomegamerus* but with longer antennae and larger eyes and pronotum. *Jur.*, USSR (Kazakh).

Pseudomegamerus MEDVEDEV, 1968, p. 158 [**P. grandis*; OD]. Similar to *Protoscelis* but distal parts of antennal segments not so enlarged; elytra with longitudinal ridges. *Jur.*, USSR (Kazakh).

Sucinagonia UHMANN, 1939, p. 18 [**S. javetana*; OD]. Similar to *Oposispa*, but antennae elongate,

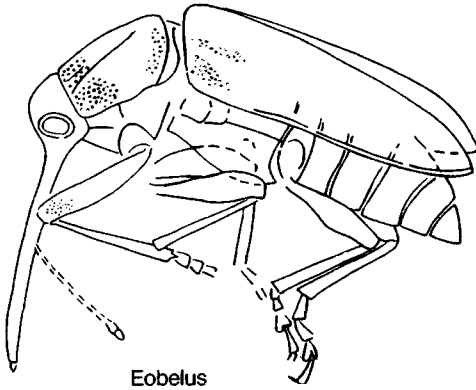


FIG. 183. Eobelidae (p. 314).

filiform, with third segment much the longest. *Oligo.*, Europe (Baltic).

Family ANTHRIBIDAE Billberg, 1820

[Antribidae BILLBERG, 1820, p. 39]

Small to moderate-sized beetles with flat rostrum; antennal scape shorter than pedicel; antennae not elbowed; antennal club occasionally present; maxillary palpi flexible; abdomen with 5 visible sternites. Adults and larvae fungivorous. *Oligo.—Holo.*

Antribus GEOFFROY, 1762, p. 306. *Holo.*

Pseudomecorhis VOSS, 1953, p. 121 [**P. simulator*; OD]. Similar to *Mecorhis* (recent); first tarsal segment elongate, obconical, 3 times as long as thick; second segment slightly shorter, triangular, broadened distally. *Oligo.*, Europe (Baltic).

Saperdirhynchus SCUDDER, 1893a, p. 160 [**S. priscotitillator*; OD]. Little-known genus, with immensely long antennae, inserted on sides of rostrum; possibly related to *Cerambyrhynchus* (recent). *Oligo.*, USA (Colorado).

Straderes SCUDDER, 1893a, p. 163 [**S. conradi*; OD]. Apparently related to *Trodideres* (recent), but prebasal ridge of prothorax slightly anterior to middle of prothorax. *Oligo.*, USA (Colorado).

Family EOBELIDAE Arnoldi, 1977

[Eobelidae ARNOLDI, 1977, p. 144]

Head rounded or transverse; frons convex; antennae usually with 11 segments and with a blunt club; first antennal segment not greatly modified and not more than twice the length of the second; pronotum with a distinct notopleural ridge. *Jur.*

Eobelus ARNOLDI, 1977, p. 147 [**E. longipes*; OD]. Frons strongly convex; eyes large; rostrum long, cylindrical, slightly curved; elytra flattened; femora thin and straight. *Jur.*, USSR (Kazakh). — FIG. 183. **E. longipes*; lateral view, $\times 7$ (Arnoldi, 1977).

Ampliceps ARNOLDI, 1977, p. 166 [**A. dentitibia*; OD]. Similar to *Oxycorynoides*, but femora conspicuously thickened; tibiae straight. *Jur.*, USSR (Kazakh).

Archaeorrhynchus MARTYNOV, 1926a, p. 23 [**A. tenuicornis*; OD]. Rostrum almost straight; fore femora strongly thickened; fore tibiae straight. ARNOLDI, 1977. *Jur.*, USSR (Kazakh).

Belonotaris ARNOLDI, 1977, p. 154 [**B. punctatissimus*; OD]. Elytra definitely convex, conspicuously punctate. *Jur.*, USSR (Kazakh).

Brenthorrhinus ARNOLDI, 1977, p. 172 [**B. mirabilis*; OD]. Rostrum short, thick, much widened at apex; antennae attached near apex; first antennal segment strongly curved; legs long, fore femora larger than middle and hind. *Jur.*, USSR (Kazakh).

Distenorhynchus ARNOLDI, 1977, p. 170 [**D. angulatus*; OD]. Antennae attached to basal one-third of rostrum; rostrum about as long as head and pronotum combined; only femora thickened. *Jur.*, USSR (Kazakh).

Eccoptarthrus ARNOLDI, 1977, p. 169 [**E. crasipes*; OD]. First tarsal segment much enlarged; legs short, femora thickened. *Jur.*, USSR (Kazakh).

Eccoptothorax ARNOLDI, 1977, p. 158 [**E. latipennis*; OD]. Rostrum short, moderately thick; pronotum strongly transverse; legs not thickened. *Jur.*, USSR (Kazakh).

Nanophydes ARNOLDI, 1977, p. 173 [**N. ovatus*; OD]. Rostrum curved; antennae attached near middle of rostrum; metathorax very short. *Jur.*, USSR (Kazakh).

Oxycorynoides ARNOLDI, 1977, p. 159 [**O. similis*; OD]. Rostrum moderately long; antennae attached near middle of rostrum; pronotum with distinct longitudinal, lateral ridge; femora only slightly thickened, tibiae straight. *Jur.*, USSR (Kazakh).

Paroxycorynoides ARNOLDI, 1977, p. 168 [**P. elegans*; OD]. Body long and narrow; pronotum small, short. *Jur.*, USSR (Kazakh).

Probelopsis ARNOLDI, 1977, p. 153 [**P. acutiapex*; OD]. Fore femora only slightly thickened; rostrum almost straight. *Jur.*, USSR (Kazakh).

Probelus ARNOLDI, 1977, p. 151 [**P. curvispinus*; OD]. Hind tibiae with large apical spur. *Jur.*, USSR (Kazakh).

Procurculio ARNOLDI, 1977, p. 157 [**P. fortipes*; OD]. Rostrum short, thick, narrowest at its proximal third; sides of pronotum strongly curved. *Jur.*, USSR (Kazakh).

Scelocampus ARNOLDI, 1977, p. 164 [**S. tenuirostris*; OD]. Similar to *Oxycorynoides*, but tibiae curved. *Jur.*, USSR (Kazakh).

Family ATTELABIDAE

Schoenherr, 1833

[Attelabidae SCHOENHERR, 1833, p. 4]

Small beetles, resembling the Anthribidae, but maxillary palpi rigid and antennae with a distinct club. Elytra not strongly convex. Adults and larvae phytophagous. *Cret.*—*Holo.*

Attelabus LINNÉ, 1758, p. 387. *Holo.*

Baisorhynchus ZHERIKHIN, 1977b, p. 176 [**B. tarsalis*; OD]. Head short, transverse; rostrum long, thin, strongly curved; elytra weakly convex; femora short, broad; tarsi with 2 lobes. *Cret.*, USSR (Asian RSFSR).

Car BLACKBURN, 1897, p. 35. Voss, 1953. *Oligo.*, Europe (Baltic)—*Holo.*

Docirhynchus SCUDDER, 1893a, p. 24 [**D. terebrans* SCUDDER, 1893a, p. 24; SD CARPENTER, herein]. Similar to *Isothea*, but body much broader. WICKHAM, 1912a. *Oligo.*, USA (Colorado).

Involvulus SCHRANK, 1798, p. 360. Voss, 1972. *Oligo.*, Europe (Baltic)—*Holo.*

Isothea SCUDDER, 1893a, p. 20 [**I. alleni*; OD]. Similar to *Paltorhynchus* but with tapered body. *Oligo.*, USA (Colorado).

Masteutes SCUDDER, 1893a, p. 12 [**M. rufis*; OD]. Little-known genus, apparently related to *Rhynchites* (recent); head small and conical; antennae with similar, slender segments. *Oligo.*, USA (Colorado).

Paltorhynchus SCUDDER, 1893a, p. 18 [**P. narubal* SCUDDER, 1893a, p. 18; SD CARPENTER, herein]. Related to *Rhynchites* (recent), but antennae inserted before middle of proximal half of rostrum. *Oligo.*, USA (Colorado).

Steganus SCUDDER, 1893a, p. 28 [**S. baranei*; OD]. Similar to *Isothea*, but head very short; elytron coarsely sculptured. *Eoc.*, USA (Colorado).

Teretrum SCUDDER, 1893a, p. 25 [**T. primulum* SCUDDER, 1893a, p. 25; SD CARPENTER, herein]. Related to *Rhynchites* (recent), but legs unusually slender; fore femora swollen apically. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado).

Toxorhynchus SCUDDER, 1893a, p. 26 [**T. minusculus* SCUDDER, 1893a, p. 26; SD CARPENTER, herein]. Little-known genus. Head conical, nearly as long as broad; rostrum slender, very slightly arcuate, nearly as long as head; elytra strongly carinate. WICKHAM, 1911, 1912b. *Oligo.*, USA (Colorado).

Trypanorhynchus SCUDDER, 1893a, p. 21 [**T. corruptivus* SCUDDER, 1893a, p. 21; SD CARPENTER,

herein]. Little-known genus. Head large basally, strongly tapered; rostrum stout, straight, longer than head; antennae as long as rostrum; fore femora only slightly enlarged distally. WICKHAM, 1913c. *Oligo.*, USA (Colorado).

Family APIONIDAE Schoenherr, 1833

[Apionidae SCHOENHERR, 1833, p. 247]

Very small to moderate-sized beetles, usually with long, curved, slender rostrum; maxillary palpi rigid; antennae not elbowed, scape shorter than 3 following segments combined; elytra strongly convex. Adults and larvae phytophagous, developing in seeds, roots, and stems of plants. *Oligo.*—*Holo.*

Apion HERBST, 1797, p. 100. WAGNER, 1924; VOSS, 1953, 1972. *Oligo.*, Europe (Baltic); *Mio./Plio.*, Mexico (Chiapas)—*Holo.*

Phyllobius SCHOENHERR, 1824, p. 447. Voss, 1972. *Oligo.*, Europe (Baltic)—*Holo.*

Family CURCULIONIDAE Latreille, 1802

[Curculionidae LATREILLE, 1802a, p. 195]

Small to large beetles, strongly sclerotized; rostrum diversely formed, often relatively short; antennae inserted on rostrum anterior to eyes, distinctly elbowed, with scape at least as long as next 3 segments combined and flagellum with a distinct club composed of 3 or 4 segments; maxillary palpi rigid; elytra convex. Larvae apodous, curved. Adults and larvae phytophagous. *Trias.*—*Holo.*

Curculio LINNÉ, 1758, p. 377. *Holo.*

Adipocephalus WICKHAM, 1916b, p. 18 [**A. hydropticus*; OD]. Little-known genus, similar to *Scolytus* (recent) but with a much larger head. *Oligo.*, USA (Colorado).

Ampharthropelma VOSS, 1972, p. 176 [**A. decipiens*; OD]. Tibiae broad and compressed, especially those of forelegs. *Oligo.*, Europe (Baltic)—*Holo.*

Anchorhorrhinus VOSS, 1953, p. 131 [**A. incertus*; OD]. Similar to *Orthorhynchus* (recent), but rostrum thin and attenuate; anterior margin of pronotum not emarginate. *Oligo.*, Europe (Baltic).

Anthribites HEER, 1847, p. 177 [collective group]. Little-known genus, apparently a curculionid. KOLBE, 1888. *Oligo.*—*Mio.*, Europe (Germany).

Antliarhinites HEER, 1865, p. 374 [**A. gracilis*; OD]. Little-known genus. HEYDEN, 1856. *Mio.*, Europe (Germany).

- Calandrites** SCUDDER, 1893a, p. 150 [**C. defessus* SCUDDER, 1893a, p. 150; SD CARPENTER, herein]. Little-known genus; elytron only. Similar to *Calandra* (recent), but elytra with 10 punctured striae. COCKERELL, 1916c, 1918. *Eoc.*, USA (Colorado, Wyoming).
- Camptorrhinites** BRITTON, 1960, p. 43 [**C. orarius*; OD]. Similar to *Pachyonyx* (recent), but prothorax and elytra lacking tubercles. *Eoc.*, England.
- Cenocephalus** CHAPUIS, 1866, p. 325. SCHEDL, 1962. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*
- Centron** SCUDDER, 1893a, p. 69 [**C. moricollis*; OD]. Little-known genus, similar to *Alophus* (recent) but with first abdominal segment nearly twice as long as second. *Oligo.*, USA (Colorado).
- Charphoborites** CARPENTER, herein [**C. keilbachi* SCHEDL, 1947, p. 32; OD]. Similar to *Charphoborus* (recent), but front margin of prothorax armed with tubercles. [The original generic name, *Charphoborites*, was a *nomen nudum* (SCHEDL, 1947).] *Oligo.*, Europe (Baltic).
- Cleonolithus** BASSI, 1841, p. 401 [**C. antiquus*; OD]. Little-known genus. *Plio.*, Europe (Italy).
- Cretonanophyes** ZHERIKHIN, 1977b, p. 178 [**C. longirostris*; OD]. Rostrum very long; frons wide; second tarsal segment with 2 lobes. *Cret.*, USSR (Asian RSFSR).
- Cryphalites** COCKERELL, 1917g, p. 368 [**C. rugosissimus*; OD]. Related to *Cryphalus* (recent); thorax and elytra strongly tuberculate and bearing small, clavate hairs; tarsal segments bearing long, flat hairs. *Mio.*, Burma.
- Cryptorhynchus** ILLIGER, 1807, p. 330. ZIMMERMAN, 1971. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*
- Cryptorhynchites** HAUPT, 1950, p. 159 [**C. sculpturatus*; OD]. Little-known genus, elytral fragments. *Eoc.*, Europe (Germany).
- Dorotheus** KUSCHEL, 1959, p. 50 [**D. guidensis*; OD]. Little-known genus; elytron with seventh and ninth striae entire. *Cret.*, Chile.
- Eccoptus** DEJEAN, 1821, p. 86. ZIMMERMAN, 1971; O'BRIEN & WIBMER, 1982. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*
- Electrorribus** HUSTACHE, 1942, p. 108 [**E. thergi*; OD]. Similar to *Phytotribus* (recent), but scape shorter, not reaching base of rostrum. *Oligo.*, Europe (Baltic).
- Eocleonus** SCUDDER, 1893a, p. 95 [**E. subjectus*; OD]. Little-known genus, related to *Lixus* (recent), but head much larger; rostrum relatively short. *Oligo.*, USA (Colorado).
- Erirrhinites** BRITTON, 1960, p. 40 [**E. bognoensis*; OD]. Anterior coxae globular, almost contiguous; prothorax without anterior ventral emarginations. *Eoc.*, England.
- Eudomus** SCUDDER, 1893a, p. 62 [**E. robustus* SCUDDER, 1893a, p. 62; SD CARPENTER, herein]. Similar to *Promecops* (recent) but with larger size and heavier body. *Oligo.*, USA (Colorado).
- Eugnamptidea** WICKHAM, 1912b, p. 42 [**E. tertiaria*; OD]. Similar to *Eugnamptus* (recent), but antennal club with 4 segments. *Oligo.*, USA (Colorado).
- Euvopes** SCUDDER, 1893a, p. 53 [**E. veneratus* SCUDDER, 1893a, p. 53; SD CARPENTER, herein]. Little-known genus, similar to *Lachnopus* (recent), but elytron with coarser punctures on striae. *Oligo.*, USA (Colorado).
- Geralophus** SCUDDER, 1893a, p. 72 [**G. anti-quarius* SCUDDER, 1893a, p. 72; SD CARPENTER, herein]. Related to *Trichalophus* (recent). Body compact and stout; head short, smaller than thorax; elytra broad. *Oligo.*, USA (Colorado).
- Hipporhinops** COCKERELL, 1926b, p. 314 [**H. sternbergi*; OD]. Large weevils, related to *Hipporhinus* (recent) but with more slender rostrum. *Oligo.*, USA (Colorado).
- Hylastes** ERICHSON, 1836, p. 47. BLAIR, 1943; SCHEDL, 1947. *Oligo.*, Europe (Baltic)—*Holo.*
- Hylescierites** SCHEDL, 1947, p. 29 [**H. granulatus*; OD]. Similar to *Scierus* (recent); flagellum of antenna with 7 segments; antennal club short and weakly developed. *Oligo.*, Europe (Baltic).
- Hylesinites** GERMAR, 1813, p. 15 [**H. electrinus*; OD]. Little-known genus. *Oligo.*, Europe (Baltic).
- Isalcidodes** VOSS, 1953, p. 134 [**I. macellus*; OD]. Similar to *Alcidodes* (recent), but tarsal claws free, without denticles, and undivided. *Oligo.*, Europe (Baltic).
- Korystina** BRITTON, 1960, p. 42 [**K. gracilis*; OD]. Middle of anterior margin of pronotum projecting anteriorly over head and curving downward. *Eoc.*, England.
- Laccopygus** SCUDDER, 1893a, p. 93 [**L. nilesii*; OD]. Related to *Hylobius* (recent) but with funiculus of antenna consisting of 7 similar, elongate segments; antennal club stout and oval. *Oligo.*, USA (Colorado), Europe (Germany).
- Lithophthorus** SCUDDER, 1893a, p. 153 [**L. rugosicollis*; OD]. Related to *Dryophthorus* (recent), but funiculus with not more than 3 segments. VOSS, 1953. *Oligo.*, USA (Colorado).
- Lithopissodes** BEIER, 1952, p. 132 [**L. luschtzensis*; OD]. Little-known genus, possibly related to *Pissodes* (recent). *Oligo.*, Europe (Austria).
- Lutago** BRITTON, 1960, p. 38 [**L. fetosus*; OD]. Similar to *Pissodites* but much broader across elytra. *Eoc.*, England.
- Metrioxena** PASCOE, 1870, p. 442 [= *Archimetrioxena* VOSS, 1953, p. 123 (type, *A. electrica*, Baltic amber)]. MARSHALL, 1955; VOSS, 1957. *Oligo.*, Europe (Baltic)—*Holo.*
- Miogeraeus** WICKHAM, 1916b, p. 16 [**M. recurrens*; OD]. Similar to *Geraeus* (recent), but elytral striae confluent at base. *Oligo.*, USA (Colorado).
- Mononychites** HAUPT, 1956, p. 83 [**M. rotunda-*

- tus*; OD]. Little-known genus (elytron only), apparently similar to *Mononychus* (recent). *Eoc.*, Europe (Germany).
- Necrodryophthorus** VOSS, 1953, p. 135 [**N. inquilinus*; OD]. Similar to *Psilodryophthorus* (recent), but rostrum elongate and curved. *Oligo.*, Europe (Baltic).
- Numitor** SCUDDER, 1893a, p. 103 [**N. claviger*; OD]. Related to *Erirhinus* (recent) with very stout body and long legs; antennae strongly clavate. *Oligo.*, USA (Colorado).
- Oligocryptus** CARPENTER, 1986, p. 577, *nom. subst. pro* *Eucriptus* SCUDDER, 1893a, p. 63, *non* HALDEMAN, 1842 [**Eucriptus sectus* SCUDDER; OD]. Similar to *Eudomus* but with rostrum stouter and body more slender. *Oligo.*, USA (Colorado).
- Ophryastites** SCUDDER, 1893a, p. 38 [collective group]. Elytra similar in general appearance to those of *Ophryastes* (recent). WICKHAM, 1912b; COCKERELL, 1916c, 1918, 1920b. *Eoc.*, USA (Colorado, Utah), England; *Oligo.*, USA (Colorado).
- Oryctorhinus** SCUDDER, 1893a, p. 149 [**O. tenuirostris*; OD]. Related to *Sphenophorus* (recent), but antennae unusually small; antennal club oval. *Oligo.*, USA (Colorado).
- Otioryhynchites** FRITSCH, 1882, p. 5 [collective group]. Little-known group of curculionids resembling *Otioryhynchus* (recent) but usually larger. SCUDDER, 1878a, 1890, 1900; WICKHAM, 1911, 1912b, 1929; TURNER, 1912; PITON & RUDEL, 1936; CROWSON, 1960; ZIMMERMAN, 1971. *Cret.*, Europe (Czechoslovakia); *Cret.-Eoc.*, Hong Kong (Peng Chau Island); *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (France); *Paleoc.-Plio.*, Argentina (Jujuy).
- Palaeotanymericides** MANI, 1947a, p. 55 [**P. hislopi*; OD]. Little-known genus (elytral fragment). [Family assignment doubtful.] *Paleoc.-Plio.*, India (Nagpur).
- Paleopissodes** ULKE, 1947, p. 1 [**P. weigangae*; OD]. Similar to *Pissodes* (recent), but rostrum more slender and with less angular slope. *Oligo.*, Europe (Baltic).
- Paonaupactus** VOSS, 1953, p. 127 [**P. sitonitoides*; OD]. Similar to *Naupactus* (recent), but eyes larger and rostrum more slender. *Oligo.*, Europe (Baltic).
- Phloeosinites** HAGEDORN, 1906, p. 118 [**P. rebi*; OD]. Similar to *Phloeosinus* (recent), but fore coxae very slender. SCHEDL, 1947. *Oligo.*, Europe (Baltic).
- Pissodes** GERMAR, 1817, p. 340. VOSS, 1972. *Oligo.*, Europe (Baltic)—*Holo.*
- Pissodites** BRITTON, 1960, p. 37 [**P. argillosus*; OD]. Similar to *Pissodes*, but body more slender; punctuation more dense. *Eoc.*, England.
- Pityophthoridaea** WICKHAM, 1916b, p. 18 [**P. diluvialis*; OD]. Similar to *Pityophthorus* (recent) but with shorter and stouter body. *Oligo.*, USA (Colorado).
- Pliocleonus** GERSDORF, 1976, p. 122 [**P. gibbosus*; OD]. Little-known genus. *Plio.*, Europe (Germany).
- Polydrosus** GERMAR, 1817, p. 341. PITON, 1939; VOSS, 1953. *Plio.*, Europe (France)—*Holo.*
- Pristorhynchus** HEER, 1847, p. 190 [**P. ellipticus*; OD]. SCUDDER, 1885b. *Mio.*, Europe (Germany).
- Rhyncolus** GERMAR, 1824, p. 341. SLEEPER, 1968. *Plio.*, USA (Nevada)—*Holo.*
- Rhysosternum** SCUDDER, 1893a, p. 124 [**R. longirostre* SCUDDER, 1893a, p. 124; SD CARPENTER, herein]. Similar to *Rhysomatus* (recent), but rostrum unusually long and elytra having punctate striae but lacking carinae. PITON, 1940a. *Oligo.*, USA (Colorado), Europe (France).
- Sciabregma** SCUDDER, 1893a, p. 146 [**S. rugosa*; OD]. Related to *Calandra* (recent), with dorsal-anterior part of prothorax extended to form an overarching frontal guard for head, guard nearly as long as rest of prothorax. COCKERELL, 1921e. *Eoc.*, USA (Colorado).
- Sitonitellus** CARPENTER, 1986, p. 577, *nom. subst. pro* *Sitonites* HAUPT, 1956, p. 80, *non* HEER, 1865 [**Sitonites egregius* HAUPT; OD]. Little-known genus, apparently similar to *Sitona* (recent). *Eoc.*, Europe (Germany).
- Slonik** ZHERIKHIN, 1977b, p. 180 [**A. sibiricus*; OD]. Antennae apparently without elbow; rostrum long, curved; trochanter short; femora alike, not thickened. [Family assignment doubtful.] *Cret.*, USSR (Asian RSFSR).
- Smicrorhynchus** SCUDDER, 1893a, p. 104 [**S. mageei*; OD]. Similar to *Smicronyx* (recent), but with 3 basal segments of funiculus equal. *Oligo.*, USA (Colorado).
- Spodotribus** SCUDDER, 1893a, p. 152 [**S. terrulentus*; OD]. Apparently related to *Dryophthorus* (recent), but funiculus of antenna consisting of at least 7 segments; eyes not prominent, composed of relatively few facets; head very long. *Oligo.*, USA (Colorado).
- Synommatius** WOLLASTON, 1873, p. 508. VOSS, 1953. *Oligo.*, Europe (Baltic)—*Holo.*
- Taphramites** SCHEDL, 1947, p. 41 [**T. gnathotrichus*; OD]. Similar to *Thamnurgus* (recent) but with fore tibiae strongly dilated. *Oligo.*, Europe (Baltic).
- Taphrorychus** EICHHOFF, 1878, p. 204. SCHEDL, 1947. *Oligo.*, Europe (Baltic)—*Holo.*
- Taylorius** BRITTON, 1960, p. 41 [**T. litoralis*; OD]. Related to *Cryptorhynchus* (recent); apical part of rostrum enclosed laterally by flangelike processes of pro- and mesosternum; elytra smooth. *Eoc.*, England.
- Tenillus** SCUDDER, 1893a, p. 35 [**T. firmus*; OD]. Little-known genus, apparently related to *Tri-*

- gonoscuta* (recent); rostrum long and stout. *Oligo.*, USA (Colorado).
- Thryogenosoma** VOSS, 1953, p. 138, *nom. subst. pro Eriirhinoides* MOTSCHULSKY, 1856, p. 27, *non* BLANCHARD, 1851, p. 385 [**Eriirhinoides caringer* MOTSCHULSKY, 1856, p. 27; OD]. Similar to *Eriirhinus* (recent), but rostrum and body long; elytra with a longitudinal ridge. *Oligo.*, Europe (Baltic).
- Tillyardiopsis** DUNSTAN, 1923, p. 64 [**T. tuberculata*; OD]. Little-known genus. Elytron as in *Etheridgea* but much larger. *Trias.*, Australia (Queensland).
- Xyleborites** WICKHAM, 1913c, p. 26 [**X. longipennis*; OD]. Little-known genus; similar to *Xyleborus* (recent), but body more elongate; thoracic sculpturing finer and more nearly uniform. *Oligo.*, USA (Colorado).
- Xylechinites** HAGEDORN, 1906, p. 120 [**X. anceps*; OD]. Similar to *Dendroctonus* (recent), but eyes long and slender. SCHEDL, 1947. *Oligo.*, Europe (Baltic).

SUBORDERS AND FAMILIES UNCERTAIN

The following extinct genera are based on species known only from isolated elytra or body fragments. Their family relationships and in many instances their subordinal positions are uncertain. Since most of the fossils are from Mesozoic deposits, some of the species may belong to unrecognized, extinct families. Most of these genera were not assigned to families by their original describers, chiefly HANDLIRSCH (1906b, 1907, 1908a) and BODE (1953).

- Actea** GERMAR, 1842, p. 85 [**A. sphinx*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, Europe (Germany).
- Adelidium** TILLYARD, 1918b, p. 752 [**A. cordatum*; OD]. Little-known genus, based on elytron. *Trias.*, Australia (New South Wales).
- Adikia** HANDLIRSCH, 1906b, p. 558 [**A. punctulata*; OD]. Little-known genus. *Jur.*, England.
- Adynasia** HANDLIRSCH, 1906b, p. 449 [**Buprestites lyelli* HEER, 1865, p. 88; OD]. Little-known genus, based on elytron. *Jur.*, Europe (Switzerland).
- Agrilium** WESTWOOD, 1854, p. 395 [**A. stomphax* WESTWOOD, 1854, p. 395; SD CARPENTER, herein]. Little-known genus. GIEBEL, 1856; HANDLIRSCH, 1906b. *Jur.*, England.
- Allognosis** HANDLIRSCH, 1906b, p. 450 [**Nebria nitens* GEINITZ, 1894, p. 74; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Allopliosilpha** GERSDORF, 1970, p. 631 [**A. inclavata*; OD]. Little-known genus. *Plio.*, Europe (Germany).
- Amarodes** HANDLIRSCH, 1906b, p. 545 [**Amara pseudozabrus* DEICHMÜLLER, 1886, p. 64; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Amblycephalonius** BODE, 1953, p. 228 [**A. tenuistriatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Amphoxyne** BODE, 1953, p. 217 [**A. lineata*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Anancaeon** HANDLIRSCH, 1939, p. 71 [**A. microcephalum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Anapiptus** HANDLIRSCH, 1906b, p. 552 [**A. brodiei*; OD]. Little-known genus. *Jur.*, England.
- Anepismus** HANDLIRSCH, 1906b, p. 450 [**Elater vanus* GIEBEL, 1856, p. 92; OD]. Little-known genus. DOLIN, 1973. *Jur.*, England.
- Angelinella** HANDLIRSCH, 1906b, p. 401 [**Elytridium angelini* HEER, 1878, p. 196; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Anhydrophilus** HANDLIRSCH, 1906b, p. 455 [**A. brodiei*; OD]. Little-known genus. COCKERELL, 1915. *Jur.*, England.
- Anobichnium** LINCK, 1949, p. 180 [**A. simile*; OD]. Boring in fossil wood, apparently caused by beetles. *Trias.*, Europe (Germany).
- Anomerus** HANDLIRSCH, 1939, p. 67 [**A. punctifer*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Anypostatus** HANDLIRSCH, 1939, p. 66 [**A. taurus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Apheloodes** DUNSTAN, 1923, p. 70 [**A. obliquum*; OD]. Little-known genus; elytron only. *Trias.*, Australia (Queensland).
- Aphodiites** HEER, 1865, p. 90 [**A. protogaeus*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Apicasia** BODE, 1953, p. 237 [**A. inolata*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Apioderes** HANDLIRSCH, 1939, p. 65 [**A. punctatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Apiopyrenides** BODE, 1953, p. 220 [**A. trigeminus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Apistotes** HANDLIRSCH, 1906b, p. 559 [**Elater purbeccensis* GIEBEL, 1856, p. 92; OD]. Little-known genus. *Jur.*, England.
- Aposphinctus** BODE, 1953, p. 223 [**A. conservatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Apsychus** HANDLIRSCH, 1939, p. 71 [**A. alutaceus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Aptilotus** CARPENTER, 1986, p. 577, *nom. subst. pro Aptilotus* BODE, 1953, p. 237, *non* MIK, 1898 [**Aptilotus capitecarens* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).

- Archiorhynchus** HEER, 1874b, p. 91 [**A. angusticollis*; OD]. Little-known genus. HANDLIRSCH, 1907. *Cret.*, Greenland.
- Ataktosites** HAUPT, 1956, p. 37 [**A. palustris*; OD]. Little-known genus, based on elytral fragments. *Eoc.*, Europe (Germany).
- Auchenophorites** CARPENTER, 1986, p. 577, *nom. subst. pro Auchenophorus* BODE, 1953, p. 229, *non* TURNER, 1907 [**Auchenophorus sculpturatus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Bareus** HANDLIRSCH, 1939, p. 66 [**B. strigipennis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Barocephalus** CARPENTER, 1986, p. 577, *nom. subst. pro Barycephalus* BODE, 1953, p. 228, *non* GUENTHER, 1860 [**Barycephalus nudatus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Bathygerus** HANDLIRSCH, 1906b, p. 456 [**Cistelites bellus* GEINITZ, 1894, p. 75; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Bellingera** HEER, 1852, p. 12 [**B. ovalis*; OD]. Little-known genus; pronotum and elytra. *Jur.*, Europe (Switzerland).
- Bellingeropis** HANDLIRSCH, 1906b, p. 440 [**Bellingera laticollis* HEER, 1865, pl. 8, fig. 5; OD]. Little-known genus; pronotum and elytra. *Jur.*, Europe (Switzerland).
- Biadelater** HANDLIRSCH, 1906b, p. 559 [**Elater werneri* GIEBEL, 1856, p. 92; OD]. Little-known genus. DOLIN, 1973. *Jur.*, England.
- Blapsium** WESTWOOD, 1854, p. 393 [**B. egertoni*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Blaptoides** FRITSCH, 1901, p. 172 [**B. dubius*; OD]. Little-known genus. *Cret.*, Europe (Czechoslovakia).
- Bothroptera** HANDLIRSCH, 1906b, p. 558 [**Curculionites westwoodi* GIEBEL, 1856, p. 147; OD]. Little-known genus. *Jur.*, England.
- Bothynophora** HEER, 1865, pl. 7, fig. 20 [**B. elegans*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Brachinites** FRITSCH, 1882, p. 5 [**B. truncatus*; OD]. Little-known genus. FRITSCH, 1901. *Cret.*, Europe (Czechoslovakia).
- Brachylaimon** BODE, 1953, p. 208 [**B. striatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Brachytrachelites** BODE, 1953, p. 235 [**B. striatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Brodiola** HANDLIRSCH, 1906b, p. 441 [**B. nana*; OD]. Little-known genus. *Jur.*, England.
- Bucklandula** HANDLIRSCH, 1906b, p. 556 [**B. striata*; OD]. Little-known genus. *Jur.*, England.
- Buprestites** HEER, 1847, p. 128 [collective group]. Elytra resembling those of buprestids; other structures unknown. GERMAR, 1849; HEER, 1862b, 1865, 1883; SCUDDER, 1900; MEUNIER, 1920c; PITON, 1940a. *Eoc.*, Greenland, England, Europe (France, Germany); *Oligo.*, Europe (France, Germany); *Mio.*, Europe (Germany).
- Buprestium** WESTWOOD, 1854, p. 393 [**B. gorgus*; SD HANDLIRSCH, 1906b, p. 561]. Little-known genus. *Jur.*, England.
- Byrrhydium** HEER, 1865, p. 89 [**B. arcuatum* HEER, 1865, p. 89; SD CARPENTER, herein]. Little-known genus. *Jur.*, Europe (Switzerland).
- Callistaspis** HAUPT, 1950, p. 153 [**C. punctatus*; OD]. Little-known genus, based on elytra. *Eoc.*, Europe (Germany).
- Camaricopterus** BODE, 1953, p. 217 [**C. ovalis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Carabidium** WESTWOOD, 1854, p. 396 [**C. dejean-ianum*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Carabocera** BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 18 [**C. prisca*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, USSR (Asian RSFSR).
- Cardioides** BODE, 1953, p. 221 [**C. incisus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Caryosoma** HAUPT, 1950, p. 125 [**C. rugosus*; OD]. Little-known genus; body robust and strongly arched dorsally. [Possibly a tenebrionid.] *Eoc.*, Europe (Germany).
- Cerambycinus** GERMAR, 1839, p. 208 [**C. dubius*; OD]. Little-known genus. HANDLIRSCH, 1906b; PONOMARENKO, 1971b. *Jur.*, Europe (Germany).
- Cerylonopsis** HANDLIRSCH, 1906b, p. 547 [**Cerylon striatum* BRODIE, 1845, p. 32; OD]. Little-known genus. *Jur.*, England.
- Chalepocarabus** HANDLIRSCH, 1906b, p. 546 [**Carabus elongatus* BRODIE, 1845, p. 32; OD]. Little-known genus. *Jur.*, England.
- Chlaeniopsis** HANDLIRSCH, 1906b, p. 548 [**Chlaenius solitarius* DEICHMÜLLER, 1886, p. 65; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Chrysomelidium** HANDLIRSCH, 1907, p. 665 [**Chrysomelites simplex* FRITSCH, 1901, p. 175; OD]. Little-known genus. *Cret.*, Europe (Czechoslovakia).
- Chrysomelophana** HANDLIRSCH, 1906b, p. 549 [**Chrysomela rara* WEYENBERGH, 1869, p. 287; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Chrysomelopsis** HANDLIRSCH, 1906b, p. 445 [**Chrysomela andraei* GIEBEL, 1856, p. 119; OD]. Little-known genus. *Jur.*, England.
- Cistelites** HEER, 1865, p. 89 [**C. insignis*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Clathropenna** FUJIIYAMA, 1973, p. 373 [**C. rugosa*; OD]. Little-known genus, based on elytral fragment, probably related to Cupedidae. *Trias.*, Japan.
- Clinomerus** CARPENTER, 1986, p. 577, *nom. subst. pro Catomerus* HANDLIRSCH, 1939, p. 67, *non* PILSBRY, 1916 [**Catomerus laticollis* HAND-

- LIRSCH; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Coccinellophana** HANDLIRSCH, 1906b, p. 566 [**C. marchisoni*; OD]. Little-known genus. *Jur.*, England.
- Coilotrachelus** BODE, 1953, p. 209 [**C. lineatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Colymbetopsis** HANDLIRSCH, 1906b, p. 445 [**Colymbetes arcuatus* HEER, 1852, p. 12; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Coptogyrinus** HANDLIRSCH, 1906b, p. 448 [**C. scutellatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Coreoeicos** BODE, 1953, p. 236 [**C. dilatatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Cretotaenia** PONOMARENKO, 1977b, p. 97 [**C. pallida*; OD]. Little-known genus. Larvae aquatic, with walking legs and modified, long urogomphi; head almost square; ninth abdominal segment with distinct tergite. *Cret.*, USSR (Asian RSFSR).
- Cricotrachelites** BODE, 1953, p. 210 [**C. rotundatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Critoderma** CARPENTER, 1986, p. 578, *nom. subst. pro Cycloderma* HEER, 1865, p. 89, *non* PETERS, 1854 [**Cycloderma deplanatum* HEER; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Cricotrachelus** CARPENTER, 1986, p. 578, *nom. subst. pro Cyclotrachelus* BODE, 1953, p. 222, *non* DE CHAUDOIR, 1838 [**Cyclotrachelus exsecutus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Cryptauchenia** BODE, 1953, p. 218 [**C. simplex*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Cryptocephalites** HAUPT, 1956, p. 66 [**C. auratus*; OD]. Little-known genus, based on elytron. *Eoc.*, Europe (Germany).
- Ctenicerium** WESTWOOD, 1854, p. 395 [**C. blissus* WESTWOOD, 1854, p. 395; SD CARPENTER, *herein*]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Curculidium** HANDLIRSCH, 1907, p. 665 [**Curculionites senonicus* KOLBE, 1888, p. 135; OD]. Little-known genus. *Cret.*, Lebanon.
- Curculionites** HEER, 1847, p. 199 [collective group] [= *Curculionites* GIEBEL, 1856, p. 14, homonym and synonym]. Elytra resembling those of Curculionidae. HEER, 1856, 1870a; ASSMANN, 1870; OUSTALET, 1870; COCKERELL, 1920b, 1920c, 1926a, 1936; NORTHROP, 1928; HAUPT, 1950. *Cret.*, USA (South Dakota); *Eoc.*, England, Europe (Germany); *Oligo.*, Europe (France, Germany); *Mio.*, Europe (Yugoslavia), Spitsbergen; *Paleoc.-Plio.*, Argentina (Jujuy).
- Curculiopsis** HANDLIRSCH, 1907, p. 663 [**Curculionites cretaceus* HEER, 1874b, p. 92; OD]. Little-known genus. *Cret.*, Greenland.
- Curculium** WESTWOOD, 1854, p. 393 [**C. syrictibus*; OD]. Little-known genus. GIEBEL, 1856; HANDLIRSCH, 1906b. *Jur.*, England.
- Cyphospheron** BODE, 1953, p. 220 [**C. virgatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Diachoristes** BODE, 1953, p. 209 [**D. collinus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Diatarastus** HANDLIRSCH, 1906b, p. 559 [**Carabus westwoodi* GIEBEL, 1856, p. 60; OD]. Little-known genus. *Jur.*, England.
- Diatrypamene** BODE, 1953, p. 231 [**D. angulocollis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Dicyphelus** CARPENTER, 1986, p. 578, *nom. subst. pro Dicyphus* BODE, 1953, p. 234, *non* FIEBER, 1858 [**Dicyphus concameratus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Dinoharpalus** HANDLIRSCH, 1906b, p. 450 [**Harpalus liasinus* GIEBEL, 1856, p. 62; OD]. Little-known genus. *Jur.*, England.
- Diphymation** BODE, 1953, p. 209 [**C. corrosum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Diplocelides** BODE, 1953, p. 211 [**D. minutus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Diplothece** BODE, 1953, p. 216 [**D. scissa*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Ditomoptera** GERMAR, 1839, p. 203 [**D. dubia*; OD] [= *Cerambycites* DEICHMÜLLER, 1886, p. 75 (type, *C. dubius*)]. Little-known genus. HANDLIRSCH, 1906b; PONOMARENKO, 1971b. *Jur.*, Europe (Germany).
- Doggeria** HANDLIRSCH, 1906b, p. 555 [**D. siberica* HANDLIRSCH, 1906b, p. 555; SD CARPENTER, *herein*]. Little-known genus. MANTELL, 1844. *Jur.*, England, USSR (Asian RSFSR).
- Doggeriopsis** HANDLIRSCH, 1906b, p. 556 [**D. stonessfieldiana*; OD]. Little-known genus. *Jur.*, England.
- Dysarestus** HANDLIRSCH, 1906b, p. 451 [**Elaterites vetustus* HEER, 1865, p. 88; OD]. Little-known genus. DOLIN, 1973. *Jur.*, Europe (Switzerland).
- Dysmorphus** BODE, 1953, p. 228 [**D. molestus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Echthlimma** HANDLIRSCH, 1939, p. 69 [**E. forficuloides*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Elateridopsis** ZALESSKY, 1929, p. 29 [**E. permien-sis*; OD]. Little-known genus, probably in Archostemata. ROHDENDORF, 1957; PONOMARENKO, 1963a; DOLIN, 1973. *Perm.*, USSR (European RSFSR).
- Elaterina** GARDINER, 1961, p. 87 [**E. liasina*; OD]. Little-known genus, based on elytron with bluntly rounded apex. *Jur.*, England.
- Elaterites** HEER, 1847, p. 141 [collective group].

- Little-known genus. COCKERELL, 1926b; PONOMARENKO, 1971b; DOLIN, 1973. *Eoc.*, England; *Paleoc.-Plio.*, Argentina (Jujuy).
- Elaterium** WESTWOOD, 1854, p. 387 [**E. pronaeus*; SD HANDLIRSCH, 1907, p. 748]. Little-known genus. *Jur.*, England.
- Elytridium** HEER, 1870a, p. 77 [**E. undecimstriatum*; SD HANDLIRSCH, 1907, p. 663]. Little-known genus. *Mio.*, Spitsbergen.
- Elytrulum** HANDLIRSCH, 1907, p. 663 [**Elytridium multipunctatum* HEER, 1883, p. 143; OD]. Little-known genus. *Cret.*, Greenland.
- Enamma** HANDLIRSCH, 1906b, p. 451 [**E. striatum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Entomocantharus** BODE, 1953, p. 212 [**E. convexus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eoallognosis** HAUPT, 1950, p. 137 [**E. undulatus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).
- Eocassida** HAUPT, 1950, p. 155 [**E. longula*; OD]. Little-known genus, based on elytra. *Eoc.*, Europe (Germany).
- Eocoleopteron** HANDLIRSCH, 1906b, p. 400 [**E. roemeri*; OD]. Little-known genus; elytron only. *Trias.*, Europe (Germany).
- Eodromus** PONGRÁCZ, 1935, p. 538 [collective group]. Elytron with prominent ridges. HAUPT, 1950. *Eoc.*, Europe (Germany).
- Eogaleruca** HAUPT, 1956, p. 74 [**E. punctipennis*; OD]. Little-known genus; elytron only. *Eoc.*, Europe (Germany).
- Eohelaeus** HAUPT, 1950, p. 135 [**E. sublaevus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).
- Eomelasoma** HAUPT, 1956, p. 73 [**E. incostata*; OD]. Little-known genus, based on elytral fragments. *Eoc.*, Europe (Germany).
- Episcepes** BODE, 1953, p. 208 [**E. rotundatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Epomenus** HANDLIRSCH, 1906b, p. 562 [**E. rugosus*; OD]. Little-known genus. *Jur.*, England.
- Erotylites** COCKERELL, 1920d, p. 71 [**E. wallacei*; OD]. Little-known genus, based on elytral fragment. *Eoc.*, England.
- Etheridgea** HANDLIRSCH, 1906b, p. 402 [**E. australis*; OD]. Little-known genus; elytra only. ETHERIDGE & OLLIFF, 1890; TILLYARD & DUNSTAN, 1916; DUNSTAN, 1923. *Trias.*, Australia (Queensland, New South Wales).
- Euenarthrus** BODE, 1953, p. 223 [**E. mandibulatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eumolpites** HEER, 1865, p. 89 [**E. liberatus*; OD]. Little-known genus; pronotum and elytra. HANDLIRSCH, 1906b. *Jur.*, Europe (Switzerland).
- Eurynotellus** CARPENTER, 1986, p. 578, *nom. subst. pro Eurynotus* BODE, 1953, p. 207, *non* KIRBY, 1819 [**Eurynotus brevicollis* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eurynucha** HANDLIRSCH, 1906b, p. 446 [**E. pseudobuprestis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eurysphinctus** BODE, 1953, p. 224 [**E. latesulcatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eurythyreites** HANDLIRSCH, 1906b, p. 542 [**Eurythyrea grandis* DEICHMÜLLER, 1886, p. 70; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Eusarcantarus** BODE, 1953, p. 212 [**E. compactus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Feronites** FRITSCH, 1884a, p. 205 [**F. velenovskiy*; OD]. Little-known genus. FRITSCH, 1901. *Cret.*, Europe (Czechoslovakia).
- Flichea** HANDLIRSCH, 1906b, p. 402 [**Glaphyrop-tera lotharingiaca* FLICHE, 1901, p. 650; OD]. Little-known genus; elytron only. *Trias.*, Europe (France).
- Gastrodelus** BODE, 1953, p. 238 [**G. decapitatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Gastroratus** BODE, 1953, p. 238 [**G. dispertitus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Glaphoptera** HANDLIRSCH, 1906b, p. 557 [**G. anglica*; OD]. Little-known genus. *Jur.*, England.
- Glaphyopterites** HANDLIRSCH, 1906b, p. 437 [**Glaphyoptera depressa* HEER, 1852, p. 14; OD]. Little-known genus; body fragments. *Jur.*, Europe (Switzerland).
- Glaphyopterodes** HANDLIRSCH, 1906b, p. 437 [**Glaphyoptera gebreti* HEER, 1852, p. 14; OD]. Little-known genus; prothorax and elytron. DOLIN, 1973. *Jur.*, Europe (Switzerland).
- Glaphyopterula** HANDLIRSCH, 1906b, p. 437 [**Glaphyoptera gracilis* HEER, 1852, p. 14; OD]. Little-known genus; pronotum and elytra. *Jur.*, Europe (Switzerland).
- Grahamelytron** ZEUNER, 1959b, p. 408 [**G. croftii*; OD]. Little-known genus; elytron only. *Jur.*, Antarctica.
- Grasselites** BODE, 1953, p. 229 [**G. pusillus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Gyrinites** HEER, 1852, p. 12 [**G. troglodytes*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Gyrinopsis** HANDLIRSCH, 1906b, p. 446 [**Gyrinites antiquus* HEER, 1865, p. 91; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Gyrinulopsis** HANDLIRSCH, 1906b, p. 455 [**G. nanus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Hadrocephalus** HANDLIRSCH, 1906b, p. 444 [**H. anglicus* HANDLIRSCH, 1906b, p. 444; SD CARPENTER, herein]. Little-known genus. *Jur.*, England.
- Halocoleus** HAUPT, 1950, p. 152 [**H. cameratus*;

- OD]. Little-known genus, based on elytral fragments. *Eoc.*, Europe (Germany).
- Halticophana** HANDLIRSCH, 1906b, p. 552 [**H. westwoodi*; OD]. Little-known genus. *Jur.*, England.
- Harpalidium** WESTWOOD, 1854, p. 393 [**H. anactus*; SD HANDLIRSCH, 1906b, p. 560]. Little-known genus. GIEBEL, 1856. *Jur.*, England.
- Harpalomimis** HANDLIRSCH, 1906b, p. 562 [**Harpalus burmeisteri* GIEBEL, 1856, p. 63; OD]. Little-known genus. *Jur.*, England.
- Heeriaopsis** CARPENTER, 1986, p. 578, *nom. subst. pro Heeriella* HANDLIRSCH, 1906b, p. 401, *non* MEUNIER, 1904a [**Elytridium laevigatum* HEER, 1878, p. 196; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Helophoropsis** HANDLIRSCH, 1906b, p. 543 [**Helophorus brodiei* GIEBEL, 1856, p. 51; OD]. Little-known genus. *Jur.*, England.
- Helopides** ROEMER, 1876, p. 351 [**H. hildesiensis*; OD]. Little-known genus. ZEUNER, 1930. *Trias.*, Europe (Germany).
- Helopidium** WESTWOOD, 1854, p. 395 [**H. neorides*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Helopium** WESTWOOD, 1854, p. 393 [**H. agabus*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Hemidonacia** HAUPT, 1956, p. 60 [**H. involuta*; OD]. Little-known genus, based on elytral fragments. *Eoc.*, Europe (Germany).
- Hemisphaericosites** HAUPT, 1956, p. 71 [**H. sphaericus*; OD]. Little-known genus; elytral fragments. *Eoc.*, Europe (Germany).
- Hexameristus** BODE, 1953, p. 210 [**H. inflatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Holcoelytrum** HANDLIRSCH, 1906b, p. 453 [**Harpalus gebeli*; OD]. Little-known genus. ZEUNER, 1962a. *Jur.*, Europe (Germany).
- Holcoptera** HANDLIRSCH, 1906b, p. 453 [**Harpalus schlotbeimi* GIEBEL, 1856, p. 63; OD]. Little-known genus. *Jur.*, England.
- Hydrobiites** HEER, 1865, p. 91 [**H. veteranus*; OD]. Little-known genus. GIEBEL, 1856. *Jur.*, Europe (Germany), England.
- Hydroicetes** BODE, 1953, p. 232 [**H. affictus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Hydrophilites** HEER, 1865, p. 91 [collective group]. Little-known group. HEER, 1883. *Jur.*, Europe (Switzerland); *Mio.*, Greenland.
- Hydroporopsis** HANDLIRSCH, 1906b, p. 559 [**Hydroporus neptuni* GIEBEL, 1856, p. 58; OD]. Little-known genus. *Jur.*, England.
- Hylobiites** SCUDDER, 1895b, p. 30 [**H. cretaceus*; OD]. Little-known genus. HANDLIRSCH, 1907. *Cret.*, Canada (Manitoba).
- Hyperomima** HANDLIRSCH, 1906b, p. 567 [**Hypera antiqua* GIEBEL, 1856, p. 140; OD]. Little-known genus. MEUNIER, 1899b. *Jur.*, England.
- Ironicus** HANDLIRSCH, 1906b, p. 558 [**Harpalidium notbrus* WESTWOOD, 1854, p. 386; OD]. Little-known genus. *Jur.*, England.
- Kakoselia** HANDLIRSCH, 1906b, p. 561 [**Camptodontus angliae* GIEBEL, 1856, p. 65; OD]. Little-known genus. *Jur.*, England.
- Kamaroma** HANDLIRSCH, 1906b, p. 565 [**K. breve*; OD]. Little-known genus. *Jur.*, England.
- Katapiptus** HANDLIRSCH, 1906b, p. 558 [**K. striolatus*; OD]. Little-known genus. *Jur.*, England.
- Katapontisus** HANDLIRSCH, 1906b, p. 565 [**Elmis brodiei* GIEBEL, 1856, p. 50; OD]. Little-known genus. *Jur.*, England.
- Keleusticus** HANDLIRSCH, 1906b, p. 450 [**Buprestites zirkeli* GEINITZ, 1894, p. 75; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Kelidus** HANDLIRSCH, 1906b, p. 556 [**Buprestium bolbus* WESTWOOD, 1854, p. 386; OD]. Little-known genus. *Jur.*, England.
- Kibdelia** HANDLIRSCH, 1906b, p. 559 [**Prionus ooliticus* BRODIE, 1845, p. 47; OD]. Little-known genus. *Jur.*, England.
- Laimocenos** BODE, 1953, p. 235 [**L. striatogranulatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Lamiites** FRITSCH, 1889, p. 8 [**L. similimus*; OD]. Little-known genus. FRITSCH, 1901. *Cret.*, Europe (Czechoslovakia).
- Lamiophanes** HANDLIRSCH, 1906b, p. 557 [**Lamia schroeteri* GIEBEL, 1856, p. 131; OD]. Little-known genus. *Jur.*, England.
- Latridiites** HEER, 1865, p. 89 [**L. schaumii*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Leptomites** BODE, 1953, p. 237 [**L. procerus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Leptosolenophorus** BODE, 1953, p. 231 [**L. brevicollis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Leprynticus** BODE, 1953, p. 221 [**L. procerus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Liassocarabites** BODE, 1953, p. 226 [**L. praefricatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Loxocamarotus** BODE, 1953, p. 216 [**L. virgatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Loxostelidorus** BODE, 1953, p. 218 [**L. minutus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Macrotrachelites** BODE, 1953, p. 216 [**M. longus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Masselytron** HANDLIRSCH, 1939, p. 68 [**M. quinquestriatum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Megacentrus** HEER, 1852, p. 14 [**M. tristis*; OD]. Little-known genus, based on body fragments. DOLIN, 1973. *Jur.*, Europe (Switzerland).
- Megachorites** BODE, 1953, p. 229 [**M. brevicollis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Megelytrites** BODE, 1953, p. 227 [**M. mutilatus*;

- OD]. Little-known genus. *Jur.*, Europe (Germany).
- Melanocantharis** BODE, 1953, p. 234 [**M. bicornuta*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Melanophilites** HANDLIRSCH, 1906b, p. 453 [**Melanophila sculptilis* HEER, 1852, p. 14; OD]. Little-known genus. HEER, 1865. *Jur.*, Europe (Switzerland).
- Melanophilopsis** HANDLIRSCH, 1906b, p. 452 [**Melanophila costata* HEER, 1865, p. 88; OD]. Little-known genus. HEER, 1852. *Jur.*, Europe (Switzerland).
- Melolonthites** HEER, 1847, p. 71 [**M. aciculatus* HEER, 1847, p. 71; SD CARPENTER, herein]. *Mio.*, Europe (Germany).
- Memptus** HANDLIRSCH, 1906b, p. 563 [**M. braueri* HANDLIRSCH, 1906b, p. 563; SD CARPENTER, herein]. Little-known genus. *Jur.*, USSR (Asian RSFSR).
- Menephioides** FUJUYAMA, 1973, p. 378 [**M. minensis*; OD]. Little-known genus, based on elytron. *Trias.*, Japan.
- Mesalocistus** BODE, 1953, p. 222 [**M. constrictus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Meseumalpites** PONOMARENKO in ROHDENDORF, 1962a, p. 266, *nom. subst. pro Eumalpites* MARTYNOV, 1926a, p. 38, *non* HEER, 1865 [**Eumalpites jurassicus* MARTYNOV; OD]. Head not visible from above; pronotum with anterior margin convex, posterior angles acute. MEDVEDEV, 1968. *Jur.*, USSR (Kazakh).
- Mesoagrites** MARTYNOV, 1935b, p. 42 [**M. multipunctatus*; OD]. Elytra elongate, resembling those of *Donacia* (recent) but with 14 narrow rows of small pits. *Jur.*, USSR (Asian RSFSR).
- Mesolobites** CARPENTER, 1986, p. 578, *nom. subst. pro Lobites* DUNSTAN, 1923, p. 53, *non* MOJSISOVICIS, 1873 [**Lobites tuberculatus* DUNSTAN; OD]. Little-known genus, based on isolated elytra. *Trias.*, Australia (Queensland).
- Mesoncus** CARPENTER, 1986, p. 578, *nom. subst. pro Loxoncus* BODE, 1953, p. 218, *non* SCHMIDT-GOEBEL, 1846 [**Loxoncus procerus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Mesorhynchophora** TILLYARD in TILLYARD & DUNSTAN, 1916, p. 42 [**M. dunstani*; OD]. Little-known genus, based on elytral fragment. *Jur.*, Australia (Queensland).
- Mesotyrites** BODE, 1953, p. 233 [**M. marginatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Metacupes** GARDINER, 1961, p. 88 [**M. harrisi*; OD]. Little-known genus, based on elytral fragment. *Trias.*, England.
- Metagriliium** HANDLIRSCH, 1906b, p. 553 [**M. westwoodi*; OD]. Little-known genus. WESTWOOD, 1854. *Jur.*, England.
- Micranthaxia** HEER, 1852, p. 14 [**M. rediviva*; OD]. Little-known genus. HEER, 1865. *Jur.*, Europe (Switzerland).
- Micrelaterium** HANDLIRSCH, 1906b, p. 554 [**Elaterium triopas* WESTWOOD, 1854, p. 389; OD]. Little-known genus. DOLIN, 1973. *Jur.*, England.
- Microcoleopteron** HANDLIRSCH, 1906b, p. 550 [collective group]. Small beetles of uncertain family position. WEYENBERGH, 1869; OPPENHEIM, 1888; MEUNIER, 1898b; ALTENA, 1958. *Jur.*, Europe (Germany).
- Mikrocarpides** BODE, 1953, p. 232 [**M. lineatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Mimelater** HANDLIRSCH, 1906b, p. 449 [**Elater angulatus* GIEBEL, 1856, p. 92; OD]. Little-known genus. DOLIN, 1973. *Jur.*, England.
- Mimemala** STRAND, 1936, p. 169, *nom. subst. pro Mimema* HANDLIRSCH, 1906b, p. 557, *non* WOLLASTON, 1861 [**Mimema punctatum* HANDLIRSCH; OD]. Little-known genus, possibly a buprestid. *Jur.*, England.
- Mimohelops** HAUPT, 1950, p. 130 [**M. venosus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).
- Nannocurculionites** HANDLIRSCH, 1906b, p. 401 [**Curculionites carlsoni* HEER, 1878, p. 195; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Nannoodes** HANDLIRSCH, 1906b, p. 446 [**N. pseudocistela*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Nebrioides** HANDLIRSCH, 1906b, p. 455 [**Nebria dobertinensis* GEINITZ, 1894, p. 77; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Necronectulus** PONOMARENKO, 1977b, p. 90 [**N. avus*; OD]. Little-known genus of aquatic species. Antennae thin and short, reaching only to base of pronotum; metepisternites reaching to cavities of middle coxae. *Jur.*, USSR (Kazakh).
- Nitidulites** HEER, 1865, p. 90 [**N. argoviensis*; OD] [= *Parnidium* GEINITZ, 1894, p. 77, obj.]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, Europe (Germany, Switzerland).
- Notokistus** HANDLIRSCH, 1906b, p. 444 [**N. brodiei*; OD]. Little-known genus. *Jur.*, England.
- Ochtebiites** PONOMARENKO, 1977c, p. 106 [collective group]. Little-known genus, possibly related to the Hydraenidae. *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).
- Oligovarus** CARPENTER, 1986, p. 578, *nom. subst. pro Varus* SCHLECHTENDAL, 1894, p. 209, *non* STÅL, 1865 [**Varus ignotus* SCHLECHTENDAL; OD]. Little-known genus. *Oligo.*, Europe (Germany).
- Omogonylus** BODE, 1953, p. 213 [**O. ovatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Onkedodimus** HANDLIRSCH, 1939, p. 70 [**O. discicollis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Ooidellus** CARPENTER, 1986, p. 579, *nom. subst. pro Ooides* BODE, 1953, p. 234, *non* AGASSIZ, 1846

- [**Ooides denudatus* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Ooperiglyptus** BODE, 1953, p. 219 [**O. contractus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Ooperioristus** BODE, 1953, p. 220 [**O. applanatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Opiselleipon** BODE, 1953, p. 230 [**O. gravis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Opsis** HANDLIRSCH, 1906b, p. 544 [**O. bavarica*; OD]. Little-known genus. ALTEHA, 1958. *Jur.*, Europe (Germany).
- Otiorrhynchites** HAUPT, 1956, p. 81 [**O. densepunctatus*; OD]. Little-known genus, based on elytral fragment. *Eoc.*, Europe (Germany).
- Oxycephalites** BODE, 1953, p. 207 [**O. curculioides*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Oxytrotiptera** HANDLIRSCH, 1939, p. 68 [**O. mediocris*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pachycoleon** HANDLIRSCH, 1906b, p. 560 [**Buprestim woodlei* WESTWOOD, 1854, p. 393; OD]. Little-known genus. *Jur.*, England.
- Pachypleurites** HAUPT, 1952, p. 247 [**P. nodosus*; OD]. Little-known genus; elytral fragment. *Perm.*, Europe (Germany).
- Palaeobelostoma** MEUNIER, 1896, p. 95 [**P. hartingi*; OD]. Little-known genus, possibly a synonym of *Pseudohydrophilus* (Coptoclavidae). HANDLIRSCH, 1906b. *Jur.*, Europe (Germany).
- Palaeotrachys** BODE, 1953, p. 215 [**P. laticollis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Paleobuprestis** WALKER, 1938, p. 138 [**P. maxima*; OD]. Tunnels in fossil wood, apparently made by beetle larvae. *Trias.*, USA (Arizona).
- Paleoipidus** WALKER, 1938, p. 140 [**P. perforatus*; OD]. Tunnels in fossil wood, apparently made by beetle larvae. *Trias.*, USA (Arizona).
- Paleoscolytus** WALKER, 1938, p. 139 [**P. divergens*; OD]. Tunnels in fossil wood, apparently made by beetles. *Trias.*, USA (Arizona).
- Pallax** HANDLIRSCH, 1906b, p. 560 [**P. prevosti*; OD]. Little-known genus. *Jur.*, England.
- Pantodapus** HANDLIRSCH, 1906b, p. 564 [**Harpalus knorri* GIEBEL, 1856, p. 62; OD]. Little-known genus. MEUNIER, 1899b. *Jur.*, England.
- Parabuprestites** HANDLIRSCH, 1906b, p. 400 [**Buprestites rugulosus* HEER, 1878, p. 194; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Parabuprestium** HANDLIRSCH, 1906b, p. 554 [**Buprestium teleas* WESTWOOD, 1854, p. 386; SD CARPENTER, herein]. Little-known genus. GIEBEL, 1856. *Jur.*, England.
- Paracurculionites** HANDLIRSCH, 1906b, p. 401 [**Curculionites parvulus* HEER, 1878, p. 195; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Paracurculium** HANDLIRSCH, 1906b, p. 455 [**Curculionites punctatus* GEINITZ, 1894, p. 77; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Paradoggeria** HANDLIRSCH, 1906b, p. 556 [**P. acuminata*; OD]. Little-known genus. *Jur.*, England.
- Paragrillium** HANDLIRSCH, 1906b, p. 553 [**Elaterium barypus* WESTWOOD, 1854, p. 389; OD]. Little-known genus. *Jur.*, England.
- Paragyrrinus** HANDLIRSCH, 1906b, p. 448 [**Gyrrinus dubius* GIEBEL, 1856, p. 56; OD]. Little-known genus. *Jur.*, England.
- Parakeleusticus** HAUPT, 1950, p. 126 [**P. posthumus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).
- Parandrexia** MARTYNOV, 1926a, p. 19 [**P. parvula*; OD]. Little-known genus. MEDVEDEV, 1969. *Jur.*, USSR (Kazakh).
- Parasilphites** HANDLIRSCH, 1906b, p. 547 [**Silphites angusticollis* OPPENHEIM, 1888, p. 239; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Parnosoma** CARPENTER, 1986, p. 579, *nom. subst. pro Pedinosoma* BODE, 1953, p. 235, *non* REIBISCH, 1893 [**Pedinosoma detectum* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Paropiophorus** HAUPT, 1950, p. 132 [**P. nitidulus*; OD]. Little-known genus. *Eoc.*, Europe (Germany).
- Pausopsia** COCKERELL, 1911b, p. 71 [**P. nearctica*; OD]. Little-known genus, possibly belonging to the Carabidae. WICKHAM, 1912a; WASMANN, 1926a, 1929a; DARLINGTON, 1950. *Oligo.*, USA (Colorado).
- Peltsosyne** PONOMARENKO, 1977c, p. 105 [**P. triasica*; OD]. Little-known genus; metepisternum not reaching cavities of middle coxae; abdomen with 5 visible sternites. *Trias.*, USSR (Kirghiz).
- Periboloptera** HANDLIRSCH, 1939, p. 67 [**P. rotunda*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Peridosoma** CARPENTER, 1986, p. 579, *nom. subst. pro Perosoma* BODE, 1953, p. 217, *non* BRONN, 1862 [**Perosoma praecisum* BODE; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Petrorophus** HEER, 1852, p. 12 [**P. truncatus*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Phanerogramma** COCKERELL, 1915, p. 479 [**Akicera heeri* GIEBEL, 1856, p. 30; OD]. Little-known genus, based on elytral fragment. *Jur.*, England.
- Phaulogyrrinus** HANDLIRSCH, 1906b, p. 448 [**Gyrrinites minimus* HEER, 1865, p. 91; OD]. *Jur.*, Europe (Switzerland).
- Pholipheron** BODE, 1953, p. 206 [**P. articulatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Phytoplezion** BODE, 1953, p. 236 [**P. ovatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pimeliodes** FRITSCH, 1901, p. 172 [**P. parvus*; OD]. Little-known genus. *Cret.*, Europe (Czechoslovakia).

- Plastelater** HANDLIRSCH, 1906b, p. 438 [**Elater neptuni* GIEBEL, 1856, p. 91; OD]. Little-known genus; pronotum and elytra. DOLIN, 1973. *Jur.*, England.
- Plastobuprestites** HANDLIRSCH, 1906b, p. 444 [**Buprestites elegans* GEINITZ, 1894, p. 76; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Plastonebria** HANDLIRSCH, 1906b, p. 444 [**Nebria scudderi* GEINITZ, 1894, p. 74; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pleuralocista** BODE, 1953, p. 213 [**P. insculpta*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pliosilpha** GERSDORF, 1969, p. 307 [**P. strausi*; OD]. Little-known genus. *Plio.*, Europe (Germany).
- Polypamon** HANDLIRSCH, 1906b, p. 456 [**Cistelites byrrhoides* GEINITZ, 1894, p. 76; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Prionophana** HANDLIRSCH, 1906b, p. 557 [**Prionus antiquus* GIEBEL, 1856, p. 126; OD]. Little-known genus. *Jur.*, England.
- Procalosoma** MEUNIER, 1895a, p. 207 [**P. giardi*; OD]. Little-known genus. HANDLIRSCH, 1906b; BREUNING, 1928b; ALTENA, 1958. *Jur.*, Europe (Germany).
- Procarabites** HANDLIRSCH, 1906b, p. 440 [**Carabites bellus* HEER, 1865, p. 90; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Prochrysomela** HANDLIRSCH, 1906b, p. 550 [**Chrysomelites jurassicus* OPPENHEIM, 1888, p. 242; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Proctobuprestis** HANDLIRSCH, 1906b, p. 439 [**Glaphyoptera brevicollis* HEER, 1865, p. 88; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Proheuristes** BODE, 1953, p. 225 [**P. striatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Prophasis** HANDLIRSCH, 1906b, p. 566 [**Chrysomela ignota* GIEBEL, 1856, p. 120; OD]. Little-known genus. *Jur.*, England.
- Prosthenostictus** HANDLIRSCH, 1906b, p. 562 [**Crypticus ungeri* GIEBEL, 1856, p. 110; OD]. Little-known genus. *Jur.*, England.
- Prosynactus** BODE, 1953, p. 224 [**P. scissus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Protocuneus** COCKERELL, 1915, p. 477 [**P. punctatus*; OD]. Little-known genus; elytral fragment. *Jur.*, England.
- Prototoma** HEER, 1852, p. 12 [**P. striata*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Pseudobuprestites** HANDLIRSCH, 1906b, p. 399 [**Glaphyoptera pterophylli* HEER, 1853b, p. 133; OD]. Little-known genus. *Trias.*, Europe (Germany).
- Pseudocarabites** HANDLIRSCH, 1906b, p. 401 [**Carabites deplanatus* HEER, 1878, p. 197; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Pseudochrysomelites** HANDLIRSCH, 1906b, p. 400 [**Chrysomelites rothenbachi* HEER, 1877, p. 76; OD]. Little-known genus; elytron only. *Trias.*, Europe (Switzerland).
- Pseudocurculionites** HANDLIRSCH, 1906b, p. 399 [**Curculionites prodromus* HEER, 1853b, p. 134; OD]. Little-known genus. *Trias.*, Europe (Germany).
- Pseudocymindis** HANDLIRSCH, 1906b, p. 560 [**Cymindis antiqua* GIEBEL, 1856, p. 69; OD]. Little-known genus. *Jur.*, England.
- Pseudocyphon** HANDLIRSCH, 1906b, p. 446 [**Cyphon vetustus* GEINITZ, 1894, p. 78; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pseudoelateropsis** HANDLIRSCH, 1906b, p. 399, *nom. subst. pro Elateropsis* ROEMER, 1876, p. 351, *non* CHEVOLAT, 1862 [**Elateropsis infraliassica* ROEMER; OD]. Little-known genus; elytra only. DOLIN, 1973. *Trias.*, Europe (Germany).
- Pseudohydrophilites** HANDLIRSCH, 1906b, p. 400 [**Hydrophilites nathorsti* HEER, 1878, p. 193; OD]. Little-known genus; elytron only. *Trias.*, Europe (Sweden).
- Pseudopronites** HANDLIRSCH, 1906b, p. 453 [**Prionus liasinus* GEINITZ, 1894, p. 72; OD]. *Jur.*, Europe (Germany).
- Pseudorhynchophora** HANDLIRSCH, 1906b, p. 402 [**P. olliffi*; OD]. Little-known genus; elytron only. *Trias.*, Australia (Queensland).
- Pseudosilphites** ZEUNER, 1930, p. 462 [**P. triassicus*; OD]. Little-known genus; elytra and abdominal fragments. ZEUNER, 1961. *Trias.*, Europe (Germany), South Africa.
- Pseudotelephorus** HANDLIRSCH, 1906b, p. 454 [**Telephorus baueri* GIEBEL, 1856, p. 101; OD]. Little-known genus. COCKERELL, 1915. *Jur.*, England.
- Pseudotenebrio** HANDLIRSCH, 1906b, p. 550 [**Tenebrio innominatus* WEYENBERGH, 1869, p. 285; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Pseudothyrea** HANDLIRSCH, 1906b, p. 541 [**P. oppenheimi*; OD]. Little-known genus, possibly a buprestid. OPPENHEIM, 1888; DOLIN, 1973. *Jur.*, Europe (Germany).
- Pseudus** HANDLIRSCH, 1906b, p. 563 [**P. purbecensis*; OD]. Little-known genus. *Jur.*, England.
- Pyrochroophana** HANDLIRSCH, 1906b, p. 542 [**Pyrochroa brevipedis* DEICHMÜLLER, 1886, p. 72; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Reeveana** DUNSTAN, 1923, p. 48 [**R. minor*; OD]. Little-known genus, elytron only. *Trias.*, Australia (Queensland).
- Rhabdotus** BODE, 1953, p. 223 [**R. cingulatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Rhinohelaeites** HAUPT, 1950, p. 140 [**R. longipes*; OD]. Little-known genus. [Family assignment doubtful.] *Eoc.*, Europe (Germany).
- Rhomaleus** BODE, 1953, p. 228 [**R. ornatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).

- Rhysopsalis** BODE, 1953, p. 214 [**R. distorta*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Scalopoides** BODE, 1953, p. 225 [**S. incisus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Scaphidiopsis** HANDLIRSCH, 1906b, p. 550 [**Scaphidium hageni* WEYENBERGH, 1869, p. 281; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Semiglobus** HANDLIRSCH, 1906b, p. 566 [**S. jurasicus*; OD]. Little-known genus. *Jur.*, England.
- Siderosemion** BODE, 1953, p. 211 [**S. punctolineatum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Silicernius** HEYDEN, 1859a, p. 6 [**S. spectabilis*; OD]. Little-known genus, possibly belonging to the Elateridae. HEYDEN, 1858. *Oligo.*, Europe (Germany).
- Silphites** FRITSCH, 1869a, p. 188 [**S. priscus*; OD] [= *Silphidium* HANDLIRSCH, 1907, p. 664, obj.]. Little-known genus. FRITSCH, 1901. *Cret.*, Europe (Czechoslovakia).
- Sitonites** HEER, 1865, p. 90 [**S. melanarius*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, Europe (Switzerland).
- Smodicoptera** HANDLIRSCH, 1906b, p. 452 [**Euchroma lasina* HEER, 1852, p. 13; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Spalacoides** BODE, 1953, p. 214 [**S. simplex*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Sphaericites** BODE, 1953, p. 233 [**S. concameratus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Sphaerocantharis** BODE, 1953, p. 213 [**S. defossa*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Stenelytron** HANDLIRSCH, 1906b, p. 451 [**Elater redtenbacheri* GIEBEL, 1856, p. 92; OD]. Little-known genus. DOLIN, 1973. *Jur.*, England.
- Stictulus** HANDLIRSCH, 1906b, p. 562 [**S. brodiei*; OD]. Little-known genus. *Jur.*, England.
- Stigmenamma** HANDLIRSCH, 1906b, p. 451 [**Harpalus heeri* GIEBEL, 1856, p. 63; OD]. Little-known genus. *Jur.*, England.
- Streblocardioides** BODE, 1953, p. 210 [**S. striatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Strongylites** HEER, 1865, p. 89 [**S. stygicus* HEER, 1865, p. 89; SD CARPENTER, herein]. Little-known genus. *Jur.*, Europe (Switzerland).
- Syntomopteris** BODE, 1953, p. 209 [**S. latus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Telephorium** WESTWOOD, 1854, p. 395 [**T. abgarus*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Tentyridium** WESTWOOD, 1854, p. 393 [**T. peleus*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, England.
- Tetragonides** BODE, 1953, p. 225 [**T. magnus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Tetragonotrachelus** BODE, 1953, p. 224 [**T. gracilis*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Theornithion** BODE, 1953, p. 217 [**T. striatum*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Thoracotes** HANDLIRSCH, 1906b, p. 438 [**T. dubius*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Thurmannia** HEER, 1852, p. 11 [**T. punctata*; OD]. Little-known genus. HEER, 1865. *Jur.*, Europe (Switzerland).
- Timarchopsis** BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 17 [**T. czekanowskii*; OD]. Little-known genus. HANDLIRSCH, 1906b. *Jur.*, USSR (Asian RSFSR).
- Tolype** BODE, 1953, p. 212 [**T. rotundata*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Trapezotrachelus** BODE, 1953, p. 215 [**T. longus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Triadocoleopteron** ZEUNER, 1930, p. 466 [**T. spectabile*; OD]. Little-known genus, possibly belonging to Silphidae. *Trias.*, Europe (Germany).
- Triadogyrus** PONOMARENKO, 1977b, p. 95 [**T. sternalis*; OD]. Little-known genus. Adults apparently aquatic, possibly related to Gyrinidae. Hind coxae short; abdomen with 6 visible segments. *Trias.*, USSR (Ukraine).
- Trichelepturgetes** BODE, 1953, p. 227 [**T. procerus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Tricyrtus** BODE, 1953, p. 230 [**T. tenuistriatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Trigonocephalites** BODE, 1953, p. 239 [**T. sulcatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Tripsalis** BODE, 1953, p. 208 [**T. praecisa*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Trixagites** HEER, 1865, p. 90 [**T. floralis*; OD]. Little-known genus. *Jur.*, Europe (Switzerland).
- Trochiscites** BODE, 1953, p. 215 [**T. capitapertus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Trochmalus** BODE, 1953, p. 214 [**T. compressus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Tryoniopsis** DUNSTAN, 1923, p. 52 [**T. punctata*; OD]. Little-known genus, elytron only. *Trias.*, Australia (Queensland).
- Tychon** HANDLIRSCH, 1906b, p. 563 [**Helophorus antiquus* GIEBEL, 1856, p. 51; OD]. Little-known genus. *Jur.*, England.
- Umkomaasia** ZEUNER, 1961, p. 305 [**U. depressa*; OD]. Little-known genus, based on elytron, possibly belonging to Carabidae. *Trias.*, South Africa.
- Velenovskya** FRITSCH, 1889, p. 8 [**V. inornata*; OD]. Little-known genus. K. W. FRITSCH, 1901. *Cret.*, Europe (Czechoslovakia).

- Wollastonia** HEER, 1852, p. 13 [**W. ovalis*; OD] [= *Wollastonites* HEER, 1865, p. 91, obj.]. Little-known genus. *Jur.*, Europe (Switzerland).
- Xenogyrinus** HANDLIRSCH, 1906b, p. 448 [**Gyrinus natanis* BRODIE, 1845, p. 101; OD]. Little-known genus. HEER, 1852. *Jur.*, England.
- Xyloconites** HAUPT, 1950, p. 143 [**X. proavus*; OD]. Little-known genus; elytron only. *Eoc.*, Europe (Germany).
- Xylotupia** HANDLIRSCH, 1906b, p. 557 [**X. brodiei*; OD]. Little-known genus. *Jur.*, England.
- Zetemenos** BODE, 1953, p. 230 [**Z. sexlineatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).
- Zygadenia** HANDLIRSCH, 1906b, p. 558 [**Curculionites tuberculatus* GIEBEL, 1856, p. 148; OD]. Little-known genus. *Jur.*, England.

RECENT GENERA OF COLEOPTERA WITH DOUBTFULLY ASSIGNED SPECIES

Extinct species belonging to the recent genera listed below have been described from diverse strata, nearly all within the Tertiary. Many of the species were named and assigned to the genera before 1900 (e.g., by GERMAR, HEER, HEYDEN, and GEINITZ), well before the present concepts of coleopterous genera were reached. Many other fossil beetles were described and placed in existing genera during the early part of the present century by individuals who had little knowledge of the order (e.g., COCKERELL and MEUNIER) or who did not appreciate the difficulties of making generic assignments on the basis of isolated elytra (e.g., WICKHAM), as pointed out by DARLINGTON (1929, 1969). Several contemporary coleopterists, specialists in various families, have examined type specimens of such Coleoptera from the Eocene and Oligocene of Colorado and have reported that they were unable to discern sufficient structural details to permit generic determinations or in some instances even family positions. It seems likely, therefore, that the great majority of the genera listed below, probably as many as 90 percent, can only very doubtfully be associated with the fossils described. To emphasize the dubious nature of these generic assignments, generic names have been

enclosed in quotation marks in the following list, which is arranged by families and includes some families not otherwise known in the fossil record.

Family Carabidae

- "Abax," *Plio.*, England. LESNE, 1926a.
- "Agonum," *Eoc.*, Europe (France). PITON, 1940a.
- "Amara," *Oligo.*, USA (Colorado). WICKHAM, 1912a; EMERSON, 1942.
- "Anchromenus," *Oligo.*, Europe (France); *Mio.*, Europe (Yugoslavia). HEER, 1847; FÖRSTER, 1891.
- "Argutor," *Mio.*, Europe (Germany); *Plio.*, England. HEER, 1847; GIEBEL, 1856; LESNE, 1926b; IABLOKOV-KHNZORIAN, 1961c.
- "Badister," *Mio.*, Europe (Germany). HEER, 1847, 1862b.
- "Bembidion," *Eoc.*, USA (Colorado), Europe (France); *Oligo.*, USA (Colorado); *Mio.*, USA (California). SCUDDER, 1900; WICKHAM, 1913c; PITON, 1940a; PIERCE, 1944.
- "Brachinus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Calosoma," *Plio.*, Europe (Germany). GERSDORF, 1969, 1976.
- "Carabus," *Eoc.*, Europe (Italy); *Oligo.*, USA (Colorado); *Mio./Plio.*, Europe (France). OMBONI, 1886; SCUDDER, 1900; PITON & THÉOBALD, 1935.
- "Chlaenius," *Oligo.*, Europe (France). GRESSITT, 1963.
- "Cratacanthus," *Oligo.*, USA (Colorado). WICKHAM, 1917.
- "Cymindis," *Mio.*, Europe (Germany). HEER, 1847.
- "Dichotrichus," *Mio.*, Europe (Germany). HEER, 1862b.
- "Dromius," *Oligo.*, Europe (Baltic). GERMAR & BERENDT, 1856.
- "Elaphrus," *Plio.*, Europe (France). PITON, 1939.
- "Ergates," *Mio.*, Europe (Germany). COCKERELL, 1922g.
- "Evarthrus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Feronia," *Mio.*, Europe (Germany). HEER, 1847.
- "Galerita," *Eoc.*, USA (Colorado). SCUDDER, 1900.
- "Glenopterus," *Mio.*, Europe (Germany). HEER, 1847.
- "Harpalus," *Eoc.*, USA (Colorado), Europe (France); *Oligo.*, USA (Colorado), Europe (France). SCUDDER, 1900; WICKHAM, 1911, 1917; COCKERELL, 1920c; THÉOBALD, 1937a; PITON, 1940a.
- "Helluomorpha," *Oligo.*, Europe (Baltic). GIEBEL, 1862.
- "Lebia," *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany); *Plio.*, Europe (France); *Paleoc.-Plio.*, Argentina (Jujuy). HEYDEN & HEYDEN, 1866; COCKERELL, 1913a, 1921a, 1936.
- "Myas," *Oligo.*, USA (Colorado). SCUDDER, 1900.

- "Nebria," *Paleoc.*, Canada (British Columbia); *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEER, 1862a; SCUDDER, 1879a, 1900; PITON & THÉOBALD, 1935.
- "Nomaretus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Nothopus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Ophonus," *Mio.*, Europe (France). PITON, 1937b.
- "Panagaeus," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Peocillus," *Eoc.*, Europe (Hungary). PONGRÁCZ, 1935.
- "Petrobius," *Paleoc.-Plio.*, USSR (Asian RSFSR). COCKERELL, 1925g.
- "Platynus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1890; TILLYARD & DUNSTAN, 1916; WICKHAM, 1917.
- "Plochionus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Polystichus," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Pterosticus," *Oligo.*, USA (Colorado), England, Europe (France); *Mio.*, USA (Washington); *Paleoc.-Plio.*, Europe (Sweden). SCUDDER, 1900; WICKHAM, 1910, 1931; HATCH, 1927b; KOLBE, 1933.
- "Rembus," *Oligo.*, USA (Colorado). SCUDDER, 1890; WICKHAM, 1920.
- "Scarites," *Oligo.*, Europe (France); *Mio.*, Europe (Yugoslavia). HEER, 1861; THÉOBALD, 1937a.
- "Stenoplus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
- "Stomis," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Tachys," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
- "Trechus," *Oligo.*, USA (Colorado), Europe (France); *Plio.*, England. FÖRSTER, 1891; WICKHAM, 1912a, 1912b; LESNE, 1926b.

Family Dytiscidae

- "Acilus," *Oligo.*, USA (Colorado). WICKHAM, 1909.
- "Agabus," *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN & HEYDEN, 1866; WICKHAM, 1912b, 1913b.
- "Bidessus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
- "Coelambus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
- "Colymbetes," *Mio.*, Europe (Yugoslavia). HEER, 1847.
- "Cybister," *Mio.*, Europe (Germany). HEER, 1862a, 1865.
- "Cymatopterus," *Oligo.*, Europe (France). HEER, 1847.
- "Dytiscus," *Oligo.*, Europe (France); *Mio.*, USA (Washington), Europe (Germany); *Plio.*, Europe (Germany). HEER, 1847; WICKHAM, 1931; KOLBE, 1932; THÉOBALD, 1937a.
- "Hydaticus," *Mio.*, Europe (Germany). HEER, 1861.
- "Hydroporus," *Oligo.*, USA (Colorado), Europe (Germany); *Plio.*, England. HEER, 1862a; WICKHAM, 1914a; LESNE, 1926a; THÉOBALD, 1937a; STATZ, 1939–1940.
- "Laccophilus," *Mio.*, Europe (Germany). HEER, 1862a.
- "Necticus," *Oligo.*, USA (Colorado). AYMARD, 1854.
- "Oreodites," *Oligo.*, Europe (Germany). STATZ, 1937, 1939–1940.
- "Pelobius," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.

Family Gyrinidae

- "Dineutes," *Mio.*, Europe (Germany). HEER, 1861, 1862a.

Family Georyssidae

- "Georyssus," *Eoc.*, Europe (Germany); *Plio.*, Europe (France). PITON, 1939; HAUPT, 1956.

Family Hydrophilidae

- "Berosus," *Eoc.*, USA (Wyoming); *Oligo.*, Europe (Germany). SCUDDER, 1878a; STATZ, 1939–1940.
- "Cercyon," *Paleoc.*, Canada (British Columbia). SCUDDER, 1879a.
- "Creniphilites," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
- "Cymbisdyta," *Oligo.*, Europe (Germany). STATZ, 1939–1940.
- "Gymnochila," *Mio.*, Europe (Germany). HEER, 1862b.
- "Helophorus," *Mio.*, Europe (Germany). HEER, 1862b.
- "Hydraena," *Plio.*, England. LESNE, 1920.
- "Hydrobius," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Europe (Yugoslavia, Germany). HEER 1847, 1856, 1862b, 1870a; SCUDDER, 1890; WICKHAM, 1911, 1913c; THÉOBALD, 1937a.
- "Hydrochus," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
- "Hydrophilus," *Oligo.*, USA (Colorado), Europe (Germany, France); *Mio.*, Europe (Germany); *Paleoc.-Plio.*, Europe (Roumania). HEER, 1847, 1862b, 1865; HEYDEN, 1862; OUSTALET, 1874; SCUDDER, 1900; WICKHAM, 1920; ZEUNER, 1931, 1938; PROTESCU, 1938; PITON & THÉOBALD, 1939; STATZ, 1939–1940.
- "Hydrous," *Oligo.-Mio.*, Europe (Germany). HEER, 1847, 1862b; HEYDEN, 1859b, HEYDEN & HEYDEN, 1866; STATZ, 1939–1940.
- "Lacobius," *Eoc.*, USA (Wyoming); *Oligo.*, Europe (Germany, France). HEYDEN & HEYDEN, 1866; OUSTALET, 1870, 1874; SCUDDER, 1878b; STATZ, 1937; THÉOBALD, 1937a.
- "Ochthebius," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
- "Paracymus," *Oligo.*, Europe (Germany). STATZ, 1939–1940.
- "Peltis," *Oligo.*, Europe (Germany). HEER, 1862b.

- "Philydrus," *Eoc.*, Europe (France); *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN & HEYDEN, 1866; WICKHAM, 1909; THÉOBALD, 1937a.
 "Tropisternus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1878a, 1900.

Family Histeridae

- "Hister," *Mio.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEER, 1862b; PITON & THÉOBALD, 1935.
 "Onthophilus," *Paleoc.-Plio.*, Europe (France). HANDSCHIN, 1944.

Family Ptiliidae

- "Ptilium," *Oligo.*, Europe (Germany). STATZ & HORION, 1937.

Family Silphidae

- "Agyrtes," *Oligo.*, USA (Colorado). HATCH, 1927b.
 "Necrodes," *Oligo.*, USA (Colorado). COCKERELL, 1908p.
 "Necrophorus," *Plio.*, Europe (Germany). GERSDORF, 1969.
 "Peltis," *Mio.*, Europe (France). PITON & THÉOBALD, 1935.
 "Silpha," *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany, France, Yugoslavia), Spitsbergen. GERMAR, 1837; HEER, 1847, 1862b, 1870a; WICKHAM, 1914a; ALTENA, 1958.
 "Xylodrepa," *Plio.*, Europe (Germany). GERSDORF, 1969.

Family Scaphidiidae

- "Scaphidium," *Mio.*, Europe (Germany). HEER, 1847.
 "Scaphisoma," *Mio.*, Europe (Germany). HEER, 1862b.

Family Staphylinidae

- "Acylophorus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Atheta," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
 "Bledius," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1862b; SCUDDER, 1878b, 1900.
 "Bolitobius," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Delester," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
 "Geodomiscus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Gyrophæna," *Eoc.*, USA (Colorado). SCUDDER, 1876a.
 "Heterothrops," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Homalium," *Mio.*, Europe (Yugoslavia). HEER, 1847.

- "Homalota," *Eoc.*, USA (Colorado). SCUDDER, 1890.
 "Hygronoma," *Oligo.*, Europe (France). OUSTALET, 1874.
 "Lathrobium," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1862b; SCUDDER, 1876a, 1890; WICKHAM, 1913c.
 "Leptacinus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Lithocharis," *Oligo.*, USA (Colorado), Europe (France). HEER, 1856; SCUDDER, 1900.
 "Micropeplus," *Plio.*, Europe (Germany). GERSDORF, 1976.
 "Mycetoporus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Ocybus," *Oligo.*, Europe (Germany). OUSTALET, 1874.
 "Omalius," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
 "Ontholestes," *Eoc.*, USA (Colorado). SCUDDER, 1876a.
 "Oxyporus," *Eoc.*, Europe (France), USA (Colorado); *Mio.*, Europe (Germany). HEER, 1862b; HEYDEN & HEYDEN, 1866; PITON, 1940a.
 "Oxytelus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Germany, France); *Mio.*, Europe (Germany). HEER, 1862b; SCUDDER, 1876a; FÖRSTER, 1891; WICKHAM, 1913c.
 "Paederus," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
 "Philonthus," *Oligo.*, USA (Colorado), Europe (Germany). HEER, 1856; HEYDEN & HEYDEN, 1866; SCUDDER, 1900.
 "Platystethus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Quedius," *Oligo.*, USA (Colorado), Europe (Germany, France). OUSTALET, 1874; SCUDDER, 1890; WICKHAM, 1912a.
 "Staphylinites," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
 "Staphylinus," *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Europe (Germany). HEER, 1862a; OUSTALET, 1874; SCUDDER, 1900; WICKHAM, 1913c.
 "Stenus," *Oligo.*, Europe (Baltic, Germany, France), USA (Colorado). HEER, 1856; MOTSCHULSKY, 1856; FÖRSTER, 1891; SCUDDER, 1900; MEUNIER, 1920a, 1920c; BENICK, 1943.
 "Sunius," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
 "Tachinus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Tachyporus," *Oligo.*, USA (Colorado), Europe (Germany). GEINITZ, 1886; SCUDDER, 1900.
 "Triga," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Xantholinus," *Oligo.*, USA (Colorado), Europe (France). HEER, 1856; SCUDDER, 1900.

Family Pselaphidae

- "Europepines," *Paleoc.-Plio.*, Australia (Victoria). OKE, 1956.

Family Lucanidae

- "Ceruchus," *Oligo.*, USA (Colorado). WICKHAM, 1911.
 "Corticaria," *Oligo.*, Europe (Germany, France). HEER, 1856; SCHLECHTENDAL, 1894.
 "Dorcus," *Mio.*, England. DEICHMÜLLER, 1881.
 "Lucanus," *Oligo.*, USA (Colorado). WICKHAM, 1913b.
 "Platycerus," *Oligo.*, Europe (Germany). GERMAR, 1837.

Family Scarabaeidae

- "Aegialia," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
 "Amphicomma," *Oligo.*, USA (Colorado). WICKHAM, 1910.
 "Anomala," *Oligo.*, USA (Colorado), Europe (Germany, France); *Mio.*, Europe (Germany). HEER, 1862b; HEYDEN & HEYDEN, 1866; WICKHAM, 1914a; MEUNIER, 1923c; GRESSITT, 1963.
 "Anomalites," *Paleoc.-Plio.*, Europe (France). FRITSCH, 1884b.
 "Anoplognathus," *Oligo.*, Europe (Germany). HEYDEN, 1862.
 "Aphodius," *Oligo.*, Europe (Baltic, Germany), USA (Colorado); *Mio.*, Europe (Germany); *Plio.*, Europe (Germany). ROBERT, 1838; HEER, 1847, 1862b; HEYDEN & HEYDEN, 1866; WICKHAM, 1911, 1912a, 1913b, 1913c, 1914a, 1914b; GERSDORF, 1970.
 "Ataenius," *Oligo.*, USA (Colorado). SCUDDER, 1893a; WICKHAM, 1912a.
 "Bolboceras," *Mio.*, Europe (Czechoslovakia). DEICHMÜLLER, 1881.
 "Coprins," *Mio.*, Europe (Germany); *Plio.*, England. HEER, 1862b; CURTIS, 1840.
 "Coprologus," *Mio.*, Europe (Germany). HEER, 1847.
 "Diplotaxis," *Oligo.*, USA (Colorado). WICKHAM, 1912a, 1913b.
 "Geotrupes," *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Germany). GERMAR, 1837, 1849; HEER, 1862b; OUSTALET, 1874.
 "Glaphyrus," *Mio.*, Europe (Germany). HEER, 1862b.
 "Gymnopleurus," *Mio.*, Europe (Germany). HEER, 1847, 1862b.
 "Hoplina," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Hybosurus," *Mio.*, Europe (Germany). HEER, 1862b.
 "Lepitrix," *Mio.*, Europe (Germany). HEER, 1862b.
 "Ligyryus," *Oligo.*, USA. WICKHAM, 1911, 1914a.
 "Listrochelus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Macroductylus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
 "Melolontha," *Oligo.*, Europe (Germany, Czechoslovakia). HEER, 1847; NOVÁK, 1877.
 "Onitis," *Oligo.*, Europe (Germany). HEYDEN, 1862.

- "Onthophagus," *Oligo.*, Europe (France); *Mio.*, Europe (Germany). HEER, 1847, 1862b; OUSTALET, 1874.
 "Oryctes," *Plio.*, Europe (Germany). GERSDORF, 1970.
 "Oxyomus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Pentodon," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany). HEER, 1865; HEYDEN & HEYDEN, 1866.
 "Phyllophaga," *Oligo.*, USA (Colorado). WICKHAM, 1916b.
 "Rhizotrogus," *Mio.*, Europe (Germany). HEER, 1847.
 "Scarabaeus," *Mio.*, Europe (Germany). HEER, 1862b.
 "Serica," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1862b; WICKHAM, 1912a, 1914b.
 "Strategus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Trichius," *Mio.*, Europe (Germany). HEER, 1847, 1862b, 1865.
 "Troz," *Paleoc.*, Canada (British Columbia). SCUDDER, 1879a; WICKHAM, 1909.
 "Valgus," *Mio.*, Europe (Germany). HEER, 1862b.

Family Dascillidae

- "Ectopria," *Oligo.*, USA (Colorado). BREUNING, 1928a.
 "Protacnaeus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.

Family Byrrhidae

- "Amphicyrta," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Byrrhus," *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN, 1859b; HEYDEN & HEYDEN, 1866; SCUDDER, 1895b, 1900.
 "Cytillus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Nosodendron," *Eoc.*, USA (Colorado). SCUDDER, 1890.
 "Nosotetocus," *Oligo.*, USA (Colorado). SCUDDER, 1900.

Family Psephenidae

- "Psephenus," *Oligo.*, USA (Colorado). SCUDDER, 1900.

Family Dryopidae

- "Helichus," *Oligo.*, USA (Colorado). WICKHAM, 1911, 1912a.

Family Chelonariidae

- "Chelonarium," *Oligo.*, USA (Colorado). WICKHAM, 1914a.

Family Buprestidae

- "Acmaeodera," *Mio.*, Europe (Germany). HEER, 1862b.
 "Agrilus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1865; WICKHAM, 1914a.
 "Ancyclocheira," *Oligo.-Mio.*, Europe (Germany). HEER, 1847, 1865; HEYDEN, 1859b, 1862.
 "Anthaxia," *Oligo.-Mio.*, Europe (Germany). HEER, 1862b; HEYDEN & HEYDEN, 1865; ASSMANN, 1870; FÖRSTER, 1891; WICKHAM, 1913b.
 "Brachyspathus," *Oligo.*, USA (Colorado). WICKHAM, 1917.
 "Buprestis," *Eoc.*, Canada (British Columbia); *Oligo.*, Europe (Germany), USA (Colorado). HEYDEN, 1858, 1859b; SCUDDER, 1879a, 1890; WICKHAM, 1914a.
 "Capnodis," *Mio.*, Europe (Germany). HEER, 1847, 1862b.
 "Chalcophora," *Mio.*, Europe (Germany). HEER, 1862b.
 "Chrysobothris," *Oligo.*, USA (Colorado). SCUDDER, 1876a; COCKERELL, 1911b; WICKHAM, 1914a.
 "Dicera," *Oligo.*, Europe (Germany), USA (Colorado); *Mio.*, Europe (Germany). HEER, 1847; HEYDEN, 1856, 1859b; ASSMANN, 1870; WICKHAM, 1914a.
 "Lampra," *Oligo.*, Europe (France). BRUYANT, 1902.
 "Lomatus," *Paleoc.-Plio.*, India (Nagpur). GERMAR, 1842.
 "Melanophila," *Oligo.*, USA (Colorado). WICKHAM, 1912a, 1914b.
 "Perotis," *Oligo.-Mio.*, Europe (Germany). HEER, 1847; MASSALONGO, 1855; HEYDEN, 1862.
 "Ptosima," *Oligo.*, USA (Colorado). WICKHAM, 1912a, 1914a.
 "Sphenoptera," *Oligo.*, Europe (Germany). HEER, 1847; HEYDEN & HEYDEN, 1865.

Family Elateridae

- "Adelocera," *Mio.*, Europe (Germany). HEER, 1847.
 "Agriotes," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Alaus," *Mio.*, Europe (Germany). HEER, 1865.
 "Ampedus," *Mio.*, Europe (Germany). HEER, 1847.
 "Anchastus," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Athous," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Campso sternus," *Mio.*, Europe (Germany). DEICHMÜLLER, 1881.
 "Cardiophorus," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1847; WICKHAM, 1916a.
 "Corymbites," *Mio.*, Europe (Germany). HEER, 1861.
 "Cryptohypnus," *Paleoc.*, Canada (British Columbia); *Oligo.*, USA (Colorado). SCUDDER, 1879a; WICKHAM, 1916a.
 "Elater," *Oligo.*, Europe (Baltic), USA (Colorado);

- Mio.*, Europe (Spitsbergen). GIEBEL, 1856; HEER, 1870a; WICKHAM, 1916a.
 "Horizonotus," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Ischnodes," *Mio.*, Europe (Germany). HEER, 1847.
 "Lacon," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1847; WICKHAM, 1916a.
 "Limonium," *Paleoc.*, Canada (British Columbia); *Oligo.*, USA (Colorado), Europe (Germany). HEER, 1847; HEYDEN, 1862; SCUDDER, 1895b; WICKHAM, 1916a.
 "Ludius," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1876a; WICKHAM, 1908, 1916a.
 "Megapenthes," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Melanactes," *Oligo.*, USA (Colorado). WICKHAM, 1908.
 "Monocrepidius," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Oxygonus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado). SCUDDER, 1876a; WICKHAM, 1916a.

Family Eucnemidae

- "Deltometopus," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Epiphanis," *Eoc.*, USA (Colorado). SCUDDER, 1876a.
 "Eucnemis," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Fornax," *Oligo.*, USA (Colorado). WICKHAM, 1916a.
 "Microrhagus," *Oligo.*, USA (Colorado). WICKHAM, 1916a.

Family Trixagidae

- "Pactopus," *Oligo.*, USA (Colorado). WICKHAM, 1914b.

Family Cantharidae

- "Cantharis," *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany, Yugoslavia). HEER, 1847; HEYDEN & HEYDEN, 1866; WICKHAM, 1913a, 1914a.
 "Chauliognathus," *Oligo.*, USA (Colorado). SCUDDER, 1876a.
 "Malthodes," *Oligo.*, Europe (Germany). FÖRSTER, 1891; MEUNIER, 1915b.
 "Podabrus," *Oligo.*, USA (Colorado). WICKHAM, 1909, 1914a, 1917.
 "Polemius," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Trypherus," *Oligo.*, USA (Colorado). WICKHAM, 1913a.

Family Lampyridae

- "Lampyris," *Mio.*, Europe (Germany). HEER, 1865.
 "Lucidota," *Oligo.*, USA (Colorado). WICKHAM, 1912a.

Family Melyridae

- "Collops," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Malachus," *Oligo.*, USA (Colorado). WICKHAM, 1917.
 "Trichochrus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.

Family Dermestidae

- "Attagenus," *Oligo.*, USA (Colorado). SCUDDER, 1900; WICKHAM, 1913a.
 "Dermestes," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1847; WICKHAM, 1912a.
 "Orphilus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.

Family Anobiidae

- "Anobium," *Eoc.*, USA (Wyoming). SCUDDER, 1878a, 1893a.
 "Ernobius," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Oligomerus," *Oligo.*, USA (Colorado). WICKHAM, 1914a, 1916b.
 "Ptinus," *Oligo.*, Europe (Germany). HEYDEN, 1859b; HEYDEN & HEYDEN, 1866.
 "Sitodrepa," *Eoc.*, USA (Wyoming). SCUDDER, 1876a.
 "Vrilletta," *Oligo.*, USA (Colorado). WICKHAM, 1913a.
 "Xestobium," *Oligo.*, USA (Colorado). WICKHAM, 1913a.

Family Bostrychidae

- "Amphicerus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Dinoderus," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
 "Xylobiops," *Oligo.*, USA (Colorado). WICKHAM, 1912a.

Family Trogossitidae

- "Ostoma," *Oligo.*, USA (Colorado). WICKHAM, 1910.
 "Tenebroides," *Oligo.*, USA (Colorado). WICKHAM, 1910.
 "Trogossita," *Eoc.*, Greenland; *Oligo.-Mio.*, Europe (Germany). GERMAR, 1837, 1849; HEER, 1847, 1862b, 1868.

Family Cleridae

- "Clerus," *Oligo.*, Europe (Baltic); *Mio.*, Europe (Germany). HEER, 1847; GIEBEL, 1862.
 "Enoclerus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Hydnocera," *Oligo.*, USA (Colorado). WICKHAM, 1913c.

- "Necrobia," *Oligo.*, USA (Colorado). WICKHAM, 1914a, 1914b.

Family Lymexylidae

- "Hylecaetus," *Oligo.*, Europe (Germany). HEER, 1865.
 "Melittoma," *Oligo.*, USA (Colorado). WICKHAM, 1911.

Family Nitidulidae

- "Amartus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
 "Amphotis," *Mio.*, Europe (Germany). HEER, 1847, 1862b.
 "Carpophilus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Colopterus," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
 "Meligethes," *Oligo.*, Europe (Germany). FÖRSTER, 1891.
 "Nitidula," *Oligo.*, Europe (Germany); *Mio.*, Europe (Yugoslavia). HEER, 1847, 1862b; MEUNIER, 1923c.
 "Phenolia," *Oligo.*, USA (Colorado). SCUDDER, 1876a.
 "Prometopia," *Paleoc.*, Canada (British Columbia). SCUDDER, 1877b.

Family Cryptophagidae

- "Antherophagus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1876a; TILLYARD, 1918a.
 "Cryptophagus," *Oligo.*, USA (Colorado). WICKHAM, 1913b, 1914a, 1916b.

Family Cucujidae

- "Laemophloeus," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
 "Pediacus," *Oligo.*, USA (Colorado). SCUDDER, 1900.

Family Erotylidae

- "Atomaria," *Mio.*, Europe (Germany). HEER, 1862b.
 "Triplax," *Oligo.*, USA (Colorado). WICKHAM, 1912a, 1914a, 1916b.
 "Tritoma," *Eoc.*, USA (Wyoming). SCUDDER, 1878a.

Family Phalacridae

- "Olibrus," *Mio.*, Europe (Germany). FÖRSTER, 1891.

Family Coccinellidae

- "Adalia," *Oligo.*, USA (Colorado), Europe (Germany). FÖRSTER, 1891; SCUDDER, 1900.

- "Anatis," *Oligo.*, USA (Colorado). WICKHAM, 1917.
 "Chilocorus," *Oligo.*, USA (Colorado). SCUDDER, 1900.
 "Coccinella," *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany). HEER, 1847, 1865; HEYDEN, 1859b, 1862; HEYDEN & HEYDEN, 1866; SCHLECHTENDAL, 1894; HAGEDORN, 1906; WICKHAM, 1913a.
 "Scymnus," *Oligo.*, Europe (Germany). FÖRSTER, 1891.

Family Lathridiidae

- "Corticaria," *Oligo.*, USA (Colorado). WICKHAM, 1913c, 1914a, 1914b.

Family Cisidae

- "Cis," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.

Family Mycetophagidae

- "Mycetophagus," *Oligo.*, USA (Colorado). WICKHAM, 1913c.

Family Colydiidae

- "Bothrideres," *Oligo.*, Europe (Baltic). STEIN, 1881.
 "Eucicones," *Oligo.*, USA (Colorado). WICKHAM, 1913c.

Family Tenebrionidae

- "Blapstinus," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
 "Bolitophagus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
 "Ephalus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
 "Gonocephalum," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
 "Helops," *Eoc.*, Greenland; *Oligo.-Mio.*, Europe (Germany). HEYDEN & HEYDEN, 1865; SCUDDER, 1895b; MEUNIER, 1914a.
 "Meracantha," *Oligo.*, USA (Colorado). WICKHAM, 1909.
 "Pactostoma," *Oligo.*, USA (Colorado). WICKHAM, 1910.
 "Platydema," *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN & HEYDEN, 1866; WICKHAM, 1912a, 1913b.
 "Protopterycera," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Tenebrio," *Paleoc.*, Canada (British Columbia); *Oligo.*, Europe (Germany). GERMAR, 1837; HEYDEN, 1859b; SCUDDER, 1879a.
 "Ulnus," *Oligo.*, USA (Colorado). WICKHAM, 1914b.
 "Uloma," *Oligo.*, Europe (Germany). HEYDEN, 1862.

Family Alleculidae

- "Capnochroa," *Oligo.*, USA (Colorado). WICKHAM, 1913a.
 "Cistela," *Mio.*, Europe (Germany). HEER, 1847.
 "Isomira," *Oligo.*, Europe (Baltic), USA (Colorado). WICKHAM, 1914a, 1914b.
 "Pseudocistela," *Oligo.*, Europe (Germany), USA (Colorado). FÖRSTER, 1891; WICKHAM, 1913a, 1913b.

Family Melandryidae

- "Synchroa," *Oligo.*, USA (Colorado). WICKHAM, 1911.

Family Scraphiidae

- "Scraphia," *Oligo.*, Europe (Baltic); *Mio.*, Europe (Germany). HEER, 1847.

Family Mordellidae

- "Mordella," *Oligo.*, USA (Colorado). WICKHAM, 1908, 1914a.
 "Mordellistena," *Oligo.*, USA (Colorado). WICKHAM, 1912a, 1913c, 1914b.
 "Tomoxia," *Oligo.*, USA (Colorado). WICKHAM, 1914a.

Family Rhipiphoridae

- "Macrosiagon," *Oligo.*, USA (Colorado). SCUDDER, 1890.
 "Rhipidius," *Oligo.*, Europe (Baltic). STEIN, 1877.
 "Rhipiphorus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.

Family Oedemeridae

- "Brachymycterus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
 "Copidita," *Oligo.*, USA (Colorado). WICKHAM, 1914b.
 "Ditylus," *Oligo.*, Europe (France). THÉOBALD, 1937a.
 "Mycterus," *Mio.*, Europe (Germany). HEER, 1847.

Family Meloidea

- "Epicauta," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Gnathium," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
 "Lytta," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1847; WICKHAM, 1914a.
 "Meloe," *Mio.*, Europe (Yugoslavia). HEER, 1847.
 "Mylabris," *Eoc.*, Europe (France); *Oligo.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEYDEN & HEYDEN, 1866; PITON & THÉOBALD, 1935; PITON, 1940a.
 "Nemognatha," *Oligo.*, USA (Colorado). WICKHAM, 1912a.

- "Tetraonyx," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Zonabris," *Eoc.*, Europe (France). PITON, 1940a.
 "Zonitis," *Mio.*, Europe (Germany). HEER, 1865.

Family Cerambycidae

- "Acanthocinus," *Plio.*, Europe (Germany). GERSDORF, 1976.
 "Acanthoderes," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany, Yugoslavia). HEER, 1847, 1865; WICKHAM, 1914b.
 "Anaesthetis," *Oligo.*, Europe (Germany); *Paleoc.-Plio.*, Argentina (Jujuy). COCKERELL, 1926b; STATZ, 1938a.
 "Anthicus," *Paleoc.-Plio.*, Argentina (Jujuy). COCKERELL, 1926b.
 "Astynomus," *Oligo.*, Europe (Germany). KOLBE, 1888.
 "Callidium," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany); *Mio./Plio.*, Europe (Germany). HEER, 1865; WICKHAM, 1917; PITON & THÉOBALD, 1935.
 "Callimoxys," *Oligo.*, USA (Colorado). WICKHAM, 1911.
 "Chlorida," *Eoc.*, Europe (France). PITON, 1940a.
 "Clytus," *Oligo.*, Europe (Baltic, France). HEER, 1847, 1865; OUSTALET, 1874; WICKHAM, 1914a; PITON, 1940b.
 "Dorcadion," *Oligo.*, Europe (Germany); *Paleoc.-Plio.*, Europe (France). HEYDEN, 1862; HANDSCHIN, 1944.
 "Dorcaschema," *Oligo.*, Europe (Baltic). ZANG, 1905b.
 "Dryobius," *Oligo.*, USA (Colorado). COCKERELL, 1908p; LINSLEY, 1942.
 "Elaphidion," *Oligo.*, USA (Colorado). WICKHAM, 1911, 1914a.
 "Ergates," *Mio.*, Europe (Germany). COCKERELL, 1922g.
 "Gaurotus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Haplocnemias," *Oligo.*, Europe (Germany). STATZ, 1938a.
 "Haruspex," *Paleoc.-Plio.*, Argentina (Jujuy). COCKERELL, 1926a.
 "Hesthesis," *Oligo.*, Europe (Germany). GERMAR, 1837; HEYDEN, 1862.
 "Hylotrupes," *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN, 1859b.
 "Lamia," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany). HEYDEN, 1859b.
 "Leptostylus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Leptura," *Eoc.*, England; *Oligo.*, USA (Colorado), Europe (Germany). WICKHAM, 1912a, 1913a, 1913b, 1914a; COCKERELL, 1920b; STATZ, 1938a.
 "Megopsis," *Eoc.*, Europe (France). PITON, 1940a.
 "Mesosa," *Mio.*, Europe (Germany). HEER, 1847.
 "Notorrhina," *Oligo.*, Europe (Baltic). ZANG, 1905b.

- "Oberea," *Oligo.*, Europe (Germany). HEYDEN, 1862.
 "Phymatodes," *Oligo.*, USA (Colorado). COCKERELL, 1908p; WICKHAM, 1914a.
 "Pogonocherus," *Oligo.*, Europe (Baltic). ZANG, 1905b.
 "Prionus," *Eoc.*, Europe (France); *Oligo.-Mio.*, Europe (Germany). GERMAR, 1837; GIEBEL, 1856; HEER, 1865; COCKERELL, 1922g.
 "Saperda," *Eoc.*, Europe (France); *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Yugoslavia, Switzerland). GERMAR, 1837; HEER, 1847, 1856; COCKERELL, 1908j; WICKHAM, 1916b; THÉOBALD, 1937a; PITON, 1940a.
 "Spondylis," *Oligo.*, Europe (Baltic), USA (Colorado). GIEBEL, 1856; WICKHAM, 1917, 1920.
 "Stenophenus," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
 "Strangalia," *Oligo.*, Europe (Baltic). ZANG, 1905b.
 "Tetrops," *Oligo.*, Europe (Germany). STATZ, 1938a.
 "Trachyderes," *Oligo.*, Europe (Germany). HEYDEN, 1859b.

Family Bruchidae

- "Bruchus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Germany). GERMAR, 1837; HEER, 1847; HEYDEN, 1858; FÖRSTER, 1891; WICKHAM, 1912a, 1913b, 1913c, 1914a, 1917.
 "Caryoborus," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany). HEYDEN, 1859b; HEER, 1861.
 "Choragus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
 "Spermophagus," *Oligo.*, USA (Colorado). SCUDDER, 1876a; WICKHAM, 1914a.
 "Urodon," *Oligo.*, Europe (Germany). HEYDEN, 1862; FÖRSTER, 1891; SCHLECHTENDAL, 1894.

Family Chrysomelidae

- "Cryptocephalus," *Eoc.*, USA (Wyoming), Europe (France); *Oligo.*, USA (Colorado), Europe (France, Germany). SCHLECHTENDAL, 1894; WICKHAM, 1913c, 1914b; THÉOBALD, 1937a; PITON, 1940a.
 "Diabrotica," *Oligo.*, USA (Colorado). WICKHAM, 1911, 1914a.
 "Donacia," *Eoc.*, Europe (Germany); *Oligo.*, USA (Colorado), Europe (Germany, France); *Mio.*, Europe (Germany), Spitsbergen; *Mio./Plio.*, Europe (France). ASSMANN, 1870; SCUDDER, 1890; FÖRSTER, 1891; WICKHAM, 1912a; PITON & THÉOBALD, 1935; THÉOBALD, 1937a; GOECKE, 1943; HAUPT, 1956.
 "Galeruca," *Mio.*, Europe (Germany, Yugoslavia). HEER, 1858, 1865; HEYDEN, 1859b.
 "Galerucella," *Paleoc.*, Canada (British Columbia); *Oligo.*, Europe (France, Germany). MEUNIER, 1918; THÉOBALD, 1937a.
 "Gonioctena," *Oligo.*, Europe (Germany, France);

- Mio.*, Europe (Germany). HEER, 1847; ASSMANN, 1870; OUSTALET, 1974.
- "Haltica," *Eoc.*, Europe (France); *Oligo.*, USA (Colorado), Europe (Germany). FÖRSTER, 1891; WICKHAM, 1914a; PITON, 1940a.
- "Labidostomis," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
- "Lema," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany). HEER, 1865; HEYDEN & HEYDEN, 1865; FÖRSTER, 1891; WICKHAM, 1910, 1914a, 1914b; COCKERELL, 1920c.
- "Lina," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany). HEER, 1847; HEYDEN & HEYDEN, 1866; MEUNIER, 1918.
- "Luperodes," *Oligo.*, USA (Colorado). WICKHAM, 1914b.
- "Luperus," *Oligo.*, Europe (Germany). MEUNIER, 1923b.
- "Melasoma," *Mio./Plio.*, Europe (France). PITON & THÉOBALD, 1935.
- "Metachroma," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
- "Oreina," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany). HEER, 1847; FÖRSTER, 1891.
- "Phytodecta," *Plio.*, England. LESNE, 1926a.
- "Plagioderia," *Oligo.*, Europe (Germany, France). HEYDEN & HEYDEN, 1866; THÉOBALD, 1937a.
- "Plateumaris," *Eoc.*, Europe (Germany). HAUPT, 1956.
- "Psylliodes," *Oligo.*, Europe (France). THÉOBALD, 1937a.
- "Systema," *Oligo.*, USA (Colorado). WICKHAM, 1913b.
- "Trirhabda," *Oligo.*, USA (Colorado). WICKHAM, 1914a.
- "Anisorhynchus," *Oligo.*, Europe (France); *Mio.*, Europe (Czechoslovakia). OUSTALET, 1870; DEICHMÜLLER, 1881.
- "Anthonomus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado); *Mio.*, USSR (Asian RSFSR); *Paleoc.-Plio.*, Argentina. SCUDDER, 1876a, 1890, 1893a; WICKHAM, 1912b; COCKERELL, 1925g.
- "Apion," *Oligo.*, USA (Colorado); *Mio.*, Europe (Germany). HEER, 1865; HEYDEN & HEYDEN, 1866; FÖRSTER, 1891; SCUDDER, 1893a; WICKHAM, 1911, 1916b.
- "Argotochus," *Oligo.*, Europe (France). THÉOBALD, 1937a.
- "Artipus," *Eoc.*, USA (Colorado). SCUDDER, 1893a.
- "Attelabus," *Mio.*, Europe (Germany). HEER, 1865.
- "Auletes," *Oligo.*, USA (Colorado). SCUDDER, 1893a; WICKHAM, 1913c.
- "Aulobaris," *Eoc.-Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Bagous," *Oligo.*, Europe (Germany, France). OUSTALET, 1870; FÖRSTER, 1891.
- "Balaninus," *Eoc.*, Europe (France); *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Europe (Czechoslovakia). HOPE, 1847; DEICHMÜLLER, 1881; SCUDDER, 1893a; WICKHAM, 1911, 1912b; COCKERELL, 1918; PITON, 1940a.
- "Baris," *Eoc.*, England; *Oligo.*, USA (Colorado). SCUDDER, 1893a; WICKHAM, 1912b, 1913c, 1916b, 1917; COCKERELL, 1920b.
- "Barypeithes," *Eoc.*, USA (Colorado). SCUDDER, 1893a.
- "Brachycerus," *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Germany). GERMAR, 1837; HEER, 1847, 1865; OUSTALET, 1870.
- "Brachyderes," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Brachyrhinus," *Eoc.*, USA (Wyoming, Colorado); *Oligo.*, USA (Colorado). SCUDDER, 1876a, 1878b, 1890, 1893a.
- "Centrinus," *Eoc.*, USA (Wyoming), Europe (France); *Oligo.*, USA (Colorado). SCUDDER, 1893a; WICKHAM, 1912b, 1916b; PITON, 1940a.
- "Ceutorhynchus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (France, Germany); *Mio./Plio.*, Europe (France). HEYDEN & HEYDEN, 1866; FÖRSTER, 1891; SCUDDER, 1893a; WICKHAM, 1916b; COCKERELL, 1920b; PITON & THÉOBALD, 1935; THÉOBALD, 1937a.
- "Chalcodermus," *Mio.*, Europe (Czechoslovakia). DEICHMÜLLER, 1881.
- "Cleonus," *Oligo.*, USA (Colorado), Europe (France, Germany); *Mio.*, Europe (Germany), USSR (Asian RSFSR). HEER, 1847, 1856, 1865; GIEBEL, 1856; OUSTALET, 1870, 1874; SCUDDER, 1885a, 1893a; FÖRSTER, 1891; WICKHAM, 1911, 1912b; COCKERELL, 1925g.
- "Coelidius," *Oligo.*, Europe (France), USA (Colorado). OUSTALET, 1874; SCUDDER, 1893a.
- "Coniatus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (France); *Mio./Plio.*, Europe

Family Anthribidae

- "Anthribus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Brachytarsus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1876a; WICKHAM, 1913c.
- "Choragus," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
- "Euparius," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1878b, 1893a; WICKHAM, 1911.
- "Ormiscus," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
- "Tropideres," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN, 1859b; SCUDDER, 1893a.

Family Curculionidae (*sensu lato*)

- "Acalles," *Oligo.*, USA (Colorado). HEYDEN & HEYDEN, 1866; WICKHAM, 1913c.
- "Acalyptus," *Oligo.*, USA (Colorado). FRITSCH, 1869b.

- (France). OUSTALET, 1874; SCUDDER, 1893a; WICKHAM, 1912b.
- "Conotrachelus," *Eoc.-Oligo.*, USA (Colorado). WICKHAM, 1912b.
- "Corimalis," *Oligo.*, Europe (France). THÉOBALD, 1937a.
- "Cossonus," *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, (Germany); *Paleoc.-Plio.*, Argentina (Jujuy). HEER, 1847; SCUDDER, 1893a; MEUNIER, 1915b; COCKERELL, 1925f.
- "Cremastorhynchus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Cryptorhynchus," *Eoc.*, USA (Colorado, Wyoming); *Oligo.*, USA (Colorado), Europe (Germany, France). OUSTALET, 1874; SCUDDER, 1876a, 1893a; FÖRSTER, 1891; WICKHAM, 1912b.
- "Cyphus," *Oligo.*, USA (Colorado). WICKHAM, 1911, 1914a.
- "Dorytomus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Dryvoetes," *Eoc.*, USA (Wyoming). SCUDDER, 1876a, 1878b; HOPKINS, 1900.
- "Endiagogus," *Eoc.*, USA (Wyoming). SCUDDER, 1878b.
- "Entomus," *Eoc.*, USA (Colorado). SCUDDER, 1893a; COCKERELL, 1911b.
- "Epicaerus," *Oligo.*, USA (Colorado). SCUDDER, 1876a.
- "Erirhinoides," *Oligo.*, Europe (Baltic). MOTSCHULSKY, 1856.
- "Erirhinus," *Oligo.*, USA (Colorado), Europe (France). OUSTALET, 1874; SCUDDER, 1893a.
- "Eugnamptus," *Eoc.*, USA (Wyoming). SCUDDER, 1876a, 1878b.
- "Euychirus," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
- "Grypidius," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Gymnetron," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (Germany). SCUDDER, 1878b, 1893a; FÖRSTER, 1891.
- "Hipporhinus," *Eoc.*, Europe (France); *Oligo.*, Europe (France); *Mio./Plio.*, Europe (France); *Plio.*, Europe (France). GERMAR, 1849; HEER, 1856; PITON, 1935b, 1940a; PITON & THÉOBALD, 1935, 1936; PITON & RUDEL, 1936; THÉOBALD, 1937a.
- "Hormorus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Hylastes," *Cret.*, England; *Oligo.*, USA (Colorado). WICKHAM, 1913c; BLAIR, 1943.
- "Hylesinus," *Oligo.*, USA (Colorado), Europe (Germany, France). HEER, 1856; FÖRSTER, 1891; HOPKINS, 1900.
- "Hylobius," *Eoc.*, USA (Wyoming); *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Italy); *Plio.*, Europe (Germany). HOPE, 1847; GIEBEL, 1856; HEER, 1856; HEYDEN & HEYDEN, 1866; OUSTALET, 1870, 1874; PONZI, 1876; SCUDDER, 1876a, 1893a; GERSDORF, 1970.
- "Hylurgops," *Oligo.*, USA (Colorado). WICKHAM, 1913c.
- "Lachnopus," *Oligo.*, USA (Colorado), Europe (France); *Mio./Plio.*, Europe (France). SCUDDER, 1893a; PITON & THÉOBALD, 1935; THÉOBALD, 1937a.
- "Larinus," *Oligo.-Mio.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEER, 1861; HEYDEN & HEYDEN, 1866; FÖRSTER, 1891; PITON & THÉOBALD, 1935.
- "Leperisinus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Lepyrus," *Eoc.*, USA (Wyoming). SCUDDER, 1893a.
- "Listronotus," *Eoc.*, USA (Wyoming). SCUDDER, 1890.
- "Lixus," *Eoc.*, Europe (France); *Mio.*, Europe (Germany). PITON, 1940a.
- "Macrorhoptus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Magdalis," *Oligo.*, USA (Colorado), Europe (Germany). HEYDEN & HEYDEN, 1866; SCHLECHTENDAL, 1894.
- "Meristos," *Paleoc.-Plio.*, India (Nagpur). MURRAY, 1860.
- "Molytes," *Oligo.*, Europe (Germany). HEYDEN, 1858.
- "Nanophyes," *Oligo.*, Europe (Germany). HEYDEN & HEYDEN, 1866.
- "Naupactus," *Mio.*, Europe (Germany). HEER, 1865.
- "Notaris," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Omileus," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Ophryastes," *Eoc.*, USA (Wyoming, Colorado); *Oligo.*, USA (Colorado). SCUDDER, 1878b, 1893a; WICKHAM, 1912b.
- "Orchestes," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Otiorrhynchus," *Mio.*, Europe (Germany). ZEUNER, 1931.
- "Pachybaris," *Oligo.*, USA (Colorado). WICKHAM, 1912a.
- "Pachylobius," *Eoc.*, USA (Colorado); *Oligo.*, Europe (France); *Paleoc.-Plio.*, Europe (France). SCUDDER, 1893a; PITON & RUDEL, 1936.
- "Pandeleteius," *Oligo.*, USA (Colorado). WICKHAM, 1917.
- "Phthorophloeus," *Oligo.*, USA (Colorado). WICKHAM, 1916b.
- "Phyllobius," *Eoc.*, USA (Colorado); *Mio./Plio.*, Europe (France). SCUDDER, 1893a; PITON & THÉOBALD, 1935.
- "Phytonomus," *Eoc.-Oligo.*, Europe (France); *Mio./Plio.*, Europe (France). OUSTALET, 1874; PITON & THÉOBALD, 1935; PITON, 1940a.
- "Phyxelis," *Eoc.*, USA (Wyoming, Colorado). SCUDDER, 1893a.
- "Pissodes," *Oligo.*, Europe (Germany). HEYDEN, 1858; FÖRSTER, 1891.
- "Platypus," *Oligo.*, Europe (Baltic); *Mio.*, Europe

- (Sicily). BURMEISTER, 1831; GUÉRIN-MÉNEVILLE, 1838.
- "Plinthus," *Oligo.*, Europe (France). OUSTALET, 1870, 1874.
- "Polygraphus," *Eoc.*, USA (Colorado). SCUDDER, 1893a.
- "Prionomerus," *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Procas," *Eoc.-Oligo.*, USA (Colorado). FRITSCH, 1869b.
- "Rhinocyllus," *Oligo.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEYDEN & HEYDEN, 1866; PITON & THÉOBALD, 1935.
- "Rhynchites," *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Germany). HEER, 1847, 1865; HEYDEN & HEYDEN, 1866; SCUDDER, 1893a; SCHLECHTENDAL, 1894; WICKHAM, 1916a; MEUNIER, 1920a, 1920d.
- "Ryssematus," *Eoc.*, USA (Colorado). FRITSCH, 1869b.
- "Sciaphilus," *Oligo.*, Europe (France). THÉOBALD, 1937a.
- "Scyphophorus," *Oligo.*, USA (Colorado). SCUDDER, 1893a; WICKHAM, 1911.
- "Scythropus," *Eoc.*, USA (Colorado, Wyoming). FRITSCH, 1869b.
- "Sibynes," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Sitona," *Eoc.*, USA (Colorado, Wyoming); *Oligo.*, Europe (France, Germany); *Mio.*, Europe (Germany). HEER, 1847; GERMAR, 1849; HEYDEN & HEYDEN, 1866; OUSTALET, 1874; SCUDDER, 1893a; THÉOBALD, 1937a.
- "Smicromyx," *Oligo.*, Europe (Germany). FÖRSTER, 1891.
- "Sphenophorus," *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany); *Mio./Plio.*, Europe (France). HEER, 1847; HEYDEN & HEYDEN, 1866; PITON & THÉOBALD, 1935.
- "Strophosomus," *Oligo.*, Europe (France). THÉOBALD, 1937a.
- "Syntomostylus," *Eoc.*, USA (Colorado, Wyoming). SCUDDER, 1893a; COCKERELL, 1909l.
- "Tanymecus," *Eoc.*, USA (Colorado); *Oligo.*, Europe (France). SCUDDER, 1890; PITON & RUDEL, 1936.
- "Tanysphyrus," *Oligo.*, Europe (France). OUSTALET, 1874.
- "Thylacites," *Mio.*, Europe (Czechoslovakia). DEICHMÜLLER, 1881.
- "Trigonoscuta," *Oligo.*, USA (Colorado). SCUDDER, 1893a.
- "Tychius," *Oligo.*, USA (Colorado), Europe (Germany). FÖRSTER, 1891.

Order STREPSIPTERA

Kirby, 1815

[Strepsiptera KIRBY, 1815a, p. 86]

Small order of insects with marked sexual dimorphism and complicated reproductive

development. Males winged; females larviform in imaginal stage. Males (Fig. 184) with head strongly transverse, eyes very prominent; antennae with 4 to 7 segments, third segment and commonly some following segments distinctly flabellate; mouthparts usually reduced, mandibles very narrow, almost bristlelike; prothorax and mesothorax small, metathorax very large; tarsal segments variable but usually with a large adhesive pad; fore wings club-shaped; hind wings large with only a few, radiating veins. Females apodous, apterous, and larviform, encased in larval cuticle; head and thorax fused; antennae and eyes absent; mouthparts vestigial. Larvae of both sexes endoparasites of other insects; females continuing as endoparasites in the imaginal stage; adults of males free-living. This parasitism does not kill hosts but causes them to lose some secondary sexual characteristics. *Oligo.-Holo.*

The only fossil Strepsiptera known are preserved in ambers. The family Mengeidae, now considered to be extinct, is represented in the Baltic amber (Oligocene), and the families Elenchidae and Myrmecolacidae occur in the Dominican amber (Oligocene/Miocene).

The phylogenetic position of the Strepsiptera is uncertain. They are considered by most students of the group to represent a separate order of uncertain affinities and by others to be highly specialized members of the Coleoptera (CROWSON, 1967; KINZELBACH, 1971a, 1971b, 1978).

Family MENGEIDAE Pierce, 1907

[Mengeidae PIERCE, 1907, p. 76]

Only males known. Antennae with 7 segments, the third and fourth segments flabellate; all tarsi with 5 segments and with claws; labial palpi present. [This family was originally based on an extinct species. A few existing species were subsequently assigned to it. Recently the concept of the family has been more restricted, and it is now considered to be extinct.] KINZELBACH, 1971a, 1971b, 1978. *Oligo.*

Mengea GROTE, 1886, p. 100, *nom. subst. pro Triaena* MENGE, 1866, p. 2, *non* HUEBNER, 1818

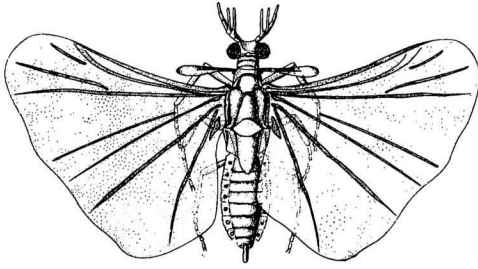


FIG. 184. Strepsiptera; dorsal view of male, *Eoxenos laboulbenei* PEYERIMHOFF, Holocene, $\times 8.5$ (Parker & Smith, 1934).

[**Triaena tertiaria* MENGE, 1866, p. 2; OD]. Hind wings with MA1 strongly developed; RS1 very short; CUA1 well developed basally, frequently coalescing with MA2 near middle of wing. PIERCE, 1907; ULRICH, 1937; KINZELBACH, 1939; KINZELBACH, 1971a, 1979. *Oligo.*, Europe (Baltic).—FIG. 185, 1. **M. tertiaria* (MENGE); a, dorsal view of holotype, $\times 20$ (Ulrich, 1937); b, antenna, $\times 80$; c, hind wing, $\times 23$ (both Kinzelbach, 1978).

Family ELENCHIDAE Perkins, 1905

[Elenchidae PERKINS, 1905, p. 98]

Only males known. Antennae with 5 segments, a flabellum on segment three only; all tarsi with 2 segments and without claws; hind wings with vein RS1 short and MA1 absent. *Oligo./Mio.—Holo.*

Elenchus CURTIS, 1831, no. 385. *Holo.*
Protelencholax KINZELBACH, 1979, p. 5 [**P. schleei*; OD]. Fourth antennal segment completely fused with the third. *Oligo./Mio.*, Dominican Republic.—FIG. 185, 2. **P. schleei*; ventral view of holotype, $\times 50$ (Kinzelbach, 1979).

Family MYRMECOLACIDAE Saunders, 1872

[Myrmecolacidae SAUNDERS, 1872, p. 34]

Only males known. Antennae with 7 segments, only third segment flabellate, the fourth very short; tarsi with 4 segments, without claws; hind wing with MA1 absent or very short and MA2 long. *Oligo./Mio.—Holo.*

Myrmecolax WESTWOOD, 1861, p. 420. KINZELBACH, 1983. *Oligo./Mio.*, Dominican Republic—*Holo.*

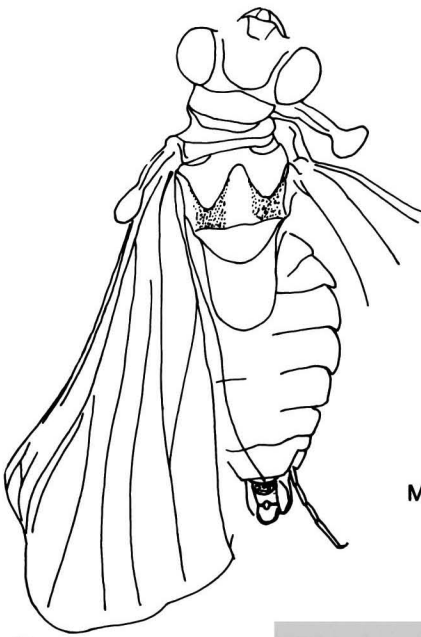
Order NEUROPTERA Linné, 1758

[Neuroptera LINNÉ, 1758, p. 543]

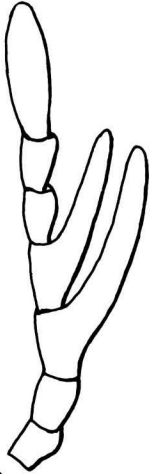
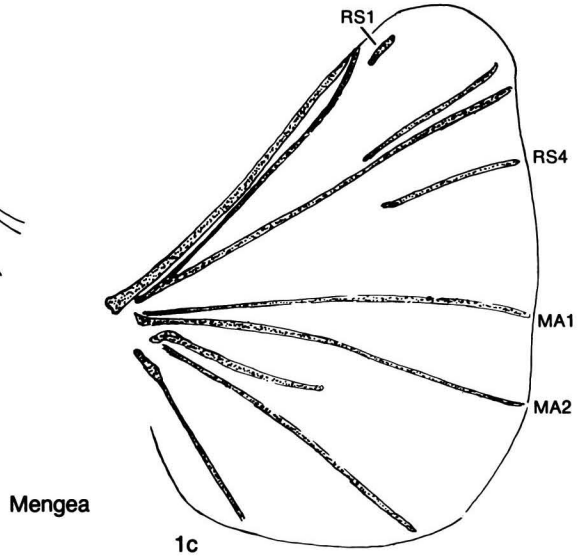
Small to large insects, mostly with soft, weakly sclerotized body. Compound eyes prominent in many; ocelli present in generalized species, absent in others; antennae prominent, commonly long and filiform, clubbed in a few; mouthparts mandibulate, hypognathous; maxillae and labium normal, with well-developed palpi. Prothorax usually well developed, about as long as mesothorax, much longer in the Mantispidae and Raphidioidea. Two pairs of membranous wings, generally subequal and typically with many veins, many forming numerous cells. Venation markedly diverse in the 3 suborders, but typically consisting of all main veins, including MA and MP; vein RS generally coalesced with MA in both wings (Fig. 186). Legs mostly slender and cursorial, with 5 tarsal segments. Abdomen with 10 distinct segments, last segment variously formed but divided into a pair of lateral plates, each bearing a group of sensilla (trichobothria).

Eggs are usually laid on foliage, bark, or the ground, or, rarely, in fresh water. The larvae are very different in the 3 suborders, but all have well-developed mandibles and are predaceous; some are aquatic and possess tracheal gills, but most are terrestrial, occurring on foliage or the ground. Pupae exarate and in leaf litter and crevices of bark; many are enclosed by silken cocoons. *Perm.—Holo.*

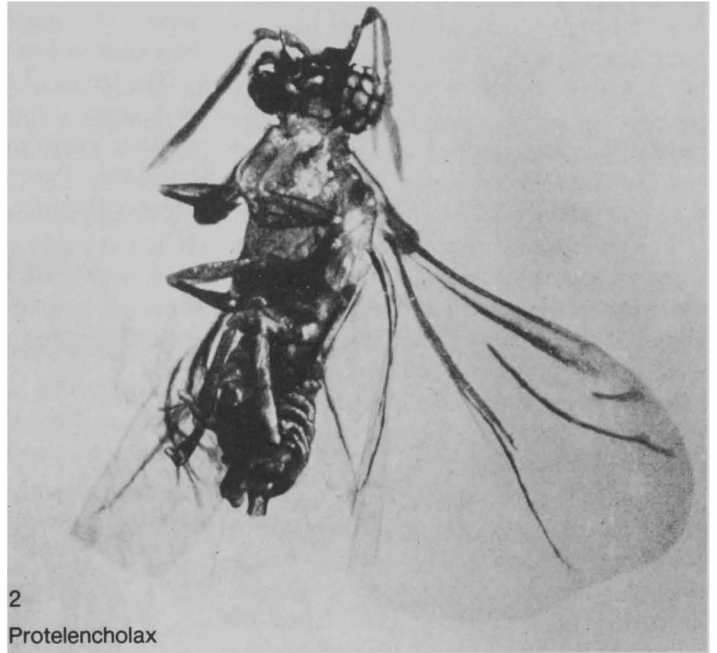
The Neuroptera include, in the suborder Sialodea, apparently the most primitive of living holometabolous insects. Precise relationships between the Neuroptera and Mecoptera are uncertain; the most that can be said is that the two orders were derived from a common ancestral stock, presumably in the Late Pennsylvanian. Some evidence has been advanced indicating that the Sialodea gave rise to the Coleoptera and Hymenoptera, but the neuropterous affinities of both of these orders are much less obvious than those of the Mecoptera.



1a



1b



2
Protelencholax

FIG. 185. Mengeidae and Elenchidae (p. 337-338).

Evidence for the present interpretation of the venation of the Neuroptera has been acquired in part from the fossil record (CARPENTER, 1936, 1940a; ADAMS, 1958; RIEK,

1970a). The coalescence of vein MA with R+RS or RS apparently took place independently in several and perhaps nearly all families. In the fore wing, the basal piece of

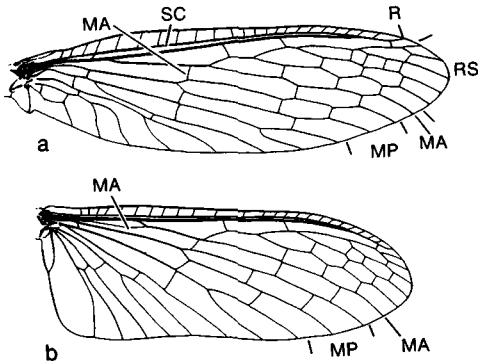


FIG. 186. Neuroptera; *a*, fore and *b*, hind wings of a recent *Archichauliodes* sp. (suborder Sialodea, family Corydalidae), indicating the usual differences between the fore and hind wings (from CSIRO, 1970).

MA (between M and R or RS) has assumed a transverse position and resembles a cross-vein, or it has been entirely lost, the coalescence having occurred at the wing base. In some genera, there is no evidence that MA has persisted. In the hind wings of more primitive genera of many families, the free piece of MA has persisted as a longitudinal or sigmoidal vein connecting M to RS (as in the recent genus *Archichauliodes*, Fig. 186*b*).

The order Neuroptera is here divided into three suborders: Sialodea, Raphidiodea, and Planipennia. These are often treated as separate orders, or, as an alternative, the Sialodea and Raphidiodea are considered to belong together in the order Megaloptera and the Planipennia to constitute the Neuroptera *sensu stricto*. However, the presence of trichobothria on the tenth tergite of all members of these three groups and the strikingly similar history of MA in their hind wings strongly suggest a common origin despite adaptive differences of their larvae. The latter are aquatic in the Sialodea and terrestrial in the Raphidiodea and Planipennia. The larvae of the Planipennia are distinguished by a groove along the inner surface of the mandibles that forms a canal for passage of fluids sucked from the bodies of their victims.

The oldest Raphidiodea and Planipennia

are found in Permian deposits. The Sialodea have a relatively poor geological record and are first found in the Jurassic. The Planipennia and possibly the Raphidiodea were apparently more extensively developed and diverse during the Jurassic than at present.

Suborder SIALODEA Hagen, 1861

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 204, *pro* Sialina HAGEN, 1861, p. 187]

Moderate-sized to large insects with normal prothorax; legs homonomous, cursorial; wings with markings in many; veins without marginal twigs. Fore wing commonly with costal area slightly broadened near midwing; pterostigma absent; veins MA and MP present; MA either coalesced with RS for a short distance or free; CUA forked. Hind wing somewhat broadened basally, markedly so in some; MA of some genera arising nearer wing base than in fore wing. *Jur.—Holo.*

The larvae of sialodeons are aquatic and have seven or eight pairs of abdominal gills; they are predaceous, with normal, chewing mandibles. Pupae are formed in soil a short distance from the water.

Family CORYDALIDAE Leach, 1815

[*nom. transl.* BURMEISTER, 1839 in BURMEISTER, 1838–1839, p. 757, *ex* Corydalida LEACH, 1815, p. 138]

Large insects with ocelli; vein MA commonly coalesced with RS for a short distance in both fore and hind wings. *Oligo.—Holo.*

Corydalus LATREILLE, 1802, p. 290. *Holo.*

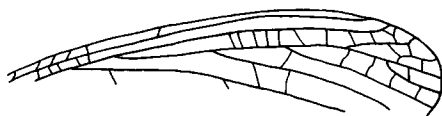
Chauliodes LATREILLE, 1796, p. 182. PICTET, 1854. *Oligo.*, Europe (Baltic)—*Holo.*

Family UNCERTAIN

The genus described below, apparently belonging to the order Neuroptera, suborder Sialodea, is too poorly known to permit family assignment.

Nematophlebia COCKERELL, 1915, p. 475 [**N. plicata*; OD]. Little-known hind wing; anal area well developed but folded over most of remigi-

um; SC long, closer to C than to R. *Jur.*, England.
 — FIG. 187. **N. plicata*; hind wing, folded
 anal area not shown, $\times 4.6$ (Cockerell, 1915).



Nematophlebia

FIG. 187. Uncertain (p. 340–341).

Suborder RAPHIDIOIDEA

Burmeister, 1838

[Raphidioidea BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 757]

Neuroptera with elongate prothorax, mostly as long as meso- and metathorax combined; legs homonomous, cursorial. Wings hyaline, without markings. Fore wings with costal area usually broadened near its middle; vein SC terminating at about midwing; pterostigma generally present and distinct; MA arising from M or MP and coalesced with RS for a short distance (Fig. 190, *a*). Hind wing similar to fore wing, but costal area narrow; MA in some genera arising nearer base than in fore wing, approximately at point of divergence of M from R. Ovipositor of female long and curved. CARPENTER, 1936. *Perm.*—*Holo.*

The raphidiodeons are terrestrial in all growth stages, larvae being predaceous on small insects, mainly Hemiptera, suborder Homoptera, and occurring on the bark of trees, in rotting wood and similar places. They have normal chewing mandibles, unlike the larvae of the Planipennia. The pupae, which have free appendages, develop in crude, unlined, oval cells in crevices of bark or decayed wood.

Family SOJANORAPHIDIIDAE

Martynova, 1952

[Sojanoraphidiidae MARTYNOVA, 1952b, p. 225]

Vein SC of fore(?) wing close to costa; costal area very narrow; pterostigma seemingly absent; RS arising near wing base; MA apparently coalesced with RS; ovipositor long and curved. [Ordinal position doubtful.] *Perm.*

Sojanoraphidia MARTYNOVA, 1952b, p. 226 [**S. rossica*; OD]. Fore(?) wing with SC long, extending nearly to end of R; veins straight, with few irregularities. CARPENTER, 1967b. *Perm.*, USSR (European RSFSR).—FIG. 188,3. **S. rossica*;

fore(?) wing and part of body, $\times 11$ (Martynova, 1952b).

Family MESORAPHIDIIDAE

Martynov, 1925

[Mesoraphidiidae MARTYNOV, 1925a, p. 234]

Fore wing slender; vein SC extending to about midwing; costal area more slender; R long, nearly parallel to costal margin; MA arising at or before origin of MP, coalesced with RS for a short distance near midwing; CU forked basally, CUA diverging anteriorly and coalesced with stem of M briefly; 1A barely touching CUP; main veins nearly straight, with few irregularities. Hind wing venation resembling that of fore wing, but costal area narrower; MA with longer free basal piece, before the coalescence with RS. Prothorax long and curved. *Jur.*

Mesoraphidia MARTYNOV, 1925a, p. 235 [**M. grandis*; OD]. Fore wing: costal area with 8 to 10 veinlets; pterostigma weakly developed but very long. MARTYNOVA, 1947a; 1952b. *Jur.*, USSR (Kazakh).—FIG. 188,1*a,b*. *M. inaequalis* MARTYNOV; *a*, fore and *b*, hind wings, $\times 3.5$ (Martynov, 1925b).—FIG. 188,1*c*. *M. pterostigmalis* MARTYNOVA; whole insect, $\times 4$ (Martynova, 1947a).

Proraphidia MARTYNOVA, 1947a, p. 636 [**P. turkestanica*; OD]. Hind wing as in *Mesoraphidia* but broader; pterostigma very short and strongly developed. *Jur.*, USSR (Kazakh).—FIG. 188,4. **P. turkestanica*; hind wing, $\times 5$ (Martynova, 1947a).

Family BAISSOPTERIDAE

Martynova, 1961

[Baissopteridae MARTYNOVA, 1961a, p. 80]

Fore wing much as in Mesoraphidiidae but with more cells between branches of veins RS and MA. MA of hind wing with long free basal piece before coalescence with RS. *Jur.*

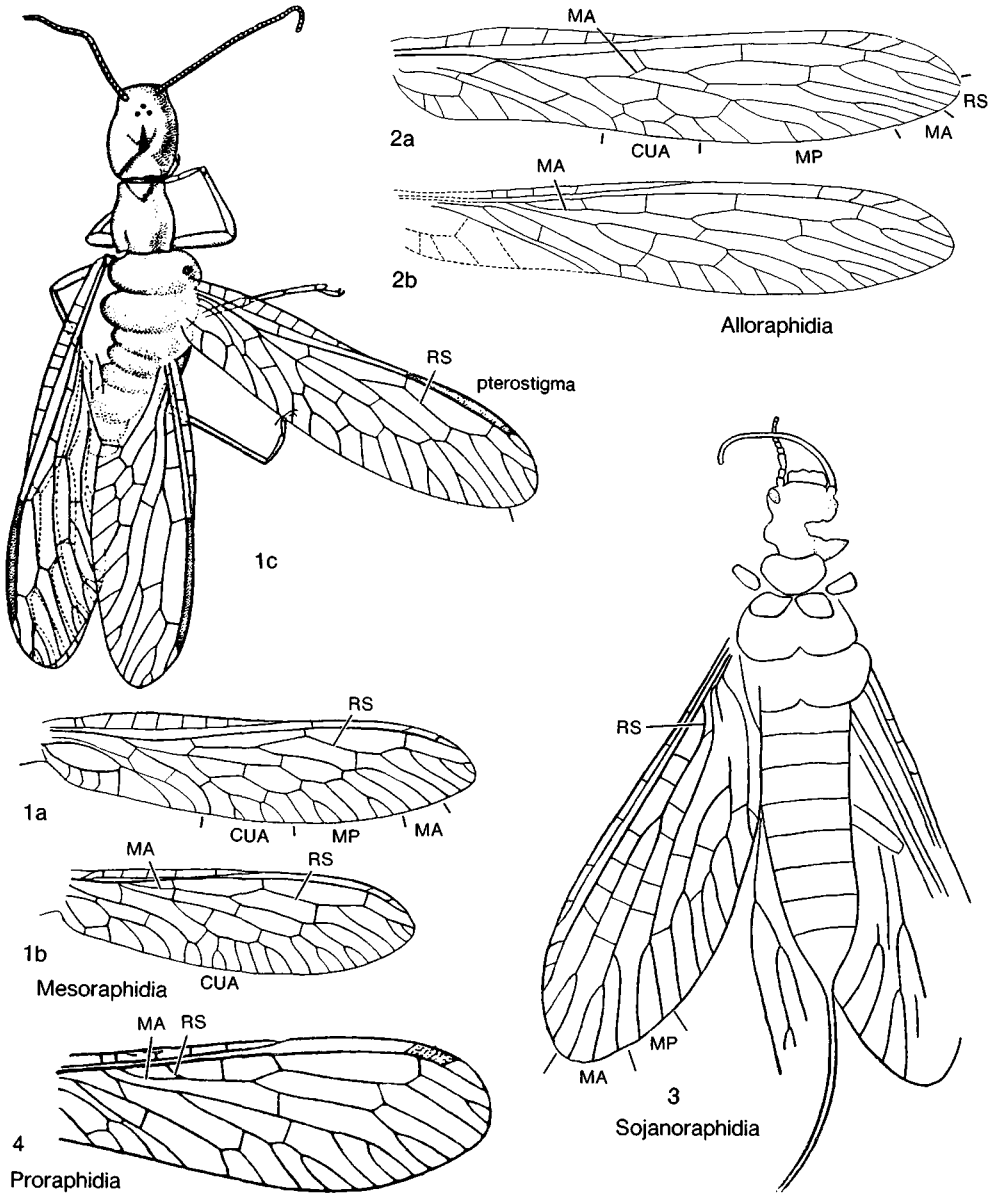


FIG. 188. Sojanoraphidiidae, Mesoraphidiidae, and Alloraphidiidae (p. 341-343).

Baissoptera MARTYNOVA, 1961a, p. 80 [**B. martinsoni*; OD]. RS of fore wing forked before end of SC; each primary branch of RS with several forks. *Jur.*, USSR (Asian RSFSR). — FIG. 189, *a*. **B. martinsoni*; fore wing, $\times 4.3$ (Martyanova, 1961a). — FIG. 189, *b*. *B. kolosnitsynae* MARTYNOVA; hind wing, $\times 4.3$ (Martyanova, 1961a).

Family ALLORAPHIDIIDAE
Carpenter, 1967

[Alloraphidiidae CARPENTER, 1967b, p. 270]

Similar to Mesoraphidiidae. Fore wing very long and slender; pterostigma well developed; vein MA arising well after origin of

MP and coalesced with RS for a short distance; CUA connected to M at its point of separation from R. Hind wing nearly same size and shape as fore wing, but costal area narrower. Body unknown. *Cret.*

Alloraphidia CARPENTER, 1967b, p. 271 [**A. dorfi*; OD]. RS and MA each with 3 well-defined branches apart from marginal fork; CUA with 1 or 2 closed submarginal cells. *Cret.*, Canada (Labrador).—FIG. 188, 2. **A. dorfi*; a, fore and b, hind wings, X3 (Carpenter, 1967b).

Family RAPHIDIIDAE

Latreille, 1810

[*nom. transl.* STEPHENS, 1829b, p. 314, ex Raphidiinae LATREILLE, 1810, p. 277]

Fore wing with vein SC terminating at midwing or slightly beyond; costal area broad, widest near its middle; pterostigma with crossveins; RS arising at midwing; MA arising from MP shortly after the origin of MP; CUA diverging anteriorly and coalesced initially with stem of M; most veins slightly irregular; crossveins few and regular in position. Hind wing similar to fore wing, but costal area narrow. Antennae slender, prothorax generally elongate; male abdomen terminating dorsally in hood-shaped epiproct; female with curved ovipositor about as long as thorax. *Oligo.*—*Holo.*

Raphidia LINNÉ, 1758, p. 552 [= *Megaraphidia* COCKERELL, 1907c, p. 607 (type, *M. elegans*); *Dictyroraphidia* HANDLIRSCH, 1910b, p. 103 (type, *Inocellia veterana* SCUDDER, 1890, p. 156)]. CARPENTER, 1936, 1956. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Family INOCELLIIDAE Navás, 1913

[*nom. transl.* NAVÁS, 1916, p. 509, ex Inocellini NAVÁS, 1913c, p. 11]

Fore and hind wings as in Raphidiidae, but pterostigmal crossveins lacking; vein MP2 branched; ocelli absent (Fig. 190). *Oligo.*—*Holo.*

Inocellia SCHNEIDER, 1843, p. 84. CARPENTER, 1956. *Oligo.*, Europe (Baltic)—*Holo.*

Fibla NAVÁS, 1915, p. 477. CARPENTER, 1936, 1956. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Family UNCERTAIN

The genus described below, apparently

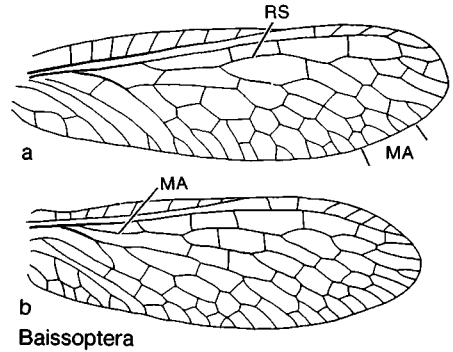


FIG. 189. Baissopteridae (p. 342).

belonging to the order Neuroptera, suborder Raphidioidea, is too poorly known to permit family assignment.

Archiinocellia HANDLIRSCH, 1910b, p. 100 [**A. oligoneura*; OD]. Little-known wing (fragments), possibly belonging to Inocelliidae. CARPENTER, 1936. *Oligo.*, Canada (British Columbia).

Suborder PLANIPPENNIA

Latreille, 1817

[*nom. correct.* HEYMONS, 1915, p. 194, pro Planipennes LATREILLE, 1817, p. 430]

Minute to large Neuroptera, usually with short prothorax and cursorial legs; wings subequal, commonly with markings; veins almost invariably with marginal twigs. Fore wing with costal area generally broad or very broad, but narrow exceptionally; pterostigma present only in the existing family Mantispidae; veins MA and MP present but not separable in some; MA mostly coalesced for a short distance with R and RS; SC terminating distally on C or R, commonly with dense cluster of veinlets near wing apex. Hind wing typically narrower than fore wing; MA arising nearer wing base than in fore wing, its free basal piece commonly sigmoidal or nearly longitudinal. *Perm.*—*Holo.*

Planipennian larvae are terrestrial (except for the Sisyridae) and have prominent, grooved mandibles, in many very long; all are predaceous and use their grooved man-

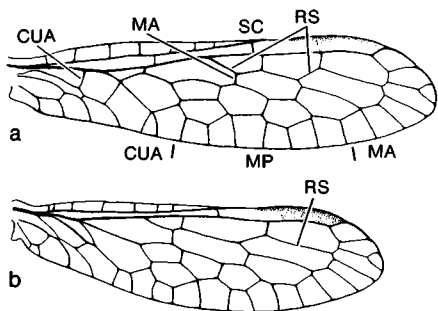


FIG. 190. Neuroptera; *a*, fore and *b*, hind wings of a recent inocelliid, *Inocellia* sp. (suborder Raphidioidea, family Inocellidae), showing the similarity of the fore and hind wings (Carpenter, new).

dibles for sucking the blood of their victims.

The existing families of Planipennia are usually grouped into several superfamilies, although considerable difference of opinion exists as to the number of these taxa and relations of some of the families (ADAMS, 1958; MACLEOD, 1964; SHEPARD, 1967). Since several extinct families from Permian and Jurassic deposits do not appear to belong to any recognized superfamily, all families are arranged herein according to their apparent phylogenetic relationships but without arrangement of them in superfamily groups.

Family PALAEMEROBIIIDAE

Martynov, 1928

[Palaemerobiidae MARTYNOV, 1928b, p. 87]

Fore wing oval with costal area narrowed basally, broader near middle; vein SC terminating on C; RS with at least 4 main branches; MA free from stem of RS; MA and MP forked at least once; CUA with a short fork; crossveins irregularly arranged, not forming a series. Hind wing unknown. *Perm.*

Palaemerobius MARTYNOV, 1928b, p. 86 [**P. proavitus*; OD]. Fore wing: RS with 5 or 6 branches; M dividing at about level of origin of RS. MARTYNOVA, 1952b, 1961c. *Perm.*, USSR (European and Asian RSFSR).—FIG. 191.1. **P. proavitus*, European RSFSR; fore wing, $\times 7$ (Martynov, 1928b).

Bianchia MARTYNOVA, 1952b, p. 214 [**B. spectabilis*; OD]. Fore wing with long SC extending

almost to end of R; only single veinlet from R to C; RS with 7 branches. MARTYNOVA, 1962d. *Perm.*, USSR (European RSFSR).—FIG. 191.2. **B. spectabilis*; fore wing, $\times 5$ (Martynova, 1952b).

Tychtobius MARTYNOVA, 1958, p. 79 [**T. brevicostatus*; OD]. Fore wing similar to that of *Palaemerobius*, but SC shorter; more veinlets from R to C; RS with 6 main branches. MARTYNOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 191.3. **T. brevicostatus*; fore wing, $\times 5$ (Martynova, 1958).

Family SIALIDOPSIDAE

Zalesky, 1928

[Sialidopsidae ZALESSKY, 1928a, p. 693]

Fore wing with vein SC about as long as in Palaemerobiidae, but costal veinlets unbranched; RS with 4 primary branches; crossveins few and scattered. Hind wing unknown. *Perm.*

Sialidopsis ZALESSKY, 1926, p. 76 [**S. kargalensis*; OD]. Fore wing oval, costal margin curved; R with 6 veinlets to costal margin. ZALESSKY, 1928a; MARTYNOVA, 1952b. *Perm.*, USSR (European RSFSR).—FIG. 191.4. *S. sojanensis* MARTYNOVA; fore wing, $\times 5.5$ (Martynova, 1952b).

Permosisyra MARTYNOV, 1933a, p. 72 [**P. latipennis*; OD]. Fore(?) wing margin apparently straight; costal area narrow and uniform in width. [Family assignment doubtful.] MARTYNOVA, 1962d. *Perm.*, USSR (European RSFSR).—FIG. 191.5. **P. latipennis*; fore(?) wing, $\times 5.5$ (Martynov, 1933a).

Family PERMITHONIDAE

Tillyard, 1922

[Permithonidae TILLYARD, 1922a, p. 289] [=Permeagalomidae MARTYNOVA, 1952b, p. 201; Permopsychopsidae RIEK, 1953, p. 83]

Fore wing with moderately broad costal area and numerous, somewhat irregular veinlets, some branched; vein SC terminating on R distally; few to many crossveins between R and RS, which has at least 4 primary branches; MA not coalesced with RS basally, but M commonly connected to it by a short crossvein; CUA with distal fork. Hind wing and body unknown. *Perm.*

Permithone TILLYARD, 1922a, p. 289 [**P. belmontensis*; OD] [=Permosmylus TILLYARD, 1926b, p. 279 (type, *P. pinocombeae*)]. Fore wing with costal area much broader basally than

distally, at least some veinlets branched; RS with 5 primary branches. *Perm.*, Australia (New South Wales).—FIG. 192,5. **P. belmontensis*; fore wing, $\times 6$ (Tillyard, 1922a).

Eopsychops MARTYNOV, 1933a, p. 69 [**E. sojanensis*; OD]. Fore wing very broad, almost triangular, with very broad costal area; M dividing well in front of fork of CU. MARTYNOVA, 1952b. *Perm.*, USSR (European and Asian RSFSR).—FIG. 192,7. **E. sojanensis*, European RSFSR; fore wing, $\times 4.2$ (Martynova, 1952b).

Permegalomus MARTYNOV, 1931c, p. 186 [**P. regularis*; OD]. Fore wing with costal area markedly narrowed basally; RS with at least 7 primary branches. MARTYNOVA, 1952b. *Perm.*, USSR (European and Asian RSFSR).—FIG. 192,6. *P. maculipennis* MARTYNOVA, European RSFSR; fore wing, $\times 5.5$ (Martynova, 1952b).

Permithonopsis MARTYNOV, 1933a, p. 67 [**P. ivensis*; OD]. Fore wing as in *Permegalomus*, but costal area not so narrow basally. MARTYNOVA, 1952b, 1961c. *Perm.*, USSR (European and Asian RSFSR).—FIG. 192,4. *P. cellulosa* MARTYNOVA, European RSFSR; fore wing, $\times 5$ (Martynova, 1952b).

Permopsychops TILLYARD, 1926e, p. 281 [**P. belmontensis*; OD]. Fore wing much as in *Permithone*; costal veinlets and branches of RS somewhat more numerous. *Perm.*, Australia (New South Wales).—FIG. 192,8. **P. belmontensis*; fore wing, $\times 4.3$ (Riek, 1953).

Permoralipisma TILLYARD, 1926e, p. 278 [**P. biserialis*; OD]. Venation of fore wing as in *Permithone*, but with many more crossveins and branches; costal area with reticulated veinlets; RS with 7 or more primary branches; MA and MP with many marginal branches. RIEK, 1953. *Perm.*, Australia (New South Wales).—FIG. 192,2. **P. biserialis*; fore wing, $\times 3$ (Tillyard, 1926e).

Family MESOPOLYSTOECHOTIDAE

Martynova, 1949

[Mesopolystoechotidae MARTYNOVA, 1949a, p. 160]

Fore wing with pointed apex; vein SC joined to R distally and gradually, before apex; MA apparently coalesced with RS basally; 2 distinct rows of crossveins. *Jur.*

Mesopolystoechus MARTYNOV, 1937a, p. 38 [**M. apicalis*; OD]. Fore wing incompletely known; MA unbranched; MP with 2 branches; branches of RS with only distal forking. MARTYNOVA, 1949a. *Jur.*, USSR (Asian RSFSR).—FIG. 192,1. **M. apicalis*; distal part of fore wing, $\times 2.5$ (Martynova, 1949a).

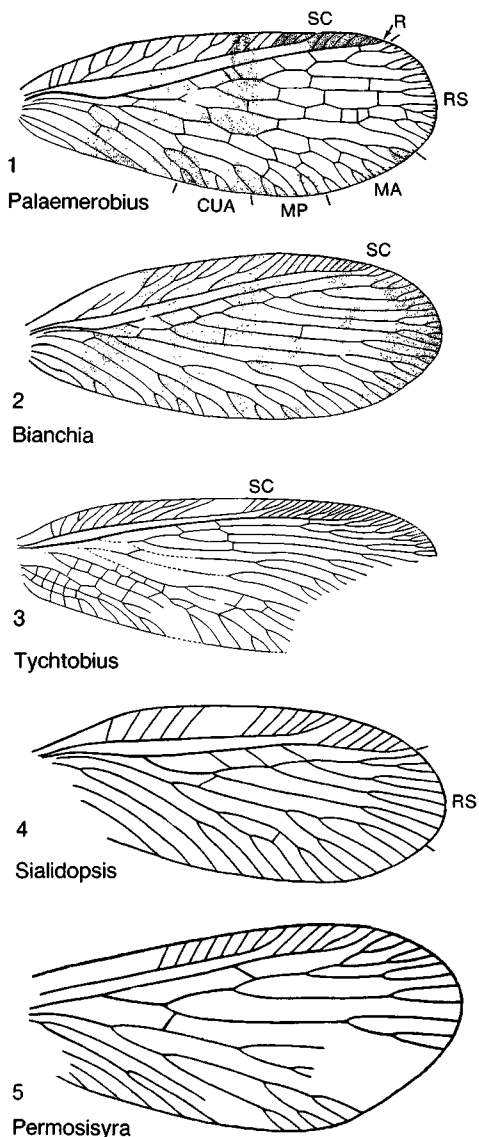


FIG. 191. Palaemerobiidae and Sialidopsidae (p. 344).

Family OSMYLITIDAE

Martynova, 1949

[Osmylitidae MARTYNOVA, 1949a, p. 159]

Vein SC of fore wing terminating on R near wing apex; RS with numerous primary branches; MA free from RS basally or coalesced with RS for a short distance. Hind

wing and body unknown. [Possibly related to the Polystoechotidae.] *Jur.*

Osmylites HAASE, 1890a, p. 22 [**Chrysopa protogaea* HAGEN, 1862, p. 108; OD]. Fore wing little known; apex pointed, slightly falcate; MA deeply forked, apparently not coalesced with RS basally. *Jur.*, Europe (Bavaria).

Kirgisellodes MARTYNOV, 1937a, p. 39, *nom. subst. pro Kirgisella* MARTYNOV, 1925b, p. 594, *non* BEKLEMICHEV, 1922 [**Kirgisella ornata*; OD]. Fore wing with SC and R merging abruptly; RS with about 15 primary branches. [Family assignment doubtful.] MARTYNOVA, 1962d. *Jur.*, USSR (Kazakh).—FIG. 192,3. **K. ornata*; fore wing, $\times 2.7$ (Martynova, 1962d).

Mesomylina BODE, 1953, p. 246 [**M. exornata*; OD]. Fore wing with numerous crossveins distributed uniformly over wing. *Jur.*, Europe (Germany).

Family SISYRIDAE Banks, 1905

[*nom. transl.* HANDLIRSCH, 1907, p. 908, *ex* Sisyriinae BANKS, 1905, p. 23]

Wings subequal, oval. Fore wing with costal area generally narrow, especially proximally; pterostigmal crossveins numerous; costal crossveins mostly unbranched; vein SC weak distally; RS with 1 or 2 primary branches arising from a single stem; CUA with almost parallel branches leading to wing margin; gradate crossveins present in some species. Hind wing with MA coalesced with MP at base, separating as a free, weak vein, then coalescing with RS for a short distance. Larvae aquatic, predaceous on freshwater sponges. *Oligo.*—*Holo.*

Sisyra BURMEISTER, 1839, p. 975. BANKS, 1905; COCKERELL, 1917b. *Oligo.*, England—*Holo.*

Rophalis HAGEN, 1866d, p. 459 [**Sisyra relicta* HAGEN in PICTET & HAGEN, 1856, p. 87; OD]. Fore wing with SC terminating on wing margin; costal area with numerous veins in front of pterostigma; inner and outer gradate series of crossveins present. PARFIN & GURNEY, 1956. *Oligo.*, Europe (Baltic).

Family HEMEROBIIDAE Leach, 1815

[*nom. correct.* KRÜGER, 1922, p. 138, *pro* Hemerobida LEACH, 1815, p. 138]

Fore wing with costal space usually broadest before midwing; vein SC terminating on C; 2 or more branches of RS arising from apparently fused stems of R and RS. Hind

wing with R not fused with RS beyond points of origin of any branches of RS; MA coalesced with RS for a short distance. Larvae terrestrial, predaceous. *Eoc.*—*Holo.*

Hemerobius LINNÉ, 1758, p. 549. JARZEMBOWSKI, 1980. *Paleog.*, England—*Holo.*

Megalomus RAMBUR, 1842, p. 418. HENRIKSEN, 1922b. *Eoc.*, Europe (Denmark)—*Holo.*

Prolachlanius KRÜGER, 1923, p. 88 [**Hemerobius resinatus* HAGEN in PICTET & HAGEN, 1856, p. 88; OD]. Similar to *Hemerobius*, but SC of fore wing terminating well before wing apex. *Oligo.*, Europe (Baltic).

Prophlebonema KRÜGER, 1923, p. 85 [**P. resinata*; OD]. Little-known hemerobiid, apparently related to *Megalomus*. *Oligo.*, Europe (Baltic).

Prospadobius KRÜGER, 1923, p. 90 [**Hemerobius moestus* HAGEN in PICTET & HAGEN, 1856, p. 88; OD]. Similar to *Symphorobius* (recent), but MA of fore wing not so deeply forked. *Oligo.*, Europe (Baltic).

Family MESOCHRY SOPIDAE Handlirsch, 1906

[Mesochrysopidae HANDLIRSCH, 1906b, p. 612]

Fore wing similar to that in Chrysopidae, but both branches of vein MP leading directly to hind margin; pseudomedia apparently well defined. [Possibly a synonym of Chrysopidae.] *Jur.*

Mesochrysopa HANDLIRSCH, 1906b, p. 613 [**Hageniotes zitteli* MEUNIER, 1898b, p. 118; OD]. Little-known fore wing with costal space of uniform width; RS straight, with about 10 primary branches. ADAMS, 1967. *Jur.*, Europe (Germany).

Mesypochochrysa MARTYNOV, 1927b, p. 764 [**M. latipennis*; OD]. Fore wing much broader than in *Mesochrysopa*; RS zigzagged, with about 7 primary branches. [Family assignment doubtful.] MARTYNOVA, 1962d; ADAMS, 1967. *Jur.*, USSR (Kazakh).—FIG. 193,1. **M. latipennis*; fore wing and body fragments, $\times 4$ (Martynov, 1927b).

Family CHRYSOPIDAE Hagen, 1866

[Chrysopidae HAGEN, 1866d, p. 371]

Wings subequal, oval. Costal area of fore wing with many unbranched crossveins; vein RS+MA arising about halfway between wing base and midwing, with a series of branches arising from zigzagged stem; 2 gradate series of crossveins generally present, one (pseudomedia) continuing the line of MP1+2 and the other (pseudocubitus) that of CUA. Hind

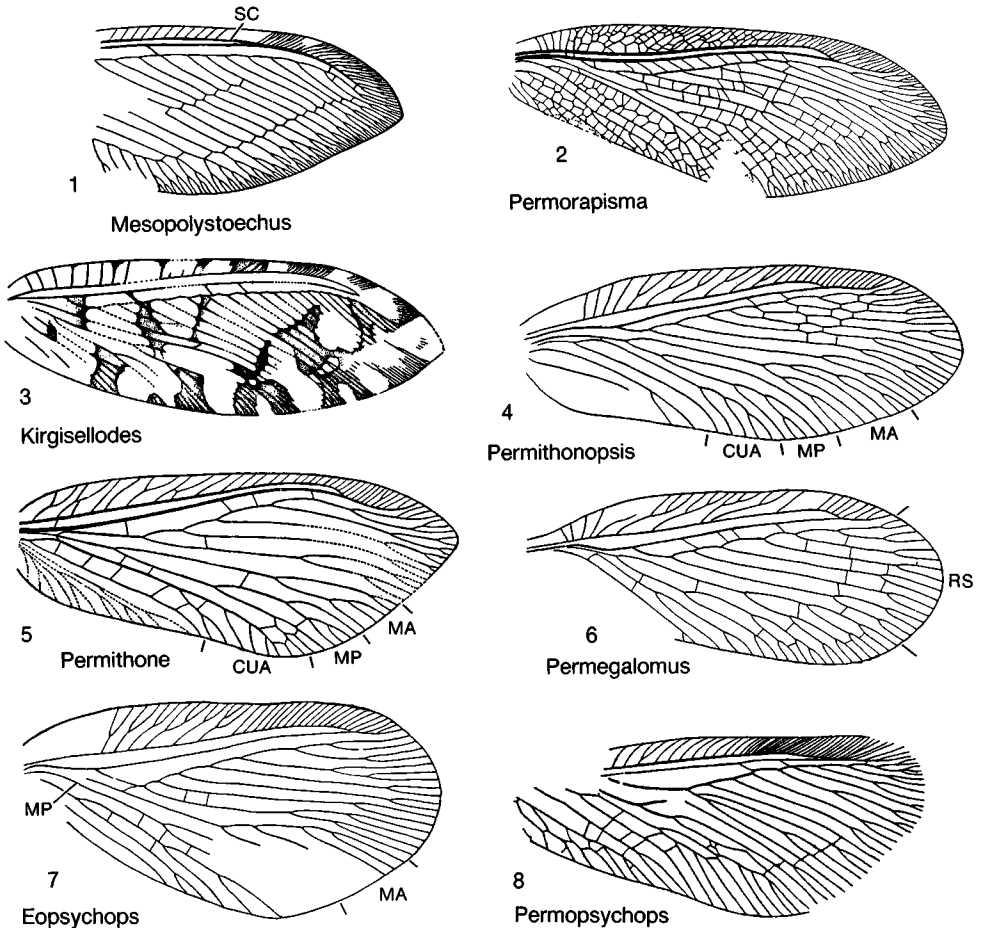


FIG. 192. Permithonidae, Mesopolystoechotidae, and Osmylitidae (p. 344–346).

wing with MP1 commonly coalesced with MA for a short distance and 2 gradate series of crossveins, mostly less irregular than in fore wing. ADAMS, 1956. *Oligo.*—*Holo.*

Chrysopa LEACH, 1815, p. 138. HANDSCHIN, 1937. *Mio.*, Europe (Germany)—*Holo.*

Archaeochrysa ADAMS, 1967, p. 229 [**Paleochrysa creedei* CARPENTER, 1935c, p. 265; OD]. Fore wing with basal subcostal crossvein distal to origin of RS+MA; MA, after leaving RS, not coalesced with MP1; pseudomedia strongly zigzagged. Hind wing with MA not coalesced with MP1. *Oligo.*, USA (Colorado).—FIG. 193,2.

**A. creedei* (CARPENTER); *a*, fore and *b*, hind wings, $\times 4.2$ (Adams, 1967).

Cimbrochrysa SCHLÜTER, 1982, p. 258 [**C. moleriensis*; OD]. Fore wing nearly triangular in shape; costal margin with a cluster of short hairs basally;

two crossveins between C and SC; MP deeply forked. *Eoc.*, Europe (Denmark).

Dyspetochrysa ADAMS, 1967, p. 229 [**Tribochrysa vetuscula* SCUDDER, 1890, p. 170; OD]. Fore wing as in *Archaeochrysa*, but MA coalesced with MP1 after leaving RS. *Oligo.*, USA (Colorado).

Nothochrysa MACLACHLAN, 1868, p. 195. STATZ, 1936a. *Oligo.*, Europe (Germany)—*Holo.*

Paleochrysa SCUDDER, 1890, p. 166 [**P. stricta*; OD] [= *Litochrysa* CARPENTER, 1935c, p. 265 (type, *Paleochrysa wickhami* COCKERELL, 1914d, p. 717)]. Venation as in *Archaeochrysa*, but in fore wing distal part of MA (after leaving RS) shorter. MA coalescing with MP1 in hind wing. ADAMS, 1967. *Oligo.*, USA (Colorado).

Tribochrysa SCUDDER, 1885b, p. 777 [**T. inaequalis*; OD]. Fore wing with RS+MA arising slightly basal of first fork of MP; inner gradate series of crossveins irregular. Hind wing with MA coalescing with MP1; pseudocubitus less

well developed than in fore wing. CARPENTER, 1935c; ADAMS, 1967. *Oligo.*, USA (Colorado). — FIG. 193,3. **T. inaequalis*; fore wing, $\times 4.5$ (Carpenter, 1935c).

Family ARCHEOSMYLIDAE

Riek, 1953

[Archeosmylidae RIEK, 1953, p. 85]

Fore wing apparently as in Osmylidae but lacking regularly arranged gradate crossveins; vein CUP deeply forked but not pectinately branched. *Perm.*–*Trias.*

Archeosmylus RIEK, 1953, p. 85 [**A. pectinatus*; OD]. Fore wing with distal costal veinlets unbranched; pterostigma long and well developed; RS with at least 8 pectinate branches. RIEK, 1955. *Perm.*, Australia (New South Wales); *Trias.*, Australia (Queensland). — FIG. 193,4. *A. stigmatus* RIEK, *Trias.*; fore wing, $\times 5.5$ (Riek, 1955).

Family OSMYLIDAE Leach, 1815

[*nom. correct.* BRAUER, 1868, p. 5, *pro* Osmylida LEACH, 1815, p. 138]

Moderate-sized to large insects with ocelli; wings covered by microtrichia; nygmata present. Fore wing with costal area only moderately broad; numerous simple veinlets from vein SC to costal margin; SC terminating on R before apex of wing; RS arising near wing base, with many branches; MA coalesced with R and RS basally and diverging as separate vein before midwing; MP having at least one fork, with division commonly basal; crossveins numerous, generally forming 1 or 2 gradate series distally. Hind wing similar to fore wing; free basal piece of MA short and sigmoidal. Larvae mainly terrestrial, some semiaquatic. *Paleoc.*–*Holo.*

Osmylus LATREILLE, 1802, p. 289. *Holo.*

Euporismites TILLYARD in TILLYARD & DUNSTAN, 1916, p. 44 [**E. balli*; OD]. Hind wing as in *Euporismus* (recent) but with basal branches of RS more widely spaced. RIEK, 1952a. *Paleoc.*, Australia (Queensland).

Lithosmylus CARPENTER, 1943c, p. 758 [**Osmylus columbianus* COCKERELL, 1908r, p. 342; OD]. Related to *Kempynus* (recent). Fore wing not falcate; M forking near wing base; MP branching distally of level of separation of MA from RS; only 1 series of gradate crossveins (outer). Hind

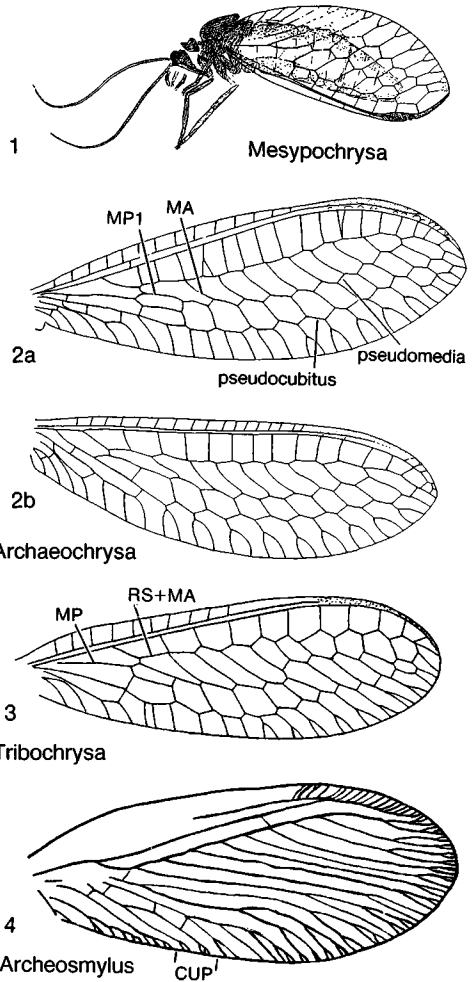


FIG. 193. Mesochrysopidae, Chrysopidae, and Archeosmylidae (p. 346–348).

wing with proximal piece of MA fully developed. *Oligo.*, USA (Colorado). — FIG. 194,4. **L. columbianus* (COCKERELL); a, fore and b, hind wings, $\times 2$ (Carpenter, 1943c).

Osmylidia COCKERELL, 1908r, p. 342 [**Osmylus requietus* SCUDDER, 1890, p. 34; OD] [= *Oligosmylus* KRÜGER, 1913, p. 19, obj.]. Related to *Gryposmylus* (recent). Fore wing more slender and pointed than hind wing and with about 10 crossveins between R and RS; radial-medial crossveins in 2 gradate series, inner of about 7 and outer of about 9; MP forked in proximal region of wing. WALTHER, 1904. *Oligo.*, USA (Colorado). — FIG. 194,2. **O. requietus* (SCUDDER); fore wing, $\times 3.7$ (Carpenter, 1943c).

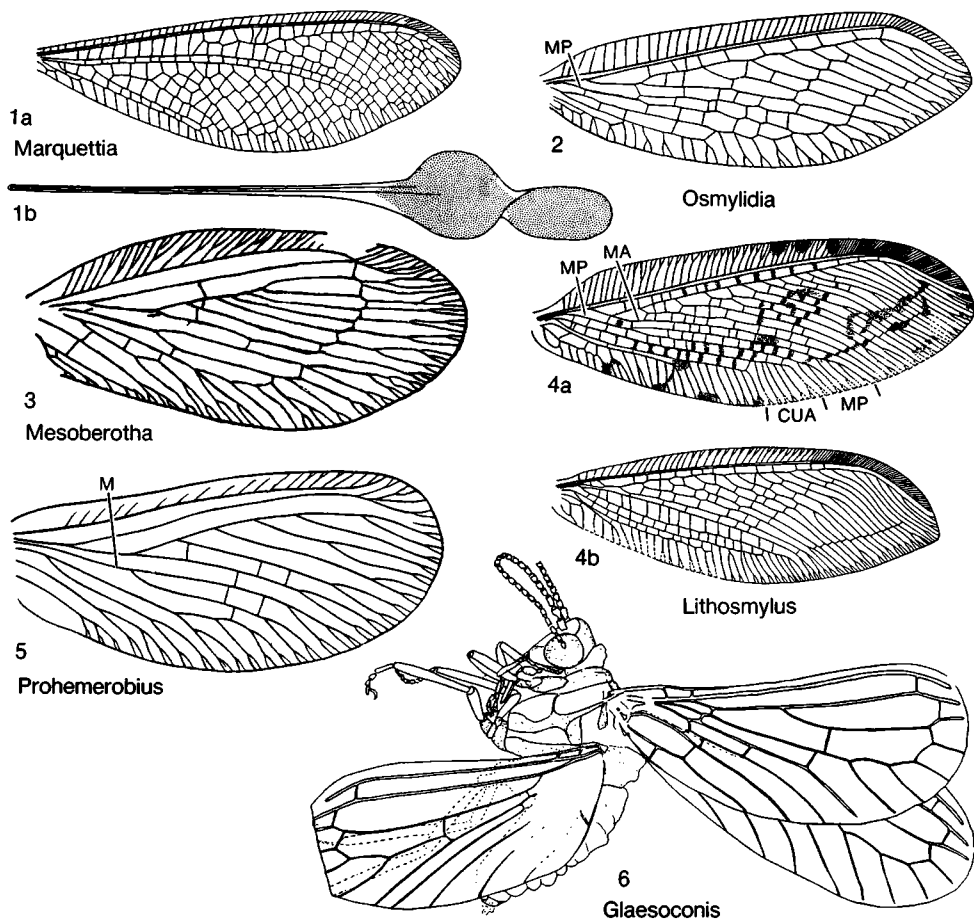


FIG. 194. Osmylidae, Mesoberothidae, Prohemerobiidae, Coniopterygidae, and Nemopteridae (p. 348–351).

Family MESOBEROTHIDAE
Carpenter, 1991

[Mesoberothidae CARPENTER, 1991, p. 87] [=Proberothidae RIEK, 1955, p. 674]

Little-known family, apparently related to Berothidae, but with more crossveins between branches of veins RS and M. *Trias.*

Mesoberotha CARPENTER, 1991, p. 87, *nom. subst. pro Proberotha* RIEK, 1955, p. 674, *non* KRÜGER, 1923 [**Proberotha superba*; OD]. Fore wing with costal area strongly widened at middle; MA and RS apparently joined by a crossvein, not coalesced. *Trias.*, Australia (Queensland).—FIG. 194,3. **M. superba* (RIEK); fore wing, ×8 (Riek, 1955).

Proberothella RIEK, 1955, p. 676 [**P. elongata*; OD]. Fore wing as in *Mesoberotha* but with MA

and RS coalesced basally for a short distance. *Trias.*, Australia (Queensland).

Family BERTHIDAE
Handlirsch, 1906

[*nom. transl.* HANDLIRSCH, 1908a, p. 1251, *ex* Berothinae HANDLIRSCH, 1906b, p. 42]

Wings subequal. Fore wing commonly falcate; vein RS with at least 4 branches, all arising from a single stem; MA coalesced with RS for a short distance proximally; single series of gradate veins. Hind wing with basal free piece of MA appearing as transverse crossvein, not longitudinal. Larvae terrestrial, with long and straight mandibles. *Cret.—Holo.*

- Berotha** WALKER, 1860, p. 186. *Holo.*
Banoberothes WHALLEY, 1980a, p. 160 [**B. enigmatica*; OD]. Fore wing with costal veinlets unbranched; R terminating on SC very close to wing apex; RS with several terminal branches; MP deeply forked. *Cret.*, Lebanon.
Paraberothes WHALLEY, 1980a, p. 161 [**P. acra*; OD]. Similar to *Rhachiberothes* (recent) but with a shorter pronotum; SC of fore wing terminating on R well before wing apex. *Cret.*, Lebanon.
Proberothes KRÜGER, 1923, p. 81 [**P. prisca*; OD]. Little-known berothid. *Oligo.*, Europe (Baltic).

Family MANTISPIDAE

Westwood, 1840

[Mantispidae WESTWOOD, 1840, p. 58]

Wings slender, subequal; pterostigma well developed; both pairs of wings with 2 gradate series of crossveins. Antennae short; pronotum slender; forelegs very long, raptorial. All species predaceous in larval and adult stages. *Paleog.*—*Holo.*

- Mantispa** ILLIGER, 1798, p. 499. *Holo.*
Promantispa JARZEMBOWSKI, 1980, p. 255 [**Mantispa relicta* COCKERELL, 1921d, p. 477; OD]. Wings apparently similar to those of *Mantispa* but with much longer pterostigma. *Paleog.*, England.

Family PROHEMEROBIIDAE

Handlirsch, 1906

[Prohemerobiidae HANDLIRSCH, 1906b, p. 473]

Fore wing small, oval; costal area not very broad; vein SC ending on C, not markedly curved; RS arising near wing base, with pectinate series of branches having small terminal forks; M with 2 branches. Hind wing unknown. [Probably related to the Dilariidae.] *Jur.*

- Prohemerobius** HANDLIRSCH, 1906b, p. 474 [**P. dilaroides*; OD]. Fore wing with costal margin straight or nearly so; costal area of moderate width; RS with 6 to 8 branches; CU forked more deeply than M. *Jur.*, Europe (Germany).—FIG. 194,5. **P. dilaroides*; fore wing, $\times 7$ (Handlirsch, 1906a).

Family CONIOPTERYGIDAE

Burmeister, 1838

[Coniopterygidae BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 701]

Very small to minute insects. Wings usually subequal, lacking marginal forks of veins characteristic of other Planipennia. Fore wing

with costa reduced, present only near base; costal area very narrow, traversed by only 1 or 2 crossveins; vein SC unbranched; RS arising near midwing, generally with 2 terminal branches; M not coalesced with RS, commonly with 2 terminal branches; CUA and CUP diverging from stem CU near base, both unbranched; 1A and 2A present. Hind wing with RS arising very near wing base, mostly forked distally; CU forked basally; CUA either very close to M or remote. Adults with wax glands, wax secreted tending to cover legs and wings. Larvae terrestrial, predaceous, feeding on aphids, scale insects, mites, etc.; mandibles straight and sharply pointed.

Jur.—*Holo.*

- Coniopteryx** CURTIS, 1834, pl. 528. MEINANDER, 1972. *Oligo.*, Europe (Baltic)—*Holo.*
Archiconiocompsa ENDERLEIN, 1910b, p. 675 [**A. prisca*; OD]. Fore wing as in *Coniocompsa* (recent); hind wing as in *Aleuropteryx* (recent); 16 antennal segments. MEINANDER, 1972. *Oligo.*, Europe (Baltic).
Archiconiopteryx ENDERLEIN, 1909, p. 774 [**A. liasina*; OD]. Fore wing with thickenings on M, as in *Aleuropteryx* (recent). MEINANDER, 1972. *Jur.*, Europe (Germany).
Archiconis ENDERLEIN, 1930, p. 111 [**A. electrica*; OD]. Fore wing as in *Fontellenea* (recent); plicaturae (paired organs) on several abdominal segments. MEINANDER, 1972. *Oligo.*, Europe (Baltic).
Glaesoconis MEINANDER, 1975, p. 54 [**G. cretica*; OD]. Head dorsoventrally elongate. Fore wing with 2 crossveins between RS and M; M with 4 terminal branches in both pairs of wings. WHALLEY, 1980a. *Cret.*, USSR (Asian RSFSR), Lebanon.—FIG. 194,6. **G. cretica*, wings and body, $\times 20$ (Meinander, 1975).
Heminiphethia ENDERLEIN, 1930, p. 105 [**H. fritschii*; OD]. Fore wing much as in *Neosemidalis* (recent). MEINANDER, 1972. *Oligo.*, Europe (Baltic).
Hemisemidales MEINANDER, 1972, p. 290. MEINANDER, 1975. *Oligo.*, Europe (Baltic)—*Holo.*
Juraconiopteryx MEINANDER, 1975, p. 53 [**J. zberichini*; OD]. Little-known genus, based on incomplete specimen; wing venation not preserved. Head capsule elongate; antennae with 28 segments. *Jur.*, USSR (Kazakh).

Family NEMOPTERIDAE

Rambur, 1842

[*nom. correct.* HAGEN, 1866d, p. 374, *pro* Nemopterides RAMBUR, 1842, p. 332]

Fore wing broadly oval or subtriangular; costal area with numerous undivided cross-

veins; vein SC coalesced with R distally; RS arising near midwing, with several irregular branches; MA coalesced with RS near origin of RS; MP1 a straight vein; MP2+CUA with several long branches to posterior margin; crossveins regularly distributed over wing but not forming a gradate series. Hind wing highly reduced, usually consisting of a long, slender petiole, terminating in 1 or 2 dilations. Larvae terrestrial, commonly with an elongate cervix. *Oligo.—Holo.*

Nemoptera LATREILLE, 1802, p. 296. *Holo.*

Marquettia NAVÁS, 1913c, p. 7 [**Halter americana* COCKERELL, 1907f, p. 446; OD] [= *Olivierina* PIERCE & KIRKBY, 1959, p. 47 (type, *O. metzeli*)]. Head shaped as in *Lertha* (recent); rostrum not elongate. RS of fore wing with 10 or more main branches; pterostigma small. Hind wing slender, with 2 dilations. CARPENTER, 1959. *Oligo.*, USA (Colorado, Montana). — FIG. 194, I. **M. americana* (COCKERELL, Colorado; *a*, fore and *b*, hind wings, $\times 1.8$ (Carpenter, 1959).

Family KALLIGRAMMATIDAE Handlirsch, 1906

[*nom. correct.* MARTYNOVA, 1947c, p. 2055, *pro* Kalligrammatidae HANDLIRSCH, 1906b, p. 610]

Large insects, related to the Psychopsidae. Fore wing with costal area of moderate width; vein SC joining R near wing apex; MA branched only near wing margins; MP extensively branched, sending several main branches anteriorly; crossveins very numerous over entire wing. Hind wing nearly as long as fore wing and at least as broad, with narrower costal area; venational pattern as in fore wing. Body little known. *Jur.*

Kalligramma WALTHER, 1904, p. 184 [**K. haeckeli*; OD]. RS of fore wing with about 12 primary branches; hind wing much broader than fore; wings with a conspicuous eye-spot. HANDLIRSCH, 1906b; MARTYNOVA, 1947c; PANFILOV, 1968. *Jur.*, Europe (Germany), USSR (Kazakh). — FIG. 195, 4. **K. haeckeli*, Germany; *a*, fore and *b*, hind wings, $\times 0.5$ (Handlirsch, 1906b).

Kalligrammula HANDLIRSCH, 1919a, p. 62 [**K. senckenbergiana*; OD]. Similar to *Kalligramma*, but RS with only 5 to 8 primary branches; wing eye-spot absent. HANDLIRSCH, 1906b; MARTYNOVA, 1947c. *Jur.*, Europe (Germany), USSR (Kazakh).

Lithogramma PANFILOV, 1968, p. 172 [**L. oculatum*; OD]. Fore wing broad, almost oval; cos-

tal area unusually broad; MA with numerous branches arising basally. *Jur.*, USSR (Kazakh). **Meioneurites** HANDLIRSCH, 1906b, p. 612 [**M. schlosseri*; OD]. Fore wing with first branch of RS remote from wing base; crossveins more widely spaced than in *Kalligramma*. MARTYNOVA, 1947c; PANFILOV, 1968. *Jur.*, Europe (Germany), USSR (Kazakh).

Family PSYCHOPSIDAE Handlirsch, 1906

[*nom. transl.* HANDLIRSCH, 1908a, p. 1170, *ex* Psychopsinae HANDLIRSCH, 1906b, p. 42]

Moderate-sized to large insects, almost mothlike in appearance. Fore wing generally very broad; costal area very wide, with numerous forked veinlets; veins SC, R, and RS close together and parallel, forming the *vena triplica*; numerous branches arising pectinately from RS; M apparently deeply forked, MA and MP not clearly identifiable; crossveins not numerous, mainly restricted to a few gradate series. Hind wing shorter than fore wing; costal area nearly as broad as in fore wing; *vena triplica* present. Larvae terrestrial. *Trias.—Holo.*

Psychopsis NEWMAN, 1842, p. 415. *Holo.*

Angaropsychops MARTYNOVA, 1949a, p. 163 [**A. turgensis*; OD]. Little-known fore wing; SC, R, and RS forming smooth curve; crossveins numerous, irregularly distributed. *Jur.*, USSR (Asian RSFSR). — FIG. 195, 3. **A. turgensis*; fore wing fragment, $\times 1.6$ (Martynova, 1949a).

Embaneura ZALESSKY, 1953a, p. 164 [**E. vachrameevi*; OD]. Fore wing as in *Angaropsychops*, but branches of RS more numerous and closer together. MARTYNOVA, 1962d. *Cret.*, USSR (Kazakh). — FIG. 195, 2. **E. vachrameevi*; fore wing, $\times 1.2$ (Martynova, 1962d).

Grammopsychops MARTYNOVA, 1954, p. 1167 [**G. lebedevi*; OD]. Fore wing very similar to that of *Embaneura*, but crossveins arranged in several concentric rows. [Probably a synonym of *Embaneura*.] *Cret.*, USSR (Asian RSFSR). — FIG. 195, 1. **G. lebedevi*; fore wing, $\times 1.3$ (Martynova, 1954).

Propropsychops KRÜGER, 1923, p. 84 [**P. helmi*; OD]. Fore wing apparently with no anastomosis between branches of MP or between posterior parts of MP and CUA. Hind wing with free basal piece of MA longitudinal in position. MACLEOD, 1970. *Oligo.*, Europe (Baltic).

Triassopsychops TILLYARD, 1922b, p. 467 [**T. superba*; OD]. Fore wing triangular in shape, almost as broad as long; crossveins not forming a definite series. *Trias.*, Australia (Queensland).

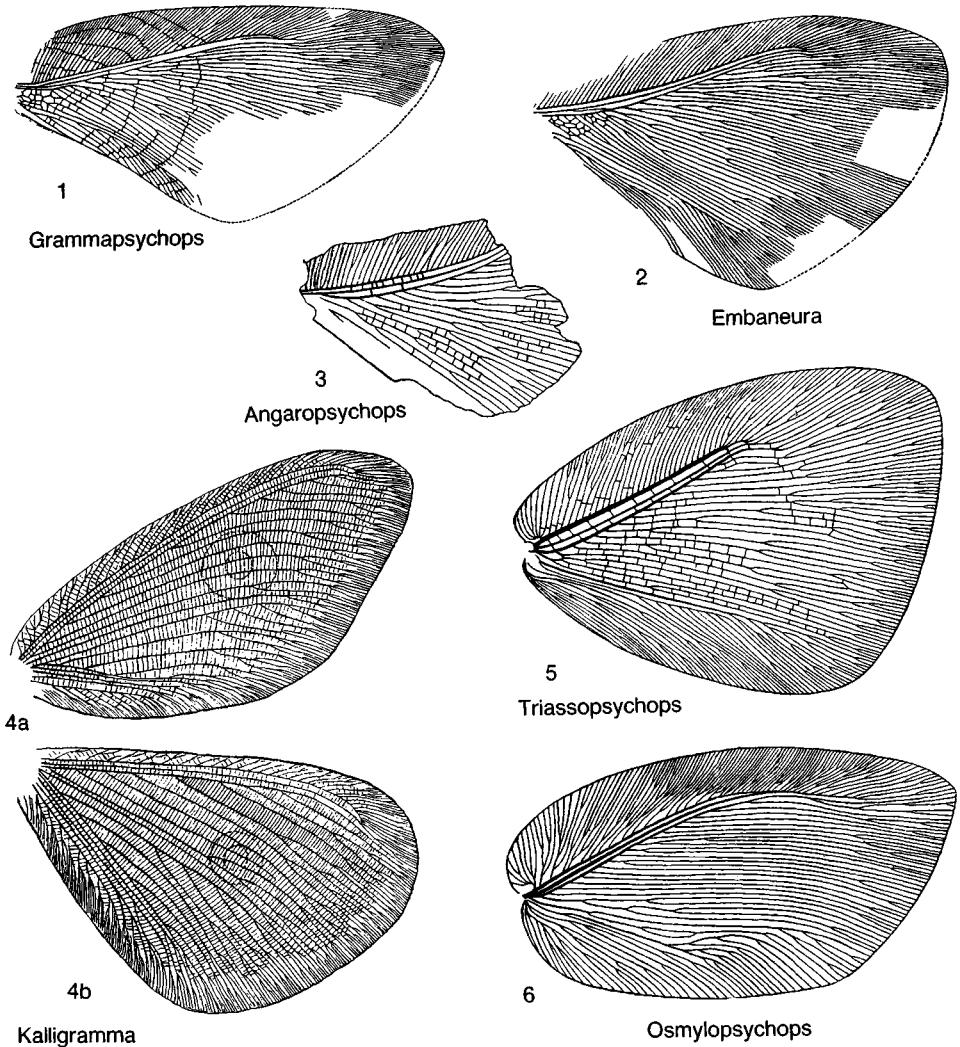


FIG. 195. Kalligrammatidae, Psychopsidae, and Osmylopsychopidae (p. 351–352).

—FIG. 195,5. **T. superba*; fore wing, partially restored, $\times 1.7$ (Tillyard, 1922b).

Family OSMYLOPSYCHOPIDAE Martynova, 1949

[*nom. correct.* MARTYNOVA, 1962d, p. 277, *pro* Osmylopsychopidae MARTYNOVA, 1949a, p. 166] [=Osmylopsychopidae RIEK, 1955, p. 680, junior synonym and homonym]

Fore wing as in Psychopsidae, but veins SC and R joined well before apical region; crossveins few and very weakly developed. Hind wing unknown. *Trias.*

Osmylopsychops TILLYARD, 1923b, p. 496 [**O. spillerae*; OD]. Fore wing with costal veinlets mostly forked and connected by scattered cross-

veins. RIEK, 1955. *Trias.*, Australia (Queensland), Europe (France). — FIG. 195,6. **O. spillerae*; fore wing, partially restored, $\times 2$ (Tillyard, 1923b).

Petropsychops RIEK, 1956, p. 104 [**P. superba*; OD]. Fore wing similar to that of *Osmylopsychops*, but M much more extensive, with many anterior, pectinate branches. *Trias.*, Australia (Queensland).

Family BRONGNIARTIELLIDAE Martynova, 1949

[Brongniartiellidae MARTYNOVA, 1949a, p. 165]

Fore wing as in Osmylopsychopidae, but costal area narrowed markedly by vein SC

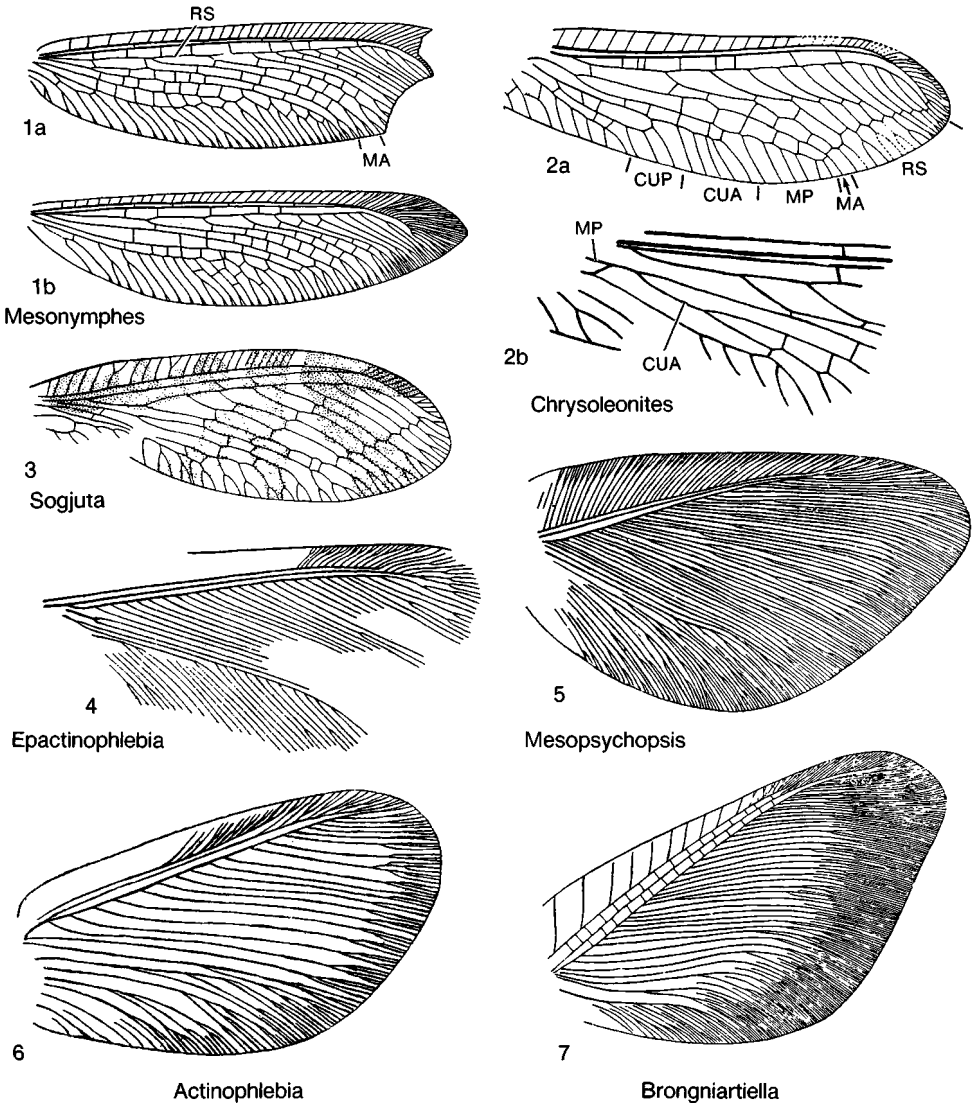


FIG. 196. Brongniartiellidae, Nymphidae, and Nymphitidae (p. 352-354).

terminating on C; distal branches of R and RS mostly straight, only a few curved posteriorly. Hind wing unknown. *Jur.*

Brongniartiella MEUNIER, 1898a, p. 237 [**B. problematica*; OD]. Fore wing with branches of RS forking at about half their lengths. MARTYNOVA, 1949a. *Jur.*, Europe (Germany).—FIG. 196,7. *B. inconditissimi* HANDLIRSCH; fore wing, $\times 0.8$ (Handlirsch, 1906b).

Actinophlebia HANDLIRSCH, 1906b, p. 476 [**Pterinoblattina megapolitana* GEINITZ, 1887, p. 198; OD]. Fore wing as in *Brongniartiella*, but terminal branches of RS shorter. TILLYARD, 1933;

MARTYNOVA, 1949a. *Jur.*, Europe (Germany), England. — FIG. 196,6. **A. megapolitana* (GEINITZ); fore wing, $\times 3.7$ (Handlirsch, 1906b). **Epactinophlebia** MARTYNOV, 1927b, p. 766 [**E. karabasi*; OD]. CUA of fore wing straight, with several pectinate branches distally, directed posteriorly; crossveins apparently absent. MARTYNOVA, 1962d. *Jur.*, USSR (Kazakh).—FIG. 196,4. **E. karabasi*; fore wing, $\times 2.5$ (Marty-nov, 1927b).

Mesopsychopsis HANDLIRSCH, 1906b, p. 607 [**Ricania hospes* GERMAR, 1839, p. 220; OD]. Similar to *Brongniartiella*, but costal area much broader; forks of branches of RS long. MARTYNOVA, 1949a. *Jur.*, Europe (Germany).—FIG.

196,5. **M. hospes* (GERMAR); fore wing, $\times 2.5$ (Handlirsch, 1906b).

Family NYMPHIDAE Rambur, 1842

[*nom. correct.* BRAUER, 1868, p. 5, *pro* Nymphides RAMBUR, 1842, p. 412]

Insects of moderate size, similar in general appearance to Osmylidae, but lacking ocelli, and wings without nygmata and covering of microtrichia. Wings similar to those of Osmylidae, but costal area of fore wing narrower; hind wing with basal piece of vein MA apparently absent. Larvae terrestrial, resembling those of Myrmeleontidae. *Jur.*—*Holo.*

Nymphes LEACH, 1814, p. 101. *Holo.*

Mesonymphes CARPENTER, 1929a, p. 191 [**M. bageni*; OD]. Wings as in *Nymphes* (recent) but wider basally and with fewer crossveins. ADAMS, 1958. *Jur.*, Europe (Germany).—FIG. 196,1. **M. bageni*; *a*, fore and *b*, hind wings, $\times 1.4$ (Carpenter, 1929a).

Pronymphes KRÜGER, 1923, p. 75 [**Nymphes mengeanus* HAGEN in PICTET & HAGEN, 1856, p. 85; OD]. Fore wing as in *Nesydrion* (recent), but fork of CUA apparently distal of level of separation of MA from RS. MACLEOD, 1970. *Oligo.*, Europe (Baltic).

Family NYMPHITIDAE

Handlirsch, 1906

[Nymphitidae HANDLIRSCH, 1906b, p. 608]

Wings as in Nymphidae but with 2 series of gradate crossveins; vein CUA of hind wing coalesced with CUP for short distance. *Trias.*—*Jur.*

Nymphites HAASE, 1890a, p. 23 [**Hemerobius priscus* WEYENBERGH, 1869, p. 264; OD]. Fore wing subtriangular with pointed apex; costal area nearly uniform in width. MARTYNOVA, 1949a. *Jur.*, Europe (Germany).

Chrysoleonites MARTYNOV, 1925b, p. 591 [**C. ocellatus*; OD]. Fore wing with costal area somewhat narrowed distally; tornus of hind margin less pronounced than in *Nymphites* and apex more rounded. Hind wing with costal area much narrower than in fore wing; CUA coalesced with MP for a short distance basally. MARTYNOVA, 1949a, 1962d. *Jur.*, USSR (Kazakh).—FIG. 196,2. **C. ocellatus*; *a*, fore wing, $\times 3.5$; *b*, hind wing, $\times 5.0$ (Martynova, 1949a).

Sialium WESTWOOD, 1854, p. 396 [**S. sipylus*; OD]. Fore wing with venation similar to that of *Nymphites*, but wing more elongate, not trian-

gular. HANDLIRSCH, 1906b. *Jur.*, Europe (Germany).

Sogjuta MARTYNOVA, 1958, p. 77 [**S. speciosa*; OD]. Fore wing as in *Chrysoleonites* but more oval; costal area nearly uniform in width; RS with fewer branches. *Trias.*, USSR (Kirghiz).—FIG. 196,3. **S. speciosa*; fore wing, $\times 4.6$ (Martynova, 1958).

Family SOLENOPTILIDAE

Handlirsch, 1906

[Solenoptilidae HANDLIRSCH, 1906b, p. 478]

Similar to Nymphitidae; vein R not parallel to costal margin distally; crossveins numerous and regularly distributed over wing. *Jur.*

Solenoptilon HANDLIRSCH, 1906b, p. 478 [**Abia kochi* GEINITZ, 1887, p. 200; OD]. Little-known wing; both SC and R slightly curved posteriorly in apical region. MARTYNOVA, 1949a. *Jur.*, Europe (Germany), USSR (Kazakh).

Family MYRMELEONTIDAE

Latreille, 1804–1805

[*nom. correct.* BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 757, *pro* Myrmeleonides LATREILLE, 1804–1805, p. 22]

Fore wing with veins SC and R coalesced at apex for considerable distance; subcostal crossveins almost entirely absent; CUA branching to form large triangle; wing bordered by dense series of marginal veinlets; MP2 and CUA coalesced proximally, base of MP2 appearing as oblique crossvein. Antennae at least slightly clavate, short. Larvae terrestrial, flattened. *Oligo.*—*Holo.*

Myrmeleon LINNÉ, 1767, p. 913. *Holo.*

Dendroleon BRAUER, 1866, p. 42. STATZ, 1936a. *Oligo.*, Europe (Germany)—*Holo.*

Family ASCALAPHIDAE

Lefebure, 1842

[*nom. correct.* SCHNEIDER, 1845, p. 341, *pro* Ascalaphides LEFEBURE, 1842, p. 10]

Similar to Myrmeleontidae, but antennae strongly clavate and at least half as long as fore wing. Larvae terrestrial, with prominent processes (scoli) along sides of thorax and abdomen. *Oligo.*—*Holo.*

Ascalaphus FABRICIUS, 1775, p. 313. *Holo.*

Borgia NAVÁS, 1913a, p. 132 [**Ascalaphus proavus* HAGEN, 1858b, p. 125; OD]. Fore wings with

very few veins in apical region. *Oligo.*, Europe (Germany).—FIG. 197,1. **B. proavus* (HAGEN); *a*, antenna and *b*, fore wing, $\times 2.6$ (Hagen, 1858b).

Neadelphus MACLEOD, 1970, p. 153 [**N. protae*; OD]. First stage larva: head capsule quadrate with cordate posterolateral margins; meso- and metathorax with 2 elongate setigerous scoli on each lateral margin; abdominal segments 1 to 8 with bilateral pair of similar scoli. HENRY, 1976. *Oligo.*, Europe (Baltic).—FIG. 197,2. **N. protae*; larva, $\times 15$ (MacLeod, 1970).

Family UNCERTAIN

The following genera, apparently belonging to the order Neuroptera, suborder Planipennia, are too poorly known to permit assignment to families.

Archedilaropsis MARTYNOV, 1935b, p. 39 [**A. furcata*; OD]. Little-known wing fragments; possibly related to Prohemerobiidae. *Jur.*, USSR (Asian RSFSR).

Archepsychos TILLYARD, 1919a, p. 205 [**A. triassica*; OD]. Little-known wing fragment, possibly related to Psychopsidae. RIEK, 1955, 1956. *Trias.*, Australia (New South Wales, Queensland).

Bothriomicromus SCUDDER, 1878d, p. 462 [**B. lachlani*; OD]. Little-known fore wing with very broad costal area basally and numerous branches of RS; 2 rows of crossveins. [Probably belonging either to Psychopsidae or Hemerobiidae.] SCUDDER, 1890. *Oligo.*, Canada (British Columbia).

Creagroptera HANDLIRSCH, 1906b, p. 605 [**C. schwertschlagerei*; OD]. Little-known fore wing, possibly related to Prohemerobiidae. *Jur.*, Europe (Germany).

Dicranoptila HANDLIRSCH, 1906b, p. 608 [**D. deichmulleri*; OD]. Little-known insect; venation unknown. [Ordinal position doubtful.] *Jur.*, Europe (Germany).

Dilarites MARTYNOV, 1925b, p. 596 [**D. incertus*; OD]. Little-known wing fragment. *Jur.*, USSR (Kazakh).

Epigambria HANDLIRSCH, 1939, p. 76 [**E. longipennis*; OD]. Little-known, small, oval wing, with strongly curved cubitus and anal veins. [Type of family Epigambridae.] *Jur.*, Europe (Germany).

Glottidia BODE, 1953, p. 268 [**G. multivenosa*; OD]. Little-known oval wing with wide costal area at base; SC apparently extending nearly to wing apex. *Jur.*, Europe (Germany).

Hondelagia BODE, 1953, p. 269 [**H. reticulata*; OD]. Little-known wing, with several anal veins. [Possibly belonging to Raphidiodea.] *Jur.*, Europe (Germany).

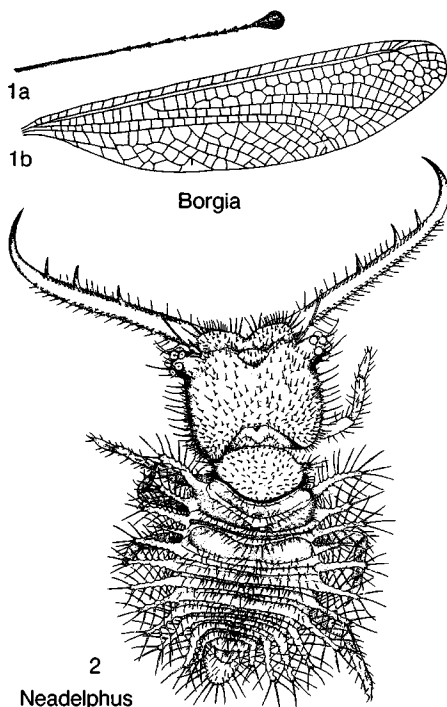


FIG. 197. Ascalaphidae (p. 354–355).

Ineptia HANDLIRSCH, 1906b, p. 614 [**I. meunieri*; OD]. Little-known insect with wing-length of 40 mm; numerous crossveins. *Jur.*, Europe (Germany).

Liassopsychops BODE, 1953, p. 248 [**L. curvata*; OD]. Little-known wing fragments; several veins with numerous marginal branches. *Jur.*, Europe (Germany).

Lithosmylidia RIEK, 1955, p. 678 [**L. lineata*; OD]. Little-known wing fragment, possibly related to Polysotechotidae. *Trias.*, Australia (Queensland).

Loxophleps HANDLIRSCH, 1939, p. 76 [**L. costalis*; OD]. Little-known wing fragment, possibly belonging to Solenoptilidae. *Jur.*, Europe (Germany).

Megapolystoechus TILLYARD, 1933, p. 11 [**M. magnificus*; OD]. Little-known wing fragment; RS with numerous branches; SC not fused with R distally. *Jur.*, England.

Melamnus HANDLIRSCH, 1939, p. 77 [**M. indistinctus*; OD]. Little-known wing fragment; SC terminating on R distally, both directed posteriorly in distal region. MARTYNOVA, 1961c. *Jur.*, Europe (Germany).

Melaneimon HANDLIRSCH, 1939, p. 77 [**M. dubium*; OD]. Small wing fragment. MARTYNOVA, 1961c. *Jur.*, Europe (Germany).

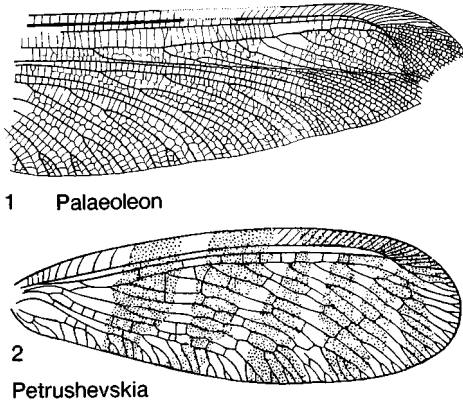


FIG. 198. Uncertain (p. 356).

Mesoleon HANDLIRSCH, 1906b, p. 477 [**M. dobertinianus*; OD]. Little-known wing fragment. *Jur.*, Europe (Germany).

Osmypopsis HANDLIRSCH, 1906b, p. 614 [**Abia duplicata* GIEBEL, 1856, p. 264; OD]. Little-known wing, about 10 mm long. *Jur.*, Europe (Germany).

Palaeoleon RICE, 1969, p. 3 [**P. ferrogeticus*; OD]. Little-known wing with myrmeleontoid features; intercalary veins well developed along posterior border. [Possibly related to the Stilbopterygidae.] *Cret.*, Canada (Labrador).—FIG. 198,1. **P. ferrogeticus*; apical half of wing, $\times 1.5$ (Rice, 1969).

Palparites HANDLIRSCH, 1906b, p. 614 [**P. deichmulleri*; OD]. Little-known insect with fore wing 80 mm long. *Jur.*, Europe (Germany).

Paractinophlebia HANDLIRSCH, 1906b, p. 477 [**Pterinoblattina curtisii* SCUDDER, 1886b, p. 471; OD]. Little-known wing fragment. *Jur.*, England.

Parasisyra ZALESSKY, 1933, p. 143 [**P. kargalica*; OD]. Little-known fragment, possibly related to Sialidopsidae. [Type of family Parasisyridae.] MARTYNOV, 1937b. *Perm.*, USSR (European RFSR).

Parhemerobius BODE, 1953, p. 260 [**P. dilatatus*; OD]. Fore wing nearly as broad as long; SC relatively short; R and RS strongly curved posteriorly in distal region. *Jur.*, Europe (Germany).

Petrushevskia MARTYNOVA, 1958, p. 76 [**P. borisi*; OD]. Fore wing(?) with rounded apex; MA coalesced with RS for short distance basally. [Probably representing an undescribed family.] *Trias.*, USSR (Kirghiz).—FIG. 198,2. **P. borisi*; fore wing(?), $\times 3.5$ (Martynova, 1958).

Protopsychoopsis TILLYARD, 1917a, p. 178 [**P. venosa*; OD]. Little-known wing, possibly related to Osmypopsychopidae. TILLYARD, 1919b; RIEK, 1956. *Trias.*, Australia (Queensland).

Pseudomyrmeleon HANDLIRSCH, 1906b, p. 614

[**Myrmeleon extinctus* WEYENBERGH, 1869, p. 265; OD]. Little-known insect, with wing 36 mm long. [Possibly related to Mesochrysopidae.] *Jur.*, Europe (Germany).

Pterinoblattina SCUDDER, 1885f, p. 105 [**Blatta pluma* GIEBEL, 1856, p. 322; SD HANDLIRSCH, 1906b, p. 607]. Little-known wing fragment. [Possibly related to Psychopsidae.] BODE, 1953. *Jur.*, Europe (Germany).

Ricartus NAVÁS, 1913a, p. 133 [**Ascalaphus edwardsi* OUSTALET, 1870, p. 93; OD]. Wing fragments. *Oligo.*, Europe (France).

Trichophlebia BODE, 1953, p. 263 [**T. multistriata*; OD]. Little-known fore wing, very broad and subtriangular, with short SC. *Jur.*, Europe (Germany).

Order GLOSSELYTRODEA Martynov, 1938

[Glosselytrodea MARTYNOV, 1938c, p. 189]

Small insects, apparently related to the Neuroptera. Wings subequal, fore wing in some species tegminous. Fore wing with precostal area commonly well developed, forming a prominent bulge at base of wing margin; vein R extending to or nearly to apex of wing, even forming a submarginal vein along anterior wing border; RS with 2 or more branches; MA coalesced with RS basally, then branching off as a nearly straight vein, often with a posterior branch; MA and MP often very close together and almost coalesced; CUA coalesced basally with MP, usually long, extending at least to midwing, often continuing as a submarginal vein nearly to apex; CUP usually straight; anal veins close together. Crossveins numerous or very numerous, forming many regular or, in a few genera, irregular cells over wing, including anal area; veins, in some species at least, with numerous setae. Hind wing slightly smaller than fore wing; precostal area apparently absent; SC short; R long, extending nearly to apex as a submarginal vein; RS, MA, and MP much as in fore wing; CUP extending only to about midwing. Body structure poorly known; head small, hypognathous; legs slender; cerci (possibly in female only) very short, with 1 to 4 segments (ZALESSKY, 1932b).

Some difference of opinion exists about the homologies of the wing venation (CAR-

PENTER, 1943a; ROHDENDORF, 1962a). The family Permoberothidae, which appears to be the most generalized of the families, provides the best evidence for interpretation of venation. In the fore wing of *Permoberotha* (see Fig. 199,2a), veins R and MA are readily identifiable as convex veins; the longitudinal veins between these two are concave and are presumably RS. The vein just below MA is concave and is therefore regarded as MP; its basal branch is weakly concave and is considered to be MP2. CUA is easily recognized as a strongly convex vein and the anal veins present no difficulty. Between MA and MP there is a faint but distinct groove, extending nearly from the wing base to the apex; the functional significance of this groove is unknown, but a similar groove occurs in the wings of the Hemerobiidae and other Neuroptera. The foregoing interpretation of the venation is different from those previously suggested; it assumes no unusual structure of the veins other than the partial coalescence of MA with RS and MP with CUA, a condition that occurs in many orders and families of insects.

The Archoglossopteridae appear to represent a somewhat more specialized stage than the Permoberothidae in the evolution of the wings of the Glosselytrodea: the precostal area is weakly developed, R terminates before the wing apex, and the cells of the wings are relatively large. In most other families, such as the Jurinidae, the precostal area is more pronounced, R terminates at the very apex of the wings, and the crossveins are usually more numerous and small.

The affinities of the Glosselytrodea are uncertain. Originally considered by MARTYNOV (1938c) to be orthopteroid, the order has more recently been regarded as endopterygote and most closely related to the Neuroptera (ZALESSKY, 1932b; CARPENTER, 1964c). In this connection it should be noted that TILLYARD (1932a) originally placed the Permoberothidae in the Neuroptera (Planipennia). It now seems certain that the Permoberothidae are, in fact, members of the Glosselytrodea; nonetheless, it seems prob-

able that TILLYARD was correct in detecting neuropterous traits in the Permoberothidae. Neuropterous traits now found in most of the other Glosselytrodea are the rows of setae on the wing veins, crossveins, and wing margins; as well as the general structure of the thorax and the position of the wings at rest. The evidence is certainly suggestive, though not conclusive, for the endopterygote position of the Glosselytrodea. *Perm.—Jur.*

Family PERMOBEROTHIDAE Tillyard, 1932

[Permoberothidae TILLYARD, 1932a, p. 23]

Wings subequal. Fore wing membranous, with setae on main veins; costa marginal; anterior border of wing with only a slight bulge proximally; vein R strongly curved distally, not quite reaching apex of wing; RS with 2 long branches; MA unbranched, straight; a distinct groove, apparently bearing a spurious vein, between MA and MP; MP coalesced basally with CUA for a short distance, giving rise to basal branch after the separation of CUA; stem of CU free at base, dividing shortly into CUA and CUP, both of which are unbranched; 3 anal veins; crossveins numerous, forming irregular network between branches of RS. Hind wing slightly smaller than fore wing; costal margin straight or smoothly curved; SC shorter than in fore wing, terminating on R before midwing; rest of venation as in fore wing. Body structure little known; abdomen with short cerci, composed of 4 or 5 segments. *Perm.*

Permoberotha TILLYARD, 1932a, p. 24 [**P. villosa*; OD] [= *Dictyobiella* TILLYARD, 1937a, p. 104 (type, *D. nervosa*)]. RS forked just before midwing; 2A in fore wing terminating on 3A. *Perm.*, USA (Kansas).—FIG. 199,2. **P. villosa*; a, fore and b, hind wings, ×6 (Carpenter, 1943a).

Family ARCHOGLOSSOPTERIDAE Martynova, 1958

[Archoglossopteridae MARTYNOVA, 1958, p. 74]

Fore wing with costa submarginal; pre-costal area present, forming a small bulge; vein R nearly straight, terminating just before apex of wing; MP without basal branch; 2

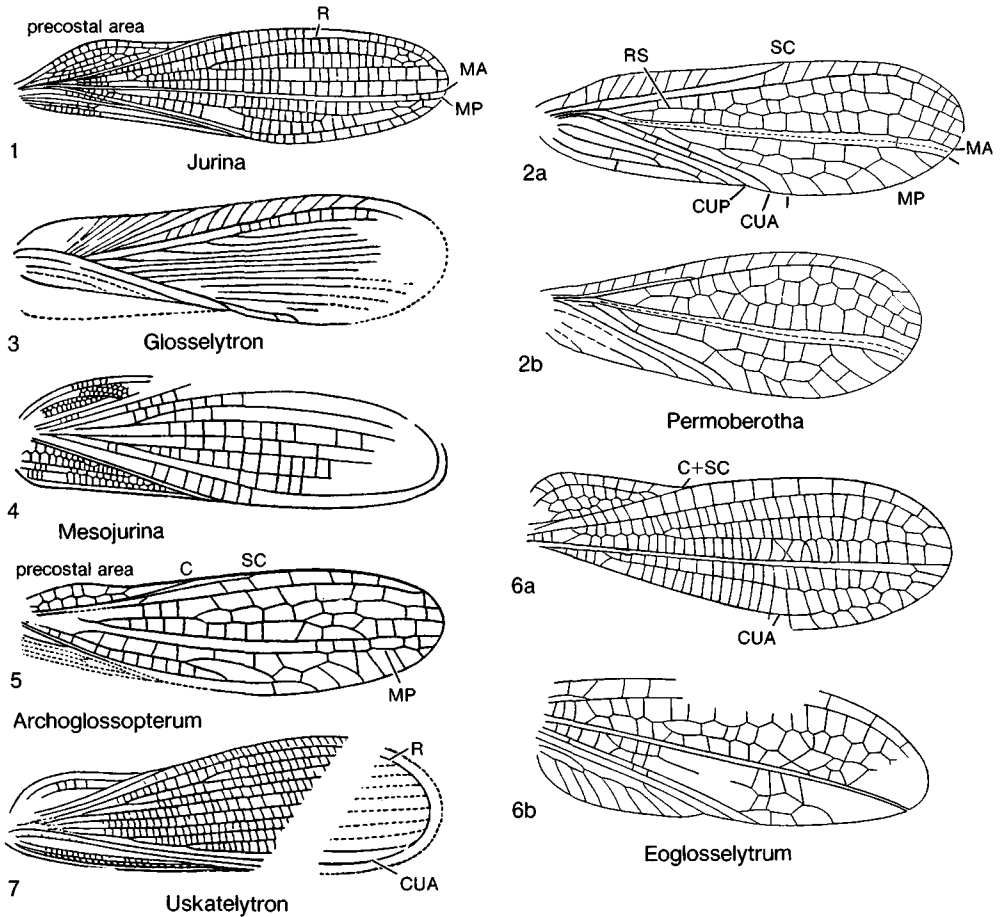


FIG. 199. Permoberothidae, Archoglossopteridae, Glosselytridae, Jurinidae, and Uskatelytridae (p. 357-359).

rows of cellules in precostal area; crossveins about as numerous as in *Permoberotha*. Hind wing and body unknown. *Perm.*

Archoglossopterm MARTYNOVA, 1958, p. 74 [**A. shoricum*; OD]. RS forked before midwing; MP diverging from CU before origin of RS. *Perm.*, USSR (Asian RSFSR). — FIG. 199,5. **A. shoricum*; fore wing, ×7 (Martynova, 1958).

Family GLOSSELYTRIDAE
Martynov, 1938

[Glosselytridae MARTYNOV, 1938c, p. 204]

Anterior margin of fore wing nearly straight; precostal area with numerous radiating veins, and vein RS with at least 5 branches. *Perm.*

Glosselytron MARTYNOV, 1938c, p. 204 [**G. multivenosum*; OD]. Little-known genus. Fore wing: branches of RS very close together and parallel. *Perm.*, USSR (European RSFSR). — FIG. 199,3. **G. multivenosum*; fore wing, ×3 (Martynov, 1938c).

Family JURINIDAE Zalessky, 1929

[Jurinidae ZALESSKY, 1929, p. 28] [=Anorthoneuridae MARTYNOV, 1938c, p. 197; Eoglosselytridae MARTYNOVA, 1952a, p. 191]

Fore wing: precostal area prominent, with at least 4 rows of cells; vein R following curvature of wing margin nearly to wing apex; RS with 2 or 3 branches; MA and MP very close together; anal veins straight and parallel; MP with a basal branch; CUA extending as a submarginal vein nearly to wing

apex. Hind wing venation as in fore wing, but branches of RS irregular and crossveins less numerous and less regular. *Perm.*

Jurina ZALESSKY, 1929, p. 28 [**J. scutulata*; OD] [= *Anorthoneura* MARTYNOV, 1938c, p. 198, *nom. nud.*]. Crossveins of fore wing very numerous, close together, and straight. *Perm.*, USSR (European and Asian RSFSR). — FIG. 199, 1. *J. marginata* MARTYNOV, Asian RSFSR; fore wing, $\times 5.5$ (Martynova, 1938c).

Eoglosselytrum MARTYNOVA, 1952a, p. 191 [**E. kondomense*; OD]. C and SC of fore wing fused; RS with 2 branches; posterior branch of MP simple; cells somewhat larger than in *Jurina*. Hind wing with cells more irregular than in fore wing. *Perm.*, USSR (Asian RSFSR). — FIG. 199, 6. **E. kondomense*; a, fore and b, hind wings, $\times 9$ (Martynova, 1952a).

Permoberothella RIEK, 1953, p. 80 [**P. perplexa*; OD]. Little-known fore wing, with most cells irregular in shape, not with straight sides, as in *Jurina*. [Family position doubtful.] MARTYNOVA, 1952a. *Perm.*, Australia (New South Wales).

Protojurina MARTYNOVA, 1958, p. 75 [**P. cellulosa*; OD]. Little-known fore wing, similar to that of *Jurina* but with crossveins even closer together and cells of precostal area smaller. *Perm.*, USSR (Asian RSFSR).

Surijoka MARTYNOVA, 1958, p. 75 [**S. grandicella*; OD]. Little-known fore wing, similar to that of *Eoglosselytrum*, but RS with 3 branches. *Perm.*, USSR (Asian RSFSR).

Family USKATELYTRIDAE

Martynova, 1952

[Uskatelytridae MARTYNOVA, 1952a, p. 190]

Precostal area of fore wing with a submarginal vein; vein RS with 2 to 4 branches. *Perm.*—*Jur.*

Uskatelytron MARTYNOVA, 1952a, p. 190 [**U. sibiricum*; OD]. Little-known fore wing; RS with 4 branches; crossveins numerous; anal area long. *Perm.*, USSR (Asian RSFSR). — FIG. 199, 7. **U. sibiricum*; fore wing, $\times 3.5$ (Martynova, 1952a).

Mesojurina MARTYNOVA, 1943, p. 285 [**M. sogjutensis*; OD]. RS with 2 branches; crossveins not so numerous as in *Uskatelytron*. *Jur.*, USSR (Kirghiz). — FIG. 199, 4. **M. sogjutensis*; fore wing, $\times 12$ (Martynova, 1943).

Family UNCERTAIN

The genus described below, apparently belonging to the order Glosselytrodea, is too poorly known to permit family assignment.

Polycytella TILLYARD, 1922b, p. 460 [**P. triasica*; OD]. Little-known fore wing; crossveins very numerous over entire wing; MA and MP apparently very close together. [Type of family Polycytellidae MARTYNOVA, 1952a.] *Trias.*, Australia (Queensland).

Order TRICHOPTERA

Kirby, 1815

[Trichoptera Kirby, 1815b, p. 88]

Small or moderate-sized insects, commonly known as caddis flies, usually with slender body. Antennae filiform, generally about as long as fore wings. Mouthparts mandibulate, but mandibles weakly formed or absent in some species; maxillae and labium normal; both pairs of palpi ordinarily well developed, terminal segments commonly modified. Prothorax small, meso- and metathorax well developed. Two pairs of membranous wings, fore pair having a somewhat heavier texture than hind pair; at rest wings held roof-wise over abdomen; hind wings generally shorter than fore wings, in some species possessing an expanded anal area. Fore wings, almost without exception, covered with hairs (micro- and macrotrichia), pubescence extending beyond wing margin as a fringe. Scales in certain wing areas in some. Wing venation in general similar to that of Mecoptera, but veins 2A and 3A of fore wing typically terminating on 1A, instead of directly on wing margin. In fore wing, SC usually long, not uncommonly with 1 or more veinlets leading to costal margin; R generally without branches and ordinarily terminating on costa; RS typically forked dichotomously, its two main branches simple or forked; M similarly formed; CUA generally deeply forked; CUP unbranched; 3 anal veins, 1A best developed, usually receiving termination of 2A, 2A usually receiving termination of 3A. Crossveins generally few and weakly developed. A crossvein between RS1+2 and RS3+4 (or branches of these veins) may close radial (discoidal) cell and a comparable crossvein between M1+2 and M3+4 may close median cell (see Fig. 203, *Electrodipteron*); presence or absence of these cross-

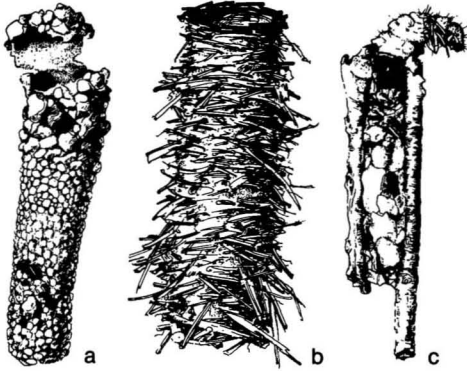


FIG. 200. Trichoptera, larval cases of recent genera; *a*, *Hesperophylax*, *b*, *Platycentropus*, and *c*, *Pycropsyche* (Orcutt, 1934).

veins, their locations, and shapes of radial and median cells diagnostic. Hind wing venation similar to that of fore wing in some, many displaying differences in branching of RS and M and in radial and median cells; anal veins better developed than in fore wing and not looped. Legs cursorial, generally long; tibiae ordinarily with apical and preapical spurs, typically arranged in pairs; tarsi with 5 segments. Abdomen with 9 or 10 distinct cerci and rarely with a prominent ovipositor. *Perm.*—*Holo.*

Eggs of Trichoptera are laid in or near water. The larvae are aquatic, some species occurring in rapidly flowing water and others in quiet ponds. Many larvae are active swimmers, but most are more sedentary and construct silken webs or cases composed of sand or plant debris fastened together by silk (Fig. 200, *a-c*). Most larvae possess a pair of terminal hooks by which they may be anchored to their webs or cases. Although many are carnivorous, most larvae appear to feed on vegetable material. Pupae are formed in cases similar to those of larvae.

The Trichoptera are clearly close relatives of the Lepidoptera. This relationship is indicated by the structure of the mouthparts and body in general as well as by the wing venation and occurrence of female heterogamety in both orders. The relationship between Tri-

choptera and Mecoptera is somewhat more remote, the similarities being chiefly in wing venation. Indications are that the Trichoptera and Lepidoptera arose from common mecopteroid stock.

Twenty-four existing families of the order are generally recognized (FISCHER, 1960, 1971), but several of these are small. The family classification is based on such diverse features as wing venation, antennae, tibial spurs, palpi, and ocelli. Grouping of families into two suborders on the basis of the maxillary palpi of males, which frequently has been done in the past, almost certainly does not represent actual evolution of the order. Convergence has obviously been most important in the history of caddis flies. The fossil record, although extending into the Permian, contributes little to our understanding of their evolution. Members of the Permian family Microptysmatidae have a more extensive branching of vein RS but otherwise show nothing remarkable. The Jurassic Necrotauliidae, except for development of the pterostigma and weak crossveins, closely resemble some existing genera. Several caddis larval cases are known from Tertiary deposits. Adults preserved in Baltic amber and described in detail by ULMER (1912) represent an essentially modern fauna.

Family MICROPTYSMATIDAE Martynova, 1958

[Microptysmatidae MARTYNOVA, 1958, p. 92]

Fore wing with vein SC joined by a distal crossvein to R; R forking distally; RS arising about one-quarter wing length from base, with 4 primary and 6 terminal branches. Hind wing unknown. *Perm.*

Microptysma MARTYNOVA, 1958, p. 92 [**M. sibiricum*; OD]. Stem of M nearly straight; M4 coalesced with anterior branch of CUA. *Perm.*, USSR (Asian RSFSR).—FIG. 201, 1. **M. sibiricum*; fore wing, $\times 14$ (Martynova, 1958).

Microptysmodes MARTYNOVA, 1958, p. 93 [**M. uralicus*; OD]. Stem of M strongly curved; M4 not joined with anterior branch of CUA. ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 201, 4. **M. uralicus*; fore wing, $\times 12$ (Martynova, 1958).

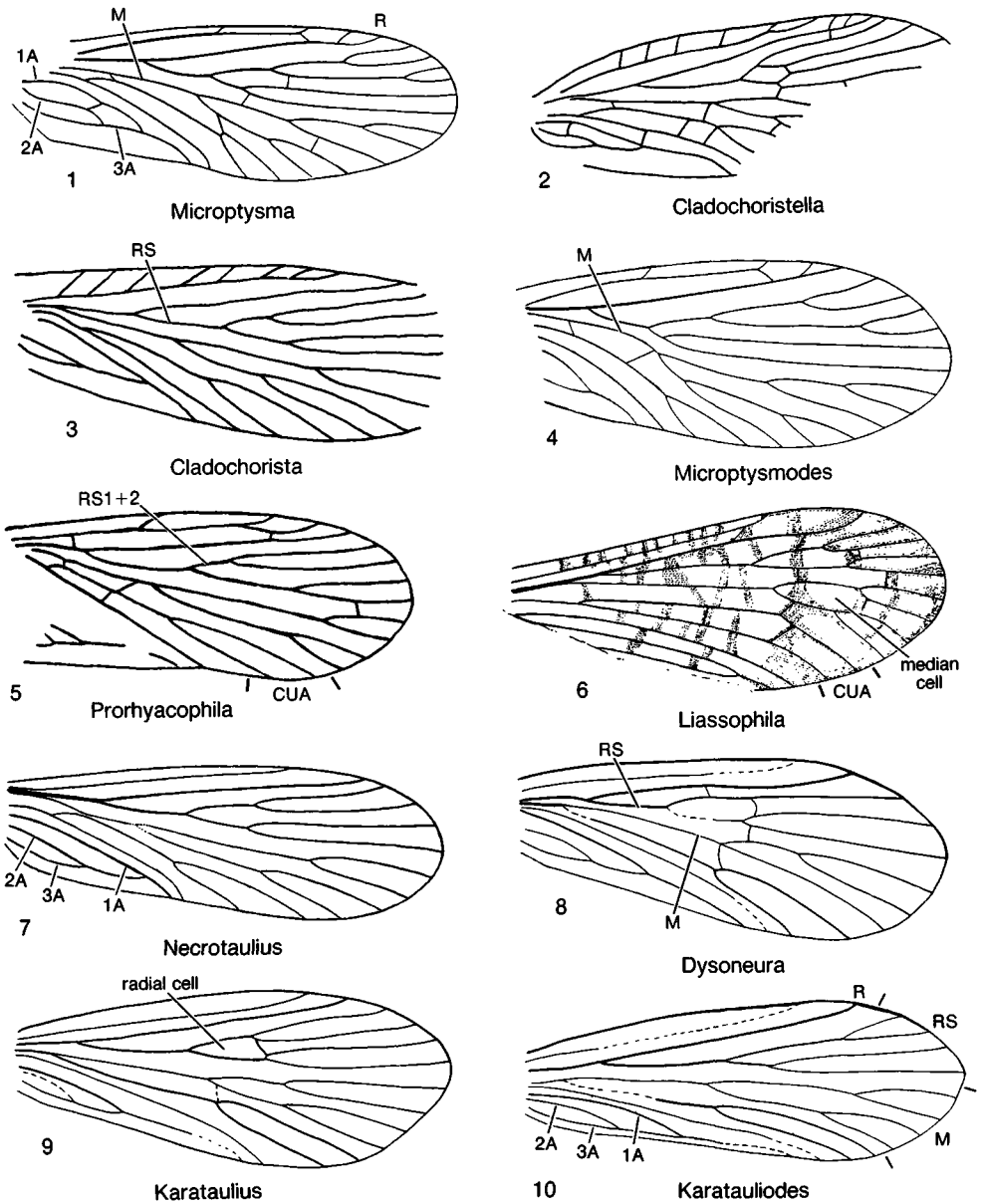


FIG. 201. Microptysmatidae, Cladochoristidae, Prorhyacophilidae, Liassophilidae, Necrotauliidae, and Dysoneuridae (p. 360-362).

Family CLADOCHORISTIDAE

Riek, 1953

[Cladochoristidae RIEK, 1953, p. 78]

Fore wing with veins RS and M with 4 branches; at least several crossveins in costal area. Hind wing little known. [Considered

by WILLMANN (1978) to belong to the ancestral stock of the Trichoptera and Lepidoptera.] *Perm.-Trias.*

Cladochorista TILLYARD, 1926e, p. 272 [**C. belmontensis*; OD]. Costal area of fore wing with numerous oblique veinlets. SUKATSCHEVA, 1973;

WILLMANN, 1979. *Perm.*, Australia (New South Wales); *Trias.*, USSR (Kirghiz).—FIG. 201,3. **C. belmontensis*; fore wing, $\times 7$ (Riek, 1953).
Cladochoristella RIEK, 1955, p. 671 [**C. bryani*; OD]. Costal area of fore wing with only 4 veinlets. *Trias.*, Australia (Queensland).—FIG. 201,2. **C. bryani*; fore wing, $\times 5.3$ (Riek, 1955).

Family PRORHYACOPHILIDAE

Riek, 1955

[Prorhyacophilidae RIEK, 1955, p. 672]

Vein SC of fore wing with prominent distal fork and single veinlet to C; CUA with deep fork. Hind wing unknown. *Trias.*

Prorhyacophila RIEK, 1955, p. 673 [**P. colliveri*; OD]. Fore wing with RS1+2 forking well before RS3+4. SUKATSHEVA, 1973. *Trias.*, Australia (Queensland), USSR (Kirghiz).—FIG. 201,5. **P. colliveri*; fore wing, $\times 11$ (Riek, 1955).

Family LIASSOPHILIDAE

Tillyard, 1933

[Liassophilidae TILLYARD, 1933, p. 551]

Fore wing with costal space narrow; complete series of veinlets from SC to costal margin; veins RS and M each with 4 branches; CUA very deeply forked, forking slightly basad of origin of RS. Hind wing unknown. *Jur.*

Liassophila TILLYARD, 1933, p. 56 [**L. hydromanicoidea*; OD]. Fore wing with costal area with about 9 veinlets; crossveins between branches of RS and M1+2; median cell closed. *Jur.*, England.—FIG. 201,6. **L. hydromanicoidea*; fore wing, $\times 2.5$ (Tillyard, 1933).

Family NECROTAULIIDAE

Handlirsch, 1906

[Necrotauliidae HANDLIRSCH, 1906b, p. 483]

Fore wing with vein SC long, extending into pterostigmal region; pterostigma variously developed; RS with 4 primary branches; M usually with 4, rarely 3 branches; crossveins weakly developed or absent. Hind wing little known; M with apparently only 3 branches; anal veins not joined. *Jur.*

Necrotaulius HANDLIRSCH, 1906b, p. 483 [**N. dobertinensis*; SD TILLYARD, 1933, p. 60]. Very small Trichoptera. Fore wing slender, with rounded apex; branches of RS1+2 and RS3+4 nearly equal in length; fork of CUA at about same level

as first fork of RS. SUKATSHEVA, 1973. *Jur.*, England, Europe (Germany), USSR (Kirghiz).—FIG. 201,7. *N. westwoodi* TILLYARD, England; fore wing, $\times 13$ (Tillyard, 1933).
Epididontus HANDLIRSCH, 1939, p. 98 [**E. geinitzianus*; OD]. Fore wing: M with 3 branches; CUA with very shallow fork. [Family assignment doubtful.] *Jur.*, Europe (Germany).

Karatauliodes SUKATSHEVA, 1968, p. 176 [**K. minutus*; OD]. Fore wing similar to that of *Necrotaulius*, but CUP much longer; basal part of 3A and portions fused with 2A and 1A forming straight line. [Possibly a synonym of *Necrotaulius*.] *Jur.*, USSR (Kazakh).—FIG. 201,10. **K. minutus*; fore wing, $\times 20$ (Sukatsheva, 1968).

Karataulius SUKATSHEVA, 1968, p. 175 [**K. aeternus*; OD]. Fore wing much as in *Necrotaulius*, but radial cell closed. *Jur.*, USSR (Kazakh).—FIG. 201,9. **K. aeternus*; fore wing, $\times 8.6$ (Sukatsheva, 1968).

Liadoptilia HANDLIRSCH, 1939, p. 98 [**L. misera*; OD]. Fore wing: RS3+4 with a very shallow fork; M with 3 branches. *Jur.*, Europe (Germany).

Liadotaulius HANDLIRSCH, 1939, p. 97 [**L. acutipennis*; OD]. Fore wing as in *Necrotaulius*, but M4 connected to CUA; 1A terminating on CUP. *Jur.*, Europe (Germany).

Metarchitaulius HANDLIRSCH, 1939, p. 96 [**M. longus*; OD]. Fore wing little known, slender; apex rounded; RS with 4 branches, M with 3. *Jur.*, Europe (Germany).

Palaeotaulius HANDLIRSCH, 1939, p. 95 [**P. vicinus*; OD]. Fore wing with broad costal area; R deeply forked; RS and M each with 4 branches. *Jur.*, Europe (Germany).

Pararchitaulius HANDLIRSCH, 1939, p. 95 [**P. ovalis*; OD]. Fore wing with broad costal area; RS with 4 branches, M apparently with 3; CUA deeply forked. *Jur.*, Europe (Germany).

Parataulius HANDLIRSCH, 1939, p. 96 [**P. jurasicus*; OD]. SC of fore wing with prominent veinlet to C; strong crossvein between RS3 and RS4 and between RS5 and M1. *Jur.*, Europe (Germany).

Phryganeidium WESTWOOD, 1854, p. 396 [**P. pytho*; OD]. Little-known fore wing; RS with 4 branches, M with 3. *Jur.*, Europe (Germany).

Family DYSONEURIDAE

Sukatsheva, 1968

[Dysoneuridae SUKATSHEVA, 1968, p. 178]

Fore wing as in Necrotauliidae, but both veins RS and M with only 3 branches. *Jur.*

Dysoneura SUKATSHEVA, 1968, p. 178 [**D. trifurcata*; OD]. Fore wing with first fork of M far distal of first fork of RS. *Jur.*, USSR (Kazakh).—FIG. 201,8. **D. trifurcata*; fore wing, $\times 10$ (Sukatsheva, 1968).

Family PROSEPIDIDONTIDAE Handlirsch, 1920

[Prosepididontidae HANDLIRSCH, 1920, p. 200]

Fore wing with very wide costal area; vein SC short, terminating slightly beyond mid-wing; R without fork; RS with 2 primary and 3 terminal branches; M with 4 branches; CUA deeply forked, apparently arising from stem M. Hind wing unknown. *Jur.*

Prosepididontus HANDLIRSCH, 1920, p. 200 [**P. calopteryx*; OD]. Fore wing with fork of M1+2 very shallow and marginal, at wing apex. HANDLIRSCH, 1939. *Jur.*, Europe (Germany).—FIG. 202,3. **P. calopteryx*; fore wing, $\times 5.3$ (Handlirsch, 1920).

Family RHYACOPHILIDAE Stephens, 1835

[Rhyacophilidae STEPHENS, 1835, p. 154]

Antennae about equal in length to wings or slightly longer, generally slender; tibial spurs variable but middle and hind tibiae each with 4 spurs; hind tibia very long. Radial and median cells open in both wings. Larvae in moving, clear water, without portable cases. *Cret.—Holo.*

Rhyacophila PICTET, 1834, p. 181. ULMER, 1912; ROSS, 1944; BOTOSANEANU & WICHARD, 1983. *Cret.*, USSR (Asian RSFSR); *Oligo.*, Europe (Baltic)—*Holo.*

Family GLOSSOSOMATIDAE Wallengren, 1891

[Glossosomatidae WALLENGREN, 1891, p. 163]

Similar to Rhyacophilidae, but radial cell in fore wing closed. Larvae in portable cases. *Oligo.—Holo.*

Glossosoma CURTIS, 1834, p. 216. *Holo.*

Electragapetus ULMER, 1912, p. 33 [**E. scitulus*; OD]. Similar to *Catagapetus* (recent), but SC about as long as R and parallel to it; RS1+2 forked. *Oligo.*, Europe (Baltic).—FIG. 202,4. **E. scitulus*; hind wing, $\times 16$ (Ulmer, 1912).

Family HYDROBIOSIDAE Ulmer, 1905

[Hydrobiosidae ULMER, 1905b, p. 72]

Antennae slender, about as long as fore wings, basal segment thick; ocelli present; venation irregular, commonly with accessory crossveins. *Cret.—Holo.*

Hydrobiosis McLACHLAN, 1870, p. 206. *Holo.*
Palaeohydrobiosis BOTOSANEANU & WICHARD, 1983, p. 191 [**P. siberambra*; OD]. Fore wing similar to that of *Hydrobiosis*, but RS forked basally, radial cell open, and anal area broad. *Cret.*, USSR (Asian RSFSR).

Family ELECTRALBERTIDAE Botosaneanu & Wichard, 1983

[Electralbertidae BOTOSANEANU & WICHARD, 1983, p. 192]

Small insects, without ocelli; antennae shorter than fore wing. Fore wing elongate; vein RS1+2 not forked. Hind wing only slightly narrower than fore wing. *Cret.*

Electralberta BOTOSANEANU & WICHARD, 1983, p. 193 [**E. cretatica*; OD]. With the characters of the family. *Cret.*, Canada (Alberta).

Family PHILOPOTAMIDAE Stephens, 1829

[Philopotamidae STEPHENS, 1829a, p. 316]

Antennae stout, relatively short; ocelli present; tibial spur formula 2,4,4. Wing fringes not unusually long. Fore wing with radial and median cells closed. Hind wing with radial cell closed, median cell open. Larvae in silken nets, in rapidly flowing streams. *Cret.—Holo.*

Philopotamus STEPHENS, 1829a, p. 317. ULMER, 1912; KIMMINS, 1950. *Oligo.*, Europe (Baltic)—*Holo.*

Dolophilus McLACHLAN, 1868, p. 301. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Electracanthinus ULMER, 1912, p. 54 [**E. klebsi*; OD]. Similar to *Dolophilus*, but RS1+2 of hind wing more deeply forked. COCKERELL, 1916c. *Cret.*, USA (Kentucky); *Oligo.*, Europe (Baltic).—FIG. 202,7. **E. klebsi*, *Oligo.*; hind wing, $\times 9$ (Ulmer, 1912).

Prophiloptamus SUKATSheVA, 1973, p. 101 [**P. asiaticus*; OD]. Apparently similar to *Electracanthinus*. RS of fore wing with 4 branches, but M with only 3. *Trias.*, USSR (Kirghiz).

Family HYDROPTILIDAE Stephens, 1835

[Hydroptilidae STEPHENS, 1835, p. 148]

Antenna shorter than fore wing; wings long, narrow, usually with acute apex, very long fringes; veins weakly formed, commonly reduced; tibial spurs variable. Larvae with portable cases, at least in late instars. *Oligo.—Holo.*

- Hydroptila** DALMON, 1819, p. 125. *Holo.*
Agraylea CURTIS, 1834, p. 217. WESTWOOD, 1840; ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*
Allotrichia McLACHLAN, 1880, p. 508. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*
Electrotrichia ULMER, 1912, p. 42 [**E. subtilis*; OD]. Similar to *Allotrichia*, but RS1+2 unbranched in fore wing; wings very pointed. *Oligo.*, Europe (Baltic).
Palaeagapetus ULMER, 1912, p. 35. FISCHER, 1970. *Oligo.*, Europe (Baltic)—*Holo.*

Family STENOPSYCHIDAE

Martynov, 1924

[Stenopsychidae MARTYNOV, 1924b, p. 19]

Similar to Philopotamidae, but antenna longer than fore wing; tibial spur formula 3,4,4; hind wing with expanded anal lobe. *Oligo.*—*Holo.*

- Stenopsyche** McLACHLAN, 1866, p. 264. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Family POLYCENTROPIDAE

Ulmer, 1906

[*nom. correct.* BRUES & MELANDER, 1915, p. 47, *pro* Polycentropidae ULMER, 1906, p. 83]

Antenna stout; length variable, but only a little shorter or longer than fore wing; tibial spur formula 3,4,4; ocelli absent. Fore wing with radial and median cells closed; all main branches of veins RS and M forked. Hind wing with radial cell open or closed. Larvae usually in moving water, with silken nets. *Cret.*—*Holo.*

- Polycentropus** CURTIS, 1835, p. 544. SCUDDER, 1890; COCKERELL, 1907c. *Oligo.*, USA (Colorado)—*Holo.*

- Archaeoneureclipsis** ULMER, 1912, p. 69 [**A. fortis*; OD]. Similar to *Phylocentropus*, but forking of RS1+2 of fore wing more acute; radial cell slender. *Oligo.*, Europe (Baltic).

- Archaeopolycentra** BOTOSANEANU & WICHARD, 1983, p. 198 [**A. zberikbini*; OD]. Little-known genus. Body of male similar to that of *Polycentropus*, but R of fore wing joining costal margin at level of crossvein closing radial cell; radial cell very short; medial cell apparently open; oblique crossvein connecting the apex of radial cell to M1. *Cret.*, USSR (Asian RSFSR).

- Holocentropus** McLACHLAN, 1878, p. 400. ULMER, 1912; BOTOSANEANU & WICHARD, 1983. *Cret.*, USSR (Asian RSFSR); *Oligo.*, Europe (Baltic)—*Holo.*

- Neureclipsis** McLACHLAN, 1864, p. 30. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

- Nyctiophylacodes** ULMER, 1912, p. 172 [**N. curtula*; OD]. Similar to *Nyctiophylax*, but radial cell of hind wing as large as that of fore wing. *Oligo.*, Europe (Baltic).—FIG. 202.8. **N. curtula*; hind wing, $\times 12$ (Ulmer, 1912).

- Nyctiophylax** BRAUER, 1865, p. 419. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

- Phylocentropus** BANKS, 1907, p. 130. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

- Plectrocnemia** STEPHENS, 1836, p. 168. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

- Tinodes** CURTIS, 1834, p. 216. SCUDDER, 1890; COCKERELL, 1907c. *Oligo.*, USA (Colorado)—*Holo.*

Family PSYCHOMYIDAE

Curtis, 1835

[Psychomyidae CURTIS, 1835 in CURTIS, 1823–1840, pl. 561]

Antenna stout, not longer than fore wing; tibial spur formula 2,4,4 or 3,4,4; ocelli absent. Wing fringes not unusually long. Fore wing with radial cell short, usually about one-quarter length of vein RS; median cell at least twice as long as radial cell. Larvae either free or with cases. *Oligo.*—*Holo.*

- Psychomyia** PICTET, 1834, p. 222. ULMER, 1912. *Holo.*

- Archaeotinodes** ULMER, 1912, p. 178 [**Rhyacophila prisca* PICTET in PICTET & HAGEN, 1856, p. 116; OD]. Similar to *Ecnomus* (recent), but radial cell of hind wing closed; M1+2 forked. [Family position uncertain.] BOTOSANEANU & WICHARD, 1983. *Oligo.*, Europe (Baltic).—FIG. 202.9. *A. grossa* (HAGEN); hind wing, $\times 7$ (Ulmer, 1912).
Lype McLACHLAN, 1878, p. 409. PITON, 1936a; ROSS, 1944. *Oligo.*, Europe (Baltic)—*Holo.*

Family HYDROPSYCHIDAE

Curtis, 1835

[Hydropsychidae CURTIS, 1835 in CURTIS, 1823–1840, pl. 544]

Antennae usually slender, at least as long as wings; ocelli absent; terminal segment of maxillary palpus multiarticulate, longer than all others combined. Fore wing with radial cell short, not more than half length of its stem, vein RS; median cell slightly longer than radial. Larvae in rapidly flowing water, usually forming silken net attached to stones or wood. *Oligo.*—*Holo.*

- Hydropsyche** PICTET, 1834, p. 199. COCKERELL, 1909h; ULMER, 1912; ROSS, 1944. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

- Diplectrona** WESTWOOD, 1840, p. 49. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

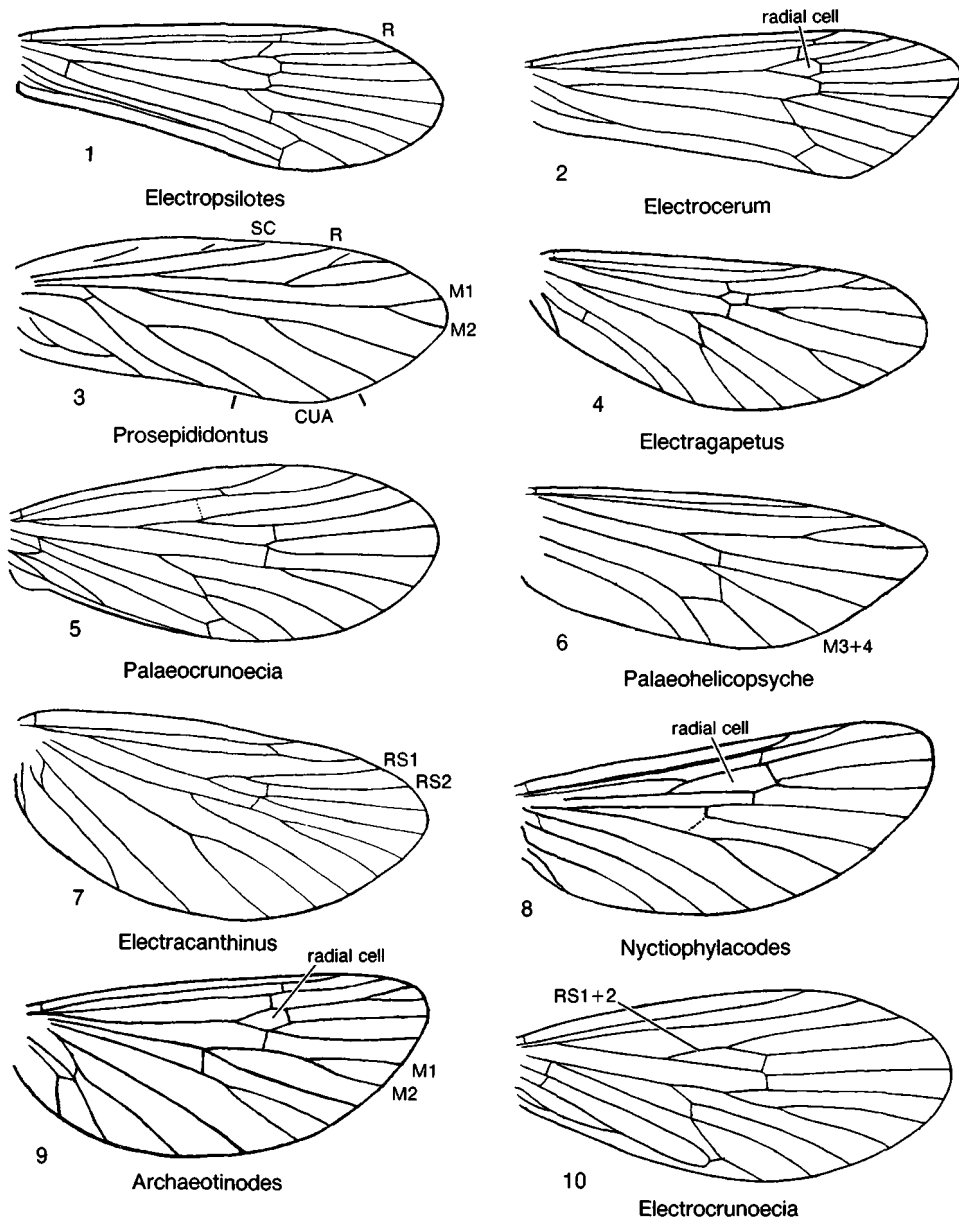


FIG. 202. Prosepidodontidae, Glossosomatidae, Philopotamidae, Polycentropodidae, Psychomyidae, Odontoceridae, Lepidostomatidae, and Helicopsychidae (p. 363–368).

Electrodipletrona ULMER, 1912, p. 216 [**E. decipiens*; OD]. Similar to *Dipletrona*, but last segment of maxillary palpus longer than third and fourth together. *Oligo.*, Europe (Baltic).—
FIG. 203. **E. decipiens*; *a*, fore and *b*, hind wings, $\times 5.5$ (Ulmer, 1912).

Potamyia BANKS, 1900, p. 259. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Family TAYMYRELECTRONIDAE
Botosaneanu & Wichard, 1983

[Taymyrelectronidae BOTOSANEANU & WICHARD, 1983, p. 202]

Male: ocelli absent; radial and median cells of fore wing absent; area between veins RS

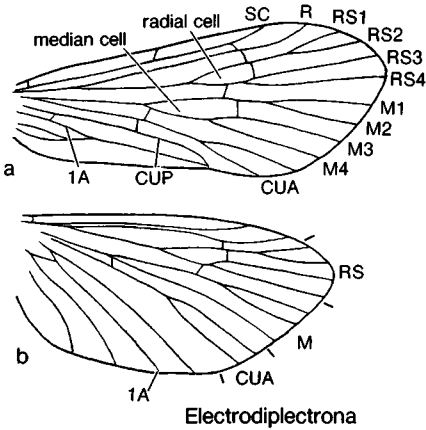


FIG. 203. Hydropsychidae (p. 365).

and M unusually large; CUP and anal veins absent. *Cret.*

Taymyrelectron BOTOSANEANU & WICHARD, 1983, p. 202 [**T. sukatshevae*; OD]. With the characters of the family. *Cret.*, USSR (Asian RSFSR).

Family PHRYGANEIDAE

Leach, 1815

[*nom. correct.* BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 922, *pro* Phryganides LEACH, 1815, p. 136]

Antenna not longer than fore wing, generally shorter; legs usually stout; tibial spur formula usually 2,4,4. Fore wing with radial cell closed and at least as long as stem of vein RS; RS1+2 forking before distal end of radial cell. Larvae in quiet water, larval cases of plant material. *Eoc.*–*Holo.*

Phryganea LINNÉ, 1758, p. 547. CURTIS, 1836 in CURTIS, 1823–1840; ULMER, 1912; FISCHER, 1963. *Eoc.*, Europe (Denmark); *Oligo.*, Europe (Germany), USA (Colorado); *Mio.*, Europe (Germany, France), USSR (Asian RSFSR)–*Holo.*

Oligotricha RAMBUR, 1842, p. 472. STATZ, 1936a. *Oligo.*, Europe (Germany)–*Holo.*

Family MOLANNIDAE

Wallengren, 1891

[Molannidae WALLENGREN, 1891, p. 116]

Antenna at least as long as fore wing; tibial spur formula 2,4,4. Wings usually very hairy; fore wing with open radial cell and vein RS

usually touching M1+2 for short distance. Larval cases of sand. *Oligo.*–*Holo.*

Molanna CURTIS, 1834, p. 214. ULMER, 1912. *Oligo.*, Europe (Baltic)–*Holo.*

Molannodes McLACHLAN, 1866, p. 178. ULMER, 1912. *Oligo.*, Europe (Baltic)–*Holo.*

Family CALAMOCERATIDAE

Ulmer, 1905

[Calamoceratidae ULMER, 1905, p. 80]

Antenna longer than fore wing, in some species only slightly so; fore tibial spurs 2, middle tibial spurs 4, hind tibial spurs variable (2 to 4). Fore wing generally broad; vein R ending on RS1; radial cell about as long as its stem, RS. Hind wing much shorter than fore. Larval cases of plant fragments. *Oligo.*–*Holo.*

Calamoceras BRAUER, 1865, p. 417. *Holo.*

Ganonema McLACHLAN, 1866, p. 253 [**G. pallicorne*; OD]. ULMER, 1912. *Oligo.*, Europe (Baltic).

Georgium FISCHER, 1964, p. 106. ULMER, 1912. *Oligo.*, Europe (Baltic)–*Holo.*

Family ODONTOCERIDAE

Wallengren, 1891

[Odontoceridae WALLENGREN, 1891, p. 12]

Antennal length variable, commonly very long; ocelli absent; tibial spur formula generally 2,4,4. Fore wing typically with radial cell longer than its stem, vein RS; median cell open; venation variable in genera and commonly also in sexes. Larval cases of fine sand. *Oligo.*–*Holo.*

Odontocerus LEACH, 1815, p. 136. *Holo.*

Electrocera ULMER, 1912, p. 243 [**E. pedestre*; OD]. Similar to *Marilia*, but radial cell of both wings much shorter. *Oligo.*, Europe (Baltic). —FIG. 202.2. **E. pedestre*; fore wing, $\times 5.5$ (Ulmer, 1912).

Electropsilotes ULMER, 1912, p. 246 [**E. rara*; OD]. Similar to *Marilia*, but R terminating on costal margin. *Oligo.*, Europe (Baltic). —FIG. 202.1. **E. rara*; fore wing, $\times 4.6$ (Ulmer, 1912).

Marilia MÜLLER, 1880, p. 127. ULMER, 1912; MOSELY & KIMMINS, 1953. *Oligo.*, Europe (Baltic)–*Holo.*

Phenacopsyche COCKERELL, 1909h, p. 385 [**P. vexans*; OD]. Little-known fore wing, with long radial cell. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Family LEPTOCERIDAE

Leach, 1815

[*nom. correct.* STEPHENS, 1829a, p. 319, *pro* Leptocerides LEACH, 1815, p. 136]

Antenna very long and slender, 2 or 3 times as long as fore wing; tibial spurs variable. Fore wing long and narrow; radial cell closed, median cell open; veins RS3+4 and M1+2 without forks. Larval cases usually of fine sand, rarely of detritus. *Cret.*—*Holo.*

Leptocerus LEACH, 1815, p. 136. SCUDDER, 1890; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*

Erotesis McLACHLAN, 1877, p. 325. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Praeathripsodes BOTOSANEANU & WICHARD, 1983, p. 209 [**P. jantar*; OD]. Little-known genus, based on incomplete female. Both RS and M with 3 branches, those of M very long. *Cret.*, USSR (Asian RSFSR).

Setodes RAMBUR, 1842, p. 515. ULMER, 1912; MILNE, 1934. *Oligo.*, Europe (Baltic)—*Holo.*

Tripletides KOLENATI, 1858, p. 169. ULMER, 1912; MOSELY, 1936. *Oligo.*, Europe (Baltic)—*Holo.*

Family GOERIDAE Ulmer, 1903

[*nom. transl.* ROSS, 1944, p. 256, *ex* Goerinae ULMER, 1903, p. 81]

Similar to Lepidostomatidae, but vein M1+2 forked in hind wing. *Oligo.*—*Holo.*

Goera STEPHENS, 1829, p. 28. WESTWOOD, 1840; ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Lithax McLACHLAN, 1876, p. 242. ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Silo CURTIS, 1830, p. 136. WESTWOOD, 1840; ULMER, 1912. *Oligo.*, Europe (Baltic)—*Holo.*

Family LIMNOPHILIDAE

Rambur, 1842

[*nom. correct.* BRAUER, 1857, p. 45, *pro* Limnophilides RAMBUR, 1842, p. 470]

Antenna about as long as fore wing; tibial spurs variable. Fore wing generally broad; radial cell long, median cell open; vein M with 3 branches. Hind wing with expanded anal area. Larval cases of sand or vegetable debris. *Eoc.*—*Holo.*

Limnophilus LEACH, 1815, p. 136 [= *Miopsyche* CARPENTER, 1931d, p. 320 (type, *M. alexanderi*)]. COCKERELL, 1920c, 1925g, 1926b. *Eoc.*,

USA (Colorado); *Mio.*, Burma, USSR (Asian RSFSR), USA (Washington)—*Holo.*

Chilostigma McLACHLAN, 1876, p. 187. BRADLEY, 1924. *Eoc.*, USA (Wyoming)—*Holo.*

Tricheopteryx COCKERELL, 1927f, p. 184, *nom. subst. pro* *Eopteryx* COCKERELL, 1907c, p. 608, *non* MEYER, 1887 [**Eopteryx florissantius* COCKERELL; OD]. Fore wing as in *Platyphylax* (recent), but R straight and radial cell very long. *Oligo.*, USA (Colorado).

Family LEPIDOSTOMATIDAE

Ulmer, 1903

[*nom. transl.* ROSS, 1944, p. 258, *ex* Lepidostomatinae ULMER, 1903, p. 89]

Antenna about as long as fore wing; tibial spur formula generally 2,4,4. Fore wing of male bearing thick hairs, commonly broad and bearing scales; M3+4 without fork; venation variable in genera and often different in sexes. Hind wing with M1+2 and M3+4 unbranched. Larval cases of sand or plant fragments. *Oligo.*—*Holo.*

Lepidostoma RAMBUR, 1842, p. 493. *Holo.*

Archaeocrunoecia ULMER, 1912, p. 288 [**A. tenuicornis*; SD FISCHER, 1970, p. 32]. Similar to *Crunoecia* (recent). First antennal segment much longer than head; antenna about 1.5 times as long as fore wing; subapical outer spur of middle tibia minute. *Oligo.*, Europe (Baltic).

Electraulax ULMER, 1912, p. 296 [**E. breviscula*; SD FISCHER, 1971, p. 83]. Fore wing with RS4 arising very close to origin of M1. *Oligo.*, Europe (Baltic).

Electrocrunoecia ULMER, 1912, p. 293 [**E. turbata*; OD]. Similar to *Archaeocrunoecia*, but subapical outer spur of middle tibia normal in size; RS1+2 of fore wing forking before end of radial cell. *Oligo.*, Europe (Baltic).—FIG. 202,10. **E. turbata*; fore wing, $\times 10$ (Ulmer, 1912).

Maniconeurodes ULMER, 1912, p. 302 [**M. conventzi*; OD]. Similar to *Electrocrunoecia*, but fork of RS1+2 distal to radial cell. *Oligo.*, Europe (Baltic).

Palaeocrunoecia ULMER, 1912, p. 282 [**P. crenata*; SD FISCHER, 1970, p. 70]. Similar to *Crunoecia* (recent) but with first antennal segment shorter. *Oligo.*, Europe (Baltic).—FIG. 202,5. **P. crenata*; fore wing, $\times 11$ (Ulmer, 1912).

Palaeolepidostoma ULMER, 1912, p. 297 [**Trichostomum proavum* HAGEN in PICTET & HAGEN, 1856, p. 103; OD]. Similar to *Palaeocrunoecia*, but first antennal segment much longer than head; antenna only about as long as fore wing. *Oligo.*, Europe (Baltic).

Family BRACHYCENTRIDAE

Ulmer, 1903

[*nom. transl.* Ross, 1944, p. 260, *ex* Brachycentrinae ULMER, 1903, p. 85]

Similar to Lepidostomatidae, but middle tibia with 2 or 3 spurs. *Oligo.-Holo.*

Brachycentrus CURTIS, 1834, p. 215. ULMER, 1912.

Oligo., Europe (Baltic)-*Holo.*

Micrasema McLACHLAN, 1876, p. 259. ULMER, 1912. *Oligo.*, Europe (Baltic)-*Holo.*

Family BERAEDIAE

Wallengren, 1891

[Beraeidae WALLENGREN, 1891, p. 111]

Antenna about as long as fore wing; tibial spur formula 2,2,4. Wings very hairy. Fore wing generally oval; vein RS touching M1+2 for a short distance. Larval cases of sand. *Oligo.-Holo.*

Beraea STEPHENS, 1833, p. 118. *Holo.*

Bereodes EATON, 1867, p. 400. COCKERELL, 1921d; FISCHER, 1969. *Oligo.*, England, Europe (Baltic)-*Holo.*

Family HELICOPSYCHIDAE

Ulmer, 1906

[*nom. transl.* Ross, 1944, p. 266, *ex* Helicopsychinae ULMER, 1906, p. 104]

Antenna not longer than fore wing. Fore wing with radial cell closed, long; veins RS1+2 and M3+4 generally with forks. Hind wing considerably shorter and smaller than fore wing; radial cell open. Larval cases of sand. *Oligo.-Holo.*

Helicopsyche VON SIEBOLD, 1856, p. 38. ULMER, 1912; FLINT, 1964. *Oligo.*, Europe (Baltic)-*Holo.*

Electrohelicopsyche ULMER, 1912, p. 310 [**E. taeniata*; OD]. Fore wing as in *Helicopsyche*, but radial cell very long and with very short stem; RS3+4 arising near origin of RS. *Oligo.*, Europe (Baltic).

Palaeohelicopsyche ULMER, 1912, p. 308 [**P. serricornis*; OD]. Similar to *Helicopsyche*, but M3+4 of hind wing unbranched. *Oligo.*, Europe (Baltic).—FIG. 202,6. **P. serricornis*; hind wing, ×11 (Ulmer, 1912).

Family UNCERTAIN

The following genera, apparently belonging to the order Trichoptera, are too poorly

known to permit family assignment. Included also are fossil caddis cases, which are very common in some deposits. For many years the collective group names, *Indusia* (BOSC, 1803) and *Folindusia* (BERRY, 1927), have been used for these fossil cases, but recently SUKATSHEVA (1982), in a review of the historical development of the Trichoptera, has added many other generic names. These are not included in the present account.

Adelomyia ULMER, 1912, p. 331 [**A. exularis*; OD]. Fore wing with RS3+4 and M1+2 unbranched; radial cell open; M dividing very near base of wing; tibial spur formula 2,2,4. *Oligo.*, Europe (Baltic).

Archiptilia HANDLIRSCH, 1939, p. 97 [**A. ovata*; OD]. Fore wing broad and oval; SC short, ending slightly beyond midwing; RS and M with 4 branches. [Probably represents an undescribed family.] *Jur.*, Europe (Germany).

Aulacomyia ULMER, 1912, p. 321 [**A. infuscata*; OD]. Fore wing with RS3+4 unbranched; M1+2 very long, arising near wing base, unbranched; tibial spur formula of male 0,4,4; antenna as long as fore wing. *Oligo.*, Europe (Baltic).

Calamodontus BOTOSANEANU & WICHARD, 1983, p. 206 [**C. grandaevus*; OD]. Little-known genus, apparently related to the recent Calamoceratidae and Odontoceridae. R of fore wing not merging with RS1 but joined to it by a crossvein near fork of RS1+2; radial and median cells closed. *Cret.*, USSR (Asian RSFSR).

Derobrochus SCUDDER, 1885b, p. 779 [**D. frigescens*; OD]. Little-known trichopteron, possibly belonging to the Polycentropodidae. SCUDDER, 1890. *Oligo.*, USA (Colorado).

Folindusia BERRY, 1927, p. 1 [**F. urilcoxiana*; OD]. Larval cases composed mainly of leaf fragments, not referable to established family or genus. BERRY, 1928. *Eoc.*, USA (Tennessee); *Mio.*, USA (Washington).

Indusia BOSC, 1803, p. 397 [**I. tubulosa*; OD]. Larval cases composed mainly of pebbles and not referable to established family or genus. SCUDDER, 1890; COCKERELL, 1910c, 1924b, 1925g; FISCHER, 1968. *Eoc.*, USA (Colorado, Wyoming); *Oligo.*, USA (Colorado), Europe (France); *Mio.*, Asia (Mongolia), USSR (Asian RSFSR).

Mesotrichopteridium HANDLIRSCH, 1906b, p. 485 [**M. pusillum*; SD FISCHER, 1960, p. 4]. Fore wing with costal area very narrow; pterostigma well developed; RS with 4 branches, M with 3. [Possibly a synonym of *Phryganeidium*.] *Jur.*, Europe (Germany).

Metatrichopteridium HANDLIRSCH, 1939, p. 98

- [**M. confusum*; OD]. Little-known wing; RS with 4 branches, M with 3. *Jur.*, Europe (Germany).
- Nannotrichopteron** HANDLIRSCH, 1906b, p. 486 [**N. gracile*; OD]. Fore(?) wing very broad; SC short; RS with 4 branches. [Ordinal position doubtful.] *Jur.*, Europe (Germany).
- Ocnertes** OPPENHEIM, 1885, p. 347 [**O. macroceraticus*; OD]. Little-known insect with very small wings. STATZ, 1936a. [Possibly a pupa.] *Oligo.*, Europe (Germany).
- Ogmomyia** ULMER, 1912, p. 333 [**O. cuspidata*; OD]. Fore wing with RS arising well before midwing, unbranched; radial cell closed, very long; M1+2 unbranched; tibial spur formula 2,4,4. *Oligo.*, Europe (Baltic).
- Paratrichopteridium** HANDLIRSCH, 1906b, p. 486 [**P. areatum*; OD]. Hind(?) wing broad; RS with 4 branches, M with 3; radial cell closed. [Probably representing an undescribed family.] *Jur.*, Europe (Germany).
- Perissomyia** ULMER, 1912, p. 328 [**P. sulcata*; OD]. Antenna twice as long as fore wing, very thin. Fore wing with RS1+2 and RS3+4 forked; radial cell closed; M1+2 unbranched. Hind wing with radial cell open. FISCHER, 1969. *Oligo.*, Europe (Baltic).
- Pseudoberaeodes** ULMER, 1912, p. 323 [**P. mira*; OD]. Antenna not longer than fore wing, its first segment as long as head; fore wing with RS1+2 and M1+2 unbranched; tibial spur formula of male 2,2,4. *Oligo.*, Europe (Baltic).
- Pseudorthophlebia** HANDLIRSCH, 1906b, p. 485 [**P. platyptera*; OD]. Fore wing very broad; SC short; pterostigma large; RS with 5 branches, M with 2. *Jur.*, Europe (Germany).
- Sphaleropalpus** ULMER, 1912, p. 318 [**S. pumicatus*; OD]. Fore wing with RS1+2 unbranched; RS3+4 forking from radial cell; radial cell long. Tibial spur formula 2,4,4. *Oligo.*, Europe (Baltic).
- Stenoptilomyia** ULMER, 1912, p. 314 [**Sericostoma hyalinum* HAGEN in PICTET & HAGEN, 1856, p. 106]. Antenna at least as long as fore wing; fore wing with RS3+4 unbranched, radial cell long, RS1+2 forking after radial cell; tibial spur formula of male apparently 2,2,2. *Oligo.*, Europe (Baltic).
- Tipulidites** WIELAND, 1925, p. 25 [**T. affinis*; OD]. Small wing fragment with closed radial cell. WIELAND, 1926. *Trias.*, South America (Argentina).
- Trichopterella** COCKERELL, 1924b, p. 140 [**T. torta*; OD]. Little-known wing. *Cret.*, Asia (Mongolia).
- Trichopteridium** GEINITZ, 1880, p. 528 [**T. gracile*; OD]. Little-known hind(?) wing; RS arising near wing base. HANDLIRSCH, 1906b. [Ordinal position doubtful.] *Jur.*, Europe (Germany).

Order LEPIDOPTERA

Linné, 1758

[Lepidoptera LINNÉ, 1758, p. 458]

Very small to very large insects, commonly known as moths, skippers, and butterflies. Antennae generally much shorter than fore wing, usually with partial scale covering; filiform but often modified (clubbed, serrate, or pectinate). Mouthparts of adults diverse but most commonly haustellate. Mandibles present in more primitive suborders (Zeugloptera and Dacnonypha) but entirely absent in the great majority of Lepidoptera. Maxillae also more generalized in these primitive suborders but extensively modified in others, the laciniae being vestigial or absent and the galeae typically elongate and joined together to form a tubular proboscis, the haustellum. Maxillary palpi usually well developed, with diverse segmentation and commonly with a covering of scales. Labium usually small but palpi prominent. Prothorax small and weakly sclerotized; mesothorax well developed; metathorax somewhat smaller than the mesothorax, especially in suborder Ditrysia. Fore and hind wings membranous, similar to one another in the Zeugloptera and Dacnonypha, but different in size and venation in most other Lepidoptera. Both wing surfaces covered with overlapping scales, which may contain pigments or produce iridescence by interference. Basic venational pattern in some Zeugloptera and Dacnonypha as in Trichoptera (Fig. 204,1): veins SC and R with 2 branches, RS with 4 branches, and M with 3 branches; CUP present and anal veins commonly looped distally. Venational pattern in the Ditrysia reduced by coalescence or loss of veins, with many modifications occurring independently in several superfamilies and also independently in fore and hind wings. In the more primitive Ditrysia (e.g., Cossidae), separate radial and medial areas present in proximal half of fore wings (Fig. 204,2); in more specialized families (e.g., Nymphalidae), proximal parts of veins RS3+4 and M3 lost, resulting in the formation of a

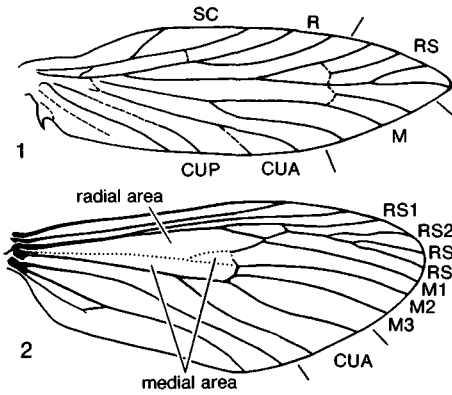


FIG. 204. Wing venation in the Lepidoptera.—
1. Generalized wing venation of the suborder Zeugloptera, family Micropterygidae (*Sabatinca*); diagram of fore wing (after CSIRO, 1970).—
2. Modified wing venation of the suborder Ditryisia, family Cossidae; diagram of fore wing of *Prionoxystus robiniae*. If the basal parts of veins M1 + M2 and M3 are absent (dotted in figure), the entire area is usually termed the discal cell (courtesy of Prof. G. W. Byers).

single, large area (commonly termed the discal cell; see Fig. 208, 1). Legs typically adapted for walking, but 1 or more pairs may be reduced and nonfunctional (as in most Nymphalidae). Middle and hind tibiae usually bearing spurs; tarsi with 5 segments. Abdomen with 10 segments, lacking cerci; a true, exserted ovipositor absent, although sclerotized papillae at genital pore may function as ovipositor. *Cret.—Holo.*

The eggs of the Lepidoptera are ordinarily deposited on or near the source of food for the larvae, usually plants. The larvae have chewing mouthparts and are mainly phytophagous, though some are predaceous; a few feed on animal products. Pupae are either naked or encased in a cocoon of silk or of a combination of silk and leaves.

With nearly 100,000 described species, the Lepidoptera constitute one of the larger orders of insects. Their higher classification has been controversial for nearly a century, but during the past 20 years there has been a more general agreement on a subordinal classification, based mainly on evolution of the adult mouthparts, of the female reproductive system, and of the wing venation, as

well as on the structure of larvae and pupae. Four suborders are recognized: Zeugloptera, Dacnonypha, Monotryisia, and Ditryisia.

The Zeugloptera, consisting of a single family (Micropterygidae), are the most primitive of the series. The functional mandibles and normal maxillae of these insects are indicative of their primitive position and of the origin of the Lepidoptera from mandibulate insects. The Dacnonypha and Monotryisia, although probably not in the direct line of ancestry leading to the Ditryisia, show intermediate conditions of the mouthparts, with slight to moderate modification of the mandibles and maxillae. The Ditryisia, which include by far most of the Lepidoptera, have complete loss of mandibles and full development of the tubelike proboscis. The female reproductive system and the wing venation show a comparable series of changes throughout the suborders. This subordinal classification, which has recently been reviewed in detail by COMMON (1970, 1975), is used here.

The family classification is still controversial, with 90 to 120 families recognized by different specialists. The family classification presented by COMMON, which is relatively conservative, is also adopted here. Distinguishing family traits are usually found in the detailed structure of the maxillary palpi, external genitalia, and wing venation.

Fossils have contributed little to our present understanding of the evolution of the Lepidoptera. Ordinarily, little more than one wing is preserved in the fossils, excepting, of course, those in amber. The oldest unquestionable record of the order consists of an exceptionally well-preserved micropterygid (Fig. 205, 2c, *Undopteryx*) from the Lower Cretaceous of the Soviet Union (SKALSKI, 1979a). A second species, also a micropterygid, has been found in amber from a slightly younger Cretaceous formation in Lebanon (WHALLEY, 1978). However, the suborder Zeugloptera is the only suborder of the Lepidoptera definitely known to have existed in the Mesozoic. The Dacnonypha and Monotryisia extend to the lower Oligocene and the

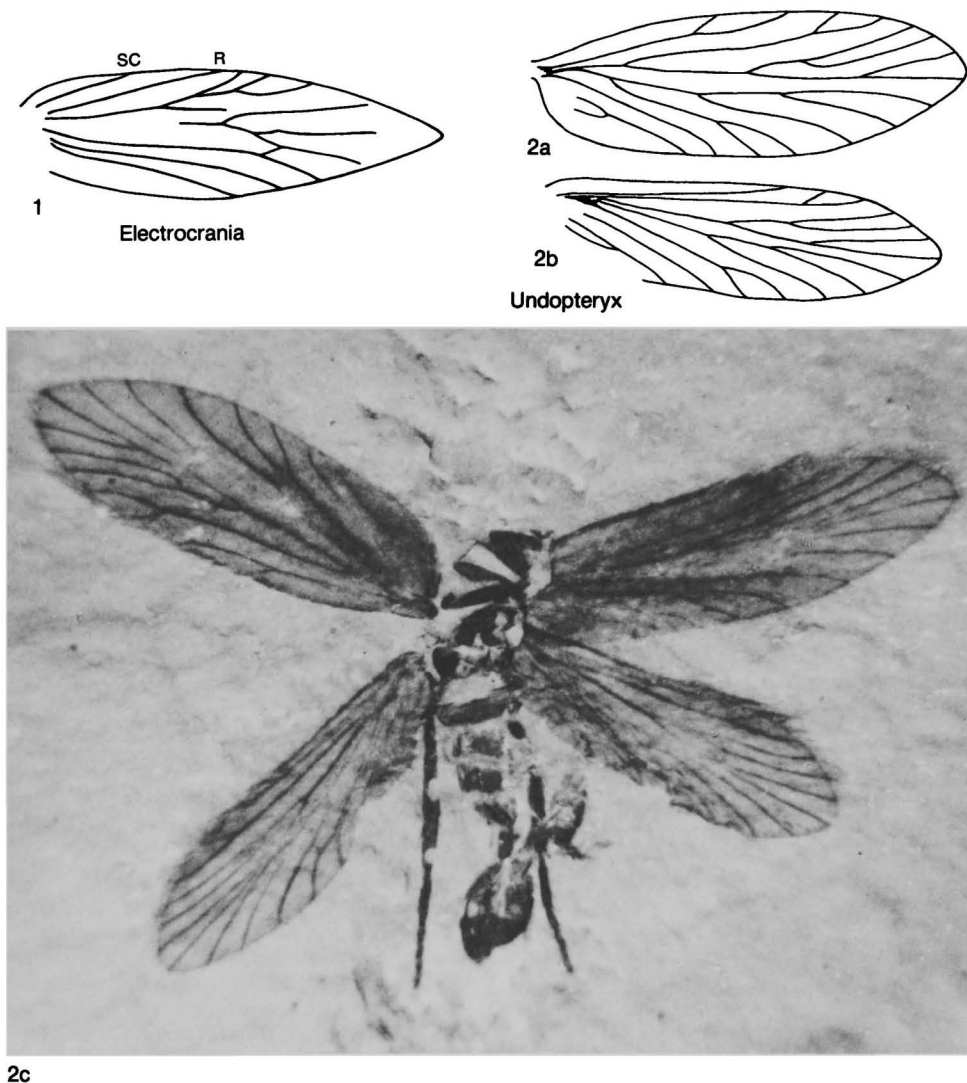


FIG. 205. Micropterygidae and Eriocraniidae (p. 372).

Ditrysia to the Eocene, but since the first records are representatives of existing families, both suborders will almost certainly eventually be found in the Cretaceous or Upper Jurassic. The Tertiary record of the Lepidoptera is very meager, at least relative to those of other existing orders of insects now of comparable size, probably because the Lepidoptera normally inhabit environments that are not conducive to their preservation as fossils. Nevertheless, the Tertiary record, small as it is, includes about 22 exist-

ing families, among which the Nymphalidae and Pieridae predominate. About 80 percent of the Tertiary genera are extinct, but in general they are not less specialized than their existing relatives, differing only about as much as existing genera do among themselves. Lepidopterous larvae, although rare, have been found in several Tertiary deposits, including Baltic amber (COCKERELL, 1907a; KUSNEZOV, 1941); and a head capsule of a small larva, apparently a micropterigid, has been reported from Cretaceous amber in Canada (MACKEY,

1970). Also, evidence of leaf mining in Miocene plants by larvae of Eriocraniidae, Nepitculidae, Lyonetiidae, and Gracillariidae has been recorded (OPLER, 1973, 1974).

The presence of Jurassic and Triassic Lepidoptera in the known geological record is controversial. TINDALE (1945, 1980) has described two genera from the Triassic of Australia that he considers to belong here; but as pointed out by RIEK (1955), the evidence for that is far from convincing. During the late Permian and early Mesozoic, the mecopteroid orders, especially the Trichoptera and Mecoptera, were extraordinarily diverse, producing a population that contained many homeomorphs suggestive of existing Trichoptera, Mecoptera, and Lepidoptera. In the present state of our knowledge, based almost entirely on wings, it seems advisable to consider these controversial homeomorphs as members of the Trichoptera or Mecoptera, which have a clear and continuous record as far back as the Permian, until better-preserved specimens have been found.

Suborder ZEUGLOPTERA

Chapman, 1917

[Zeugloptera CHAPMAN, 1917, p. 312]

Small moths with functional and dentate mandibles; laciniae present, galeae normal. Venation similar in fore and hind wings. Female with single, common opening for reproductive duct and rectum. Larvae with paired groups of 5 ocelli. Adults pollen feeders; larvae apparently feeders on moss and liverworts, although some may be detritus feeders. *Cret.—Holo.*

Family MICROPTERYGIDAE

Cotes, 1889

[Micropterygidae COTES in SWINHOE & COTES, 1889, p. 706]

Only known family of suborder; characters of suborder. *Cret.—Holo.*

Micropterix HÜBNER, 1826, p. 426. WHALLEY, 1978; JARZEMBOWSKI, 1980. *Paleoc.*, England—*Holo.*

Parasabatinca WHALLEY, 1978, p. 73 [**P. affimacra*; OD]. Similar to *Sabatinca* (recent) but with unusually large spines on legs; ocelli absent. *Cret.*, Lebanon.

Sabatinca WALKER, 1863, p. 54. REBEL, 1935, 1936; WHALLEY, 1978; SKALSKI, 1979c. *Oligo.*, Europe (Baltic); *Mio.*, Burma—*Holo.*

Undopteryx SKALSKI, 1979a, p. 91 [**U. sukatshevae*; OD]. Similar to *Sabatinca* (recent), but vein R forked in hind wing. SKALSKI, 1979b. *Cret.*, USSR (Asian RSFSR).—FIG. 205,2. **U. sukatshevae*; *a*, fore and *b*, hind wings, $\times 12$ (Skalski, 1979a); *c*, entire insect, $\times 12.7$ (Carpenter, new, courtesy of A. W. Skalski).

Suborder DACNONYPHA

Hinton, 1946

[Dacnonypha HINTON, 1946, p. 4]

Small moths, with or without mandibles and laciniae; galeae either normal or forming a short haustellum. Venation similar in fore and hind wings. Female with a single genital opening. Larvae apodous; leaf miners or feeders within seeds. *Oligo.—Holo.*

Family ERIOCRANIIDAE

Meyrick, 1927

[Eriocraniidae MEYRICK, 1928, p. 870]

Mandibles present. *Oligo.—Holo.*

Eriocrania ZELLER, 1851, p. 323. *Holo.*

Dyseriocrania SPULER, 1910, p. 483. COCKERELL, 1919d; SKALSKI, 1973b. *Mio.*, Burma—*Holo.*

Electrocrania KUSNEZOV, 1941, p. 19 [**E. immensipalpa*; OD]. Similar to *Dyseriocrania* but without supplementary branches on veins SC and R. SKALSKI, 1976. *Oligo.*, Europe (Baltic).—FIG. 205,1. **E. immensipalpa*; fore wing, $\times 11.4$ (Kusnezov, 1941).

Suborder MONOTRYZIA

Börner, 1939

[Monotryzia BÖRNER, 1939, p. 1401]

Very small to large moths, lacking mandibles and laciniae; galeae usually in form of short haustellum. Venation usually similar in fore and hind wings but sometimes reduced in hind wings and even in both pairs of wings. Female with 1 or 2 genital openings. Most larvae miners in leaves, stems, or roots. *Oligo.—Holo.*

Family INCURVARIIDAE

Spuler, 1910

[Incurvariidae SPULER, 1910, p. 464]

Small moths, without ocelli; haustellum scaled basally. Hind wing with strong frenulum. *Oligo.*—*Holo.*

Incurvaria HAWORTH, 1828, p. 559. *Holo.*

Adelites REBEL, 1934, p. 15 [**A. electrella*; OD]. Little-known adult. REBEL, 1935. *Oligo.*, Europe (Baltic).

Incurvarites REBEL, 1934, p. 14 [**I. alienella*; OD]. Little-known genus. [Family assignment uncertain.] *Oligo.*, Europe (Baltic).

Prophalonia REBEL, 1935, p. 167 [**P. gigas*; OD]. Little-known incurvariid with costal area of fore wing abruptly narrowed at midwing. SKALSKI, 1973c. *Oligo.*, Europe (Baltic).

Suborder DITRYZIA

Börner, 1939

[Ditryzia BÖRNER, 1939, p. 1401]

Small to very large moths, skippers, or butterflies, with mandibles and laciniae absent; galeae forming a haustellum; venation differing in fore and hind wings. Female with 2 genital openings. Most larvae phytophagous but very diverse. *Paleoc.*—*Holo.*

Family COSSIDAE Leach, 1815

[Cossidae LEACH, 1815, p. 131]

Haustellum very short; maxillary palpi minute. Larvae wood-boring. *Oligo.*—*Holo.*

Cossus FABRICIUS, 1793, pl. 1. *Holo.*

Adelopsyche COCKERELL, 1926c, p. 16 [**A. frustans*; OD]. Similar to *Macrocyttara* (recent), but radial cell of fore wing very short; RS2 not forked; M2 fully developed. *Oligo.*, USA (Colorado).

Xyleutites KOZHANCHIKOV, 1957, p. 675 [**X. miocenicus*; OD]. Radial cell of fore wing elongate; RS2 forked; M2 obsolescent proximally. MARTYNOVA, 1960. *Mio.*, USSR (European RSFSR).—FIG. 206,3. [**X. miocenicus*; fore wing, $\times 2.5$ (Martynova, 1960)].

Family TORTRICIDAE Latreille, 1802

[Tortricidae LATREILLE, 1802a, p. 415]

Small moths; maxillary palpi very small, with 2 to 4 segments. Costal margin of fore wing often strongly arched. *Oligo.*—*Holo.*

Tortrix LINNÉ, 1758, p. 530. [Generic assignment of fossils doubtful.] COCKERELL, 1907h, 1916c. *Oligo.*, USA (Colorado)—*Holo.*

Electresia KUSNEZOV, 1941, p. 62 [**E. zaleskii*; OD]. Close to *Laspeyresia* HÜBNER (recent); differing in minor venational details. SKALSKI, 1973c. *Oligo.*, Europe (Baltic).—FIG. 206,2. [**E. zaleskii*; fore wing, $\times 12$ (Kusnezov, 1941)].

Tortricidrosis SKALSKI, 1973c, p. 339 [**T. inclusa*; OD]. Little-known genus, probably belonging to the Olethreutinae (recent). *Oligo.*, Europe (Baltic).

Family TINEIDAE Latreille, 1810

[Tineidae LATREILLE, 1810, p. 347]

Small moths, without ocelli; antennae usually simple; haustellum short or even absent; head rough and hairy; vein M often present in fore wing. Larvae sometimes case bearing. *Paleoc.*—*Holo.*

Tinea LINNÉ, 1758, p. 534. *Holo.*

Architinea REBEL, 1934, p. 10 [**A. balticella*; OD]. Little-known adult. *Oligo.*, Europe (Baltic).

Dysmasites KUSNEZOV, 1941, p. 28 [**D. carpenteri*; OD]. Similar to *Ateliotum* (recent) but without intercalary cell in hind wing; proboscis reduced. *Oligo.*, Europe (Baltic).—FIG. 206,4. [**D. carpenteri*; entire insect, $\times 18$ (Kusnezov, 1941)].

Ethmia HÜBNER, 1819, p. 163. [Generic assignment of fossil doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Glossocardia KUSNEZOV, 1941, p. 39 [**G. gerasimovi*; OD]. Larva with chaetotaxy much as in *Scardia* (recent). *Oligo.*, Europe (Baltic).

Martynea KUSNEZOV, 1941, p. 24 [**M. rebeli*; OD]. Similar to *Nemapogon* (recent), but RS3+4 fully developed. *Oligo.*, Europe (Baltic).

Monopibaltia SKALSKI, 1974, p. 98 [**M. ignitella*; OD]. Similar to *Monopis* (recent); fore wing oval; median cell small, about three-fifths length of wing; SC extending to level of distal end of median cell; R, RS1, RS2 parallel; RS2 arising close to origin of RS3+4; R4 terminating at wing apex. *Oligo.*, Europe (Baltic).

Palaeoscardiites KUSNEZOV, 1941, p. 36 [**P. mordvilkoii*; OD]. Similar to *Scardia* (recent), but vestiges of mandibles present; antennal scape not pectinate. *Oligo.*, Europe (Baltic).

Paratriaxomasia JARZEMBOWSKI, 1980, p. 267 [**P. solentensis*; OD]. Similar to *Triaxomasia* (recent) but with broader fore wing; hind wing lacking marginal indentation near end of SC+R. *Paleoc.*—*Oligo.*, England.

Proscardiites KUSNEZOV, 1941, p. 33 [**P. mar-*

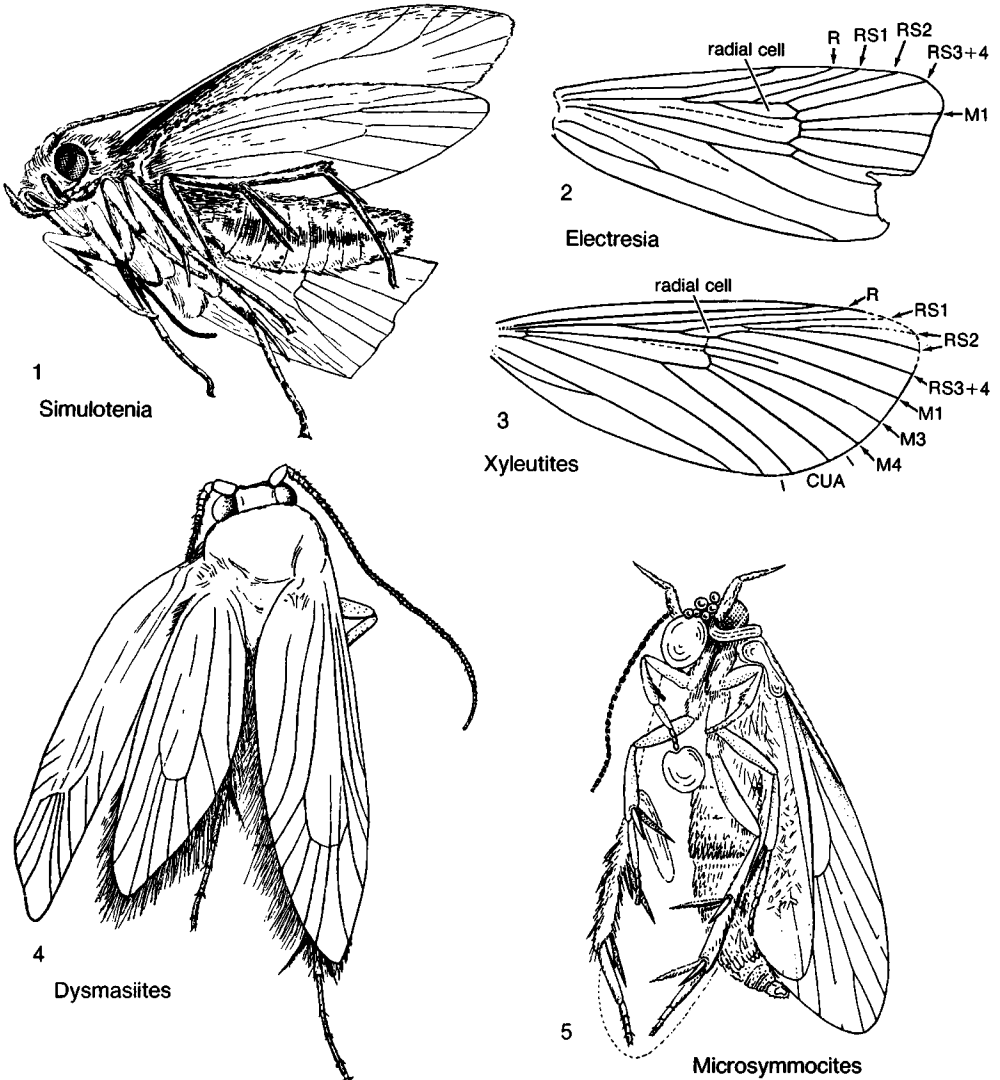


FIG. 206. Cossidae, Tortricidae, Tineidae, and Oecophoridae (p. 373–375).

tynovi; OD]. Similar to *Palaeoscardiites*, but antennae and proboscis shorter. *Oligo.*, Europe (Baltic).
Scardiites KUSNEZOV, 1941, p. 30 [**P. meyricki*; OD]. Similar to *Palaeoscardiites*, but vestiges of mandibles absent; veins M1 and M2 of hind wing forming a long stalk, M1+2. *Oligo.*, Europe (Baltic).
Simulotenia SKALSKI, 1977, p. 16 [**S. intermedia*; OD]. Fore wing moderately ovate; hind wing as broad as fore wing, apex rounded; M1 terminating on costal margin; maxillary palpus about twice as long as labial palpus; metatibia with

pair of long spurs near middle of segment. *Oligo.*, Europe (Baltic). — FIG. 206, 1. **S. intermedia*; lateral view, $\times 15$ (Skalski, 1977).
Tillyardinea KUSNEZOV, 1941, p. 22 [**T. eocaenica*; OD]. Similar to *Phylloporia* (recent), but RS of fore wing with 4 branches; labial palpi as long as maxillary palpi. SKALSKI, 1974. *Oligo.*, Europe (Baltic).
Tineolamima REBEL, 1934, p. 13 [**T. aurella*; OD]. Little-known adult. *Oligo.*, Europe (Baltic).
Tineosemopsis SKALSKI, 1974, p. 97 [**T. decurtatus*; OD]. Similar to *Tillyardinea*, but maxillary palpi longer than labial palpi; RS1+2 more

than half as long as RS3 + 4. *Oligo.*, Europe (Baltic).

Family PSYCHIDAE Boisduval, 1828

[Psychidae BOISDUVAL, 1828, p. 44]

Usually small moths; head with roughened hairs; haustellum vestigial or absent. Larvae case bearing. *Oligo.*—*Holo.*

Psyche SCHRANK, 1801, p. 156. [Generic assignment of fossil doubtful.] HEER, 1849. *Mio.*, Europe (Germany)—*Holo.*

Sterrhopteryx HÜBNER, 1825, p. 399. [Generic assignment of fossil doubtful.] REBEL, 1934. *Oligo.*, Europe (Baltic)—*Holo.*

Family PROLYONETIIDAE

Kusnezov, 1941

[Prolyonetiidae KUSNEZOV, 1941, p. 45]

Related to Lyonetiidae but having long labial palpi, fully developed maxillary palpi, and less reduced venation of both wings. [Probably a synonym of Lyonetiidae.] *Oligo.*

Prolyonetia KUSNEZOV, 1941, p. 43 [**P. cockerelli*; OD]. R and RS3 + 4 present in fore wing; proboscis fully developed. *Oligo.*, Europe (Baltic).

Family OECOPHORIDAE

Bruand, 1849

[Oecophoridae BRUAND, 1849, p. 45]

Small moths. Scale covering of head usually smooth; ocelli commonly absent; antennae simple; maxillary palpi with 4 segments; labial palpi recurved. In fore wing, vein RS3 + 4 commonly forked to about half its length. Larvae usually leaf rollers. *Oligo.*—*Holo.*

Oecophora LATREILLE, 1796, p. 146. *Holo.*

Borkhausenites REBEL, 1934, p. 6, non *Borkhausenites*, *lapsus calami* [**B. bachofeni*; OD]. Similar to *Borkhausenia* (recent) but differing in venational details; R not parallel to RS1. *Oligo.*, Europe (Baltic).

Depressarites REBEL, 1935, p. 175 [**D. levipalpella*; OD]. Similar to *Schistodepressaria* (recent) but differing in scale covering of maxillary palpi. *Oligo.*, Europe (Baltic).

Epiborkhausenites SKALSKI, 1973a, p. 153 [**E. obscuroidimaculatus*; OD]. Similar to *Paraborkhausenites* but with different spacings of origins of R, RS1, and RS2. *Oligo.*, Europe (Baltic).

Glesseumeyrickia KUSNEZOV, 1941, p. 47 [**G. henrikseni*; OD]. Similar to *Eumeyrickia* (recent) but in fore wing SC terminating well beyond midwing. *Oligo.*, Europe (Baltic).

Microsymmocites SKALSKI, 1977, p. 18 [**M. kuznetzovi*; OD]. Fore wing broadly ovate, with costal margin strongly curved; hind wing with apex rounded; labial palpus long, recurved; metatibia with a pair of spurs at middle. *Oligo.*, Europe (Baltic).—FIG. 206,5. **M. kuznetzovi*; lateral view, $\times 15$ (Skalski, 1977).

Neoborkhausenites SKALSKI, 1977, p. 20 [**Borkhausenites incertella* REBEL, 1935, p. 178; OD]. Similar to *Microsymmocites*. Fore wing broadly ovate, 3 times as long as broad; apex very broadly rounded. *Oligo.*, Europe (Baltic).

Paraborkhausenites KUSNEZOV, 1941, p. 49 [**Borkhausenites vicinella* REBEL, 1935, p. 181]. Similar to *Borkhausenites* but with R, RS1, and RS2 parallel and RS3 and RS4 with a long stalk. SKALSKI, 1977. *Oligo.*, Europe (Baltic).

Schiffermuelleria HÜBNER, 1826, p. 421. SKALSKI, 1977. *Oligo.*, Europe (Baltic)—*Holo.*

Family ELACHISTIDAE Stainton, 1854

[Elachistidae STAINTON, 1854, p. 244]

Very small moths. Head scaling smooth; haustellum almost always present; in hind wing vein RS straight, extending along wing axis to apex. Larvae leaf miners. *Oligo.*—*Holo.*

Elachista TREITSCHKE, 1833, p. 177. *Holo.*

Anybia STAINTON, 1854, p. 244. [Family assignment of fossil doubtful.] REBEL, 1934. *Oligo.*, Europe (Baltic)—*Holo.*

Family COPROMORPHIDAE

Meyrick, 1905

[Copromorphidae MEYRICK, 1905, p. 606]

Wings broad, venation not reduced, or wings deeply cleft, hind wing divided into at least 6 plumes; vein M in hind wing with 3 branches and RS and M1 parallel. *Paleoc.*—*Holo.*

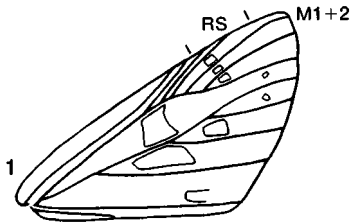
Copromorpha MEYRICK, 1886, p. 281. JARZEMBOWSKI, 1980. *Paleoc.*, England—*Holo.*

Family SYMMOCIDAE

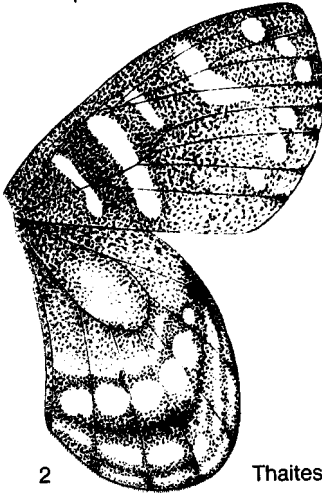
Gozmány, 1957

[Symmocidae GOZMÁNY, 1957, p. 326]

Similar to the Gelechiidae (recent), but hind wing without a projecting apex above a deeply arcuate termen, and with less com-



Pamphilites



2 Thaites

FIG. 207. HesperIIDae and PapilionIDae (p. 376–377).

plicated genital structures. Larvae feeding on vegetable debris. *Oligo.*—*Holo.*

Symmoca HÜBNER, 1825, p. 403. *Holo.*

Oegoconites KUSNEZOV, 1941, p. 51 [**O. borisjaki*; OD]. Similar to *Oegoconia* (recent), but stem of M3 + CUA long. *Oligo.*, Europe (Baltic).

Family ZYGAENIDAE Latreille, 1809

[Zygaenidae LATREILLE, 1809, p. 189]

Small moths with dilated antennae, bipectinate in male; maxillary palpi with 1 or 2 segments; vein CUP present in both fore and hind wings; in hind wing SC + R coalescing for a short distance with RS beyond middle of discal cell. Larvae with dense covering of short setae; foliage feeders. *Mio.*—*Holo.*

Zygaena FABRICIUS, 1775, p. 550. REISS, 1936; BURGEFF, 1951. *Mio.*, Europe (Germany)—*Holo.*

Zygaenites BURGEFF, 1951, p. 3 [**Z. controversus*; OD]. Similar to *Zygaena* but with basal wing spots nearer wing apex. *Mio.*, Europe (Germany).

Family PYRALIDAE Latreille, 1809

[Pyralidae LATREILLE, 1809, p. 192]

Small to large moths. Antennae usually simple; haustellum commonly densely covered with scales near base; vein CUP usually absent in fore wing, present in hind wing. Larvae commonly in shelters of leaves, stems, or galls; feeding habits diverse. *Paleoc.*—*Holo.*

Pyralis LINNÉ, 1758, p. 533. *Holo.*

Glendotricha KUSNEZOV, 1941, p. 64 [**G. olgae*; OD]. Similar to *Endotricha* (recent) but having a narrower fore wing, with strongly acute apex. *Oligo.*, Europe (Baltic).

Pyralites HEER, 1856, p. 30 [**P. obscurus*; OD]. Little-known genus, based on wing fragments; venation apparently similar to that of several recent genera of Pyralidae. JARZEMBOWSKI, 1980. *Paleoc.*—*Oligo.*, England; *Oligo.*, Europe (France).

Family THYRIDIDAE Herrich-Schaeffer, 1846

[Thyrididae HERRICH-SCHAEFFER, 1846, p. 81]

Small to large moths; ocelli usually absent; haustellum without scales; maxillary palpi very small, with 1 or 2 segments. Vein CUP absent in fore wing, vestigial in hind wing. Larvae usually in stems or twigs. *Eoc.*—*Holo.*

Thyris LASPEYRES, 1803, p. 39. *Holo.*

Hexerites COCKERELL, 1933b, p. 480 [**H. primalis*; OD]. Similar to *Hexeris* (recent), but labial palpi shorter and fore wings more obtuse and less falcate distally. *Eoc.*, USA (Colorado).

Family HESPERIIDAE Leach, 1815

[HesperIIDae LEACH, 1815, p. 128]

Small to medium-sized skippers. Antennae dilated apically and terminating in a hook; widely separated at base. Maxillary palpi and ocelli absent. Vein CUP absent in both wings. Larvae foliage feeders, usually occurring in rolled leaves. *Oligo.*—*Holo.*

Hesperia FABRICIUS, 1793, p. 258. *Holo.*

Pamphilites SCUDDER, 1875a, p. 66 [**P. abdita*; OD]. Fore wing similar to that of *Atalopedes* (recent) but with M1+2 terminating on outer wing margin just below wing apex. *Oligo.*, Europe (France).—FIG. 207.1. **P. abdita*; fore wing, $\times 2.5$ (Scudder, 1875a).

Thanatites SCUDDER, 1875a, p. 62 [**Vanessa vetula* HEYDEN, 1859a, p. 12; OD]. Similar to *Erynnis*

(recent) but with more numerous small spots on the fore wing. [Possibly a synonym of *Erynnis*.] *Oligo.*, Europe (Germany).

Family PAPILIONIDAE

Latreille, 1802

[Papilionidae LATREILLE, 1802a, p. 387]

Large butterflies with maxillary palpi vestigial; forelegs normal; fore wing with normal apex; discal cell of both wings closed. Larvae foliage feeders. *Eoc.*—*Holo.*

Papilio LINNÉ, 1758, p. 458. [*P. maachii* MÉNÉTRIÉS occurs in the Pleistocene and Holocene of Japan.] FUJIYAMA, 1968a. *Pleist.*—*Holo.*

Luehdorfia KRÜGER, 1878, p. 128 [= *Dorites* REBEL, 1898, p. 734 (type, *D. bosniaskii*); *Luehdorfia* BRYK, 1912, p. 53 (type, *Dorites bosniaskii* REBEL, 1898, obj.). REBEL, 1898; BRYK, 1934. *Mio.*, Europe (Italy)—*Holo.*

Praepapilio DURDEN & ROSE, 1978, p. 5 [*P. colorado*; OD]. Fore wing with costa concave at end of SC; labial palpi longer than head; R terminating on costal margin. *Eoc.*, USA (Colorado).

Thaites SCUDDER, 1875a, p. 57 [**T. ruminianus*; OD] Similar to *Thais* (recent), but fore wing markings without crescentic spots. *Mio.*, Europe (Germany). — FIG. 207,2. **T. ruminianus*; fore and hind wings, $\times 2$ (Scudder, 1875a).

Family PIERIDAE Boisduval, 1836

[Pieridae BOISDUVAL, 1836, p. 163]

Medium-sized butterflies, lacking maxillary palpi; forelegs normal; vein RS in fore wing with 3 branches or less. Larvae foliage feeders. *Oligo.*—*Holo.*

Pieris SCHRANK, 1801, p. 152. *Holo.*

Aporia HÜBNER, 1819, p. 90. Fossil consists of a small fragment of wing. [Generic assignment doubtful.] KERNBACH, 1967; BRANSCHIED, 1969. *Plio.*, Europe (Germany)—*Holo.*

Coliades SCUDDER, 1875a, p. 52 [**C. proserpina*; OD]. Similar to *Delias* (recent), but anterior border of discal cell straight. *Oligo.*, Europe (France).

Mylothrites SCUDDER, 1875a, p. 44 [**Vanessa pluto* HEER, 1849, p. 179; OD]. Venation similar to that of *Mylothris* (recent), but wing form as in *Hebomoia* (recent). *Mio.*, Europe (Yugoslavia).

Oligodonta F. M. BROWN, 1976, p. 1 [**O. florissantensis*; OD]. Little-known genus, based on specimen with folded wings. *Oligo.*, USA (Colorado).

Pontia FABRICIUS, 1807, p. 283 [= *Pierites* HEER, 1849, p. 182 (type, *P. freyeri*)]. HEER, 1849; SCUDDER, 1875a. *Mio.*, Europe (Germany)—*Holo.*

Stolopsyche SCUDDER, 1889, p. 467 [**S. libytheoides*; OD]. Similar to *Pieris* (recent) but with longer labial palpi and shorter basal antennal segments. *Oligo.*, USA (Colorado).

Family NYMPHALIDAE

Swainson, 1837

[Nymphalidae SWAINSON in RICHARDSON, SWAINSON, & KIRBY, 1837, p. 289]

Small to large butterflies. Maxillary palpi with 1 segment; forelegs reduced, nonfunctional; vein RS in fore wing with 4 or more branches. Larvae foliage feeders. *Paleoc.*—*Holo.*

Nymphalis LINNÉ, 1758, p. 473. *Holo.*

Aglais DALMAN, 1816, p. 56. SCUDDER, 1878a; MARTYNOVA, 1960; NEKRUTENKO, 1965a. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Apanthesis SCUDDER, 1889, p. 459 [**A. leuce*; OD]. Allied to *Cirrochroa* (recent) but differing in venational details and in greater sinuosity of inner margin of fore wing. *Oligo.*, USA (Colorado). — FIG. 208,1. **A. leuce*; fore wing, $\times 1.5$ (Scudder, 1889).

Chlorippe DOUBLEDAY, 1844, p. 108. COCKERELL, 1907g. *Oligo.*, USA (Colorado)—*Holo.*

Eugonia HÜBNER, 1819, p. 36. SCUDDER, 1875a. *Mio.*, Europe (Yugoslavia)—*Holo.*

Jupitellia CARPENTER, 1986, p. 579, *nom. subst. pro Jupitertia* SCUDDER, 1889, p. 448, *non* BELLARDI, 1875 [**Jupitertia charon* SCUDDER, 1889, p. 450; OD]. Similar to *Lithodryas*, but fore wing narrower and SC closer to costal margin; hind wing relatively longer. *Oligo.*, USA (Colorado). — FIG. 208,3. **J. charon* (SCUDDER); *a*, fore and *b*, hind wings, $\times 1.9$ (Scudder, 1889).

Lethites SCUDDER, 1875a, p. 34, *nom. subst. pro Satyrites* SCUDDER, 1872, p. 66, *non* BLANCH-BRULLÉ, 1871 [**Satyrites reynesii* SCUDDER, 1872, p. 66; OD]. Similar to *Lethe* (recent) but with RS1+2 and RS3+4 arising before distal end of discal cell. *Oligo.*, Europe (France). — FIG. 208,2. **L. reynesii* (SCUDDER); fore wing, $\times 1.8$ (Scudder, 1875a).

Lithodryas COCKERELL, 1909c, p. 79, *nom. subst. pro Lithopsyche* SCUDDER, 1889, p. 454, *non* BUTLER, 1889 [**Lithopsyche styx* SCUDDER, 1889, p. 454; OD]. Similar to *Jupitellia* but having much broader fore wing with less pointed apex. *Oligo.*, USA (Colorado).

Neorinopsis BUTLER, 1873, p. 127 [**Cyllo sepulta* BOISDUVAL, 1840, p. 371; OD]. Similar to *Neorina* (recent) but with different form and markings of hind wing. SCUDDER, 1875a. *Oligo.*, Europe (France).

Nymphalites SCUDDER, 1889, p. 457 [**N. obscurum*; OD]. Little-known genus, apparently sim-

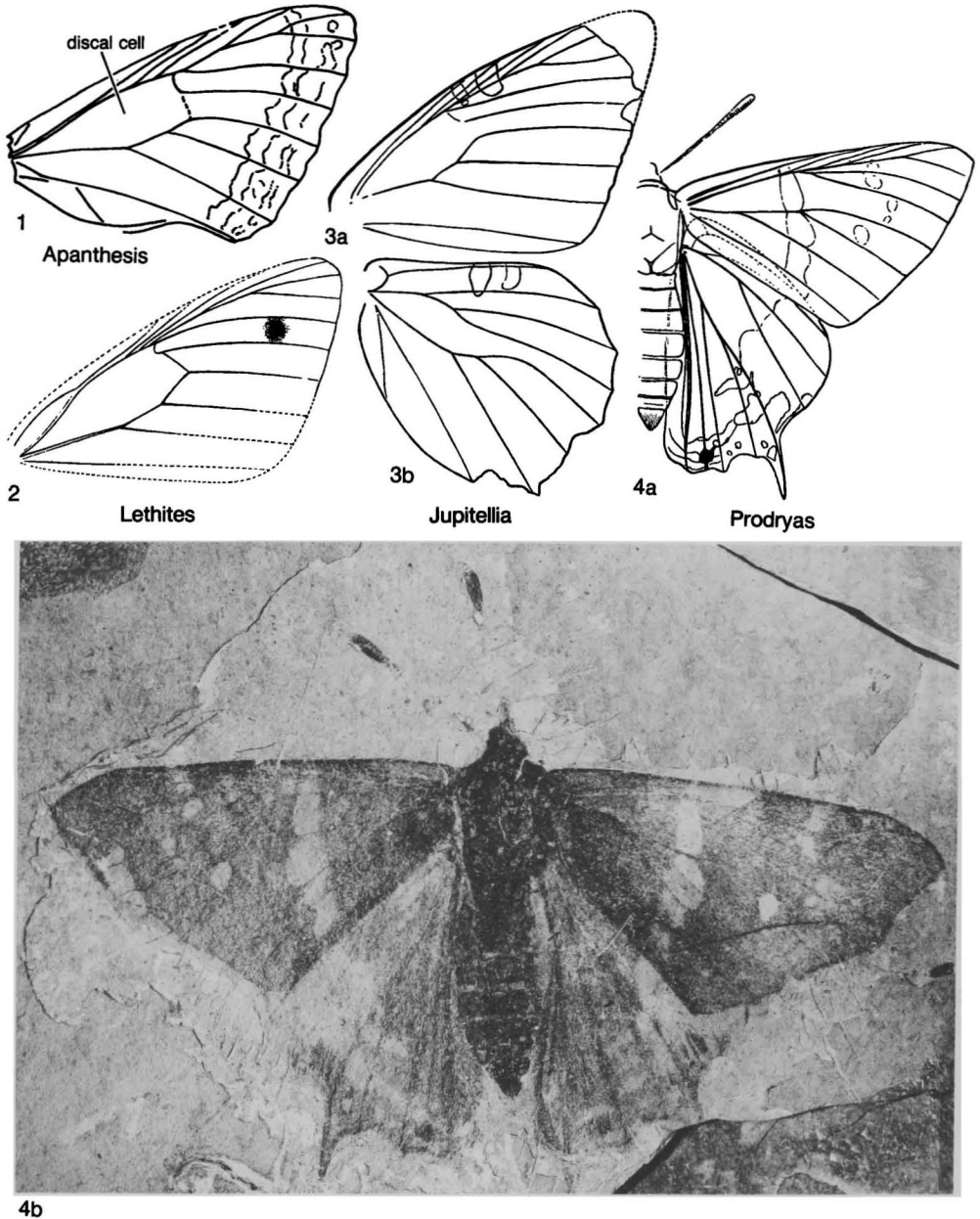


FIG. 208. Nymphalidae (p. 377-378).

ilar to such recent nymphalid genera as *Neurosigma* and *Abrota*, but M2 of fore wing more remote from M1 basally; hind wing with relatively narrow anterior area. JARZEMBOWSKI, 1980. *Paleoc.-Oligo.*, England; *Oligo.*, USA (Colorado).

Prodryas SCUDDER, 1878a, p. 520 [**P. persephone*; OD]. Similar to *Hypanartia* (recent), but fore

wing more elongate; costal and outer margins uniformly straight; discal cell open. FORBES, 1932. *Oligo.*, USA (Colorado). — FIG. 208.4. **P. persephone*; a, wings and body, $\times 1.6$ (Scudder, 1878a); b, whole insect, $\times 2$ (Carpenter, new). **Vanessa** FABRICIUS, 1807, p. 281. NEKRUTENKO, 1965a, 1965b. *Mio.*, USSR (European RSFSR)–*Holo.*

Family LIBYTHEIDAE

Boisduval, 1836

[Libytheidae BOISDUVAL, 1836, p. 167]

Medium-sized butterflies; maxillary palpi vestigial; forelegs reduced in male only; fore wing truncate apically. Larvae foliage feeders. *Oligo.*—*Holo.*

Libythea FABRICIUS, 1807, p. 284. *Holo.*

Barbarothea SCUDDER, 1892, p. 21 [**B. florissanti*; OD]. Similar to *Libythea* (recent), but hind wing much broader relative to its length. *Oligo.*, USA (Colorado). — FIG. 209,2. **B. florissanti*; *a*, fore and *b*, hind wings, $\times 1.8$ (Scudder, 1892).

Prolibythea SCUDDER, 1889, p. 465 [**P. vagabunda*; OD]. Similar to *Dichora* (recent) but with costal margin of hind wings not lobed. *Oligo.*, USA (Colorado). — FIG. 209,1. **P. vagabunda*; *a*, fore and *b*, hind wings, $\times 1.7$ (Scudder, 1889).

Family LYCAENIDAE Leach, 1815

[Lycaenidae LEACH, 1815, p. 129]

Small to medium-sized butterflies, lacking maxillary palpi; forelegs slightly reduced in male, normal in female; fore wing with normal apex but often lacking 1 or 2 branches of RS. Larvae mostly foliage feeders, some predaceous. *Paleoc.*—*Holo.*

Lycaena FABRICIUS, 1807, p. 285. *Holo.*

Aquisextana THÉOBALD, 1937b, p. 160 [**A. irenaei*; OD]. Similar to *Curetis* (recent) but with a smaller thorax. *Oligo.*, Europe (France).

Lithopsyche BUTLER, 1889, p. 294 [**L. antiqua*; OD] [= *Calospilites* VAN SCHEPDAEL, 1974, p. 15, obj.]. Little-known genus, based on wing fragments, apparently similar to *Mesene* and *Anteros* and other recent genera of subfamily Riodininae, but fork of RS3+4 of fore wing apparently absent. JARZEMBOWSKI, 1980. *Paleoc.*—*Oligo.*, England.

Riodinella DURDEN & ROSE, 1978, p. 15 [**R. nympha*; OD]. Venation as in *Ancyluris* (recent), but RS4 terminating distinctly posterior of wing apex. *Eoc.*, USA (Colorado).

Family GEOMETRIDAE Leach, 1815

[Geometridae LEACH, 1815, p. 134]

Small to large moths. Antennae simple or pectinate; maxillary palpi commonly with 1 segment; ocelli usually absent. Wings broad, venation very diverse. In fore wing partial coalescence of radial veins often forming narrow accessory cells (areoles); veins RS3 and

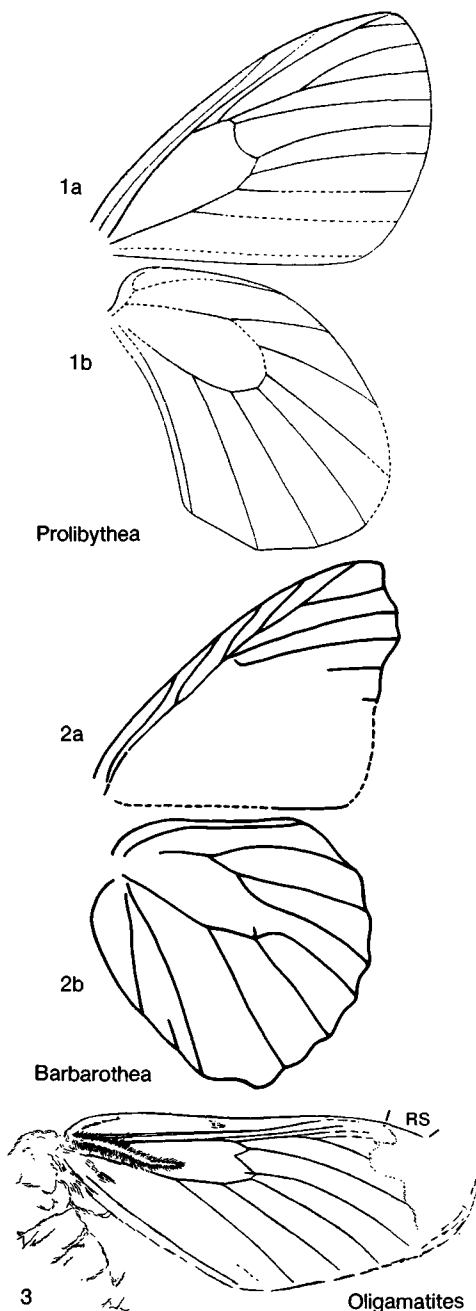


FIG. 209. Libytheidae and Ctenuchidae (p. 379–380).

RS4 stalked. In hind wing SC usually strongly bent basally. Larvae with anterior 2 or 3 pairs of ventral prolegs much reduced or even absent; foliage feeders. *Paleoc.*—*Holo.*

- Geometra** LINNÉ, 1758, p. 326. *Holo.*
Geometridites CLARK & others, 1971, p. 582 [**G. repens* KERNBACH, 1967, p. 107]. Little-known genus, based on larva; additional wing fragments also placed here. KERNBACH, 1967; JARZEMBOWSKI, 1980. *Paleoc.-Oligo.*, England; *Plio.*, Europe (Germany).
Hydriomena HÜBNER, 1825, p. 322. [Generic assignment of fossil doubtful.] COCKERELL, 1922c. *Oligo.*, USA (Colorado)—*Holo.*

Family CTENUCHIDAE Kirby, 1837

[Ctenuchidae Kirby in RICHARDSON, SWAINSON, & KIRBY, 1837, p. 305]

Small to medium-sized moths; antennae simple or complex; maxillary palpi with only 1 segment. Fore wing narrow, areole absent; hind wing with vein SC+R completely coalesced with RS. Larvae with dense setal cover; mostly foliage feeders. *Oligo.—Holo.*

- Ctenucha** KIRBY, 1837, p. 305. *Holo.*
Oligamatites KUSNEZOV, 1928, p. 431 [**O. martynovi*; OD]. Similar to *Ctenucha* (recent), but costal margin of fore wing concave in basal half; branches of RS arising very close together; RS₃ strongly diverging from RS₂. *Oligo.*, USSR (Kazakh).—FIG. 209,3. **O. martynovi*; fore wing, $\times 1.3$ (Kusnezov, 1928).

Family UNCERTAIN

The following genera, apparently belonging to the order Lepidoptera, suborder Ditrysia, are too poorly known to permit assignment to families.

- Arctiites** REBEL, 1898, p. 732 [**A. deletus*; OD]. Little-known adult moth. *Mio.*, Europe (Italy).
Argyresthites REBEL, 1934, p. 5 [**A. succinella*; OD]. Little-known adult, possibly an yponomeutid. *Oligo.*, Europe (Baltic).
Cerurites KERNBACH, 1967, p. 107 [**C. wagneri*; OD]. Little-known genus, based on poorly preserved specimen. *Plio.*, Europe (Germany).
Chionaemopsis COCKERELL & LEVEQUE, 1931, p. 354 [**C. quadrifasciatus*; OD]. Little-known moth, possibly belonging to the Yponomeutidae. FORBES, 1931. *Eoc.*, USA (Colorado).
Epinomeuta REBEL, 1935, p. 172 [**E. truncatipennella*; OD]. Little-known adult, possibly a tineid. *Oligo.*, Europe (Baltic).
Eriocranites KERNBACH, 1967, p. 104 [**E. hercynicus*; OD]. Little-known genus, based on a poorly preserved wing. *Plio.*, Europe (Germany).
Gallerites KERNBACH, 1967, p. 106 [**G. keleri*; OD]. Little-known genus, based on poorly preserved specimen. *Plio.*, Europe (Germany).
Gurnetia COCKERELL, 1921d, p. 472 [**G. durranti*;

- OD]. Little-known genus, based on wing fragments. JARZEMBOWSKI, 1980. *Paleoc.—Oligo.*, England.
Lycaenites REBEL, 1898, p. 734 [**L. gabbroensis*; OD]. Little-known adult. *Mio.*, Europe (Italy).
Miopieris ZEUNER, 1942c, p. 409 [**M. talboti*; OD]. Little-known butterfly; probably a lycaenid. *Mio.*, Europe (Germany).
Phylledestes COCKERELL, 1907a, p. 188 [**P. vorax*; OD]. Little-known larva, with several stout hairs on body segments 2 through 10. *Oligo.*, USA (Colorado).
Prohepialus PITON, 1940a, p. 217 [**P. incertus*; OD]. Little-known genus, based on wing fragments. [Placed in the Hepialidae by PITON (1940a) and JARZEMBOWSKI (1980).] *Paleoc.—Oligo.*, Europe (France), England.
Scythropites REBEL, 1935, p. 169 [**S. balticella*; OD]. Little-known adult, possibly an yponomeutid. *Oligo.*, Europe (Baltic).
Sphingidites KERNBACH, 1967, p. 108 [**S. weidneri*; OD]. Little-known genus, based on several segments of a larva with a posterior horn. *Plio.*, Europe (Germany).
Symmocites KUSNEZOV, 1941, p. 54 [**S. robdendorfi*; OD]. Little-known genus, with maxillary palpi much reduced. [Placed in Symmocidae by KUSNEZOV (1941) and in Oecophoridae by SKALSKI (1976).] *Oligo.*, Europe (Baltic).

Suborder UNCERTAIN

The following genera, apparently belonging to the order Lepidoptera, are too poorly known to allow assignment to suborders.

- Noctuites** HEER, 1849, p. 185 [**N. effossus* HEER, 1849, p. 185; SD CARPENTER, herein]. Little-known adult moths; venation not preserved. HEER, 1849; OUSTALET, 1870; KERNBACH, 1967. *Oligo.*, Europe (France); *Mio.*, Europe (Yugoslavia); *Plio.*, Europe (Germany).
Stigmellites KERNBACH, 1967, p. 104 [**S. heringi*; OD]. Form genus, based on mines in foliage. *Plio.*, Europe (Germany).

Order MECOPTERA

Packard, 1886

[Mecoptera COMSTOCK & COMSTOCK, 1895, p. 184, *nom. correct. pro* Mecaptera PACKARD, 1886, p. 808] [=Paratrichoptera TILLYARD, 1919a, p. 194; Paramecoptera TILLYARD, 1919b, p. 231]

Small or moderate-sized insects, usually with slender body. Compound eyes prominent; ocelli usually present; antennae filiform, with 15 to 50 segments. Head produced into a rostrum; rostrum often elongate

and normally held in a vertical position; mouthparts with chewing mandibles situated at distal end of rostrum; maxillae and labium normal, with well-developed palpi. Prothorax typically small, meso- and metathorax well developed. Two pairs of similar wings, a distinct pterostigma usually present; branching of veins typically dichotomous. Vein SC usually conspicuous, commonly submarginal, but more remote from costal margin in some families, the costal area being broad, containing oblique veinlets; in some genera SC apparently bearing 1 or more branches; R strongly convex, usually with short veinlets in pterostigmal area; RS typically arising at or before midwing, with 3 to 18 terminal branches; media (M) showing no convexity or concavity, with 4 to 12 branches; CU dividing near wing base into CUA and CUP. In fore wing, CUA usually unbranched, rarely forked; shortly after its origin CUA either connected to stem of M by a crossvein (formerly termed M5) or actually coalesced with M for a short distance; the free basal piece of CUA (before connection to M by crossvein or coalescence) very short or long. In hind wing, CUA coalesced with M near base, commonly continuing the straight line of stem of M beyond coalescence. Three anal veins typically present in both fore and hind wings. Legs usually slender, with 5 tarsal segments. Abdomen showing 10 distinct segments; ninth abdominal segment of male variously modified with copulatory structures, often in form of genital bulb, including large claspers; in female, last 3 abdominal segments cylindrical, slender, apical segment terminating in a pair of very short cerci with 2 segments. *Perm.—Holo.*

The eggs of Mecoptera are usually laid in damp soil. The larvae are caterpillarlike but possess groups of ocelli on each side of the head; they are saprophagous or phytophagous (rarely predaceous), usually living in soil. The pupae are formed in earthen cells in the ground.

The Mecoptera appear to occupy a central position in the evolution of the Endopterygota. There is reasonably good evidence that

the Trichoptera, Lepidoptera, and Diptera have evolved from ancestral stock close to the Mecoptera or even within the order itself. The relationship of the Mecoptera with the Neuroptera is more obscure; mecopterons apparently share many adult features with the suborder Planipennia (TILLYARD, 1929, 1933, 1935d; MARTYNOVA, 1948a; RIEK, 1953, 1955).

Although nine existing families of Mecoptera are usually recognized, three of these (Notiothaumidae, Meropeidae, and Apteropanorpidae) include only one or two species; another family, the Boreidae, are flightless species and live in the cooler parts of the Holarctic region. The Panorpidae and Bittacidae are the largest existing families. The family classification is based mainly on the nature of the rostrum, the terminal abdominal structures of the male, and the wing venation.

The geological record of the Mecoptera is a long one, extending into the Lower Permian. It is obvious from the geological record of the order that the existing Mecoptera are only a small remnant of a very diverse series of families that lived during the Permian and into the Jurassic.

The evolution of the Mecoptera has clearly centered on such body structures as the rostrum and the terminal abdominal structures of the male and also on the wing venation (PENNY, 1975). Unfortunately, little is known about the body structures in the Paleozoic and Mesozoic genera, except for a very few species. Since the rostrum is well developed in the existing Meropeidae and Notiothaumidae, which appear to be the most generalized of the recent species, the long rostrum is probably an archaic trait in the order; the shortened rostra of the Panorpididae and Choristidae are presumably specializations and independently evolved. The modification of the terminal abdominal segments in the male has apparently reached a peak in Panorpidae, in some genera of which the entire abdomen has become very attenuate (see Fig. 214,1, *Holcorpa*). In the males of some Permian Mecoptera there is slight enlarge-

ment of the terminal abdominal segments but no evidence of the discrete genital bulb of the Panorpidae.

Evolution of the wing venation in the Mecoptera has involved extensive convergence. In general there seems to have been a definite trend toward reduction in the number of branches of main veins, especially the radius and media. However, it is clear that this reduction has occurred independently in a number of lines of evolution within families and genera. It is not realistic, therefore, to set family limits by definite and restricted patterns of venation without considering all other available characteristics.

Of special interest is the structure of CUA in the fore wing. As noted above, in some families (e.g., Permochoristidae) this vein is entirely independent of M except for a connecting crossvein (formerly termed M5). This is presumably the original or primitive condition. In other families (e.g., Nannochoristidae), CUA diverges anteriorly shortly after its origin and then coalesces for a short distance with M before branching off again as a separate vein. The free basal piece of CUA, before the coalescence, appears in a variety of forms and seems to be a useful taxonomic character at the generic level. However, the coalescence with M seems to have taken place independently in several families and genera of Mecoptera, and it does not by itself indicate close phylogenetic relationship. In a few families (e.g., Agetopanorpidae), the coalescence of CUA with M seems to have taken place near the wing base, there being no free piece of CUA remaining.

The family classification of the Mecoptera has been complicated by the existence of Permian and Mesozoic species that are mecopteroid but not apparently closely related to the existing families. At various times three separate orders were established for these families. The order Protomecoptera was erected by TILLYARD (1917a) for a fragmentary Triassic fossil (*Archipanorpa*); subsequently (1935d), TILLYARD considered the Protomecoptera to be a suborder of the

Mecoptera, assigning to it the recent families Meropeidae and Notiothaumidae. The genus is now considered to be of uncertain ordinal position (WILLMANN, 1978). The remaining families of Mecoptera were placed in the suborder Eumecoptera. A second order, the Paramecoptera, was erected by TILLYARD (1919b) for *Belmontia*, which had a forked CUA in the fore wing; this group has subsequently been treated as a suborder of Mecoptera. The third order, Paratrichoptera, was erected by TILLYARD (1919a) for several Triassic genera; this has also been regarded as a suborder. As more Permian, Triassic, and Jurassic Mecoptera have been found, it has become increasingly difficult to distinguish among these suborders. For example, the well-branched SC and the forked CUA, supposedly characteristic of the Protomecoptera, have turned up in species that, in other respects, belong to the Eumecoptera. The evidence now suggests that these supposed suborders do not represent divergent evolutionary lines within the Mecoptera. There has apparently been so much convergent evolution of the wing venation of the Mecoptera that subordinal divisions on this basis are not meaningful. The separation of the order into the suborders Protomecoptera and Eumecoptera works out satisfactorily for the existing families but not for the entire geological record of the order as it now stands. Obviously, greater knowledge of body structures of the extinct species is necessary before the main phylogenetic lines can be derived.

Family KALTANIDAE Martynova, 1958

[Kaltanidae MARTYNOVA, 1958, p. 79]

Fore wing with costal area of moderate width and with few to many veinlets; pterostigma absent; basal piece of vein CUA transverse or oblique; anal veins reaching wing margin independently, not looped. Hind wing unknown. *Perm.*

Altajopanorpa MARTYNOVA, 1948b, p. 113 [**A. kaltanica*; OD] [= *Kaltana* MARTYNOVA, 1958, p. 80 (type, *K. pilosa*)]. M with 6 branches; RS

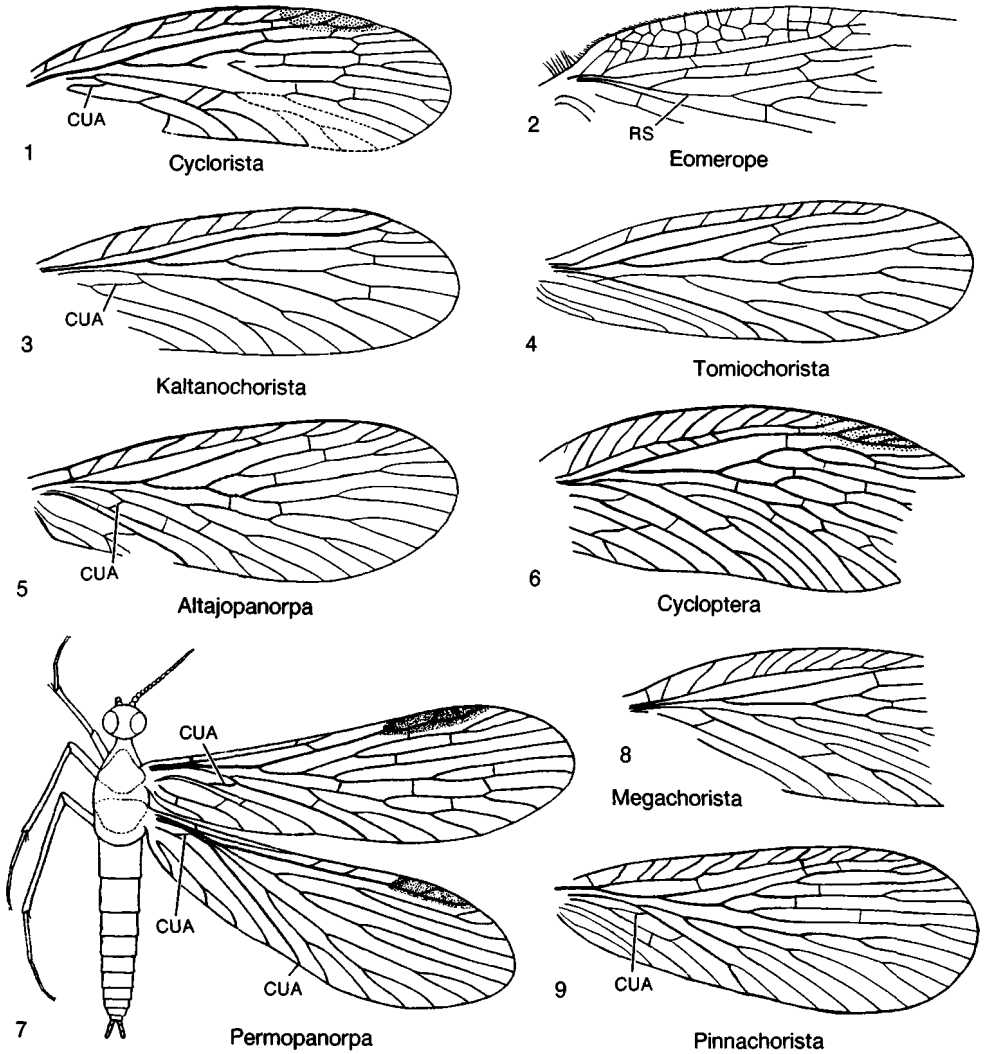


FIG. 210. Kaltanidae, Cycloristidae, Cyclopteridae, Tomiochoristidae, Permopanorpidae, and Eomeropidae (p. 382–384).

and proximal portions of its main branches with tubercles. MARTYNOVA, 1961d, 1962e. *Perm.*, USSR (Asian RSFSR).—FIG. 210,5. *A. pilosa* (MARTYNOVA); fore wing, $\times 8$ (Martyanova, 1961d).

Megachorista MARTYNOVA, 1958, p. 81 [**M. khal-fini*; OD]. M with 6 branches; longitudinal veins without tubercles. MARTYNOVA, 1961d, 1962e. *Perm.*, USSR (Asian RSFSR).—FIG. 210,8. **M. khal-fini*; fore wing, $\times 4$ (Martyanova, 1961d). **Pinnachorista** MARTYNOVA, 1958, p. 80 [**P. sar-balensis*; OD]. M with more than 6 branches. MARTYNOVA, 1961d. *Perm.*, USSR (Asian

RSFSR).—FIG. 210,9. **P. sarbalensis*; fore wing, $\times 9$ (Martyanova, 1961d).

Family CYCLORISTIDAE
Martyanova, 1958

[Cycloristidae MARTYNOVA, 1958, p. 84]

Fore wing with costal margin strongly convex; pterostigma present; costal area only slightly broader than subcostal; some main veins with tubercles; anal veins not looped distally. Hind wing unknown. *Perm.*

Cyclorista MARTYNOVA, 1958, p. 84 [**C. convexicosta*; OD]. M with 6 branches; basal piece of CUA short but sigmoidal and longitudinal. *Perm.*, USSR (Asian RSFSR). — FIG. 210,1. **C. convexicosta*; fore wing, $\times 8$ (Martynova, 1958).

Family CYCLOPTERIDAE
Martynova, 1958

[Cyclopteridae MARTYNOVA, 1958, p. 84]

Fore wing shaped as in Cycloristidae; costal area much wider than subcostal; pterostigma present; anterior branches of vein RS curved anteriorly near wing margin; anal veins not looped distally. Hind wing unknown. *Perm.*

Cycloptera MARTYNOVA, 1958, p. 85 [**C. autumnale*; OD]. M with 8 branches; basal piece of CUA transverse. *Perm.*, USSR (Asian RSFSR). — FIG. 210,6. **C. autumnale*; fore wing, $\times 10$ (Martynova, 1958).

Family TOMIOCHORISTIDAE
Martynova, 1958

[Tomiochoristidae MARTYNOVA, 1958, p. 85]

Fore wing with costal margin only slightly curved; pterostigma absent; numerous costal veinlets; tubercles on some longitudinal veins; vein CUA with a shallow fork; anal veins not looped. Hind wing unknown. *Perm.*

Tomiochorista MARTYNOVA, 1958, p. 85 [**T. nubila*; OD]. Costal area about as wide as subcostal; basal piece of CUA short and straight; M with 4 to 7 branches. MARTYNOVA, 1961d. *Perm.*, USSR (Asian RSFSR). — FIG. 210,4. *T. minuta* MARTYNOVA; fore wing, $\times 12$ (Martynova, 1961d).

Kaltanochorista MARTYNOVA, 1958, p. 86 [**K. grjasevi*; OD]. Fore wing with costal area about twice as wide as subcostal; basal piece of CUA long and sigmoidal; M with 4 branches. MARTYNOVA, 1961d. *Perm.*, USSR (Asian RSFSR). — FIG. 210,3. **K. grjasevi*; fore wing, $\times 6.5$ (Martynova, 1961d).

Family PERMOPANORPIDAE
Tillyard, 1926

[Permopanorpidae TILLYARD, 1926c, p. 139]

Small insects, with wings commonly slender. Fore wing with costal space traversed by 1 to a few veinlets; vein SC extending to about midwing; pterostigma well developed; RS with 4 to 9 terminal branches; basal piece

of CUA joined to M by a prominent crossvein; CUA unbranched. Hind wing slightly smaller than fore wing; SC short; CUA fused basally with M. Head with a very short rostrum; tarsi with 5 segments; female with vestigial cerci; male with terminal abdominal structures resembling those of the Bittacidae (recent). *Perm.*

Permopanorpa TILLYARD, 1926c, p. 143 [**P. formosa*; OD]. Fore wing with costal area narrow or moderately broad, with few veinlets; M with 6 branches; basal piece of CUA sigmoidal. Hind wing with SC much shorter than in fore wing. WILLMANN, 1978. *Perm.*, USA (Kansas), USSR (European RSFSR). — FIG. 210,7. *P. inaequalis* TILLYARD, Kansas; whole insect, $\times 10$ (Carpenter, 1930b).

Family EOMEROPIDAE
Cockerell, 1909

[*nom. transl.* PONOMARENKO & RASNITSYN, 1974, p. 68, ex Eomeropinae COCKERELL, 1909h, p. 384]

Wing venation reticulate. Fore wing with costal area very broad, traversed by numerous veinlets and crossveins; stems of veins R and M coalesced basally but each distinct; RS with 12 to 18 terminal branches; M with 10 to 12 terminal branches; CUA forked distally. Hind wing slightly smaller than fore wing and costal area narrower, with fewer veinlets; RS and M with 10 to 14 terminal branches. Male with terminal abdominal segments forming a small but distinct bulb. PONOMARENKO & RASNITSYN, 1974; WILLMANN, 1978. *Paleoc.*—*Holo.*

Eomerope COCKERELL, 1909h, p. 381 [**E. tortriciformis*; OD]. Fore wing as in *Notiothauma* (recent), but costal area narrower and with fewer cellules. PONOMARENKO & RASNITSYN, 1974. *Paleoc.*, USSR (Asian RSFSR); *Oligo.*, USSR (Asian RSFSR), USA (Colorado)—*Holo.* — FIG. 210,2. **E. tortriciformis*; basal part of fore wing, $\times 5.6$ (Cockerell, 1909h).

Family PERMOCHORISTIDAE
Tillyard, 1918

[Permochoristidae TILLYARD, 1918b, p. 732] [=Mesochoristidae TILLYARD, 1926e, p. 267; Idelopanorpidae ZALESSKY, 1932b, p. 192; Xenochoristidae RIEK, 1953, p. 69]

Fore wing with vein SC long, extending at least to midwing, usually prominently forked or branched; pterostigma distinct; R

commonly unbranched, rarely with a terminal twig; RS with 4 to 10 terminal branches; M usually with 5 or 6 terminal branches; CUA connected to M by crossvein, not coalesced with it. Hind wing similar to fore wing, but SC slightly shorter; R with distal twigs; RS arising near base. *Perm.-Jur.*

Mesochorista TILLYARD in TILLYARD & DUNSTAN, 1916, p. 29 [**M. proavita*; OD] [= *Permochorista* TILLYARD, 1918b, p. 732 (type, *P. australica*); *Caenoptilon* ZALESSKY, 1933, p. 141 (type, *C. minutum*)]. Fore wing with costal space no wider than subcostal; SC long, extending to pterostigma; branching of RS and M diverse but stem RS3+4 shorter than stem of RS. *Perm.*, USSR (Asian and European RSFSR), Australia (New South Wales); *Trias.*, Australia (Queensland).—FIG. 211,1a. *M. fedotovi* MARTYNOVA, *Perm.*, USSR; fore wing, $\times 8$ (Martynova, 1961d). — FIG. 211,1b. *M. australica* (TILLYARD), *Perm.*, New South Wales; fore wing, $\times 5$ (Tillyard, 1918b).

Agetochorista MARTYNOV, 1933a, p. 24 [**A. ornata*; OD] [= *Neoageta* RIEK, 1953, p. 67 (type, *N. elongata*); *Agetochoristella* RIEK, 1953, p. 68 (type, *A. adscita*)]. Fore wing with costal area at its maximum much wider than subcostal; veinlets from SC long and usually curved; RS with 5 branches; basal piece of CUA short but distinct. MARTYNOVA, 1948a, 1962e. *Perm.*, USSR (Asian and European RSFSR), Australia (New South Wales). — FIG. 211,2. **A. ornata*, USSR; a, fore and b, hind wings, $\times 5$ (Martynov, 1933a).

Asiachorista MARTYNOVA, 1958, p. 87 [**A. neuburgae*; OD]. RS with 4 branches; stem RS1+2 and stem RS3+4 of same length. PINTO, 1972a. *Perm.*, USSR (Asian RSFSR), Brazil. — FIG. 211,3. **A. neuburgae*; fore wing, $\times 6$ (Martynova, 1958).

Calliethira MARTYNOVA, 1958, p. 90 [**C. khalfini*; OD]. Fore wing as in *Asiachorista*, but apex more pointed and asymmetrical. *Perm.*, USSR (Asian RSFSR). — FIG. 212,3. **C. khalfini*; fore wing, $\times 7$ (Martynova, 1958).

Liassochorista TILLYARD, 1933, p. 21 [**L. anglicana*; OD]. Fore wing as in *Mesochorista* but oval in shape; basal piece of RS straight. [Family assignment doubtful.] MARTYNOVA, 1961d; WILLMANN, 1978. *Trias.*, USSR (Kirghiz); *Jur.*, England. — FIG. 212,7. *L. asiatica* MARTYNOVA, *Trias.*; fore wing, $\times 8$ (Martynova, 1948a).

Parachorista TILLYARD, 1926e, p. 273 [**P. pincombeae*; OD] [= *Tillyardina* HANDLIRSCH, 1937, p. 110 (type, *Parachorista splendida* TILLYARD, 1926e); *Phipoides* RIEK, 1953, p. 66 (type, *P. elegans*)]. In fore wing, RS with RS1+2 directed anteriorly, with its branches arising pectinately,

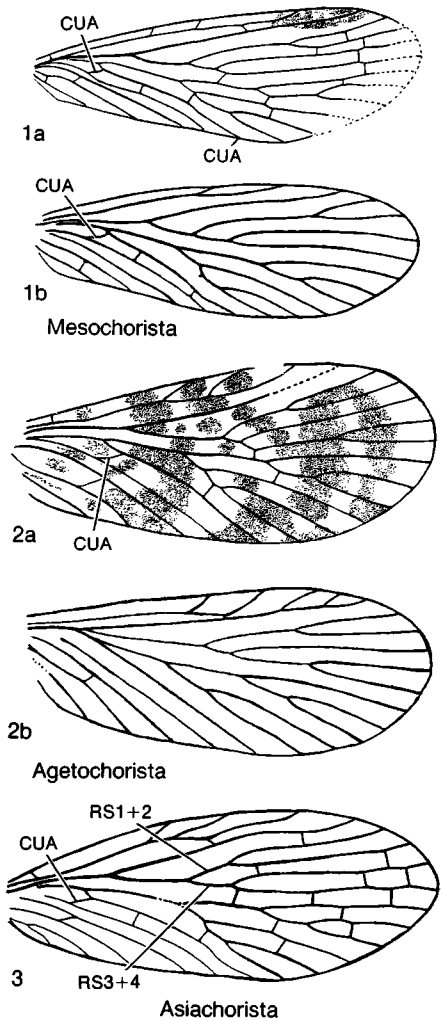


FIG. 211. Permochoristidae (p. 385).

or nearly so; RS and M with 6 branches; basal piece of CUA straight. MARTYNOVA, 1962e. *Perm.*, Australia (New South Wales). — FIG. 212,1. **P. pincombeae*; fore wing, $\times 4$ (Riek, 1953).

Petrochorista MARTYNOV, 1931c, p. 182 [**P. elegantula*; OD] [= *Neopetromantis* RIEK, 1953, p. 67 (type, *N. australis*)]. Fore wing with SC long, costal area narrow; stem R diverging from SC to a marked extent; RS with 4 branches; M with 6 branches; basal piece of CUA long and straight. MARTYNOVA, 1962e. *Perm.*, USSR (Asian and European RSFSR), Australia (New South Wales). — FIG. 212,2. **P. elegantula*; fore wing, $\times 8$ (Martynov, 1931c).

Petromantis HANDLIRSCH, 1904b, p. 5 [**P. rossica*; OD] [= *Idelopanorpa* ZALESSKY, 1929, p. 18 (type, *I. elegans*); *Martynowiella* HANDLIRSCH, 1937, p.

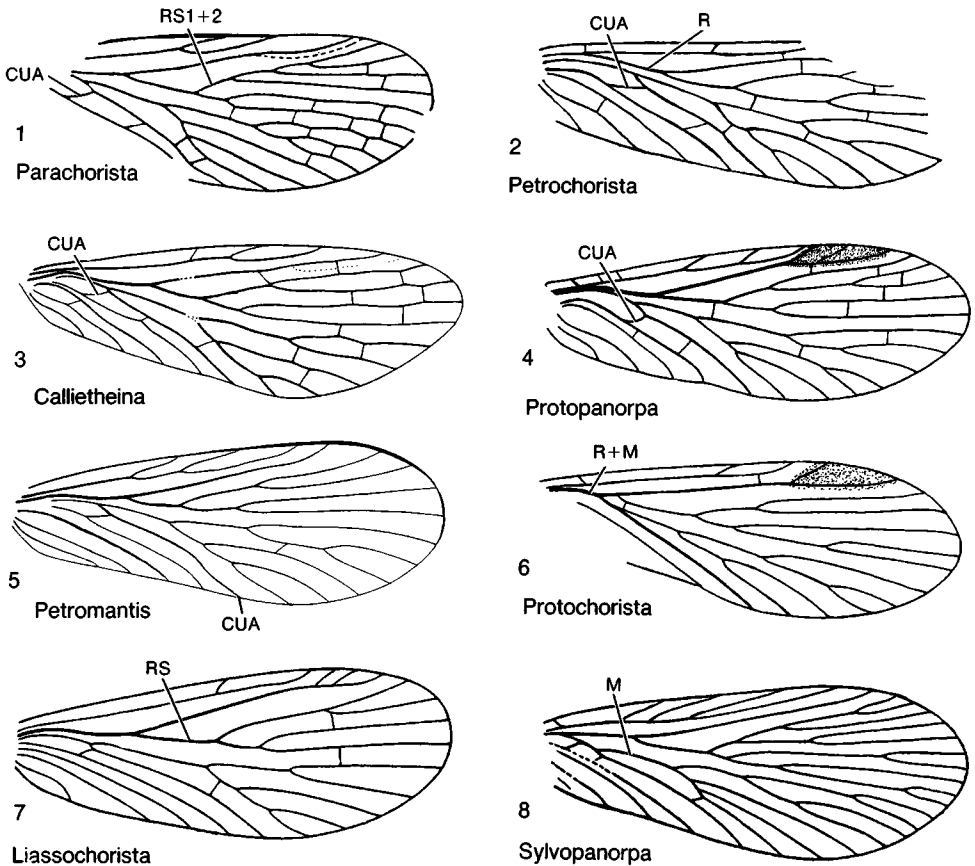


FIG. 212. Permochoristidae (p. 385–386).

109, *nom. nud.*]. Fore wing with branches of SC long, both arising before midwing; stem RS1+2 usually longer than stem RS3+4; CUA curved and irregular. MARTYNOVA, 1948a, 1961d, 1962e; PINTO, 1972a. *Perm.*, USSR (Asian and European RSFSR), Brazil. — FIG. 212, 5. *P. grandis* MARTYNOVA; fore wing, $\times 5.5$ (Martynova, 1961d).

Protochorista TILLYARD, 1926c, p. 140 [**P. tetraclada*; OD]. Hind wing oval; SC parallel to R; stem R+M very short, RS arising close to wing base; CUA coalesced with M for a short distance basally. *Perm.*, USA (Kansas). — FIG. 212, 6. **P. tetraclada*; hind wing, $\times 10$ (Carpenter, 1930b).

Protopanorpa TILLYARD, 1926c, p. 151 [**P. permiana*; OD]. Fore wing oval in shape, broad; venation very similar to that of *Petrochorista*; SC with 3 terminal branches; basal piece of CUA curved. *Perm.*, USA (Kansas). — FIG. 212, 4. **P. permiana*; fore wing, $\times 10$ (Carpenter, 1930b).

Stigmorista MARTYNOVA, 1958, p. 87 [**S. captiosa*;

OD]. Little-known fore(?) wing; M1 long and unbranched; pterostigma unusually large, almost touching RS1+2. *Perm.*, USSR (Asian RSFSR).

Sylvopanorpa MARTYNOV, 1940, p. 42 [**S. carpenteri*; OD]. Fore wing: SC with 3 long, oblique branches; RS with 10 branches; basal part of M strongly arched. [Probably representing a distinct family.] *Perm.*, USSR (Asian RSFSR). — FIG. 212, 8. **S. carpenteri*; fore wing, $\times 5.5$ (Martynov, 1940).

Xenochorista RIEK, 1953, p. 69 [**X. splendida*; OD]. Fore wing as in *Agetochochista*, but RS with only 4 branches (possibly an individual variation). [Type of family Xenochoristidae RIEK, 1953.] MARTYNOVA, 1962e. *Perm.*, Australia (New South Wales).

Family AGETOPANORPIDAE Carpenter, 1930

[Agetopanorpidae CARPENTER, 1930b, p. 97]

Fore wing somewhat broader than in Permochoristidae; vein SC remote from costal

margin, with long branches; RS with 5 to 6 branches; M with 6 branches; CUA coalesced with M from wing base to near level of origin of RS; no free basal piece of CUA present. Hind wing unknown. *Perm.*

Agetopanorpa CARPENTER, 1930b, p. 97 [**A. maculata*; OD]. Stems of RS1+2 and RS3+4 subequal. *Perm.*, USA (Kansas).—FIG. 213,4. **A. maculata*; fore wing, $\times 6$ (Carpenter, 1930b).
Oochorista MARTYNOV, 1933a, p. 32 [**O. gunderseni*; OD]. Stem of RS1+2 much longer than stem of RS3+4. *Perm.*, USSR (European RSFSR).—FIG. 213,6. **O. gunderseni*; fore wing, $\times 4.5$ (Martynov, 1933a).

Family LITHOPANORPIDAE Carpenter, 1930

[Lithopanorpidae CARPENTER, 1930b, p. 95]

Fore wing similar to that of Permopanorpidae, but free basal piece of vein CUA very long, sigmoidal, and coalesced with M near its origin. *Perm.*

Lithopanorpa CARPENTER, 1930b, p. 95 [**Protopanorpa pusilla* TILLYARD, 1926c, p. 153; OD]. SC not extending to pterostigma, with only 1 distal veinlet; costal area very narrow; RS with 4 branches. [The species described as *L. kuznetskiensis* from the Permian of USSR (Asian RSFSR) by MARTYNOVA (1961d) almost certainly does not belong to *Lithopanorpa*.] MARTYNOVA, 1962e. *Perm.*, USA (Kansas).—FIG. 213,3. **L. pusilla* (TILLYARD); fore wing, $\times 14$ (Carpenter, 1930b).

Family TYCHTOPSYCHIDAE Martynova, 1958

[Tychtopsyichidae MARTYNOVA, 1958, p. 91]

Fore wing broadly oval, about twice as long as wide; stem of vein R + M curved away from SC; RS and M each with 4 branches; CUA almost touching M, connected by a short crossvein. *Perm.*

Tychtopsyche MARTYNOVA, 1958, p. 91 [**T. beljanini*; OD]. Veins RS1+2 and RS3+4 forking at about same level. MARTYNOVA, 1962e. *Perm.*, USSR (Asian RSFSR).—FIG. 213,10. **T. beljanini*; fore wing, $\times 10$ (Martynova, 1958).

Family MESOPANORPODIDAE Tillyard, 1918

[Mesopanorpodidae TILLYARD, 1918c, p. 436]

Fore wing relatively broad; vein SC extending to pterostigmal area; M coalesced

with CUA basally and diverging anteriorly at its separation from CUA; RS and M with 4 branches. Hind wing little known. MARTYNOVA, 1962e; RIEK, 1953; WILLMANN, 1978. *Perm.*—*Trias.*

Mesopanorpodes TILLYARD, 1918c, p. 435, *nom. subst. pro Mesopanorpa* TILLYARD, 1918b, p. 747, *non* HANDLIRSCH, 1906b [**Mesopanorpa wianamattensis*; OD]. CUA of fore wing straight, continuing the line of CUA + M. *Perm.*—*Trias.*, Australia (New South Wales).—FIG. 213,2. *M. belmontensis* RIEK; fore wing, $\times 6.3$ (Riek, 1953).
Afristella RIEK, 1974c, p. 22 [**A. delicatula*; OD]. Little-known genus, based on incomplete wing. Similar to *Prochoristella*, but SC touching R distally and M and CUA in brief contact beyond wing base. WILLMANN, 1978. *Trias.*, South Africa.

Prochoristella RIEK, 1953, p. 72 [**P. megaloprepia*; OD]. Fore wing as in *Mesopanorpodes*, but SC remote from R distally; M and CUA separating very near wing base. MARTYNOVA, 1962e; WILLMANN, 1978. *Perm.*, Australia (New South Wales).

Family LAURENTIPTERIDAE Martynova & Willmann, 1978

[Laurentipteridae MARTYNOVA & WILLMANN in WILLMANN, 1978, p. 61, *nom. subst. pro Pseudodipteridae* MARTYNOVA in KOLOSITSYNA & MARTYNOVA, 1961, p. 163]

Fore wing triangular in form, much narrowed basally; vein SC extending much beyond midwing; costal area narrow; RS and M with 4 branches; CUA apparently coalesced with stem of M basally. Hind wing much shorter than fore wing. WILLMANN, 1978. *Trias.*—*Jur.*

Laurentiptera MARTYNOVA & WILLMANN in WILLMANN, 1978, p. 61, *nom. subst. pro Pseudodiptera* LAURENTIAUX & GRAUVOGEL in LAURENTIAUX, 1953, p. 488, *non* KAYE, 1918 [**Pseudodiptera gallica* LAURENTIAUX & GRAUVOGEL in LAURENTIAUX, 1953, p. 488; OD]. Fore wing with very narrow costal area; SC and R very close together; crossveins apparently absent from costal area; CUA not branched. Hind wing about half as long as fore wing. *Trias.*, Europe (France).—FIG. 213,11. **L. gallica*; fore wing and part of hind wing, $\times 10$ (Martynova, 1962e).

Ijapsyche KOLOSITSYNA & MARTYNOVA, 1961, p. 163 [**I. sibirica*; OD]. Fore wing similar to that of *Laurentiptera*, but costal area broader and including several crossveins. Hind wing unknown. WILLMANN, 1978. *Jur.*, USSR (Asian RSFSR).

Family PERMOCENTROPIDAE

Martynov, 1933

[Permocentropidae MARTYNOV, 1933a, p. 49]

Fore wing much as in Agetopanorpidae, but vein SC close to costal margin, with a short branch; costal margin slightly concave; RS with 4 branches; M with 6 branches; CUA coalesced with M from wing base, as in Agetopanorpidae. *Perm.*

Permocentropus MARTYNOV, 1933a, p. 49 [**P. philopotamoides*; OD]. Forks of RS1+2 and RS3+4 of subequal length; R with a short veinlet in pterostigmal area. *Perm.*, USSR (European RSFSR). — FIG. 213,9. **P. philopotamoides*; fore wing, $\times 8$ (Martynov, 1933a).

Family DINOPANORPIDAE

Carpenter, 1972

[Dinopanorpidae CARPENTER, 1972, p. 83]

Large Mecoptera, similar to Orthophlebiidae and Panorpidae. Hind wing with several strong crossveins between vein SC and costal margin; R extending almost to wing apex, curving posteriorly near its termination; RS with at least 8 terminal branches; CUA coalesced with M for short distance; CUP coalesced with 1A; crossveins more numerous than in Panorpidae or Orthophlebiidae. Fore wing and body unknown. *Mio.*

Dinopanorpa COCKERELL, 1924a, p. 2 [**D. megarche*; OD]. Hind wing with costal space relatively broad, with 5 to 6 strong veinlets from SC to margin. CARPENTER, 1972; WILLMANN, 1978. *Mio.*, USSR (Asian RSFSR). — FIG. 213,7. **D. megarche*; hind wing, $\times 2$ (Cockerell, 1924a).

Family ORTHOPHLEBIIDAE

Handlirsch, 1906

[*nom. correct.* HANDLIRSCH, 1920, p. 196, ex Orthophlebiidae HANDLIRSCH, 1906b, p. 479]

Fore wing slightly broader than in Panorpidae; vein SC with only 1 branch to costal margin; R not forked; RS with 5 to 9 branches; M with 5 branches (rarely more); CUA not fused with M basally, but connected to it by short crossvein. Hind wing similar to fore wing but slightly smaller and SC a little shorter; CUA coalesced with M

basally for short distance, free piece of CUA resembling crossvein. Rostrum little known, apparently a little shorter than in Panorpidae; tarsi with 5 segments; abdominal structure of male unknown. *Trias.*—*Jur.*

Orthophlebia WESTWOOD in BRODIE, 1845, p. 102 [**O. communis*; OD] [= *Orthophlebioides* HANDLIRSCH, 1906b, p. 481, *nom. nud.*; *Orthophlebiites* HANDLIRSCH, 1939, p. 83 (type, *O. radialis*); *Synorthophlebia* HANDLIRSCH, 1939, p. 84, *nom. nud.*]. Fore wing with RS1+2 and RS3+4 forking at about same level; RS1 forking at least 3 times. Hind wing with distal crossvein between M4 and CUA absent. TILLYARD, 1933; MARTYNOV, 1937a; MARTYNOVA, 1948a, 1962e; BODE, 1953; WILLMANN, 1978. *Trias.*, USSR (Kirghiz); *Jur.*, England, Europe (Germany), USSR (Kazakh). — FIG. 213,1. *O. liassica* (MANTELL), England; *a*, fore and *b*, hind wings, $\times 3.5$ (Tillyard, 1933).

Mesopanorpa HANDLIRSCH, 1906b, p. 615 [**Panorpa hartungi* BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 16; OD]. Fore wing as in *Protorthophlebia*, but stem RS1+2 twice as long as stem RS3+4. MARTYNOV, 1927a; MARTYNOVA, 1948a, 1962e; RIEK, 1950; WILLMANN, 1978. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Asian RSFSR, Kazakh, Kirghiz, Tadzhik), Europe (Germany), England. — FIG. 213,8. **M. hartungi* (BRAUER, REDTENBACHER, & GANGLBAUER), *Jur.*, USSR; fore wing, $\times 5$ (Martynov, 1927a).

Protorthophlebia TILLYARD, 1933, p. 28 [**P. latipennis*; OD] [= *Choristopanorpa* RIEK, 1950, p. 254 (type, *C. bifasciata*)]. Similar to *Orthophlebia*, but RS1 with only 2 branches. MARTYNOVA, 1948a, 1962e; BODE, 1953; WILLMANN, 1978. *Trias.*, USSR (Kirghiz), Australia (Queensland); *Jur.*, England. — FIG. 213,5. **P. latipennis*, England; fore wing, $\times 6$ (Tillyard, 1933).

Family NANNOCHORISTIDAE

Tillyard, 1917

[Nannochoristidae TILLYARD, 1917b, p. 289] [= Robinjohniidae MARTYNOVA, 1948a, p. 42]

Rostrum very slender. Fore wing venation as in Choristidae (recent), but vein RS with 3 branches; M usually with 4 branches; CUA coalesced with M for a considerable distance basally. Hind wing similar to fore wing, but SC shorter and CUA coalesced with M for a greater distance. *Perm.*—*Holo.*

Nannochorista TILLYARD, 1917b, p. 292. *Holo.*

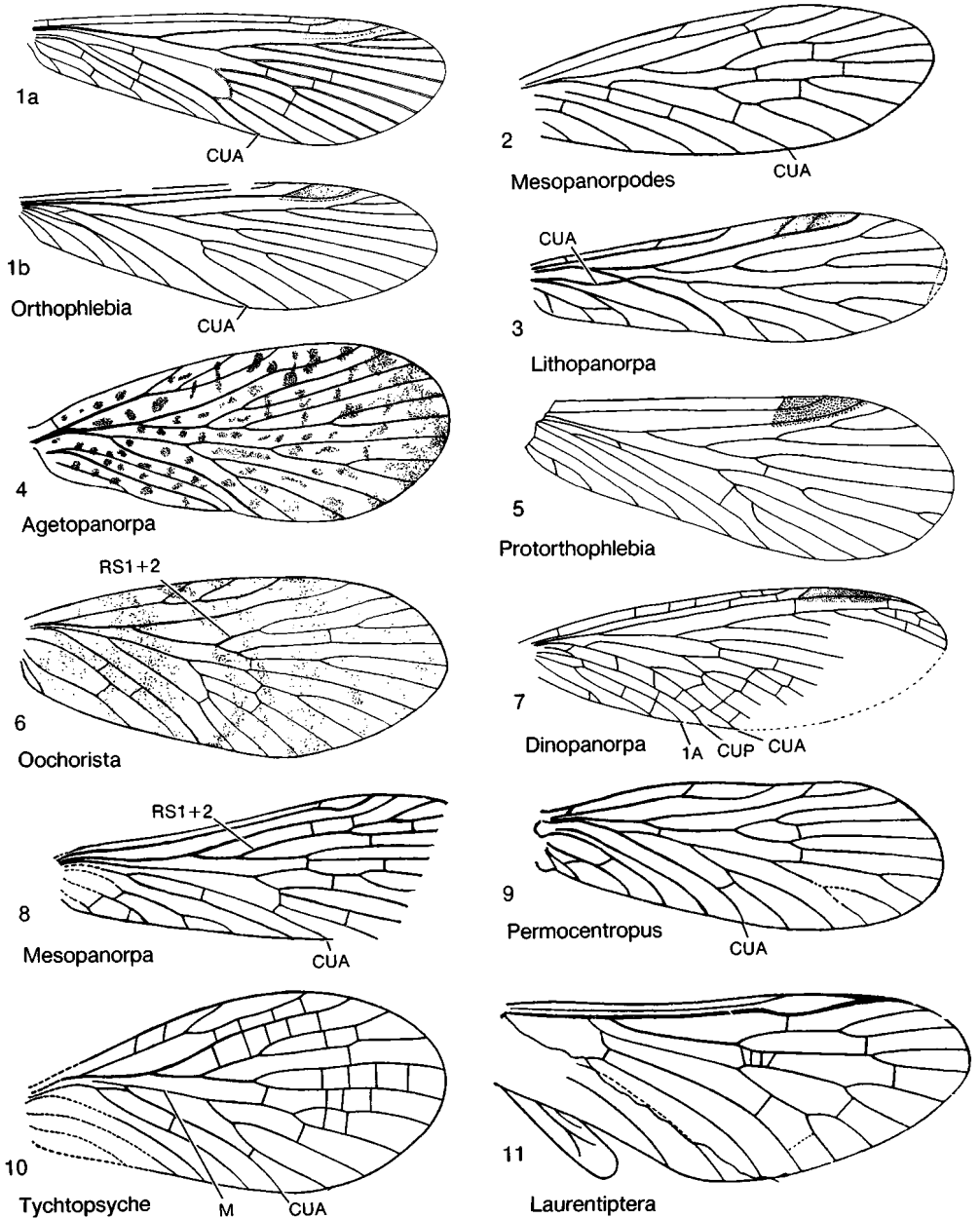


FIG. 213. Agetopanorpidae, Lithopanorpidae, Tychtopsychidae, Mesopanorpididae, Laurentipteridae, Permocentropidae, Dinopanorpidae, and Orthophlebiidae (p. 387–388).

Nannochoristella RIEK, 1953, p. 74 [**N. reducta*; OD]. Fore wing as in *Neochoristella*, but M with 3 branches. *Perm.*, Australia (New South Wales). — FIG. 214,8. **N. reducta*; fore wing, $\times 10$ (Riek, 1953).

Neochoristella RIEK, 1953, p. 74 [**N. optata*; OD].

Fore wing with SC long; R unbranched; M with 4 branches. *Perm.*, Australia (New South Wales). — FIG. 214,9. **N. optata*; fore wing, $\times 14$ (Riek, 1953).

Robinjohnia MARTYNOVA, 1948a, p. 42 [**R. tillyardi*; OD]. Fore wing as in *Nannochoristella*,

but SC very short, not reaching to midwing; M with 4 branches. Hind wing slightly smaller than fore wing. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).—FIG. 214.7. **R. tillyardi*; *a*, fore and *b*, hind wings, $\times 11$ (Riek, 1968a).

Family PANORPIDAE Latreille, 1804–1805

[*nom. correct.* LEACH, 1815, p. 137, *pro* Panorpidae LATREILLE, 1804–1805, p. 19]

Rostrum well developed. Fore wing slender; vein SC long, extending to pterostigmal region; RS usually with 5 branches; M usually with 4 branches, rarely 5; CUA not coalesced with M, but joined to it by a short crossvein. Hind wing: SC extending to about midwing; CUA coalesced with M basally. *Paleoc.*—*Holo.*

Panorpa LINNÉ, 1758, p. 551. COCKERELL, 1908p; STATZ, 1936a; CARPENTER, 1954. WILLMANN, 1976. *Oligo.*, Europe (Baltic, Germany), England, USA (Colorado)—*Holo.*

Holcorpa SCUDDER, 1878a, p. 540 [**H. maculosa*; OD]. Related to *Neopanorpa* (recent); sixth to eighth abdominal segments very elongate; genital bulb of male large, with long forceps. Fore wing: RS with 5 to 6 branches; M with 5 branches. *Oligo.*, USA (Colorado).—FIG. 214.1. **H. maculosa*; whole insect, $\times 1.6$ (Carpenter, 1931c).

Family PANORPODIDAE Handlirsch, 1920

[*nom. transl.* BYERS, 1965, p. 123, *ex* Panorpodinae HANDLIRSCH, 1920, p. 842]

Wing venation as in Panorpidae, but rostrum much shorter. *Oligo.*—*Holo.*

Panorpodes MACLACHLAN, 1875, p. 188 [= *Electropanorpa* CARPENTER, 1931c, p. 409 (type, *Panorpa brevicauda* HAGEN in PICTET & HAGEN, 1856)]. CARPENTER, 1954. *Oligo.*, Europe (Baltic)—*Holo.*

Family NEORTHOPHLEBIIDAE Handlirsch, 1939

[Neorthophlebiidae HANDLIRSCH, 1939, p. 86]

Fore wing more slender than in Orthophlebiidae; vein SC ending near midwing, without branches to front margin; pterostigma usually weak; RS1 forked at about level of pterostigma; RS and M usually with 4 branches; terminal branches of RS and M

straight; CUA coalesced with M basally. *Trias.*—*Jur.*

Neorthophlebia HANDLIRSCH, 1906b, p. 479 [**N. maculipennis*; OD] [= *Mesobittacus* HANDLIRSCH, 1939, p. 88 (type, *M. minutus*); *Pleobittacus* BODE, 1953, p. 289 (type, *P. retroflexus*)]. SC not quite reaching midwing; M and CUA coalesced basally, diverging close to wing base; pterostigma small. MARTYNOVA, 1948a; WILLMANN, 1978. *Jur.*, Europe (Germany), USSR (Asian RSFSR, Kirghiz).—FIG. 214.5. **N. maculipennis*, Germany; fore wing, $\times 5$ (Handlirsch, 1906b).

Auxobittacus BODE, 1953, p. 285 [**A. praeacutus*; OD]. Fore wing as in *Protobittacus*, but forks of RS1+2 and M4 very shallow. [Probably a synonym of *Protobittacus*.] *Jur.*, Europe (Germany).

Bittacopanorpa ZALESSKY, 1935, p. 688 [**B. javorskii*; OD]. Little-known wing, with SC not reaching midwing. [Probably a synonym of *Neorthophlebia*.] *Trias.*, USSR (Asian RSFSR).

Haplobittacus BODE, 1953, p. 291 [**H. parvus*; OD]. Little-known fore wing, similar to that of *Neorthophlebia* but M1+2 apparently unbranched. *Jur.*, Europe (Germany).

Protobittacus TILLYARD, 1933, p. 48 [**P. liassicus*; OD] [= *Metaxybittacus* BODE, 1953, p. 287 (type, *M. vittatus*); *Polydicrobittacus* BODE, 1953, p. 290 (type, *P. lingula*); *Archebittacus* RIEK, 1955, p. 666 (type, *A. exilis*)]. Fore wing as in *Neorthophlebia*, but SC extending slightly beyond midwing; pterostigma large. MARTYNOVA, 1949c, 1962e; RIEK, 1953. *Trias.*, Australia (Queensland); *Jur.*, England, Europe (Germany), ?China (Xinjiang).—FIG. 214.3. **P. liassicus*, England; fore wing, $\times 3.5$ (Tillyard, 1933).

Family BITTACIDAE Handlirsch, 1906

[*nom. correct.* ENDERLEIN, 1910a, p. 387, *pro* Bittacidae HANDLIRSCH, 1906b, p. 43]

Wings usually very narrow basally, broadened distally; pterostigma commonly well developed. Fore wing with vein SC extending beyond midwing; RS and M usually with 4 somewhat zigzagged branches; CUA coalesced with M basally, at least for a short distance. *Jur.*—*Holo.*

Bittacus LATREILLE, 1805, p. 19 [= *Electrobittacus* CARPENTER, 1931c, p. 410 (type, *B. antiquus* PICTET, 1854)]. CARPENTER, 1954, 1955; JARZEMBOWSKI, 1980. *Eoc.*, USA (Utah); *Oligo.*, England, Europe (Baltic)—*Holo.*

Palaeobittacus CARPENTER, 1928, p. 242 [**P. eocenicus*; OD]. Fore wing as in *Bittacus* but with more diffuse pterostigma and crossvein between stem of RS and stem of M. MARTYNOVA,

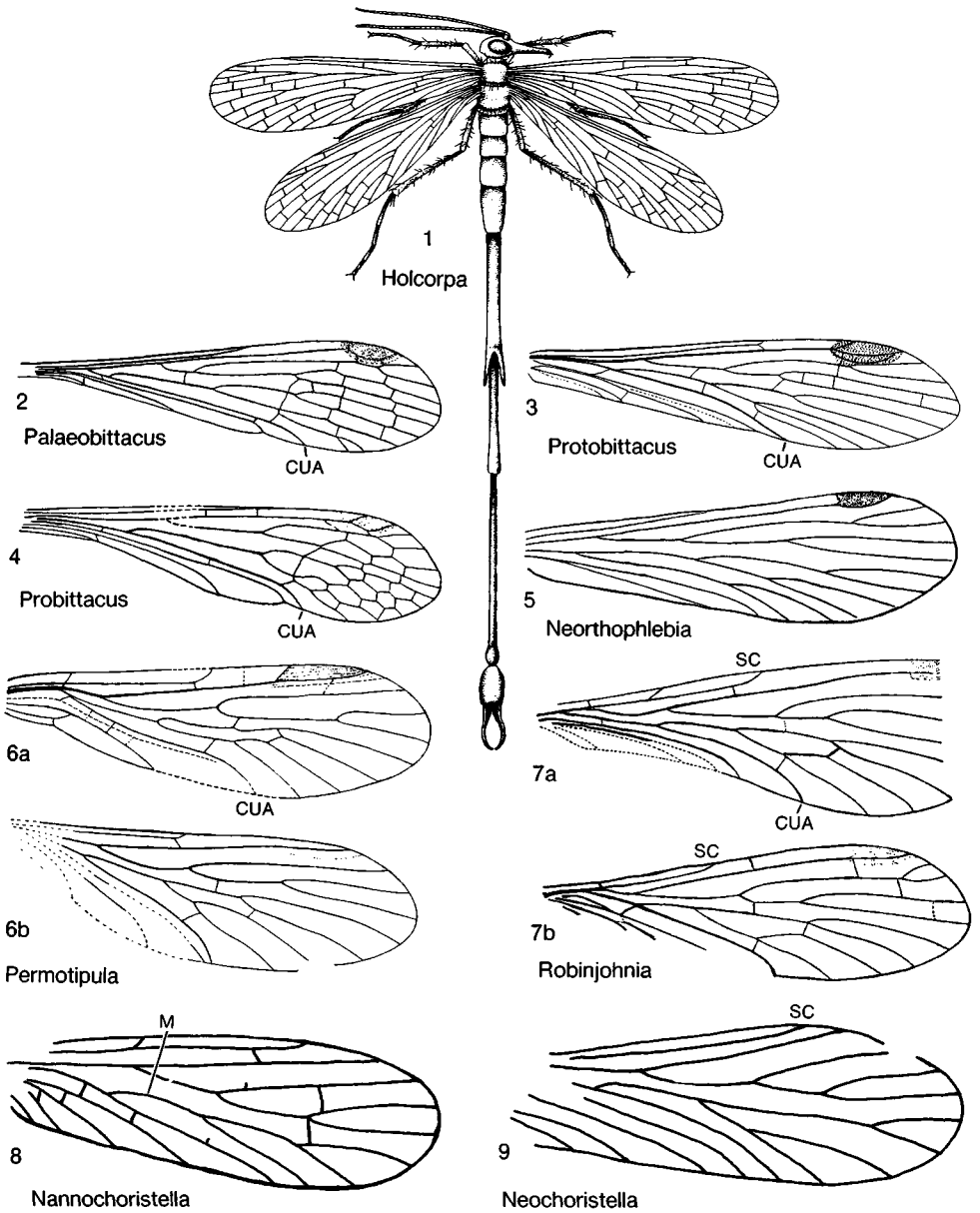


FIG. 214. Nannochoristidae, Panorpidae, Neorthopplebiidae, Bittacidae, and Permotipulidae (p. 389–392).

1949c. *Eoc.*, USA (Colorado). — FIG. 214, 2. **P. eocenicus*; fore wing, $\times 4.5$ (Carpenter, 1928). *Probittacus* MARTYNOV, 1927a, p. 658 [**P. avitatus*; OD]. Fore wing with branches of M strongly zigzagged; marked incision of wing margin at end of CUP. CARPENTER, 1931c; ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh). — FIG. 214, 4. **P. avitus*; fore wing, $\times 3.5$ (Martynov, 1927a).

Family CHORISTIDAE
Esben-Petersen, 1915

[*nom. transl.* TILLYARD, 1926d, p. 300, *ex* Choristinae
 ESSEN-PETERSEN, 1915, p. 232]

Fore wing as in Panorpidae, but costal margin convex basally; vein CUA coalesced

for short distance with M; RS with 4 branches; M usually with 5 branches. *Paleoc.*—*Holo.*

Chorista KLUG, 1836, p. 87. RIEK, 1952a. *Paleoc.*, Australia (Queensland)—*Holo.*

Family PERMOTIPULIDAE

Tillyard, 1929

[Permotipulidae TILLYARD, 1929, p. 779]

Fore wing subpetiolate; vein RS with 3 branches; M with 4 branches; CUA unbranched, touching M shortly after its origin; CUP obsolescent. Hind wing unknown. [Ordinal position uncertain.] *Perm.*,

Permotipula TILLYARD, 1929, p. 779 [**P. patricia*; OD]. M forking before RS. *Perm.*, Australia (New South Wales), USSR (Asian RSFSR).—FIG. 214,6a. **P. patricia*, Australia; fore wing, $\times 11$ (Tillyard, 1935d).—FIG. 214,6b. *P. borealis* MARTYNOVA, USSR; fore wing, $\times 12.5$ (Tillyard, 1929).

Family PSEUDOPOLYCENTROPIDAE

Handlirsch, 1920

[Pseudopolycentropidae HANDLIRSCH, 1920, p. 198]

Fore wing broad distally, nearly triangular in shape; hind wing only about half size of fore wing; costal margins of both wings nearly straight. Fore wing with pterostigma present but weak; vein SC very short; RS with 4 branches; M coalesced with CUA for very short distance basally; M with 4 branches; CUA and CUP unbranched. *Jur.*

Pseudopolycentropus HANDLIRSCH, 1906b, p. 482 [**Phryganidium perlaeforme* GEINITZ, 1884, p. 575; OD]. R very straight; fork of RS1 + 2 much shorter than that of RS3 + 4. MARTYNOV, 1927a; HANDLIRSCH, 1939. *Jur.*, Europe (Germany); USSR (Kazakh).—FIG. 215,2. *P. latipennis* MARTYNOV, USSR; *a*, fore and *b*, hind wings, $\times 7$ (Martynov, 1927a).

Family CHORISTOPSYCHIDAE

Martynov, 1937

[Choristopsychidae MARTYNOV, 1937a, p. 26]

Fore wing broadly oval; vein SC long, with 2 long anterior branches; RS with 4 branches; M with 5 branches; CUA coalesced with M basally, strongly bent at about its midpoint. *Perm.*

Choristopsyche MARTYNOV, 1937a, p. 26 [**C. tenuinervis*; OD]. Origin of RS at about same level

as separation of M from CUA; several crossveins between CUP and CUA and between CUP and 1A. MARTYNOVA, 1962e. *Perm.*, USSR (Tadzhik).—FIG. 215,7. **C. tenuinervis*; fore wing, $\times 6$ (Martynov, 1937a).

Family MESOPSYCHIDAE

Tillyard, 1917

[Mesopsychidae TILLYARD, 1917a, p. 180] [=Aristopsychidae JEANNEL, 1949, p. 73]

Fore wing slender and oval; vein SC extending beyond midwing; pterostigma apparently absent or very weak; R straight at origin of RS; RS and M with 4 branches; CUA unbranched, anastomosed with M basally. RIEK, 1956; MARTYNOVA, 1962e; WILLMANN, 1978. *Trias.*

Mesopsyche TILLYARD, 1917a, p. 181 [**M. triareolata*; OD] [=Triassopsycha TILLYARD, 1917a, p. 182 (type, *T. dunstani*); Aristopsycha TILLYARD, 1919a, p. 200 (type, *A. superba* TILLYARD); Neuropsycha TILLYARD, 1919a, p. 203 (type, *N. elongata* TILLYARD)]. Fore wing usually with several costal veinlets; RS and M forking at about same level; several crossveins commonly present between branches of RS. RIEK, 1956; WILLMANN, 1978. *Trias.*, Australia (Queensland).—FIG. 215,6. *M. superba*; fore wing, $\times 2.3$ (Tillyard, 1919a).

Family UNCERTAIN

The following genera, apparently belonging to the order Mecoptera, are too poorly known to permit assignment to families.

Anormochorista TILLYARD, 1926c, p. 155 [**A. oligoclada*; OD]. Little-known genus, based on incomplete fore wing; RS with 4 branches; pterostigma present; M with at least 3 branches; basal parts of M and CUA unknown. [Type of family Anormochoristidae TILLYARD, 1926c.] CARPENTER, 1930b; WILLMANN, 1978. *Perm.*, USA (Kansas).

Austropanorpa RIEK, 1952a, p. 11 [**A. australis*; OD]. Little-known fore wing, similar to that of *Panorpa*, but RS apparently having 8 or 9 terminal branches arising pectinately. [Placed in new family Austropanorpidae by WILLMANN (1977a, p. 12).] *Paleoc.*—*Plio.*, Australia (Queensland).

Belmontia TILLYARD, 1919b, p. 234 [**B. mitchelli*; OD] [=Parabelmontia TILLYARD, 1922a (type, *P. permiana*)]. Fore wing with long SC; RS with 6 branches; M with 4 branches; CUA with prominent basal piece and shallow fork. [Type of family Belmontiidae TILLYARD, 1922a (=Parabelmontiidae TILLYARD, 1922a)]. RIEK,

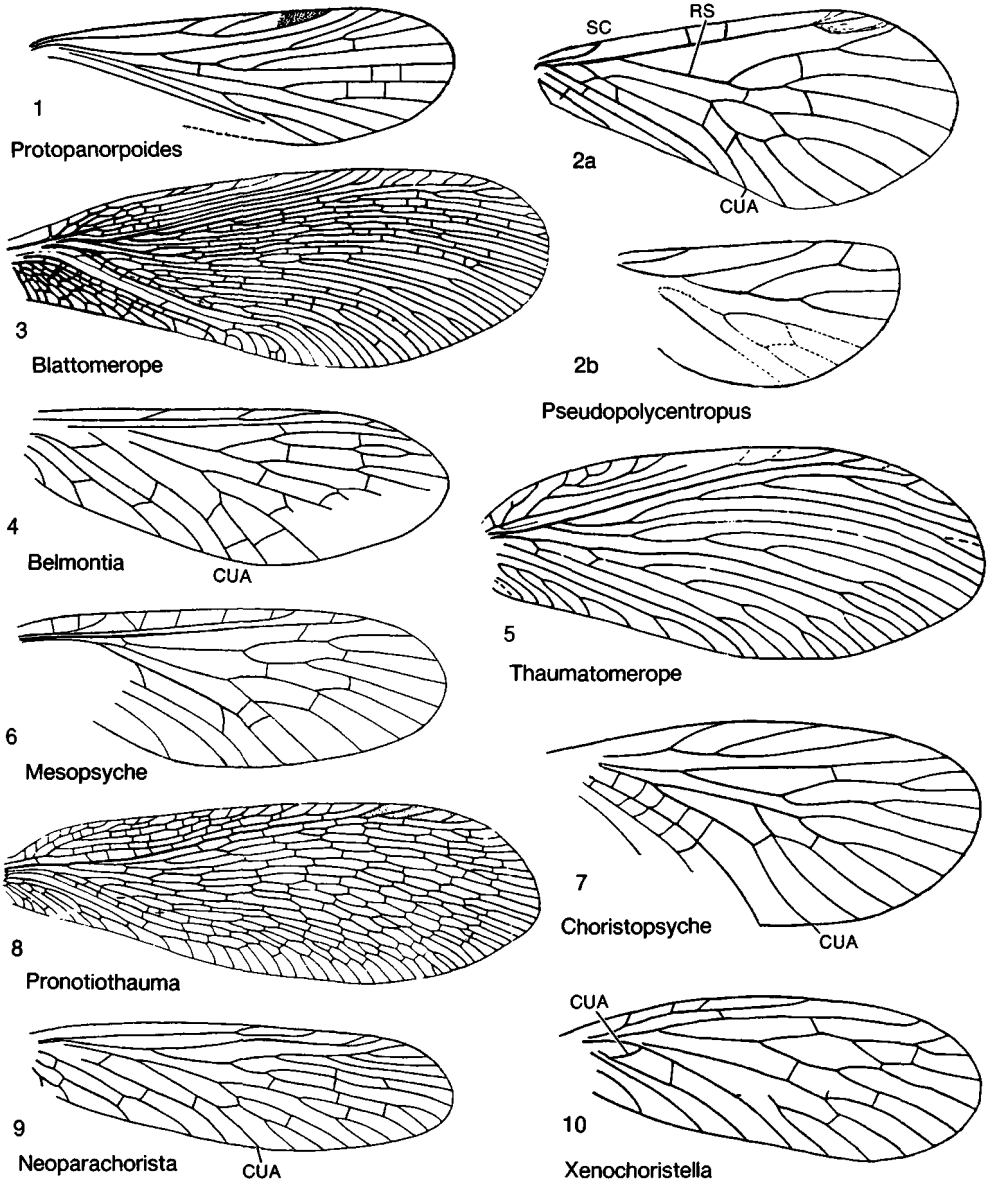


FIG. 215. Pseudopolycentropidae, Choristopsychidae, Mesopsychidae, and Uncertain (p. 392–395).

1953; WILLMANN, 1978. *Perm.*, Australia (New South Wales). — FIG. 215.4. *B. permiana* (TILLYARD); fore(?) wing, $\times 3.3$ (Riek, 1953).

Blattomerope RASNITSYN in PONOMARENKO & RASNITSYN, 1974, p. 67 [*B. polyneura*; OD]. Fore wing similar to that of *Pronotiothauma*, but costal margin nearly straight basally, SC terminating more distally, and branches of M and CUA more regular and nearly parallel. [Placed in family Meropeidae (recent) by PONOMARENKO and RASNITSYN (1974) and in the family Eome-

ropidae (recent) by WILLMANN (1978).] *Trias.*, USSR (Kirghiz). — FIG. 215.3. **B. polyneura*; fore wing, $\times 5.5$ (Ponomarenko & Rasnitsyn, 1974).

Choristotanyderus RIEK, 1953, p. 76 [**C. nanus*; OD]. Hind(?) wing with SC short, close to costal margin; rest of venation much as in *Permotanyderus*. [Possibly based on hind wing of *Permotanyderus*.] WILLMANN, 1978. *Perm.*, Australia (New South Wales).

Cimbrophlebia WILLMANN, 1977b, p. 736 [**C. bit-*

- taciformis*; OD]. Little-known genus, apparently related to Bittacidae. Wings long and slender, but RS with 4 or 5 branches and 2A with several branches. [Placed in new family Cimbrophlebiidae.] *Eoc.*, Europe (Denmark).
- Dobbertinia** HANDLIRSCH, 1920, p. 198 [**D. reticulata*; OD]. Little-known fore wing with long SC; RS and M with 4 branches; CUA with 3 branches. WILLMANN, 1978. [Ordinal position uncertain; type of family Dobbertinidae HANDLIRSCH, 1939.] *Jur.*, Europe (Germany).
- Ferghanopsyche** MARTYNOV, 1937a, p. 29 [**F. rotundata*; OD]. Little-known hind(?) wing with long SC; R forked distally; RS and M with 4 branches; CUA unbranched, apparently coalesced with M basally. MARTYNOVA, 1962e. *Trias.*, USSR (Tadzhik).
- Liassopanorpa** MARTYNOV, 1937a, p. 24 [**L. crassinervis*; OD]. Little-known wing (base only); CUA not touching M, its basal piece longitudinal. *Jur.*, USSR (Tadzhik).
- Limfjordia** WILLMANN, 1977b, p. 740 [**L. breineri*; OD]. Wings broad and relatively short. Fore wing with an unusual increase in branching; R1 terminating close to pterostigma. [Placed in new family, Limfjordidae WILLMANN, 1977b.] *Eoc.*, Europe (Denmark).
- Mesotanyderus** RIEK, 1955, p. 670 [**M. jonesi*; OD]. Fore wing with SC close to costal margin as in *Permotanyderus*, but CUA coalesced with M basally. WILLMANN, 1978. *Trias.*, Australia (Queensland).
- Neoparachorista** RIEK, 1955, p. 662 [**N. perkinsi*; OD]. Fore wing slender; R with 2 or 3 branches; CUA coalesced with M briefly basally; M with 6 terminal branches. Hind wing: M with 4 branches. [Type of family Neoparachoristidae WILLMANN, 1978, p. 53.] MARTYNOVA, 1962e. *Trias.*, Australia (Queensland).—FIG. 215,9. **N. perkinsi*; fore wing, $\times 2.5$ (Riek, 1955).
- Neopermotanorpa** RIEK, 1955, p. 658 [**N. mesembria*; OD]. Little-known genus, based on wing fragments; SC longer than in *Permotanorpa*. WILLMANN, 1978. *Trias.*, Australia (Queensland).
- Parabittacus** HANDLIRSCH, 1939, p. 91 [**P. analis*; OD]. Little-known wing (base only); wing apparently slender, narrow basally; CUA coalesced with M at base of wing. WILLMANN, 1978. *Jur.*, Europe (Germany).
- Parorthophlebia** BODE, 1953, p. 275 [**P. gras-selensis*; OD]. Little-known fore wing; SC long, with numerous costal veinlets; R forked; RS with 5 branches; M with 4 branches; CUA forked. WILLMANN, 1978. *Jur.*, Europe (Germany).
- Permotanyderus** RIEK, 1953, p. 75 [**P. ableptus*; OD]. Fore wing with SC long and very close to costal margin; pterostigma distinct; RS and M with 4 branches; CUA not coalesced with M. [Ordinal position uncertain; type of family Permotanyderidae RIEK.] WILLMANN, 1978. *Perm.*, Australia (New South Wales).
- Pronotiothauma** WILLMANN, 1978, p. 15 [**Thaumatomerope neuropteroides* RASNITSYN in PONOMARENKO & RASNITSYN, 1974, p. 65; OD]. Fore wing as in *Thaumatomerope*, but costal area broader basally, with more extensive series of reticulate veins. [Placed in the family Meropeidae (recent) by PONOMARENKO & RASNITSYN (1974) and in the family Eomeropidae (recent) by WILLMANN (1978).] *Trias.*, USSR (Kirghiz). —FIG. 215,8. **P. neuropteroides*; fore wing, $\times 5$ (Ponomarenko & Rasnitsyn, 1974).
- Protopanorpoidea** MARTYNOVA, 1962e, p. 287 [**Protopanorpa elongata* MARTYNOV; OD]. SC of fore wing long, with long branches; R and RS1 curved and remote from costa; RS with 5 branches; M with 6 branches; structure of CUA unknown. [Possibly belonging to Permochoristidae.] WILLMANN, 1978. *Perm.*, USSR (European RSFSR). —FIG. 215,1. **P. elongata* (MARTYNOV); fore wing, $\times 6$ (Martyanova, 1962e).
- Ptychopteropsis** MARTYNOV, 1937a, p. 35 [**P. mirabilis*; OD]. Hind(?) wing little known, oval; SC extending to midwing; R straight, not forked; RS with 3 branches; CUA at least touching M basally. MARTYNOVA, 1962e; WILLMANN, 1978. *Trias.*, USSR (Tadzhik).
- Sogdopsyche** MARTYNOV, 1937a, p. 32 [**S. elongata*; OD]. Fore wing little known, very slender; SC extending at least to midwing; R unbranched; RS and M with 4 branches; CUA apparently coalesced with M for a considerable distance. MARTYNOVA, 1962e; WILLMANN, 1978. *Trias.*, USSR (Tadzhik).
- Stenopanorpa** HANDLIRSCH, 1906b, p. 616 [**Panorpa gracilis* GIEBEL, 1856, p. 258; OD]. Little-known genus, based on incomplete wing. WILLMANN, 1978. *Jur.*, Europe (Germany).
- Thaumatomerope** RASNITSYN in PONOMARENKO & RASNITSYN, 1974, p. 61 [**T. sogdiana*; OD]. Fore wing broadly oval; SC with 2 to 3 branches; RS and M with a total of 18 to 33 terminal branches. Venational patterns of fore and hind wings similar, except for CUA. [Placed in family Meropeidae (recent) by PONOMARENKO and RASNITSYN (1974) and in Eomeropidae (recent) by WILLMANN (1978).] *Trias.*, USSR (Kirghiz). —FIG. 215,5. **T. sogdiana*; fore wing, $\times 6.5$ (Ponomarenko & Rasnitsyn, 1974).
- Turanopsyche** MARTYNOV, 1937a, p. 37 [**T. venosa*; OD]. Little-known hind(?) wing; SC not reaching midwing; RS with 3 main branches; RS2+3 forking at wing margin; CUA straight, not coalesced with M. WILLMANN, 1978. *Trias.*, USSR (Tadzhik).
- Xenochoristella** RIEK, 1955, p. 668 [**X. billae*; OD]. SC of fore wing with short branches; CUA coalesced with M basally for a short distance. MARTYNOVA, 1962e; WILLMANN, 1978. *Perm.*,

Australia (New South Wales).—FIG. 215, 10.
 **X. billae*; fore wing, $\times 5.5$ (Riek, 1955).
Xenopanorpa RIEK, 1955, p. 659 [**X. didymovena*; OD]. Little-known wing; RS and M each with 7 or 8 branches. MARTYNOVA, 1962e; WILLMANN, 1978. *Trias.*, Australia (Queensland).

Order SIPHONAPTERA Latreille, 1825

[Siphonaptera LATREILLE, 1825, p. 334]

Small, apterous insects, body laterally compressed. Head sessile on prothorax; compound eyes absent, but 2 lateral ocelli frequently present; antennae short in female, longer in male; mouthparts modified for piercing-sucking, maxillae in form of long, cutting blades; maxillary and labial palpi well developed; prothorax and mesothorax small, metathorax large; legs well developed, hind pair long and used for jumping; abdomen with 10 distinct segments, terga with rows of setae. Combs (ctenidia) in the form of rows of thick, flattened bristles present in some on genital area, pronotum, and, rarely, metanotum. *Oligo.*—*Holo.*

The adults are blood-sucking, mostly parasites on mammals, especially rodents, and rarely on birds. The larvae are free-living and feed on organic debris, largely the feces of adult fleas.

The fleas constitute a relatively small order of ectoparasites. The only known fossils are two congeneric species in Baltic amber, belonging to a family that is considered to be among the more specialized families of the order (HOLLAND, 1964).

Two apterous insects from the Lower Cretaceous of Australia have been noted by RIEK (1970) and considered by him to belong to the order, but they have not been fully described and remain unnamed. Specialists who have examined the fossils are of the opinion that they are not fleas. Another wingless insect from the Cretaceous (*Saurophthirus longipes* PONOMARENKO, 1976) has also been placed in the Siphonaptera (RASNITSYN, 1980e), but since the specimen has long, slender legs and lacks any indication of the

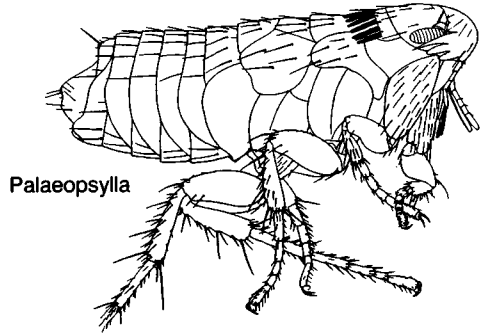


FIG. 216. Hystrichopsyllidae (p. 395).

characteristic lateral compression of the body, its placement in the Siphonaptera is very dubious. It is herein assigned to the category Order Uncertain.

The origin of the Siphonaptera is by no means clear. Several authors have suggested the derivation of the fleas from the Coleoptera, Diptera, or Mecoptera, but the evidence for each of these is weak and inconclusive (KRISTENSEN, 1975, 1981; HENNIG, 1981). About all that can be said with confidence at the present time is that they are members of the Endopterygota.

Family HYSTRICHOPSYLLIDAE Tiraboschi, 1904

[Hystrichopsyllidae TIRABOSCHI, 1904, p. 242]

Pronotal ctenidium usually present; hind margin of metanotum without spines; hind coxae without spinelike setae on inner surface. Mostly parasites on moles and shrews. [Extinct species of moles and shrews are known from the Oligocene of Europe.] *Oligo.*—*Holo.*

Palaeopsylla WAGNER, 1903, p. 137. DAMPF, 1911; HENNIG, 1939; HOPKINS & ROTHSCHILD, 1966; PEUS, 1968. *Oligo.*, Europe (Baltic)—*Holo.*—FIG. 216. *P. klebsiana* DAMPF; lateral view, $\times 30$ (Dampf, 1911).

Order DIPTERA Linné, 1758

[Diptera LINNÉ, 1758, p. 584]

Very small to medium-sized insects. Head commonly large. Most of head surface except

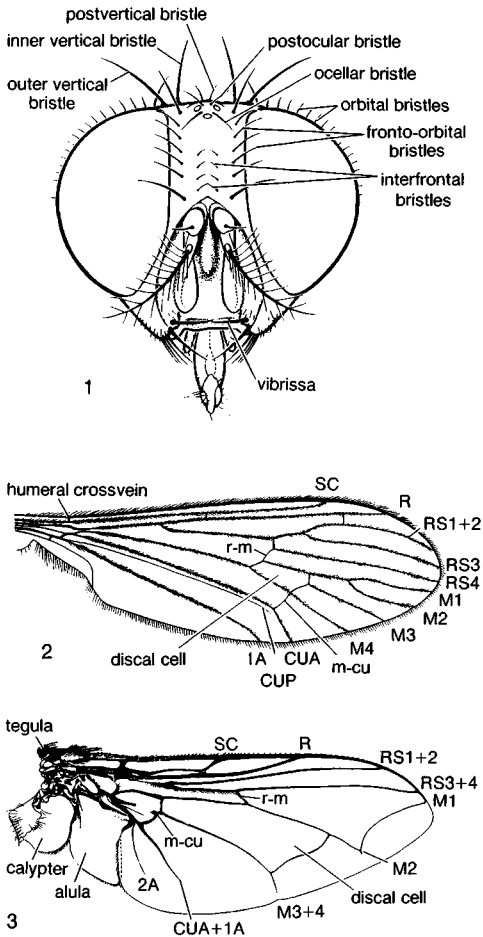


FIG. 217. Diptera; bristle arrangement and fore wing venation. —1. Muscoid fly head, showing bristle arrangement and terminology (CSIRO, 1970). —2. Fore wing of a recent genus of the suborder Nematocera, *Nothotrichocera*, showing comparatively unspecialized venation pattern (CSIRO, 1970). —3. Fore wing of a recent genus of the suborder Brachycera, *Chrysomya*, showing more specialized venational pattern (CSIRO, 1970).

The symbols for crossveins are hyphenated.

the relatively large compound eyes generally bearing prominent bristles, bristle arrangement useful in generic and family classification (Fig. 217,1). Antennae diverse; filiform in more generalized members of order (Nematocera), shorter and with fewer segments in more specialized members (Brachycera). Mouthparts of adults suctorial, forming a proboscis that may include stylets for

piercing. Mandibles present only in some nematoceros females. Maxillae commonly highly modified, though segmented palpi may be present. Labium forming proboscis, bearing distally a pair of fleshy lobes (labella). Hypopharynx long and slender. Prothorax and metathorax small, metathorax more or less fused with large mesothorax; thorax generally with prominent bristles, especially in higher Brachycera.

Fore wings membranous, with a distinct venation resembling that of generalized Mecoptera though commonly much reduced or otherwise modified. Venational homologies clear in generalized families but uncertain in some specialized families.

Several widely different terminologies have been used for venation in the past, but in recent years most dipterists have agreed on the terminology and the homologies employed here, which are those used by COLLESS and McALPINE (1970). In the tipuloids (suborder Nematocera, Fig. 217,2), which appear to have the least specialized wings among recent Diptera, veins SC and R are straight, independent, and long; RS is dichotomously forked and its branches terminate in the apical region of the wings; M, apparently coalesced with CUA basally, shows neither convexity nor concavity but divides into four terminal and nearly parallel branches; CUA is a strong vein and (in the present interpretation) terminates without forking. CUP is a weak vein, arising from the base of 1A and becoming obsolescent before the wing margin. Vein 1A is nearly straight or gently curved, reaching the hind margin remote from the wing base; 2A is short and independent of 1A. In these tipuloids and other generalized families, the wings tend to be slenderly oval, often petiolate.

In the more highly specialized families, such as the muscoids (suborder Brachycera, Fig. 217,3), veins SC and R are greatly shortened and may be coalesced; they often terminate before the wing apex. Vein M tends to fork near the base and its branches in general are reduced; CUA commonly diverges posteriorly just beyond the end of CUP and

coalesces with 1A, forming a compound vein, CUA + 1A, which may extend to the wing margin or be very short or virtually absent. Vein 2A is most commonly much reduced or absent. In these specialized families the wings tend to be broad, especially basally, with the development of one or two lobes (calypteres and alulae) along the inner posterior margin.

In all known alate Diptera the hind wings have been modified to halteres, each consisting of a small, slender stalk terminating in a knob; these structures oscillate in flight and function as balancing organs.

With some exceptions, only a few crossveins (humeral, r-m, and m-cu) occur in dipterous wings, although additional crossveins may be present near the points of origin of distal branches of the veins. In some species, parts of the longitudinal veins have become transverse in position and resemble crossveins. Ordinarily, however, there are only a few closed cells in the wings; the discal cell, formed by the forking of M, is the one most commonly present (Fig. 217,2,3).

The legs of the Diptera are basically cursorial, though the fore pair may be more or less raptorial in some species. The tarsi typically have five segments.

The abdomen in its generalized form, as seen in the tipuloids, consists of 10 or possibly 11 segments. In the more specialized Diptera the first two segments tend to coalesce, at least externally, and the posterior ones often show distinct telescoping. *Trias.*—*Holo.*

Adult Diptera occur in virtually all terrestrial habitats, from rain forests to deserts. All are limited to liquid food, which in addition to water may include blood and other tissue fluids of animals, decomposed organic matter, and plant and animal secretions.

The larvae, which typically develop from eggs deposited near the food source, lack true legs in all stages. The body form is diversely modified throughout the order. In the Nematocera the head capsule is distinct, and the mouthparts are normal (Fig. 218,1). In the Brachycera the head capsule is reduced to a few minute rods or plates retracted within

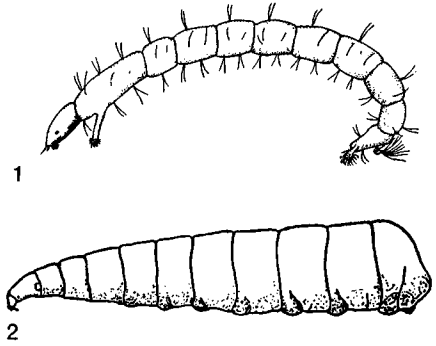


FIG. 218. Diptera; larval forms.—1. Larva of *Tanypus*, suborder Nematocera (Brues, Melander, & Carpenter, 1954).—2. Muscoid larva, suborder Brachycera (Brues, Melander, & Carpenter, 1954).

the thorax, or is completely absent (Fig. 218,2), and the mandibles may be retained or replaced by mouthhooks. Most larvae are terrestrial, obtaining oxygen from the atmosphere; others are aquatic, absorbing dissolved oxygen from the water or obtaining air from plant tissues; and still others are endoparasites of other invertebrates (chiefly insects) or occasionally of vertebrates. Pupation occurs in a variety of environments. The pupae of many Nematocera are free (not enclosed in a case), but others are formed within a silken cocoon. The pupae of most Brachycera are also free, but in the highly specialized families, they are enclosed in the hardened exuviae of the larvae (puparia).

The Diptera comprise one of the large and highly diversified orders of insects. Nearly 100,000 existing species have been described, and about half as many more probably remain to be described (COLLESS & McALPINE, 1970). Their general evolutionary development, from the lower to the higher flies, is fairly clear, but the translation of that sequence into a phylogenetic system of classification has proven difficult. The classification most widely used for many years has recognized two suborders, Nematocera and Brachycera, with the latter divided into two sections, the Orthorrhapha and Cyclorrhapha. Within the past two decades, however, doubts have been expressed about some of these taxa as phy-

logenetetic categories (ROHDENDORF, 1964; COLLESS & McALPINE, 1970; HENNIG, 1973; STEYSKAL, 1974; OLDROYD, 1977), and the diversity of the classifications now being proposed indicates the degree of differences of opinion that still exists on this subject among students of Diptera. COLLESS and McALPINE (1970), for example, follow the traditional system mentioned above; the families of the suborder Nematocera are grouped into four major divisions, and those of the Brachycera are grouped into Orthorrhapha and Cyclorrhapha. On the other hand, OLDROYD (1977) has proposed the division of the Diptera into three suborders, Superstata, Medescata, and Arescata, based on general ecology and habits, rather than directly on structure. ROHDENDORF (1961c) has proposed two suborders, Archidiptera and Eudiptera, the former to include certain extinct (Triassic) families, the latter to comprise all other families, grouped into 13 infraorders (see below, under the suborder Archidiptera). HENNIG (1973), following the completion of his extensive studies on the morphology of existing Diptera, adopted still another course, recognizing the two suborders Nematocera and Brachycera, with the latter divided into three infraorders, Homoeodactyla, Asilomorpha, and Cyclorrhapha. RICHARDS and DAVIES (1977) introduced a division into three suborders, the Nematocera, Brachycera (=Orthorrhapha), and Cyclorrhapha.

In the present treatment of the Diptera, three suborders are recognized: Archidiptera (including only the Triassic families discussed below), Nematocera, and Brachycera. In view of the arguments presented by ROHDENDORF (1961c) and OLDROYD (1977), the brachycerous families are not divided into the Orthorrhapha and Cyclorrhapha. The number of existing families recognized in the order Diptera ranges from 115 to 140 (COLLESS & McALPINE, 1970; HENNIG, 1973). About 80 percent of these families are members of the suborder Brachycera. Although family groupings such as superfamilies and infraorders are usually employed to indicate relationships of the families, there is much difference of opinion about the assignment

of certain families to these higher categories. Inclusion of extinct families and genera in the classification adds to the difficulty, because some of them appear to be intermediate between family groups, especially in the Brachycera. In the present treatment of the Diptera, superfamilies and comparable family groupings are omitted, but the sequence of families, as well as the family nomenclature, follows that of COLLESS & McALPINE (1970).

As pointed out by ROHDENDORF (1964), the fossil record of the Diptera has contributed substantially to our understanding of their evolution. Flies are not only numerous as fossils, but their wing venation, which usually provides a basis for family or generic identification, is almost always clearly preserved. The earliest known Diptera have been found in Upper Triassic beds of Kirghiz in the Soviet Union (ROHDENDORF, 1961c, 1962a, 1964). All of these belong to extinct families. Some of the families, assigned to the Archidiptera, appear to have only remote affinities with even the most generalized Nematocera; others seem clearly to belong to existing family groups of the Nematocera (i.e., superfamilies Tipulomorpha and Bibiomorpha). The earliest known Brachycera occur in Jurassic deposits and include, in addition to several extinct families, representatives of the Acroceridae, Nemestrinidae, and Rhagionidae. The few Cretaceous flies that are known support the conclusion based on the lower Tertiary record that by the end of the Mesozoic most of the living families were already in existence. Numerous recent genera have been recognized in lower Tertiary deposits; the specimens in amber are of special interest in this connection, since their excellent preservation allows positive determination of their generic affinities. As might be expected, the percentage of existing genera known from the lower Tertiary varies considerably from family to family: in general, it is higher for the Nematocera than for the Brachycera. For example, about 75 percent of the tipulid and mycetophilid genera of the lower Tertiary are extant, whereas only about 40 percent of the bombyliid and syrphid genera are still existing. Many species

in the Baltic amber are strikingly similar to existing species and one of them, according to HENNIG's very careful study (1966a), seems to be identical with an existing muscid, *Fannia scalaris* FABRICIUS.

The evidence now available indicates that the Diptera were derived from generalized Mecoptera or from ancestral mecopteroid stock, probably during the Permian. By the late Permian the mecopteroid complex had differentiated into three well-defined ordinal lines, the Neuroptera, Trichoptera, and Mecoptera, in addition to a series of little-known families with obscure relationships to those orders. The precise position in this complex of the evolutionary line leading to the Diptera, with reduction of the hind wings and their modification to halteres, is not yet certain.

Suborder ARCHIDIPTERA Rohdendorf, 1961

[Archidiptera ROHDENDORF, 1961c, p. 154]¹

Very small flies. Wings normally developed; veins of unequal thickness and development: C, R, and CUA commonly strong; RS, M, CUP, and 1A weak or obsolescent; numerous crossveins present in all areas but often weak or forming a network. Halteres, body structure, and immature stages unknown. ROHDENDORF, 1961c, 1961d, 1962a, 1964. *Trias*.

This suborder was originally based on several Triassic specimens consisting of isolated wings (ROHDENDORF, 1961d, 1962a) and belonging to four extinct families. The diagnosis of the suborder was therefore limited to the venational features cited above. In a subsequent publication, however, ROHDENDORF (1964) also placed in the suborder Archidiptera the recent family Nymphomyiidae and redefined the suborder by assigning to it the characteristics of that fam-

ily. His entire revised definition reads as follows (ROHDENDORF, 1964, translated edition): "Head of pupa directed forward, prognathous. Ocelli very large, two in number. Prothorax large, well isolated. Wings of pupa parallel-margined, elongate." Since the Triassic species on which the suborder was based originally are known only by isolated wings, this revised definition has no meaning without the assumption, for which there is no evidence, that the Triassic species had body structures and pupae like those of the Nymphomyiidae.

At the time when ROHDENDORF's revised definition was published, the recent family Nymphomyiidae was known only by a single species, *Nymphomyia alba* TUKUNAGA, from Japan. Since then several other species belonging to different genera have been found in widely scattered localities: New Brunswick and Alberta in Canada, West Bengal, and Primorsk Kray in the eastern Soviet Union (IDE, 1964, 1965; CUTTEN & KEVAN, 1970; ROHDENDORF & KALUGINA, 1974; KEVAN & CUTTEN-ALI-KHAN, 1975). These nymphomyiids collectively show a remarkable combination of generalized and specialized features. They are very small, with a body length of less than 2 mm; their wings are elongate and slender and have only minute vestiges of veins at the wing bases and a marginal fringe of very long hairs. The larvae and pupae are aquatic, and the adults, presumably after nuptial flight, shed their wings and return to water.

Although there is no close agreement among dipterists about the affinities of these remarkable flies (KEVAN & CUTTEN-ALI-KHAN, 1975), there has been a general tendency to accept ROHDENDORF's hypothesis that the family Nymphomyiidae is a member of the suborder Archidiptera (see, however, KEVAN & CUTTEN, 1981). Although the Nymphomyiidae may represent a suborder distinct from the Nematocera and Brachycera, assignment of the family to the suborder Archidiptera as that was defined by ROHDENDORF from the Triassic fossils (1964) is insupportable: the fossils show none of the characteristics of the recent Nymphomyiidae,

¹ CUTTEN and KEVAN (1970) have emended ROHDENDORF's name Archidiptera to read Archaeidiptera. However, the Greek prefix, meaning primitive or ancient, has been accepted in biological terminology in several forms, including archi- and arche- as well as archae-. The proposed emendation, therefore, seems entirely unnecessary (see NYBAKKEN, 1959, p. 135, 152, 225; BROWN, 1954, p. 99).

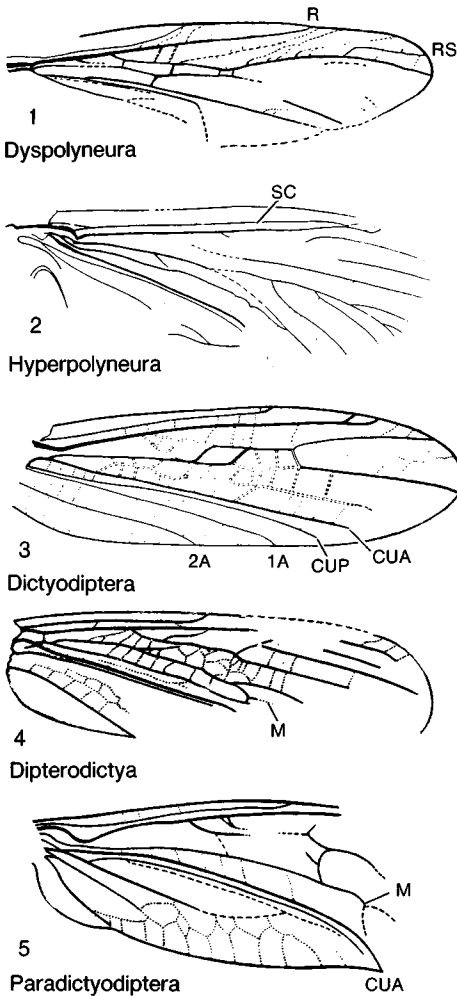


FIG. 219. Dictyodipteridae, Hyperpolyneuridae, and Dyspolyneuridae (p. 400-401).

and the nymphomyiids show none of the features known in the fossils. Accordingly, it seems advisable to consider the subordinal position of the existing family Nymphomyiidae as uncertain and to restrict the suborder Archidiptera, at least for the present, to the Triassic species, as originally proposed by ROHDENDORF. Because our knowledge of these Triassic families is limited to isolated wings, all of which possess a venation quite unlike that postulated for the early dipteran stock, even their assignment to the Diptera should probably be considered uncertain, especially since there is no evidence that they possessed only two wings and halteres.

Family DICTYODIPTERIDAE Rohdendorf, 1961

[Dictyodipteridae ROHDENDORF, 1961d, p. 90]

Small species; wings less than 3.5 mm long and broad basally; veins R and CUA very strong; RS, M, and CUP weak; base of stem R with a prominent bend; RS and M with few branches; crossveins numerous over most of wing including anal area. *Trias.*

Dictyodiptera ROHDENDORF, 1961d, p. 91 [**D. multinervis*; OD]. Crossveins present basally between CUA and CUP; 1A and 2A well developed and nearly parallel. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 219,3. **D. multinervis*; wing, $\times 20$ (Rohdendorf, 1964).

Dipterodictya ROHDENDORF, 1961d, p. 92 [**D. tipuloides*; OD]. Bend in stem of R much less pronounced than in *Paradictyodiptera*; M dividing basally. ROHDENDORF, 1962a, 1964. *Trias.*, USSR (Kirghiz).—FIG. 219,4. **D. tipuloides*; wing, $\times 16$ (Rohdendorf, 1961d).

Paradictyodiptera ROHDENDORF, 1961d, p. 93 [**P. trianalis*; OD]. Base of stem R strongly bent; M dividing distally; crossveins absent between CUA and CUP; 3 anal veins, connected by a network of crossveins. ROHDENDORF, 1962a, 1964. *Trias.*, USSR (Kirghiz).—FIG. 219,5. **P. trianalis*; wing, $\times 22$ (Rohdendorf, 1961d).

Family HYPERPOLYNEURIDAE Rohdendorf, 1961

[Hyperpolyneuridae ROHDENDORF, 1961d, p. 94]

Wing: stem of vein R with sharp break, developed into a short projection towards base of M; SC long, parallel to R and terminating just before end of R; RS apparently with 3 branches; M with 6 branches; crossveins weak and absent from anal area. *Trias.*

Hyperpolyneura ROHDENDORF, 1961d, p. 95 [**H. phryganeoides*; OD]. Wing with M forked just basad of break in stem of R. ROHDENDORF, 1962a, 1964. *Trias.*, USSR (Kirghiz).—FIG. 219,2. **H. phryganeoides*; wing, $\times 20$ (Rohdendorf, 1961d).

Family DYSPOLYNEURIDAE Rohdendorf, 1961

[Dyspolyneuridae ROHDENDORF, 1961d, p. 95]

Wing: stem of vein R with sharp break, forming a strong strut joined to base of M; SC short, terminating before midwing; R terminating well before apex of wing. *Trias.*

Dyspolyneura ROHDENDORF, 1961d, p. 96 [**D. longipennis*; OD]. Little-known wing, with all branches of RS directed anteriorly. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 219, 1. **D. longipennis*; wing, $\times 18$ (Rohdendorf, 1964).

Suborder NEMATOCERA

Latreille, 1825

[*nom. transl.* BRAUER, 1883, p. 4, *ex Nematocera* LATREILLE, 1825, p. 482]

Antennae of adults usually filiform, at least as long as thorax, differentiated into scape, pedicel, and flagellum of 6 or more segments; maxillary palpi commonly with 3 to 5 segments; wings very commonly slender; vein CUA not coalesced with 1A and rarely diverging toward it. Larvae with head capsule usually distinct and complete; mandibles typically generalized, dentate and opposite, their chewing movements in horizontal plane of head. Pupae free, usually capable of some movement. HENNIG, 1973. *Trias.*—*Holo.*

Family DIPLOPOLYNEURIDAE

Rohdendorf, 1961

[Diplopolyneuridae ROHDENDORF, 1961d, p. 98]

Wing with crossveins restricted to distal third of wing; veins SC and R very short, terminating about one-quarter wing length from base. Body unknown. [Subordinal position uncertain.] *Trias.*

Diplopolyneura ROHDENDORF, 1961d, p. 98 [**D. mirabilis*; OD]. Little-known wing; characters as in family. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 220, 1. **D. mirabilis*; wing, $\times 12.5$ (Rohdendorf, 1964).

Family TIPULODICTYIDAE

Rohdendorf, 1962

[Tipulodictyidae ROHDENDORF, 1962a, p. 310]

Very small insects. Wing with costal area narrow; vein SC terminating beyond midwing; R smoothly curved basally; RS apparently arising close to wing base, branches usually parallel and terminating on apical margin; CUA, CUP, and posterior branch of M close together and parallel. Body unknown. *Trias.*

Tipulodictya ROHDENDORF, 1962a, p. 311 [**T. minima*; OD]. Costal area with several weak crossveins; main branch of RS arising just before

end of SC. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 220, 6. **T. minima*; wing, $\times 22$ (Rohdendorf, 1964).

Family EOPOLYNEURIDAE

Rohdendorf, 1962

[Eopolyneuridae ROHDENDORF, 1962a, p. 311]

Very small insects. Wing broader than in Tipulodictyidae; costal area broad; vein SC weakly formed; stem R with a small break, strut absent; RS arising well before midwing, dividing into 3 branches at midwing; anal area broad. Body unknown. *Trias.*

Eopolyneura ROHDENDORF, 1962a, p. 311 [**E. tenuinervis*; OD]. Termination of RS1+2 remote from end of R; no crossveins between SC and R. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 220, 3. **E. tenuinervis*; wing, $\times 18$ (Rohdendorf, 1964).

Pareopolyneura ROHDENDORF, 1962a, p. 311 [**P. costalis*; OD]. Venation as in *Eopolyneura*, but RS1+2 terminating close to end of R; crossveins present between SC and R. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Family MUSIDOROMIMIDAE

Rohdendorf, 1962

[Musidoromimidae ROHDENDORF, 1962a, p. 311]

Very small insects. Wing with narrow costal area; vein SC extending almost to midwing; RS with 2 apparent origins from R, one near midwing, the other basal; crossveins mostly weak. Body unknown. *Trias.*

Musidoromima ROHDENDORF, 1962a, p. 311 [**M. crassinervis*; OD]. Branches of M nearly equally spaced; CUA nearly straight for most of its length, with an abrupt bend distally. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 220, 5. **M. crassinervis*; wing, $\times 18$ (Rohdendorf, 1964).

Family ARCHITIPULIDAE

Handlirsch, 1906

[Architipulidae HANDLIRSCH, 1906b, p. 490]

Small flies. Wing slightly narrowed basally; costal area narrow; stem of vein R without an abrupt bend or break; RS usually arising slightly before midwing; branches of RS and M arising distad of midwing; CUA generally straight for most of its length; CUP weak or absent, parallel to CUA; commonly 3 anal veins, 2 of them long. Body unknown. *Trias.*—*Jur.*

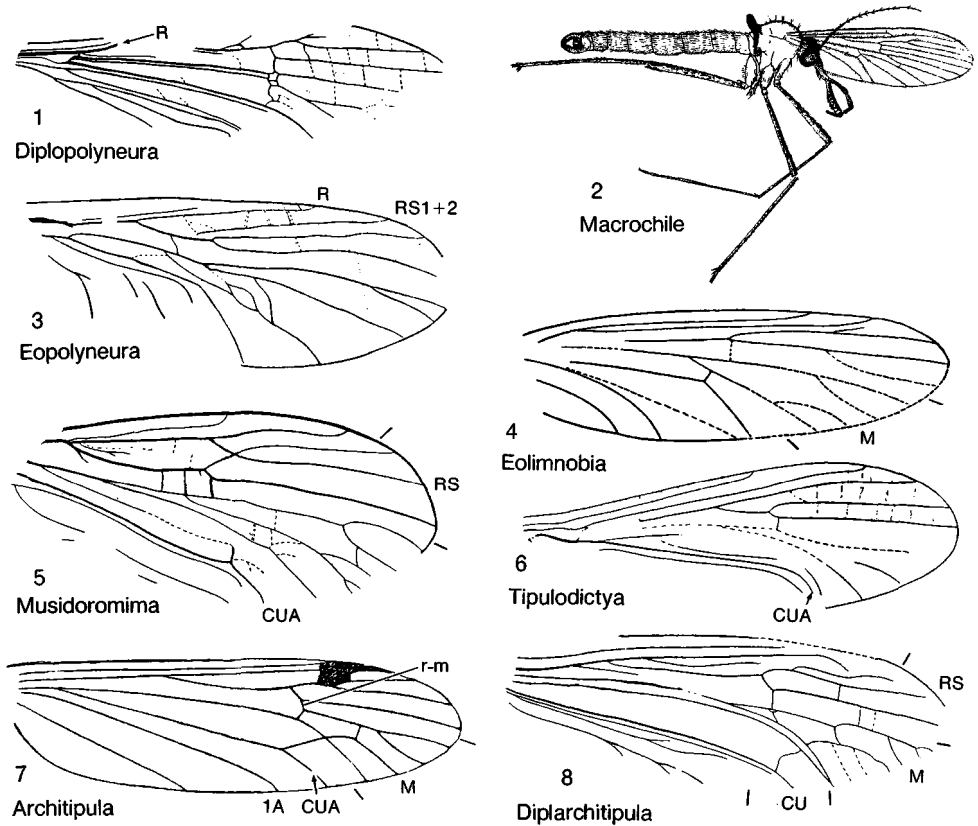


FIG. 220. Diplopolyneuridae, Tipulodictyidae, Eopolyneuridae, Musidoromimidae, Architipulidae, Eolimnobiidae, and Tanyderidae (p. 401–403).

Architipula HANDLIIRSCH, 1906b, p. 490 [**A. seebachiana*; SD ROHDENDORF, 1962a, p. 313 [= *Protipula* HANDLIIRSCH, 1906b, p. 491 (type, *P. crassa*); *Mesotipula* HANDLIIRSCH, 1939, p. 107 (type, *M. brachyptera*); *Paratipula* BODE, 1953, p. 304 (type, *P. acuta*)]. Subcostal area narrow; RS1+2 with a long fork; M with 4 branches; crossvein r-m present. HANDLIIRSCH, 1939. *Trias.*, USSR (Kirghiz); *Jur.*, Europe (Germany), USSR (Kazakh).—FIG. 220,7. **A. seebachiana*, *Jur.*, Germany; wing, $\times 8$ (Handlirsch, 1907).

Dictyotipula ROHDENDORF, 1962a, p. 312 [**D. densa*; OD]. Little-known wing fragment; costal area with weak crossveins. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Diplarchitipula ROHDENDORF, 1962a, p. 313 [**D. multimediialis*; OD]. Costal area without crossveins; 1 or 2 weak veins, in addition to RS, arising from R near midwing; M with an apparent second main branch arising from wing base, close to and paralleling anterior branch. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

— FIG. 220,8. **D. multimediialis*; wing, $\times 12$ (Rohdendorf, 1964).

Eotipula HANDLIIRSCH, 1906b, p. 491 [**E. parva*; OD]. Similar to *Architipula*, but much smaller and with less branching of M. ROHDENDORF, 1964. *Jur.*, Europe (Germany).

Haplotipula BODE, 1953, p. 311 [**H. majalis*; OD]. Similar to *Architipula*, but RS1+2 with a very shallow, marginal fork. *Jur.*, Europe (Germany).

Leptotipuloides CARPENTER, 1986, p. 576, *nom. subst. pro Leptotipula* BODE, 1953, p. 312, *non* ALEXANDER, 1917 [**Leptotipula fastigata* BODE, 1953, p. 312; OD]. Similar to *Architipula*, but both RS1+2 and RS3+4 forked. *Jur.*, Europe (Germany).

Liassotipula TILLYARD, 1933, p. 74 [**L. anglicana*; OD]. Similar to *Architipula*, but discal cell longer; fork of M1+2 much longer than that of M3+4. PRIESNER, 1924. *Jur.*, England.

Ozotipula BODE, 1953, p. 313 [**O. tarda*; OD] [= *Mikrotipula* BODE, 1953, p. 314 (type, *M.*

dixaeformis]). Similar to *Architipula*, but RS2 and RS3 forked. *Jur.*, Europe (Germany).

Family EOLIMNOBIIDAE

Rohdendorf, 1962

[Eolimnobiidae ROHDENDORF, 1962a, p. 313]

Wing base slightly narrowed; vein SC long, ending on costa; discal cell absent; crossvein r-m at center of wing; 2 anal veins. Body unknown. *Jur.*

Eolimnobia HANDLIRSCH, 1906b, p. 489 [**E. geinitzi*; OD]. Wing length 3.2 times width. MARTYNOV, 1938c; ROHDENDORF, 1962a. *Jur.*, Europe (Germany).—FIG. 220,4. **E. geinitzi*; wing, $\times 4.6$ (Rohdendorf, 1962a).

Family TANYDERIDAE

Osten-Sacken, 1879

[Tanyderidae OSTEN-SACKEN, 1879, p. 517]

Wing similar to that of Tipulidae, but vein RS with 4 parallel branches; only 1 anal vein. *Oligo.*—*Holo.*

Tanyderus PHILIPPI, 1865, p. 780. *Holo.*

Macrochile LOEW, 1850, p. 37 [**M. spectrum*; OD] [= *Idioplasta* MEUNIER, 1906a, p. 390, obj.]. SC terminating a little beyond level of fork of RS1 + 2; crossvein m-cu at fork of M3 + 4. Maxillary palpi very long. ALEXANDER, 1931. *Oligo.*, Europe (Baltic).—FIG. 220,2. **M. spectrum*; whole insect, $\times 5.3$ (Alexander, 1931).

Family TIPULIDAE Leach, 1815

[Tipulidae LEACH, 1815, p. 161]

Wing long; vein RS commonly with 3 branches reaching wing margin; discal cell usually present; 2 anal veins leading to wing margin. Ocelli absent; mesonotal suture prominent and V-shaped; legs very long and slender. Larvae aquatic or subaquatic. *Paleoc.*—*Holo.*

Tipula LINNÉ, 1758, p. 585 [= *Tipulidea* SCUDDER, 1894, p. 238 (type, *T. consumpta*); *Micrapsis* SCUDDER, 1894, p. 242 (type, *M. paludis*)]. HANDLIRSCH, 1910b; MEUNIER, 1914a, 1915a; COCKERELL, 1921d; HENRIKSEN, 1922a; ALEXANDER, 1931; THÉOBALD, 1937a; CARPENTER & others, 1938; ZEUNER, 1938; PITON & THÉOBALD, 1939; STATZ, 1944b; DRAKE & RUHOFF, 1960; POPOV, 1961; HENNIG, 1967c; LEWIS, 1973; WIGHTON, 1980. *Paleoc.*, Canada (Alberta); *Eoc.*, USA (Colorado), Europe (Denmark); *Oligo.*, USA (Colo-

rado, Montana), Canada (British Columbia), England, Europe (Baltic, France, Germany); *Mio.*—*Plio.*, Europe (France); *Mio.*, Europe (Germany)—*Holo.*

Adelphomyia BERGROTH, 1891, p. 134. ALEXANDER, 1931. *Oligo.*, England, Europe (Baltic)—*Holo.*

Antocha OSTEN-SACKEN, 1859, p. 219. SCUDDER, 1894. *Oligo.*, USA (Colorado)—*Holo.*

Atarba OSTEN-SACKEN, 1869, p. 127. COCKERELL, 1915. *Oligo.*, England—*Holo.*

Austrolimnophila ALEXANDER, 1920b, p. 4. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*

Ceratocheilus WESCHE, 1910, p. 358. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*

Cladoneura SCUDDER, 1894, p. 212 [**C. willistoni*; OD]. Similar to *Cladura*, but RS arising more basally; crossvein between R and RS1 near end of SC. *Oligo.*, USA (Colorado).

Cladura OSTEN-SACKEN, 1859, p. 229. SCUDDER, 1894. *Oligo.*, USA (Colorado)—*Holo.*

Cylindrotoma MACQUART, 1834, p. 107. COCKERELL, 1920c. *Eoc.*, USA (Colorado)—*Holo.*

Cyttaromyella MEUNIER, 1915b, p. 229 [**C. bastini*; OD]. Little-known genus. [Family assignment uncertain.] STATZ, 1934a. *Oligo.*, Europe (Germany).

Cyttaromyia SCUDDER, 1877a, p. 751 [**C. fenestrata*; OD]. Little-known genus (wing fragment).

COCKERELL, 1920c, 1924a; COCKERELL & HAINES, 1921; SÉGUY, 1934. *Paleoc.*—*Plio.*, Europe (France); *Eoc.*, USA (Colorado).

Dactylolabis OSTEN-SACKEN, 1859, p. 240. ALEXANDER, 1931; STATZ, 1944b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Dasymolophilus GOETGHEBUER, 1920, p. 132. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*

Dicranomyia STEPHENS, 1829, p. 53. SCUDDER, 1894; COCKERELL, 1908a, 1922a; MEUNIER, 1916b; COCKERELL & HAINES, 1921. *Oligo.*, England, USA (Colorado)—*Holo.*

Dicranoptycha OSTEN-SACKEN, 1859, p. 217. ALEXANDER, 1931; STATZ, 1944b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Electrolabis ALEXANDER, 1931, p. 58 [**E. extincta*; OD]. Stem of RS aligned with RS3 + 4; antennae with 16 segments. *Oligo.*, Europe (Baltic).

Elephantomyia OSTEN-SACKEN, 1859, p. 220. ALEXANDER, 1931; STATZ, 1934a. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Empeda OSTEN-SACKEN, 1869, p. 183. COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Epiphragma OSTEN-SACKEN, 1859, p. 238. COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Eriocera MACQUART, 1838, p. 74. HENRIKSEN, 1922b; ALEXANDER, 1931; STATZ, 1944b. *Eoc.*, Europe (Denmark); *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Erioptera MEIGEN, 1803, p. 262. ALEXANDER, 1931; THÉOBALD, 1937a (as *Ilisia* RONDANI, generic

- assignment of fossil doubtful); STATZ, 1944b. *Oligo.*, Europe (Baltic, Germany, France)—*Holo.*
- Gnophomyia** OSTEN-SACKEN, 1859, p. 223. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Gonomyia** MEIGEN, 1818, p. 147. COCKERELL, 1921a; COCKERELL & HAINES, 1921; ALEXANDER, 1931; STATZ, 1944b. *Oligo.*, USA (Colorado), England, Europe (Baltic, Germany)—*Holo.*
- Gymnastes** BRUNETTI, 1911, p. 96. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Helius** LEPELETIER & SERVILLE, 1828, p. 831. ALEXANDER, 1931; STATZ, 1944b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*
- Hexatoma** LATREILLE, 1809, p. 260. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Holorusia** LOEW, 1863, p. 276. COCKERELL & HAINES, 1921. *Oligo.*, England—*Holo.*
- Limnobia** MEIGEN, 1818, p. 116. COCKERELL, 1921d; STATZ, 1934a; THÉOBALD, 1937a. *Oligo.*, England, Europe (Germany, France)—*Holo.*
- Limnocema** SCUDDER, 1894, p. 201 [**L. marcescens* SCUDDER, 1894, p. 201; SD CARPENTER, herein]. Similar to *Limnobia* but with a crossvein between R and RS1 near wing apex. *Oligo.*, USA (Colorado).
- Limnophila** MACQUART, 1834, p. 95. COCKERELL, 1921d; COCKERELL & HAINES, 1921; ALEXANDER, 1931; THÉOBALD, 1937a; STATZ, 1944b; CARPENTER, 1951; WIGHTON, 1980. *Paleoc.*, Canada (Alberta); *Oligo.*, England, Europe (France, Germany, Baltic)—*Holo.*
- Limonia** MEIGEN, 1803, p. 262. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Macromastix** OSTEN-SACKEN, 1886, p. 185. COCKERELL & HAINES, 1921; ALEXANDER, 1931. *Oligo.*, England, Europe (Baltic)—*Holo.*
- Manapsis** SCUDDER, 1894, p. 222 [**M. anomala*; OD]. Similar to *Tipula*, but vein M1+2 not forked. CARPENTER & others, 1938. *Oligo.*, USA (Colorado).
- Megistocera** WIEDEMANN, 1828, p. 55. COCKERELL & HAINES, 1921. *Oligo.*, England—*Holo.*
- Mongoma** WESTWOOD, 1881, p. 364. COCKERELL, 1917b, 1921d. *Oligo.*, England—*Holo.*
- Ormosia** RONDANI, 1856, p. 180. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Oryctogma** SCUDDER, 1894, p. 194 [**O. sackenii*; OD]. Similar to *Cylindrotoma*, but SC deflected distally and ending on R; discal cell short. *Oligo.*, USA (Colorado).
- Palaeopocecilostola** MEUNIER, 1899c, p. 334 [**P. longicornis* MEUNIER, 1906a, p. 377; SD ALEXANDER, 1931, p. 45]. SC terminating at level of fork of RS; RS1+2 elongate, in alignment with RS. Antennae elongate, segments elongate-cylindrical. ALEXANDER, 1931. *Oligo.*, Europe (Baltic).
- Phyllolabis** OSTEN-SACKEN, 1877, p. 202. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Pilaria** SINTENIS, 1889, p. 398. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Polymera** WIEDEMANN, 1821, p. 40. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Pronophlebia** SCUDDER, 1877a, p. 750 [**P. rediviva*; OD]. Little-known genus; venation obscure. SCUDDER, 1890. *Eoc.*, USA (Colorado).
- Pseudolimnophila** ALEXANDER, 1919, p. 917. ALEXANDER, 1931; WIGHTON, 1980. *Paleoc.*, Canada (Alberta); *Oligo.*, Europe (Baltic)—*Holo.*
- Rhabdomastix** SKUSE, 1889, p. 828. ALEXANDER, 1931; STATZ, 1944b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*
- Rhadinobrochus** SCUDDER, 1894, p. 223 [**R. extinctus*; OD]. Similar to *Tipula*, but basal cell between M1 and M2 unusually narrow. CARPENTER & others, 1938. *Oligo.*, USA (Colorado).
- Ripidia** RONDANI, 1856, p. 186. COCKERELL, 1917b. *Oligo.*, England—*Holo.*
- Spiladomyia** SCUDDER, 1877a, p. 749 [**S. simplex*; OD]. Little-known genus, similar to *Dicranomyia*. SCUDDER, 1890. *Eoc.*, USA (Colorado).
- Stibadocerites** ZEUNER, 1941a, p. 96 [**S. europeus*; OD]. Similar to *Stibadocerella* (recent), but SC almost reaching to wing apex. *Eoc.*, Scotland.
- Tanymera** ALEXANDER, 1931, p. 75 [**T. fritschii*; OD]. SC and RS relatively short; RS in alignment with RS1+2. *Oligo.*, Europe (Baltic).
- Tansyphra** LOEW, 1850, p. 38 [**T. gracilis*; OD]. SC terminating at level of fork of RS; RS1 and RS2 parallel for their entire lengths. ALEXANDER, 1931. *Oligo.*, Europe (Baltic).
- Thaumastoptera** MIK, 1866, p. 302. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Trentepohlia** BIGOT, 1854, p. 473. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Trichocera** MEIGEN, 1803, p. 262. STATZ, 1934a. *Oligo.*, Europe (Germany)—*Holo.*
- Trichoneura** LOEW, 1850, p. 36 [**T. vulgaris*; OD]. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Tricyphona** ZETTERSTEDT, 1837, p. 65. ALEXANDER, 1931. *Oligo.*, Europe (Baltic)—*Holo.*
- Ula** HALIDAY, 1833, p. 153. STATZ, 1934a. *Oligo.*, Europe (Germany)—*Holo.*

Family PSYCHODIDAE Newman, 1835

[Psychodidae NEWMAN, 1835, p. 388]

Very small flies; wings commonly very hairy, held roof-wise over abdomen; vein RS usually with 4 branches; M usually with 3 branches; CUA with 2 branches, CUA2 commonly very short; anal veins reduced. V-shaped suture on mesonotum absent. Larvae usually in moist, freshwater habitats. *Cret.*—*Holo.*

Psychoda LATREILLE, 1796, p. 152. COCKERELL, 1915, 1921d; QUATE, 1963; HENNIG, 1972b. *Oligo.*, England, Europe (Baltic); *Mio.*, Mexico—*Holo.*

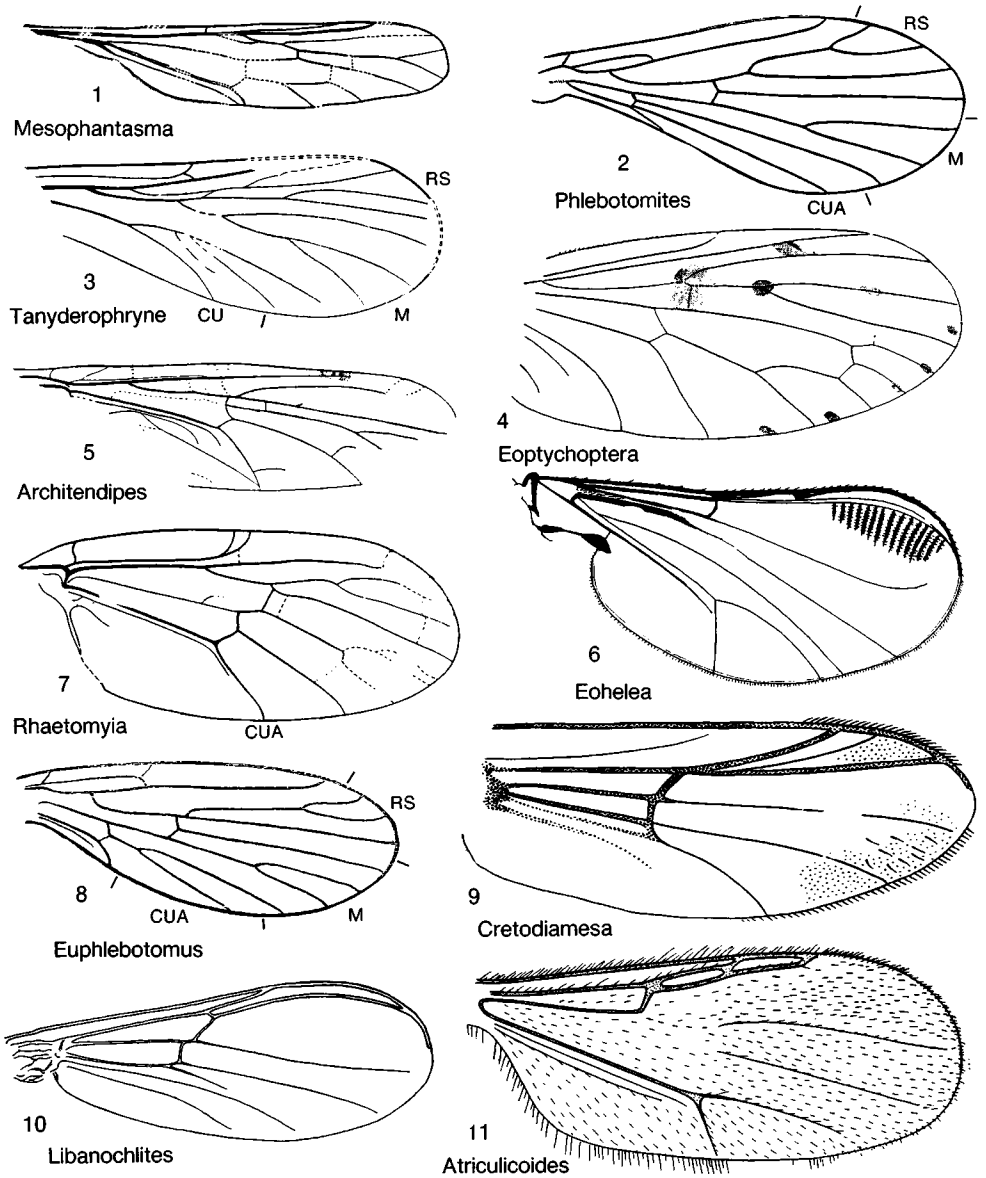


FIG. 221. Psychodidae, Eoptychopteridae, Tanyderophryneidae, Architendipedidae, Chironomidae, Ceratopogonidae, Rhaetomyiidae, and Mesophantasmatae (p. 404–409).

Brunettia ANNANDALE, 1910, p. 141. QUATE, 1963; HENNIG, 1972b. *Mio.*, Mexico—*Holo.*

Eatonisca MEUNIER, 1905c, p. 253 [**E. tertiaria*; OD]. Little-known genus. HENNIG, 1972b. *Oligo.*, Europe (Baltic)—*Holo.*

Euphlebotomus COCKERELL, 1920e, p. 212 [**E. connectens*; OD]. Similar to *Horaiella* (recent), but RS1+2 forked; RS3+4 forked at about level of origin of RS1+2. EDWARDS, 1929; HENNIG,

1972b. *Mio.*, Burma. — FIG. 221,8. **E. connectens*; wing, X49 (Edwards, 1929).

Lutzomyia FRANÇA, 1927, p. 23. QUATE, 1963; HENNIG, 1972b. *Mio.*, Mexico—*Holo.*

Nemopalpus MACQUART, 1840, p. 101 [= *Palaeosycorax* MEUNIER, 1905b, p. 50 (type, *P. tertiariae*)]. EDWARDS, 1929; HENNIG, 1972b; SCHLÜTER, 1978b. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Dominican Republic—*Holo.*

- Pericoma** WALKER, 1856, p. 256. [Generic assignment of fossils doubtful.] MEUNIER, 1905c; HENNIG, 1972b. *Oligo.*, Europe (Baltic)—*Holo.*
- Philosepedon** EATON, 1904, p. 57. QUATE, 1961; HENNIG, 1972b. *Mio.*, Mexico—*Holo.*
- Phlebotomiella** MEUNIER, 1906b, p. 103 [**Phlebotomus tipuliformis* MEUNIER, 1905c, p. 254; OD]. Similar to *Phlebotomus*, but crossvein r-m and origin of RS4 near center of wing; wing apex rounded; fifth segment of palpus very short; 4 spines on male genital style. [Probably a synonym of *Phlebotomus*.] *Oligo.*, Europe (Baltic).
- Phlebotomites** HENNIG, 1972b, p. 39 [**P. brevifilis*; OD]. Similar to *Phlebotomiella*, but with 5 spines on male genital style. *Cret.*, Lebanon. — FIG. 221,2. **P. brevifilis*; wing, $\times 40$ (Hennig, 1972b).
- Phlebotomus** RONDANI & BERTÉ, 1840, p. 12. FAIRCHILD, 1951; HENNIG, 1972b. *Oligo.*, Europe (Baltic)—*Holo.*
- Sycorax** HALIDAY, 1839, no. 745. LOEW, 1850; MEUNIER, 1905c; HENNIG, 1972b. *Oligo.*, Europe (Baltic)—*Holo.*
- Telmatoscopus** EATON, 1904, p. 58. QUATE, 1963; HENNIG, 1972b. *Mio.*, Mexico—*Holo.*
- Trichomyia** HALIDAY, 1839, no. 745. MEUNIER, 1905c; COCKERELL, 1917c, 1917g; QUATE, 1963; HENNIG, 1972b. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Mexico; *Mio.*, Burma—*Holo.*

Family EOPTYCHOPTERIDAE Handlirsch, 1906

[Eoptychopteridae HANDLIRSCH, 1906b, p. 488]

Wing with uniformly strong veins; vein SC terminating near midwing; branches of RS not close together distally; discal cell large. *Jur.*

Eoptychoptera HANDLIRSCH, 1906b, p. 489 [**Phryganidium simplex* GEINITZ, 1887, p. 203; OD] [= *Proprychoptera* HANDLIRSCH, 1906b, p. 489 (type, *P. liasina*)]. Wing very broad basally; R nearly straight; RS1+2 not forked; RS3+4 with deep fork. HANDLIRSCH, 1920; BODE, 1953. *Jur.*, Europe (Germany). — FIG. 221,4. *E. maculata* (HANDLIRSCH); wing, $\times 11$ (Handlirsch, 1920).

Family TANYDEROPHRYNEIDAE Rohdendorf, 1962

[Tanyderophryneidae ROHDENDORF, 1962a, p. 314]

Wing narrowed basally; vein SC terminating before midwing, with a crossvein connecting to R distally; stem of M much reduced or absent, its posterior branches coalesced in part with those of CU. Antennae apparently

short; legs thin; tibial spurs present; abdomen long. *Jur.*

Tanyderophryne ROHDENDORF, 1962a, p. 314 [**T. multinervis*; OD]. Posterior branches of RS apparently coalesced with anterior branches of M. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh). — FIG. 221,3. **T. multinervis*; wing, $\times 16$ (Rohdendorf, 1964).

Family DIXAMIMIDAE Rohdendorf, 1962

[Dixamimidae ROHDENDORF, 1962a, p. 314]

Wing broad; venation poorly known; vein RS arising in basal third of wing; male antennae 15-segmented; maxillary palpi 3-segmented. *Jur.*

Dixamima ROHDENDORF, 1962a, p. 314 [**D. villosa*; OD]. Little-known genus. Second segment of maxillary palpi thickest and curved. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family DIXIDAE van der Wulp, 1877

[Dixidae VAN DER WULP, 1877, p. 336]

Small flies, similar to the Culicidae. Wing veins without scales; RS1+2 strongly arched; halteres long. Mouthparts not forming a long proboscis. Larvae aquatic. *Oligo.*—*Holo.*

Dixa MEIGEN, 1818, p. 216 [= *Eriopterites* MEUNIER, 1915a, p. 15 (type, *E. hyalipennis*)]. MEUNIER, 1906a; COCKERELL, 1915, 1921d; HENNIG, 1966b. *Oligo.*, England, Europe (Baltic, France)—*Holo.*

Paradixa TONNOIR, 1924, p. 223. MEUNIER, 1906a; HENNIG, 1966b. *Oligo.*, Europe (Baltic)—*Holo.*

Family CULICIDAE Billberg, 1820

[Culicidae BILLBERG, 1820, p. 122]

Small flies. Wing veins bearing elongate or slender scales; vein RS1+2 aligned with stem RS. Mouthparts usually in form of long proboscis. Larvae aquatic. *Cret.*—*Holo.*

Culex LINNÉ, 1758, p. 602. [Generic assignment of fossils uncertain.] COCKERELL, 1915; EDWARDS, 1923. *Eoc.*, USA (Colorado, Wyoming); *Oligo.*, England—*Holo.*

Aedes MEIGEN, 1818, p. 13. COCKERELL, 1915; EDWARDS, 1923. *Oligo.*, England—*Holo.*

Anopheles MEIGEN, 1818, p. 10. [Generic assignment of fossil uncertain.] STATZ, 1944b. *Oligo.*, Europe (Germany)—*Holo.*

Chaoborus LICHTENSTEIN, 1800, p. 174 [= *Culicites* HEYDEN, 1862, p. 79 (type, *C. tertiaris*)].

[Fossils are pupae and adults.] MEUNIER, 1904b; HENNIG, 1966b, 1972b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Chironomaptera PING, 1928, p. 33 [**Samarura gregaria* GRABAU, 1923, p. 178; OD]. Little-known genus, based on fragments of adults. [Family assignment doubtful.] KALUGINA, 1977, 1980a. *Cret.*, China (Shandong), Mongolia.

Mansonia BLANCHARD, 1901, p. 1046. STATZ, 1944b; ROHDENDORF, 1961c. *Oligo.*, Europe (Baltic)—*Holo.*

Mochlonyx LOEW, 1844, p. 121. MEUNIER, 1902a; EDWARDS, 1923; HENNIG, 1966b. *Oligo.*, Europe (Baltic)—*Holo.*

Family ARCHITENDIPEDIDAE Rohdendorf, 1962

[Architendipedidae ROHDENDORF, 1962a, p. 317]

Small insects. Wing with costal margin nearly straight; costal area moderately wide, with some crossveins; vein SC very close to R; longitudinal veins mainly concentrated in anterior half of wing; main fork of RS at midwing; M very weak; crossveins present between R and M, and between M and CUA. Body unknown. *Trias.*

Architendipes ROHDENDORF, 1962a, p. 317 [**A. tschernovskiji*; OD]. Middle of costal area with several crossveins; basal part of M apparently coalesced with RS. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 221,5. **A. tschernovskiji*; wing, $\times 12$ (Rohdendorf, 1964).

Palaeotendipes ROHDENDORF, 1962a, p. 317 [**P. alexii*; OD]. Little-known wing; no crossveins in middle of costal area. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Family PROTENDIPEDIDAE Rohdendorf, 1962

[Protendipedidae ROHDENDORF, 1962a, p. 317]

Wing hairy; venation unknown; head small; female antenna with at least 7 segments. *Jur.*

Protendipes ROHDENDORF, 1962a, p. 317 [**P. dasypterus*; OD]. Posterior femora extremely elongate; third and sixth antennal segments cylindrical. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family CHIRONOMIDAE Macquart, 1838

[Chironomidae MACQUART, 1838, p. 36]

Small flies. Wings long and slender; microtrichia ordinarily present, scales absent; vein SC free but rarely well developed; RS1+2

commonly weak or absent; RS3+4 well developed and ordinarily coalesced with C near wing apex; M1+2 unbranched, extending nearly to wing apex; CUA forked. Body slender; mouthparts not piercing; legs long and thin. *Cret.*—*Holo.*

Chironomus MEIGEN, 1803, p. 260. MEUNIER, 1904a; THÉOBALD, 1937a; MANI, 1944, 1947b; MELANDER, 1949. *Paleoc.*—*Plio.*, India; *Eoc.*, USA (Colorado, Wyoming); *Oligo.*, USA (Colorado), Europe (Baltic, Germany, France); *Mio.*—*Plio.*, Europe (France); *Mio.*, Europe (Germany)—*Holo.*

Cretodiamesa KALUGINA, 1976, p. 88 [**C. tai-myrica*; OD]. Antennal flagella of male consisting of several very thin, waferlike segments and a very large terminal segment; plumage flat. Antennae of female with 15 segments. Wings with RS1+2 terminating on costa about midway between terminations of R and RS3+4. *Cret.*, USSR (Asian RSFSR).—FIG. 221,9. **C. tai-myrica*; wing of female, $\times 36$ (Kalugina, 1976).

Cricotopiella MEUNIER, 1916a, p. 282 [**C. rostrata*; OD]. Similar to *Cricotopus*, but rostrum as long as the head. *Oligo.*, Europe (Baltic).

Cricotopus VAN DER WULP, 1874, p. 132. MEUNIER, 1904a, 1916a. *Oligo.*, Europe (Baltic)—*Holo.*

Diamesa WALTJ, 1837, p. 283. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Electrotentia KALUGINA, 1980b, p. 91 [**E. brundini*; OD]. Male: antennae plumose, with 15 segments, penultimate segment elongate; wings without macrotrichia. Female: antennae with 14 segments. *Cret.*, USSR (Asian RSFSR).

Eurycnemus VAN DER WULP, 1874, p. 135. MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*

Libanochlites BRUNDIR, 1976, p. 149 [**L. neocomicus*; OD]. A podonomine genus of small species related to *Paraboreochlus* and *Boreochlus* (both recent). Female: wing with RS3+4 strongly curved and close to C; palpi reduced; at least 1 spur lacking on middle tibia. *Cret.*, Europe (Lebanon).—FIG. 221,10. **L. neocomicus*; wing of female, $\times 55$ (Brundin, 1976).

Manlayamyia KALUGINA, 1980a, p. 63 [**M. litonina*; OD]. Little-known genus, based on fragments of adults. *Cret.*, Mongolia.

Metriocnemus VAN DER WULP, 1874, p. 136. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*

Nomochirus COLLADO, 1926, p. 91 [**N. sampe-layoi*; OD]. Similar to *Telmatogeton* (recent), but male with only 7 antennal segments. *Paleoc.*—*Plio.*, Europe (Spain).

Palpomyia MEIGEN, 1818, p. 82. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Sendelia DUISBERG, 1868, p. 23. MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*

Smittia HOLMGREN, 1869, p. 47. MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*

- Spaniotoma** PHILIPPI, 1865, p. 629. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*
Tanypus MEIGEN, 1803, p. 261. MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*
Tanytarsus VAN DER WULP, 1874, p. 134. MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*

Family CERATOPOGONIDAE Skuse, 1890

[Ceratopogonidae SKUSE, 1890, p. 222]

Small to very small flies. Similar to Chironomidae but wings broader; vein M1+2 forked; RS3+4 terminating on costal margin nearer to midwing than to apex; anal area reduced. Mouthparts of females modified for piercing and sucking. Larvae aquatic or sub-aquatic. *Cret.*—*Holo.*

Ceratopogon MEIGEN, 1803, p. 261. LOEW, 1850; MEUNIER, 1904a; RUBTZOVA, 1936; CARPENTER & others, 1937; REMM, 1976. *Cret.*, Canada (Manitoba), USSR (Asian RSFSR); *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Atrichopogon KIEFFER, 1906, p. 53. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*

Atriculicoides REMM, 1976, p. 108 [**A. macrophthalmus*; OD]. Similar to *Atrichopogon* and *Culicoides*. Female: wings with abundant hairs; cells between R and RS elongate. Proboscis short; empodium and tibial spurs absent. *Cret.*, USSR (Asian RSFSR). — FIG. 221,11. **A. macrophthalmus*; fore wing of female, $\times 46$ (Remm, 1976).

Baeohelea WIRTH & BLANTON, 1970, p. 95. REMM, 1976. *Cret.*, USSR (Asian RSFSR)—*Holo.*

Culicoides LATREILLE, 1809, p. 251. PALMER, 1957; REMM, 1976. *Cret.*, USSR (Asian RSFSR); *Mio.*, USA (California)—*Holo.*

Dasyhelea KIEFFER, 1913, p. 179. CARPENTER & others, 1937; PALMER, 1957. *Cret.*, Canada (Manitoba); *Mio.*, USA (California)—*Holo.*

Eohelea PETRUNKEVITCH, 1957, p. 208 [**E. stridulans*; OD]. Wing: costa long, marginal, extending to apex; stridulatory organ (transverse ridges) in radial area distally. Antennae with 16 segments; legs slender, femora unarmed; hind tibial comb with 4 spines. WIRTH, 1974. *Oligo.*, Europe (Baltic). — FIG. 221,6. **E. stridulans*; wing, $\times 78$ (Petrunkevitch, 1957).

Johannsenomyia MALLOCH, 1915, p. 332. [Generic assignment of fossils (pupae) doubtful.] COCKERELL, 1919e; PIERCE, 1966. *Mio.*, Burma, USA (California)—*Holo.*

Lasiohelea KIEFFER, 1921, p. 115. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*

Miopalpomyia PIERCE, 1966, p. 95 [**M. shilo*; OD]. Little-known genus, based on pupa. *Mio.*, USA (California).

Neoculicoides PIERCE, 1966, p. 93 [**N. jeanneae*; OD]. Little-known genus, based on pupa. *Mio.*, USA (California).

Neopalpomyia PIERCE, 1966, p. 95 [**N. freyi*; OD]. Little-known genus, based on pupae. *Mio.*, USA (California).

Paraculicoides PIERCE, 1966, p. 94 [**P. rouseae*; OD]. Little-known genus, based on pupae. *Mio.*, USA (California).

Parapalpomyia PIERCE, 1966, p. 97 [**P. rysbkoffi*; OD]. Little-known genus, based on pupae. *Mio.*, USA (California).

Protoculicoides BOESEL, 1937, p. 50 [**P. depressus*; OD]. Similar to *Culicoides*, but RS3+4 ending about midway between R and M1+2. *Cret.*, Canada (Manitoba).

Family SIMULIIDAE Newman, 1835

[Simuliidae NEWMAN, 1835, p. 387]

Small, stout flies. Wings very broad, anal area forming a lobe; vein M1+2 forked; M3+4 arising at wing base, obsolescent. Body stout; proboscis short, females blood-sucking. Larvae in running water. *Oligo.*—*Holo.*

Simulium LATREILLE, 1802, p. 426. MEUNIER, 1904a; RUBTZOVA, 1936. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Nevermannia ENDERLEIN, 1921a, p. 199. ENDERLEIN, 1921b. *Oligo.*, Europe (Baltic)—*Holo.*

Family RHAETOMYIIDAE Rohdendorf, 1962

[Rhaetomyiidae ROHDENDORF, 1962a, p. 318]

Small insects. Wing broad, with broadly rounded apex; vein SC extending to midwing; RS arising just before midwing, with 3 branches; CUP obsolescent and close to CUA; no anal veins. Body unknown. *Trias.*

Rhaetomyia ROHDENDORF, 1962a, p. 318 [**R. necopinata*; OD]. Fork of RS1+2 about two-thirds as long as RS3+4; M3+4 unbranched. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 221,7. **R. necopinata*; wing, $\times 16$ (Rohdendorf, 1964).

Family MESOPHANTASMATIDAE Rohdendorf, 1962

[Mesophantasmatidae ROHDENDORF, 1962a, p. 319]

Wing narrow and petiolate; veins C, SC, and R close together; SC and R long; RS arising at midwing; M apparently with 3 branches; CUA and CUP close together. *Jur.*

Mesophantasma ROHDENDORF, 1962a, p. 319 [**M. tipuliforme*; OD]. Little-known wing; anterior branch of M simple; posterior branch forked near wing margin. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh). — FIG. 221, 1. **M. tipuliforme*; wing, $\times 7$ (Rohdendorf, 1964).

Family BLEPHAROCERIDAE

Loew, 1862

[Blepharoceridae Loew, 1862, p. 6]

Flies similar in general form to the Tipulidae, but wing membranes with a complicated network of veinlike markings caused, apparently, by folds within pupal wing cases. V-shaped mesonotal suture commonly absent; mouthparts elongate. Larvae and pupae in flowing water. *Eoc.*—*Holo.*

Blepharocera MACQUART, 1843, p. 61. *Holo.*

Paltostomopsis COCKERELL, 1915, p. 489 [**P. ciliatus*; OD]. Little-known genus, apparently similar to *Paltostoma* (recent), but CUA unbranched; anal vein absent. [Family assignment doubtful.] *Oligo.*, England.

Philorites COCKERELL, 1908o, p. 264 [**P. johannseni*; OD]. RS1+2 arising from RS3+4 a short distance beyond origin of RS and terminating below wing apex; proboscis longer than palpi. COCKERELL, 1920c. *Eoc.*, USA (Colorado).

Family PLECIODICTYIDAE

Rohdendorf, 1962

[Pleciodictyidae ROHDENDORF, 1962a, p. 319]

Very small insects. All wing veins weak except R and base of RS; R with basal break; RS arising about one-third wing length from base, with several short branches directed anteriorly to R; M very weak, branched. Body unknown. *Trias.*

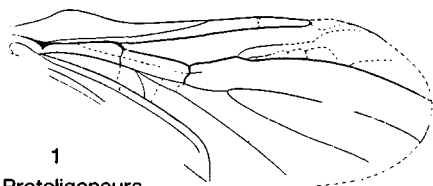
Pleciodictya ROHDENDORF, 1962a, p. 319 [**P. modesta*; OD]. Anterior margin of wing straight to midwing; R straight beyond break. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 222, 3. **P. modesta*; wing, $\times 25$ (Rohdendorf, 1964).

Family PROTOLIGONEURIDAE

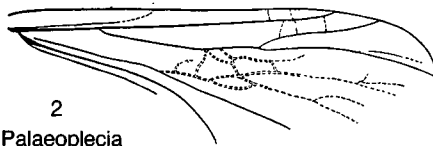
Rohdendorf, 1962

[Protoligoneuridae ROHDENDORF, 1962a, p. 319]

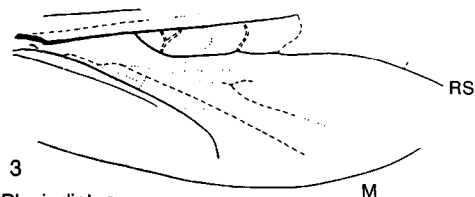
Very small insects. Wing: costal margin with a prominent bulge basally; veins nearly uniformly developed; vein RS arising about one-quarter wing length from base, its



1
Protoligoneura



2
Palaeoplecia



3
Pleciodictya

FIG. 222. Pleciodictyidae, Protoligoneuridae, and Palaeopleciidae (p. 409).

branches directed anteriorly but ending on costal margin beyond end of R; M deeply forked. Body unknown. *Trias.*

Protoligoneura ROHDENDORF, 1962a, p. 319 [**P. fusicosta*; OD]. SC terminating at midwing; RS strong, connected to M by 2 distinct but irregular crossveins. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 222, 1. **P. fusicosta*; wing, $\times 22$ (Rohdendorf, 1962a).

Family PALAEOPLECIIDAE

Rohdendorf, 1962

[Palaeopleciidae ROHDENDORF, 1962a, p. 319]

Wing elongate; basal part of vein R without break or bend; RS arising one-quarter wing length from base, with long anterior branch, parallel to end of R; crossveins present between R and C, RS1+2 and R, and between RS and M. *Trias.*

Palaeoplecia ROHDENDORF, 1962a, p. 319 [**P. rhaetica*; OD]. SC ending about one-third wing length from base; RS3+4 with a narrow fork; branches of M irregular and weak. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 222, 2. **P. rhaetica*; wing, $\times 14$ (Rohdendorf, 1962a).

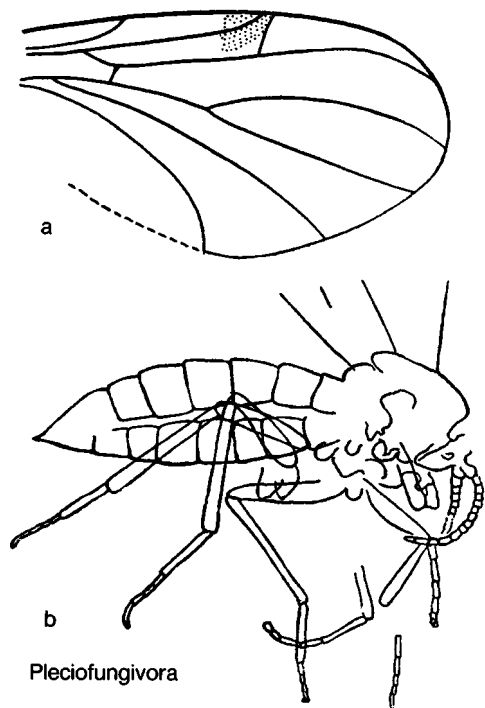


FIG. 223. Pleciofungivoridae (p. 410).

Family PLECIOfUNGIVORIDAE Rohdendorf, 1946

[Plecofungivoridae ROHDENDORF, 1946, p. 51]

Wing broad; vein SC about one-third of wing length, terminating on costa; RS arising in basal third of wing, with at least 1 branch, usually more; no strong crossveins between R and RS; posterior branch of M not thicker than other branches of M. Antennae with about 15 segments, not longer than head and thorax combined; legs slender; abdomen large, about twice length of head and thorax combined. *Trias.*—*Jur.*

Plecofungivora ROHDENDORF, 1938, p. 42 [**P. latipennis*; OD]. RS with a single weak and straight (or nearly so) branch, terminating on costal margin just beyond end of R; SC terminating slightly beyond level of origin of RS. ROHDENDORF, 1946, 1962a, 1964. *Jur.*, USSR (Kazakh).—FIG. 223. *P. major* ROHDENDORF; *a*, wing, $\times 18.5$; *b*, body, $\times 14$ (both Rohdendorf, 1962a).

Allactoneurites ROHDENDORF, 1938, p. 43 [**A. jurassicus*; OD]. Similar to *Palaeoesperinus*, but wing more slender; M3+4 arising near wing base

and strongly convex. ROHDENDORF, 1946, 1962a, 1964. *Jur.*, USSR (Kazakh).

Archihesperinus ROHDENDORF, 1962a, p. 321 [**A. pbryneoides*; OD]. Wing broad; SC branched; RS with a sigmoidal branch ending on costa. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 224,1. **A. pbryneoides*; wing, $\times 21$ (Rohdendorf, 1962a).

Archiplecofungivora ROHDENDORF, 1962a, p. 321 [**A. binerva*; OD]. Wing as in *Archihesperinus*; SC unbranched; strong crossvein in costal area. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Archipleciomima ROHDENDORF, 1962a, p. 321 [**A. obtusipennis*; OD]. Wing with broadly rounded apex; SC ending in membrane; branch of RS resembling a crossvein to R. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 224,4. **A. obtusipennis*; wing, $\times 29$ (Rohdendorf, 1962a).

Eoesperinus ROHDENDORF, 1946, p. 60 [**E. martynovi*; OD]. Wing venation as in *Palaeoesperinus*, but wing much broader. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).

Eopachyneura ROHDENDORF, 1946, p. 57 [**E. trisectoralis*; OD]. Little-known wing; RS with 2 sigmoidal branches leading to costal margin. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).

Palaeoesperinus ROHDENDORF, 1962a, p. 323 [**P. longipennis*; OD]. RS1+2 arising close to crossvein r-m; M3+4 nearly straight. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 224,2. **P. longipennis*; wing, $\times 19$ (Rohdendorf, 1962a).

Plecofungivorella ROHDENDORF, 1946, p. 54 [**P. binerva*; OD]. Little-known insect; SC short; RS with 2 oblique branches, one terminating on R, the other on costa. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).

Polyneurisca ROHDENDORF, 1946, p. 52 [**P. atavina*; OD]. Wing broadly oval; RS with several branches leading to R and costa; base of RS curved abruptly away from R. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).—FIG. 224,7. **P. atavina*; wing, $\times 32$ (Rohdendorf, 1962a).

Prohesperinus ROHDENDORF, 1946, p. 56 [**P. abdominalis*; OD]. Wing as in *Palaeoesperinus*, but M3+4 strongly curved. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).—FIG. 224,5. **P. abdominalis*; wing, $\times 17$ (Rohdendorf, 1962a).

Protallactoneura ROHDENDORF, 1962a, p. 321 [**P. turanica*; OD]. Little-known wing, similar to *Rhaetofungivorodes*, but branches of RS reticulate and weak. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Rhaetofungivora ROHDENDORF, 1962a, p. 320 [**R. reticulata*; OD]. Wing broad; no distinct crossvein in costal area; SC and M weak; R and RS strong; branches of RS variable, from 1 to several or even to a network of weak veins. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).—FIG. 224,6. **R. reticulata*; wing, $\times 29$ (Rohdendorf, 1964).

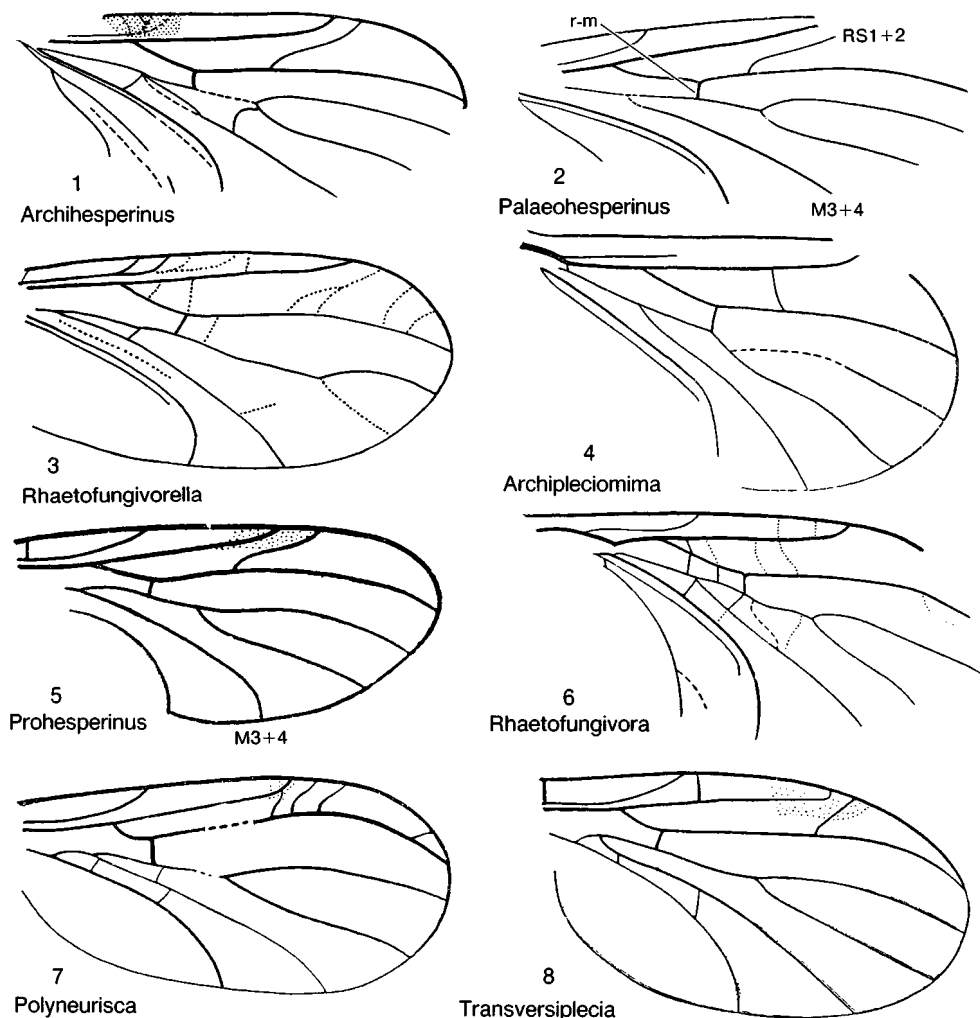


FIG. 224. Pleciofungivoridae (p. 410–411).

Rhaetofungivorella ROHDENDORF, 1962a, p. 320 [**R. subcosta*; OD]. Wing moderately slender. SC with distal branches or short crossveins; RS sigmoidal, with several weak, variable branches, leading either to R or wing margin; one strong crossvein between M and RS, others weak. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Kazakh).—FIG. 224,3. **R. subcosta*; wing, $\times 28$ (Rohdendorf, 1964).

Rhaetofungivorodes ROHDENDORF, 1962a, p. 320 [**R. defectivus*; OD]. Little-known wing, with wide costal area, long SC, and oblique branches on RS. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Transversiplecia ROHDENDORF, 1946, p. 53 [**T. transversinervis*; OD]. Wing broadly oval; 1

strong crossvein in subcostal area, 1 oblique crossvein between R and costal margin, and 2 between posterior branch of M and CUA. ROHDENDORF, 1962a, 1964. *Jur.*, USSR (Kazakh).—FIG. 224,8. **T. transversinervis*; wing, $\times 16$ (Rohdendorf, 1962a).

Family FUNGIVORITIDAE Rohdendorf, 1946

[*nom. transl.* ROHDENDORF, 1957, p. 91, ex Fungivoritinae ROHDENDORF, 1946, p. 79]

Wing with vein R extending nearly to apex; RS arising abruptly from R, without distinct, longitudinal branches; all branches of M equally strong. *Jur.*

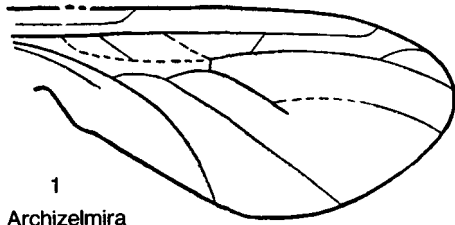
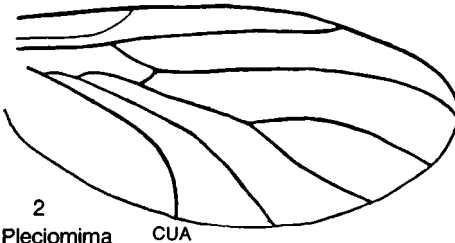
1
Archizelmira2
Pleciomima CUA

FIG. 225. Archizelmiridae and Pleciomimidae (p. 412).

Fungivorites ROHDENDORF, 1938, p. 46 [**F. latimediis*; OD]. Little-known genus; R almost straight; crossvein r-m very short. ROHDENDORF, 1946, 1962a. *Jur.*, USSR (Kazakh).

Eoboletina ROHDENDORF, 1946, p. 79 [**E. gracilis*; OD]. RS without branches; SC terminating at level of crossvein r-m. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Mesosciophila ROHDENDORF, 1946, p. 76 [**M. venosa*; OD]. Wing very broad; RS with a weak anterior branch leading to R; crossvein r-m longer than in *Fungivorites*. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Mesosciophilodes ROHDENDORF, 1946, p. 77 [**M. angustipennis*; OD]. Similar to *Mesosciophila*, but wing more slender. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Mimalycoria ROHDENDORF, 1946, p. 78 [**M. allactoneuroides*; OD]. Similar to *Eoboletina* but SC shorter. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Family ARCHIZELMIRIDAE Rohdendorf, 1962

[Archizelmiridae ROHDENDORF, 1962a, p. 326]

Wing with vein R long, extending nearly to apex of wing; RS with 2 anterior branches, 1 distal, terminating on C near end of R, the other near midwing, short and terminating on R; crossvein r-m very short. Head large; antennae not longer than thorax. *Jur.*

Archizelmira ROHDENDORF, 1962a, p. 326 [**A. kazachstanica*; OD]. Costal area rather wide; SC terminating before midwing. ROHDENDORF, 1946. *Jur.*, USSR (Kazakh).—FIG. 225, 1. **A. kazachstanica*; wing, $\times 18$ (Rohdendorf, 1962a).

Family PLECIOMIMIDAE Rohdendorf, 1946

[Pleciomimidae ROHDENDORF, 1946, p. 61]

Wing broad; vein SC present but usually weak, extending to about one-third of wing length; RS with strong base and without branches; crossveins absent between branches of M and between M and CUA. *Jur.*

Pleciomima ROHDENDORF, 1938, p. 44 [**P. sepulta*; OD]. R very straight, without basal bend; RS strongly curved posteriorly in distal region. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).—FIG. 225, 2. **P. sepulta*; wing, $\times 22$ (Rohdendorf, 1938).

Antefungivora ROHDENDORF, 1938, p. 48 [**A. prima*; OD]. Similar to *Pleciomima*, but crossveins between M and RS more remote from origin of RS. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Antiquamedia ROHDENDORF, 1938, p. 47 [**A. tenuipes*; OD]. SC very short, recurved and ending on R. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Archibio HANDLIRSCH, 1939, p. 105 [**A. mycetophilinus*; OD]. Little-known genus, with M3+4 apparently arising from CUA near wing base. ROHDENDORF, 1964. *Jur.*, Europe (Germany).

Archilycoria ROHDENDORF, 1962a, p. 328 [**A. magna*; OD]. Similar to *Antefungivora*, but crossvein r-m longer. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Lycoriomima ROHDENDORF, 1946, p. 62 [**L. ventralis*; OD]. R curved anteriorly at its distal end; RS only slightly curved posteriorly; CUP distinct. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Lycoriomimella ROHDENDORF, 1946, p. 69 [**L. minor*; OD]. R slightly wavy. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Lycoriomimodes ROHDENDORF, 1946, p. 67 [**L. deformatus*; OD]. RS sigmoidally curved. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Lycorioplecia ROHDENDORF, 1946, p. 66 [**L. elongata*; OD]. Similar to *Lycoriomima*, but CUP indistinct; weak pterostigma present. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Megalycoriomima ROHDENDORF, 1962a, p. 326 [**M. magnipennis*; OD]. Little-known insect; RS curved distally; M1+2 indistinct. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Mimallactoneura ROHDENDORF, 1946, p. 72 [**M.*

vetusta; OD]. SC very weak, indistinct; R nearly straight; M and CUP distinct. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Paralycoriomima ROHDENDORF, 1946, p. 64 [**P. sororcula*; OD]. SC and CUP distinct; R nearly straight; RS smoothly and gradually curved; CUA abruptly curved distally. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Paritonida ROHDENDORF, 1946, p. 74 [**P. brachyptera*; OD]. Crossvein r-m much shorter than basal section of RS. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Pleciomimella ROHDENDORF, 1946, p. 71 [**P. karatavica*; OD]. Similar to *Pleciomima* but SC weak distally and R slightly curved distally. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).

Family TIPULOPLECIIDAE

Rohdendorf, 1962

[Tipulopleciidae ROHDENDORF, 1962a, p. 328]

Wing much longer than abdomen; vein R straight; RS with at least 2 anterior branches, 1 ending on R. Legs very slender. *Jur.*

Tipuloplecia ROHDENDORF, 1962a, p. 328 [**T. breviventris*; OD]. Little-known genus; RS strongly curved posteriorly. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family SINEMEDIIDAE

Rohdendorf, 1962

[Sinemediidae ROHDENDORF, 1962a, p. 328]

Similar to Tipulopleciidae, but wings more narrow and vein RS without branches; legs stout. *Jur.*

Sinemedia ROHDENDORF, 1962a, p. 328 [**S. angustipennis*; OD]. Little-known genus; crossvein r-m oblique. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

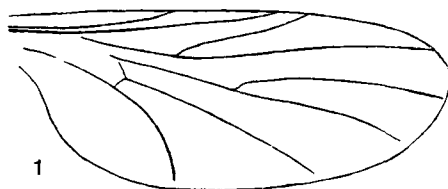
Family PARAXYMYIIDAE

Rohdendorf, 1946

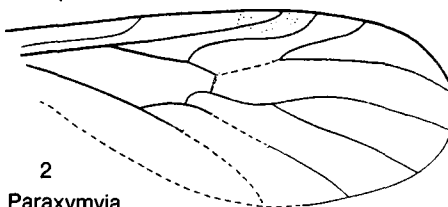
[Paraxymyiidae ROHDENDORF, 1946, p. 44]

Wing with vein SC short, not extending to midwing; RS with 2 long branches, 1 arising basad of crossvein r-m. *Jur.*

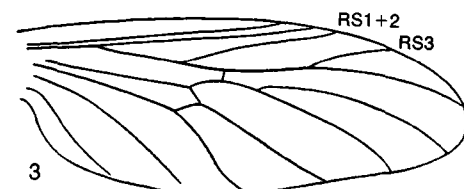
Paraxymyia ROHDENDORF, 1946, p. 45 [**P. quadriradialis*; OD]. Pterostigma present; posterior branch of RS forked. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).—FIG. 226,2. **P. quadriradialis*; wing, $\times 24$ (Rohdendorf, 1962a).



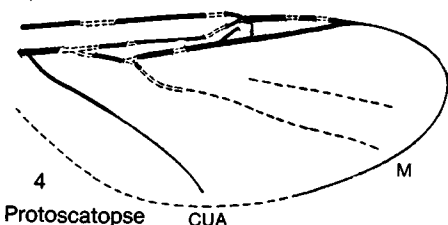
1
Protoplecia



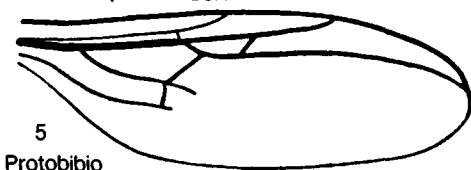
2
Paraxymyia



3
Eoplecia



4
Protoscatopse



5
Protobiblio

FIG. 226. Paraxymyiidae, Eopleciidae, Protopleciidae, Protobibionidae, and Protoscatopsidae (p. 413–414).

Family EOPLECIIDAE

Rohdendorf, 1946

[Eopleciidae ROHDENDORF, 1946, p. 43]

Wing with vein SC long, extending beyond midwing; RS with 2 long, well-developed branches to anterior margin of wing. Body unknown. *Jur.*

Eoplecia HANDLIRSCH, 1920, p. 203 [**E. primitiva*; OD]. M3 + 4 apparently anastomosed with ante-

rior branch of CUA. HANDLIRSCH, 1939; ROHDENDORF, 1946, 1962a; BODE, 1953. *Jur.*, Europe (Germany).—FIG. 226.3. **E. primitiva*; wing, $\times 18$ (Handlirsch, 1939).

Family PROTOPLECIIDAE Rohdendorf, 1946

[Protopleciidae ROHDENDORF, 1946, p. 42]

Wing with vein SC short, commonly ending before midwing; RS with an oblique anterior branch, terminating near end of R. *Jur.*

Protoplecia HANDLIRSCH, 1906b, p. 488 [**Macropiza liasina* GEINITZ, 1884, p. 582; OD]. M1 + 2 forking distally of fork on RS. ROHDENDORF, 1964. *Jur.*, Europe (Germany).—FIG. 226.1. **P. liasina* (GEINITZ); wing, $\times 16$ (Handlirsch, 1907).

Mesoplecia ROHDENDORF, 1938, p. 49 [**M. jurassica*; OD]. SC extending to about midwing; M1 + 2 forking proximally of fork RS. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Mesopleciella ROHDENDORF, 1946, p. 43 [**M. minor*; OD]. Similar to *Mesoplecia*, but SC much shorter. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family PROTOBIBIONIDAE Rohdendorf, 1946

[Protobibionidae ROHDENDORF, 1946, p. 46]

Very small insects. Wing with vein RS with 1 short branch leading directly to R near midwing; anterior veins strong. *Jur.*

Protobibio ROHDENDORF, 1946, p. 47 [**P. jurassicus*; OD]. SC extending almost to midwing; crossvein r-m long, oblique. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).—FIG. 226.5. **P. jurassicus*; wing, $\times 36$ (Rohdendorf, 1962a).

Family PROTOSCATOPSIDAE Rohdendorf, 1946

[Protoscatopsidae ROHDENDORF, 1946, p. 48]

Wing with anterior veins very strong, veins in rest of wing weak or obsolescent; RS with 2 very short anterior branches leading directly into C just beyond end of R. Antenna short. *Jur.*

Protoscatopse ROHDENDORF, 1946, p. 49 [**P. jurassica*; OD]. CUA almost straight, weak distally. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).—FIG. 226.4. **P. jurassica*; wing, $\times 26$ (Rohdendorf, 1962a).

Family SCATOPSIDAE Newman, 1835

[Scatopsidae NEWMAN, 1835, p. 387]

Small to very small flies. Wings with veins R and RS very strong, other veins much weaker; SC vestigial; RS reduced to RS3 + 4 and unbranched, commonly extending only to midwing. Larvae saprophagous, usually found in rotting vegetation. *Oligo.*—*Holo.*

Scatopse GEOFFROY, 1762, p. 450. [Generic assignment of fossils doubtful.] MEUNIER, 1904d; MELANDER, 1949. *Oligo.*, USA (Colorado), Europe (Baltic)—*Holo.*

Family BIBIONIDAE Newman, 1835

[Bibionidae NEWMAN, 1835, p. 387]

Small to moderate-sized flies. Wings without discal cell; vein SC well developed, usually extending to midwing; RS forked into RS1 + 2 and RS3 + 4 or reduced to unbranched RS3 + 4; M with 2 branches; CUA1 and CUA2 extending to hind margin of wing. Antennae typically short; eyes of male holoptic. Larvae mostly saprophagous, in soil. *Cret.*—*Holo.*

Bibio GEOFFROY, 1762, p. 568. BUTLER, 1889; COCKERELL, 1909j, 1921d; MEUNIER, 1915b; PONGRÁČZ, 1928; PITON & THÉOBALD, 1935; MANEVAL, 1936; JAMES, 1937; THÉOBALD, 1937a; STATZ, 1943; MELANDER, 1949; DÜRRENFELDT, 1968. *Oligo.*, Europe (Germany, France), England, USA (Colorado); *Mio.*, Europe (Croatia); *Plio.*, Europe (Germany)—*Holo.*

Bibiodes COQUILLET, 1904, p. 171. JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Bibiodites COCKERELL, 1915, p. 493 [**B. confluens*; OD]. Similar to *Bibiodes* (recent), but RS in very brief contact with M1 + 2. *Oligo.*, England.

Dilophus MEIGEN, 1803, p. 264. DÜRRENFELDT, 1968; HARRIS, 1983. *Eoc.*, New Zealand (North Otago); *Plio.*, Europe (Germany)—*Holo.*

Hesperinus WALKER, 1848, p. 81. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Lithosomyia CARPENTER, 1986, p. 576, *nom. subst. pro Mesomyia* PONGRÁČZ, 1928, p. 174, *non* MACQUART, 1849 [**Bibio brevis* HEER, 1849, p. 225; SD CARPENTER, 1986, p. 576]. Venation as in *Bibio*, but fork of M1 + 2 shorter. *Mio.*, Europe (Croatia).

Penthetria MEIGEN, 1803, p. 264 [= *Bibiopsis* HEER, 1849, p. 228 (type, *B. cimicoides*); *Protomyia* HEER, 1849, p. 231 (type, *Bibio lygaeoides* UNGER)]. HANDLIRSCH, 1910b; MEUNIER, 1917c, 1918; PONGRÁČZ, 1928; STATZ, 1944b; MELANDER, 1949; LEWIS, 1971b. *Eoc.*, Canada

(British Columbia); *Oligo.*, Europe (Germany), USA (Colorado, Montana); *Mio.*, Europe (Croatia)—*Holo.*

Plecia WIEDEMANN, 1828, p. 72. COCKERELL, 1914f, 1917b, 1921d; THÉOBALD, 1937a; CARPENTER & others, 1938; ZEUNER, 1941a; PETERSON, 1975. *Cret.*, Canada (Manitoba); *Paleoc.-Phio.*, Europe (France); *Eoc.*, Scotland; *Oligo.*, Europe (Germany, France), England, USA (Colorado)—*Holo.*

Family SCIARIDAE Billberg, 1820

[Sciaridae BILLBERG, 1820, p. 121]

Small flies. Wings with vein R short, usually not extending beyond midwing; RS arising from R as a short, transverse vein and connected to M1+2 by the longitudinally arranged crossvein r-m. Coxae enlarged; eyes commonly touching above antennae; tibiae without prominent spines. Larvae mostly saprophagous, in decaying vegetation. *Eoc.*—*Holo.*

Sciara MEIGEN, 1803, p. 263. SCUDDER, 1878d; COCKERELL, 1910b, 1915, 1916c, 1917c; MEUNIER, 1917c; THÉOBALD, 1937b; ARMBRUSTER, 1938; QUIÉVREUX, 1938; STATZ, 1944c; MELANDER, 1949. *Eoc.*, Canada (British Columbia); *Oligo.*, Europe (Baltic, France, Germany), England, USA (Colorado); *Mio.*, Burma, Europe (Germany)—*Holo.*

Lycoriella FREY, 1942, p. 36. [Generic assignment of fossil doubtful.] MEUNIER, 1904a. *Oligo.*, Europe (Baltic)—*Holo.*

Protosciara QUIÉVREUX, 1938, p. 83 [**P. alsatica*; OD]. Little-known genus; M3+4 apparently forked. [Family assignment doubtful.] *Oligo.*, Europe (Baltic).

Pseudosciara SCHINER, 1866, p. 930 [= *Heeriella* MEUNIER, 1904a, p. 86 (type, *H. bifurcata*)]. FREY, 1942. *Oligo.*, Europe (Baltic)—*Holo.*

Ruebsaameniella MEUNIER, 1903a, p. 165 [**R. semibrachyptera*; OD]. Similar to *Lycoriella* (recent), but female with reduced venation as well as small wings. FREY, 1942. *Oligo.*, Europe (Baltic).

Trichosia WINNERTZ, 1867, p. 173. HEER, 1849; FREY, 1942. *Oligo.*, Europe (Croatia)—*Holo.*

Family MYCETOPHILIDAE

Newman, 1835

[Mycetophilidae NEWMAN, 1835, p. 386]

Small to very small flies. Wings with diverse venation. Vein RS1+2 either absent or reduced to short, transverse vein leading to costal margin; stem of RS usually arising

as transverse crossvein and joined to M1+2 by crossvein r-m, or coalesced with M1+2 for a short distance; 1A absent. Antennae much longer than head, eyes not touching dorsally; tibiae commonly with strong spines. Larvae typically associated with fungi, developing in their fruiting bodies; some larvae making webs or tubes. *Paleoc.*—*Holo.*

Mycetophila MEIGEN, 1803, p. 263. COCKERELL, 1915; PITON & THÉOBALD, 1935; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), England, Europe (France, Croatia)—*Holo.*

Acnemia WINNERTZ, 1863, p. 798. COCKERELL, 1921d, 1924a. *Eoc.*, USA (Colorado); *Oligo.*, England—*Holo.*

Allactoneura de MEIJERE, 1907, p. 201. [Generic assignment of fossil doubtful.] THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Allodia WINNERTZ, 1863, p. 826. MEUNIER, 1916b, 1917a, 1922, 1923a; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)—*Holo.*

Anacileia MEUNIER, 1904a, p. 157. EDWARDS, 1940. *Oligo.*, Europe (Baltic)—*Holo.*

Aneura MARSHALL, 1896, p. 287. [Generic assignment of fossil doubtful.] RIEK, 1954a. *Paleoc.*—*Eoc.*, Australia (Queensland)—*Holo.*

Archaeolettina MEUNIER, 1904a, p. 160 [**A. tipuliformis*; OD]. Similar to *Speolepta* (recent) but with SC2 only slightly before RS; separation of M3+4 from CUA almost below crossvein r-m; macrotrichia absent from wing membrane and forks of veins. MEUNIER, 1904d; EDWARDS, 1940. *Oligo.*, Europe (Baltic).

Archaeomacrocera MEUNIER, 1917a, p. 88 [**A. concinna*; OD]. Similar to *Macrocera*, except in minor venational details. [Probably a synonym of *Macrocera*.] *Oligo.*, Europe (Baltic).

Asindulum LATREILLE, 1805, p. 290. [Generic assignment of fossil doubtful.] STATZ, 1944a. *Oligo.*, Europe (Baltic)—*Holo.*

Austrolocymerus FREEMAN, 1954, p. 39. [Generic assignment of fossil doubtful.] RIEK, 1954a (as *Centrocnemis*). *Paleoc.*—*Eoc.*, Australia (Queensland)—*Holo.*

Boletina STAEGER, 1840, p. 233. MEUNIER, 1916b, 1917a, 1920d, 1922, 1923a; STATZ, 1944a; MELANDER, 1949. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Brachypeza WINNERTZ, 1863, p. 806. MEUNIER, 1917a, 1917c. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Bradysia WINNERTZ, 1867, p. 180. MEUNIER, 1904a; FREY, 1942. *Oligo.*, Europe (Baltic)—*Holo.*

Burmacrocera COCKERELL, 1917h, p. 326 [**B. petiolata*; OD]. Similar to *Palaeoplasyra*, but crossvein r-m absent; thorax strongly setose. *Mio.*, Burma.

Coelosia WINNERTZ, 1863, p. 796 [= *Palaeophthibinia* MEUNIER, 1904a, p. 160 (type, *P. aberrans*)].

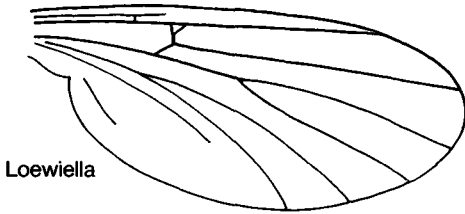


FIG. 227. Mycetophilidae (p. 416).

- MEUNIER, 1917a; EDWARDS, 1940. *Oligo.*, Europe (Baltic)-*Holo.*
- Cordyla** MEIGEN, 1803, p. 263. MEUNIER, 1917a, 1923b; STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Dianepsia** LOEW, 1850, p. 33 [**D. bisssa*; OD]. Similar to *Docosia*, but wings short and broad, with very short SC; SC2 present; macrotrichia absent on wing membrane and forks of veins. MEUNIER, 1899a; EDWARDS, 1940. *Oligo.*, Europe (Baltic).
- Ditomyia** WINNERTZ, 1846, p. 14. STATZ, 1944a. *Oligo.*, Europe (Germany)-*Holo.*
- Docosia** WINNERTZ, 1863, p. 802. MEUNIER, 1916b, 1917a, 1922, 1923a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Dziedzicka** JOHANNSEN, 1909, p. 44. [Generic assignment of fossils doubtful.] MEUNIER, 1917b, 1922, 1923a; STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Ectrepesthoneura** ENDERLEIN, 1910, p. 155, *nom. subst. pro Willistoniella* MEUNIER, 1904a, p. 85, *non* MIK, 1895. EDWARDS, 1940; STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Exechia** WINNERTZ, 1863, p. 879. COCKERELL, 1908a; PONGRÁČ, 1928; THÉOBALD, 1937a; STATZ, 1944a; MELANDER, 1949. *Oligo.*, USA (Colorado), Europe (Baltic, Germany, France); *Mio.*, Europe (Croatia)-*Holo.*
- Gnoriste** MEIGEN, 1818, p. 243. PONGRÁČ, 1928. *Oligo.*, Europe (France)-*Holo.*
- Heterotricha** LOEW, 1850, p. 33 [= *Palaeobeterotricha* MEUNIER, 1904a, p. 62 (type, *P. grandis*)]. FREY, 1942. *Oligo.*, Europe (Baltic)-*Holo.*
- Leia** MEIGEN, 1818, p. 253. COCKERELL, 1911b; MEUNIER, 1917a, 1918; STATZ, 1944a; SNYDER, 1950. *Oligo.*, USA (Colorado), Europe (Baltic, Germany, France)-*Holo.*
- Leptomorphus** CURTIS, 1831, pl. 365. MEUNIER, 1917a; COCKERELL, 1920c. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Baltic)-*Holo.*
- Loewiella** MEUNIER, 1894, p. cxi [**L. incompleta*; SD JOHANNSEN, 1909, p. 44]. Similar to *Dziedzicka*, but stem of M1+2 longer than crossvein r-m; RS3+4 straight or nearly so. EDWARDS, 1940. *Oligo.*, Europe (Baltic). — FIG. 227. **L. incompleta*; wing, $\times 16$ (Johannsen, 1909).
- Macrocera** MEIGEN, 1803, p. 261. COCKERELL, 1910b; STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Manota** WILLISTON, 1896, p. 260 [= *Cerato* MEUNIER, 1904a, p. 87 (type, *C. longipalpis*)]. JOHANNSEN, 1909; STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Mycetophaetus** SCUDDER, 1892, p. 20 [**M. intermedius*; OD]. Similar to *Sciophila* (recent), but stem of M connected to R by crossvein near wing base. *Oligo.*, USA (Colorado).
- Mycomya** RONDANI, 1856, p. 194. JOHANNSEN, 1912; COCKERELL, 1914f, 1921d, 1923b; THÉOBALD, 1937a; ROHDENDORF, 1961c. *Oligo.*, USA (Colorado), Europe (Baltic, Germany, France); *Paleoc.-Plio.*, South America (Colombia)-*Holo.*
- Necromyza** SCUDDER, 1895a, p. 121 [**N. pedata*; OD]. Little-known genus; SC appears to terminate on R just beyond origin of RS. *Mio.*, Europe (Germany).
- Neoempheria** OSTEN-SACKEN, 1878, p. 9. MEUNIER, 1922, 1923a; QUIÉVREUX, 1938. *Oligo.*, Europe (Baltic, France)-*Holo.*
- Neuratelia** RONDANI, 1856, p. 195 [= *Proanaclinia* MEUNIER, 1904a, p. 156 (type, *P. gibbosa*; SD EDWARDS, 1940)]. STATZ, 1944a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
- Palaeoanaclinia** MEUNIER, 1904a, p. 154 [**P. distincta*; SD JOHANNSEN, 1909, p. 86]. Similar to *Boletina*; wings without macrotrichia on membrane and forks of veins; SC2 absent; stem of M1+2 short. EDWARDS, 1940. *Oligo.*, Europe (Baltic).
- Palaeoboletina** MEUNIER, 1904a, p. 161 [**P. elongatissima*; SD EDWARDS, 1940, p. 122]. Similar to *Boletina* but with SC2 arising near end of SC. [Possibly a synonym of *Boletina*.] JOHANNSEN, 1909. *Oligo.*, Europe (Baltic).
- Palaeodocosia** MEUNIER, 1904a, p. 172 [**P. brachypezoides*; OD] [= *Palaeotrichonta* MEUNIER, 1904a, p. 179 (type, *P. brachycamptites*); *Paleosyntemna* MEUNIER, 1922, p. 119 (type, *P. brachypezoides*); *Sciomorpha* MEUNIER, 1923a, p. 25, *nom. nud.*]. JOHANNSEN, 1909; EDWARDS, 1940. *Oligo.*, Europe (Baltic).
- Palaeoempalia** MEUNIER, 1904a, p. 128, *nom. subst. herein pro Sciobia* LOEW, 1850, p. 34, *non* BURMEISTER, 1838 [**P. brongniarti*; SD JOHANNSEN, 1909, p. 117]. Little-known genus, apparently related to *Sciophila* and *Mycomya*; SC reaching costa. MEUNIER, 1916b, 1922, 1923a. *Oligo.*, Europe (Baltic).
- Palaeognoriste** MEUNIER, 1904a, p. 87 [**P. sciariforme*; OD]. Proboscis elongate; wing venation little known. [Possibly a sciarid.] JOHANNSEN, 1909; MEUNIER, 1912b. *Oligo.*, Europe (Baltic).
- Paraleia** ARMBRUSTER, 1938, p. 120 [**P. rhymosides*; OD]. Little-known genus. *Mio.*, Europe (Germany).

- Phronia** WINNERTZ, 1863, p. 857. MEUNIER, 1917a; COCKERELL, 1921d; THÉOBALD, 1937a. *Oligo.*, England, Europe (Baltic, France)—*Holo.*
- Phthinia** WINNERTZ, 1863, p. 779. STATZ, 1944a. *Oligo.*, Europe (Germany)—*Holo.*
- Platyura** MEIGEN, 1803, p. 264. MEUNIER, 1917a; COCKERELL, 1921d; SCHMALFUSS, 1979. *Oligo.*, England, Europe (Baltic); *Oligo./Mio.*, Dominican Republic—*Holo.*
- Proallogia** ARMBRUSTER, 1938, p. 121 [**P. rhymsides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Proapemon** MELANDER, 1949, p. 9 [**P. infernus*; OD]. Venation as in *Hesperodes* (recent) but the 3 ocelli distinct and antennal scape long. *Oligo.*, USA (Colorado).
- Proapolephthisa** ARMBRUSTER, 1938, p. 119 [**P. manorides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Proboletina** MEUNIER, 1904a, p. 162 [**P. syntemniiformis*; OD]. Venation as in *Synapba*. Eyes emarginate above antennae; lateral ocelli touching eyes; palpi 3-segmented; claws with subbasal tooth. EDWARDS, 1940. *Oligo.*, Europe (Baltic).
- Proceroplatus** EDWARDS, 1925, p. 523. SCHMALFUSS, 1979. *Oligo./Mio.*, Dominican Republic—*Holo.*
- Prodelopsis** ARMBRUSTER, 1938, p. 122 [**P. epi-cyptides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Prodocosia** ARMBRUSTER, 1938, p. 120 [**P. ronaldaniellides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Proepicypta** ARMBRUSTER, 1938, p. 121 [**P. obesa*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Prohadroneura** ARMBRUSTER, 1938, p. 119 [**P. dziedzickides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Proleia** ARMBRUSTER, 1938, p. 120 [**P. landrocki*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Promacrocera** ARMBRUSTER, 1938, p. 118 [**P. archaica*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Promycetomyia** ARMBRUSTER, 1938, p. 119 [**P. neoempherides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Proneoglyphoptera** MEUNIER, 1904a, p. 169 [**P. eocenica*; OD]. Related to *Leia* and most similar to *Paraleia* but with the 3 ocelli arranged in a straight line, lateral ones touching eyes. COCKERELL, 1926c; EDWARDS, 1940. *Oligo.*, Europe (Baltic).
- Pronovakia** ARMBRUSTER, 1938, p. 120 [**P. incerta*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Prophronia** ARMBRUSTER, 1938, p. 121 [**P. dynat-osomides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Prophthinia** ARMBRUSTER, 1938, p. 119 [**P. coe-*
- losides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Protasmanina** RIEK, 1954a, p. 60 [**P. nana*; OD]. Similar to *Tasmanina* (recent). SC ending on C after origin of RS; RS transverse from its origin to crossvein r-m; M3 + 4 arising from CUA basad of forking of M1 + 2. *Paleoc.-Eoc.*, Australia (Queensland).
- Protrichonta** ARMBRUSTER, 1938, p. 121 [**P. delop-sides*; OD]. Little-known genus. *Mio.*, Europe (Germany).
- Rymosia** WINNERTZ, 1863, p. 810 [= *Palaeoepicypta* MEUNIER, 1904a, p. 181 (type, *P. longicalcar*)]. COCKERELL, 1921d; THÉOBALD, 1937a; EDWARDS, 1940. *Oligo.*, England, Europe (Baltic, Germany)—*Holo.*
- Sciophila** MEIGEN, 1818, p. 245. COCKERELL, 1909d; MEUNIER, 1915b. *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*
- Symmerus** WALKER, 1848, p. 88. MEUNIER, 1906a. *Oligo.*, Europe (Baltic)—*Holo.*
- Synapba** MEIGEN, 1818, p. 227. MEUNIER, 1917a. *Oligo.*, Europe (Baltic)—*Holo.*
- Syntemma** WINNERTZ, 1863, p. 767. MEUNIER, 1904a, 1917a, 1917c, 1922, 1923a. *Oligo.*, Europe (Baltic)—*Holo.*
- Tetragoneura** WINNERTZ, 1846, p. 18 [= *Sciarella* MEUNIER, 1904a, p. 89 (type, *S. mycetophiliformis*), non LENDENFELD, 1884]. COCKERELL, 1909d; MEUNIER, 1914a, 1922, 1923a; EDWARDS, 1940; STATZ, 1944a. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Family OLIGOPHRYNEIDAE Rohdendorf, 1962

[Oligophryneidae ROHDENDORF, 1962a, p. 332]

Wing broad; vein SC apparently very short; RS with 2 branches, anterior one simple, posterior one forked distally; discal cell small. Body unknown. *Trias.*

Oligophryne ROHDENDORF, 1962a, p. 332 [**O. fungivoroides*; OD]. SC terminating in membrane; R strong. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 228.4. **O. fungivoroides*; wing, ×26 (Rohdendorf, 1964).

Family PROTOLBIOGASTRIDAE Rohdendorf, 1962

[Protolbiogastridae ROHDENDORF, 1962a, p. 332]

Wing with broad costal area; vein SC long; R with strong, complicated strut near wing base, joining R to CUA; anterior branch of RS sigmoidal, terminating on costa just beyond R; discal cell prominent. *Trias.*

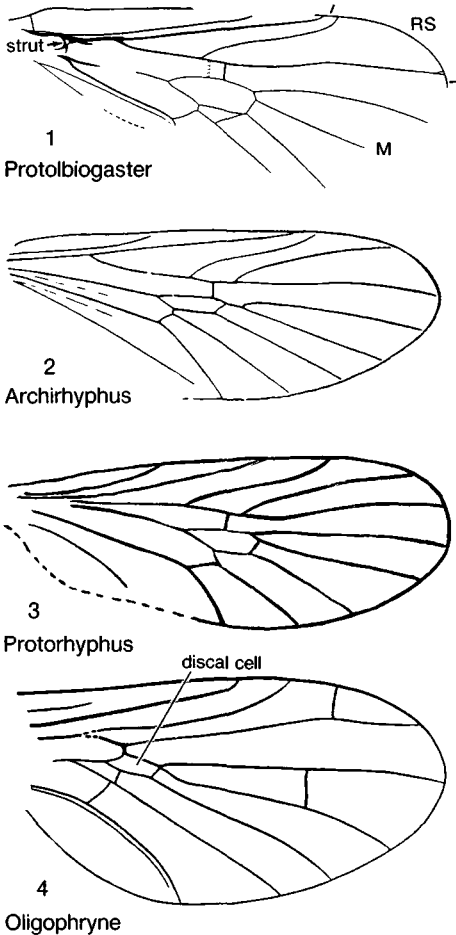


FIG. 228. Oligophryneidae, Protolbiogastridae, and Protorhyphidae (p. 417-418).

Protolbiogaster ROHDENDORF, 1962a, p. 332 [**P. rhaetica*; OD]. M1 and M2 separating before distal end of discal cell. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz). — FIG. 228,1. **P. rhaetica*; wing, $\times 12$ (Rohdendorf, 1964).

Family PROTORHYPHIDAE Handlirsch, 1906

[Protorhyphidae HANDLIRSCH, 1906b, p. 487]

Wing with vein SC strong, ending before midwing; RS with 2 long, curved branches, directed anteriorly; crossvein r-m midway between origins of these 2 branches; discal cell small. *Trias.*–*Jur.*

Protorhyphus HANDLIRSCH, 1906b, p. 487 [**Phryganidium simplex* GEINITZ, 1887, p. 203, pl. 5,

fig. 13; OD]. M1 and M2 diverging before distal end of discal cell. EDWARDS, 1928; ROHDENDORF, 1962a, 1964. *Trias.*, USSR (Kirghiz); *Jur.*, Europe (Germany). — FIG. 228,3. **P. simplex* (GEINITZ); *Jur.*, Germany; wing, $\times 18$ (Handlirsch, 1907).

Archirhyphus HANDLIRSCH, 1939, p. 102 [**A. geinitzi*; OD]. M1 and M2 diverging after distal end of discal cell. ROHDENDORF, 1964. *Jur.*, Europe (Germany), USSR (Kazakh). — FIG. 228,2. **A. geinitzi*, *Jur.*, Germany; wing, $\times 18$ (Handlirsch, 1939).

Family PHRAGMOLIGONEURIDAE Rohdendorf, 1962

[Phragmoligoneuridae ROHDENDORF, 1962a, p. 332]

Vein R with a well-developed strut (phragma), connecting base of R with CUA; basal parts of RS and M reduced; RS unbranched. Body unknown. *Trias.*

Phragmoligoneura ROHDENDORF, 1962a, p. 332 [**P. incerta*; OD]. Little-known wing; SC very weak; M forking just before crossvein between RS and M. ROHDENDORF, 1964. *Trias.*, USSR (Kirghiz).

Family ANISOPIDAE Knab, 1912

[Anisopidae KNAB, 1912, p. 111]

Flies of moderate size. Wings: vein SC usually extending about to midwing; discal cell present; RS1+2 terminating on R or C. Body stout; antennae longer than head. Larvae saprophytic, in decaying vegetation. *Jur.*–*Holo.*

Sylvicola HARRIS, 1776, p. 100 [= *Anisopus* MEIGEN, 1803, p. 264 (type, *A. fuscus*)]. HEER, 1849; MEUNIER, 1904d; COCKERELL, 1921d; EDWARDS, 1928; PONGRÁČZ, 1928. *Oligo.*, England, Europe (Baltic); *Mio.*, Europe (Croatia)–*Holo.*

Asarcomyia SCUDDER, 1890, p. 567 [**A. cadaver*; OD]. Similar to *Sylvicola*, but discal cell shorter. [Probably a synonym of *Sylvicola*.] EDWARDS, 1928. *Eoc.*, USA (Wyoming).

Olbiogaster OSTEN-SACKEN, 1886, p. 20 [= *Pseudadonia* HANDLIRSCH, 1906b, p. 628 (type, *Platyura fittoni* BRODIE, 1845, p. 3, fig. 9); *Mesorhyphus* HANDLIRSCH, 1920, p. 203 (type, *M. nanus*); *Euthereva* COCKERELL, 1920c, p. 251 (type, *E. simplex*)]. EDWARDS, 1928. *Jur.*, England, Europe (Germany); *Eoc.*, USA (Colorado)–*Holo.*

Thiras GIEBEL, 1856, p. 235 [**T. westwoodi*; OD]. Similar to *Olbiogaster*; RS1+2 and discal cell obscure. [Possibly a synonym of *Olbiogaster*.] EDWARDS, 1928. *Jur.*, England.

Family CECIDOMYIDAE

Newman, 1835

[Cecidomyiidae NEWMAN, 1835, p. 386]

Small to very small flies. Wings weak, hairy, with a reduced venation, sometimes consisting of only 1 or 2 longitudinal veins; SC usually absent; RS typically arising from R as in the Sciaridae; M weakly developed or absent; 1A commonly absent. Antennae typically long and moniliform; tibial spurs absent. Larvae mostly in plant galls; some scavengers in decaying debris; a few predators and parasites. *Cret.*—*Holo.*

Cecidomyia MEIGEN, 1803, p. 261. LOEW, 1850; MEUNIER, 1899a; KIEFFER, 1913; NAORA, 1933a. *Oligo.*, Europe (Baltic), USA (Colorado); *Paleoc.*—*Plio.*, China (Manchuria)—*Holo.*

Bryocrypta KIEFFER, 1896, p. 8. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Campatomyia KIEFFER, 1894, p. 323. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Campylomyza MEIGEN, 1818, p. 101. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Colpodia WINNERTZ, 1853, p. 185. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Cretocatocha GAGNÉ, 1977, p. 58 [**C. mcalpinei*; OD]. Related to *Anocha* (recent), but male antenna setiform, with 8 flagellomeres, distal ones tapering to a bristlike tip; RS3+4 terminating on costa before wing apex. *Cret.*, Canada (Alberta).—FIG. 229,5. **C. mcalpinei*; wing, ×40 (Gagné, 1977).

Cretocordylomyia GAGNÉ, 1977, p. 58 [**C. quadriseriis*; OD]. Similar to *Cordylomyia* (recent); flagellomeres of male antenna with 4 crenulate whorls of long setae; R3+4 terminating on costa at wing apex; fork of M3+4 and CUA acute. *Cret.*, Canada (Manitoba).—FIG. 229,3. **C. quadriseriis*; wing, ×55 (Gagné, 1977).

Cretomiastor GAGNÉ, 1977, p. 60 [**C. ferejunctus*; OD]. Similar to *Leptosyna* (recent), but wing broader and without macrotrichia; 5 tarsomeres present; M absent. *Cret.*, Canada (Alberta, Manitoba).—FIG. 229,1. **C. ferejunctus*; holotype female, ×55 (Gagné, 1977).

Cretowinnertzia GAGNÉ, 1977, p. 60 [**C. angustata*; OD]. Similar to *Parwinnertzia* (recent), but wings broader; maxillary palpi with 4 segments. *Cret.*, Canada (Manitoba).—FIG. 229,4. **C. angustata*; holotype female, ×38 (Gagné, 1977).

Dicroneurus KIEFFER, 1895, p. 122. MEUNIER,

1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Epidosis LOEW, 1850, p. 38. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Frirenia KIEFFER, 1894, p. 201. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Heteropeza WINNERTZ, 1846, p. 13. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Lasioptera MEIGEN, 1818, p. 88. SCUDDER, 1890; KIEFFER, 1913. *Eoc.*, USA (Colorado)—*Holo.*

Ledomyiella MEUNIER, 1904a, p. 44 [**L. succini* MEUNIER, 1904a, p. 44; SD CARPENTER, herein]. Similar to *Brachyneura* (recent), but M3+4 separating from CUA distally. KIEFFER, 1913. *Oligo.*, Europe (Baltic).—FIG. 229,2. **L. succini*; wing, ×90 (Meunier, 1904a).

Lestremia MACQUART, 1826, p. 173. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Lithomyza SCUDDER, 1877a, p. 746 [**L. condita*; OD]. Little-known genus, apparently similar to *Anarete* (recent), but wings broader beyond middle and tapering more basally. SCUDDER, 1890; KIEFFER, 1913. *Eoc.*, USA (Colorado).

Meunieria KIEFFER, 1904, p. 408 [**Miastor succini* MEUNIER, 1901a, p. 191; OD]. Similar to *Miastor* (recent), but maxillary palpi with 4 segments. MEUNIER, 1904a. *Oligo.*, Europe (Baltic).

Mikiola KIEFFER, 1896, p. 5. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Monardia KIEFFER, 1895, p. 111. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Monodicrana LOEW, 1850, p. 32. KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Neostenoptera MEUNIER, 1902c, p. 102, *nom. subst. pro Stenoptera* MEUNIER, 1901a, p. 200, *non* DUPONCHEL, 1838. KIEFFER, 1913. *Pleist.*, Africa—*Holo.*

Palaeocolpodia MEUNIER, 1904a, p. 29 [**P. eocenica*; OD]. Similar to *Holoneurus* (recent), but transverse part of RS straight and not oblique. KIEFFER, 1913. *Oligo.*, Europe (Baltic).

Peromyia KIEFFER, 1894, p. 205. LOEW, 1850; MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Porricondyla RONDANI, 1840, p. 13. LOEW, 1850; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Winnertzia RONDANI, 1860, p. 290. MEUNIER, 1904a; KIEFFER, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Winnertzia KIEFFER, 1912, p. 235. EDWARDS, 1928. *Mio.*, Burma—*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the order Diptera, suborder Nema-

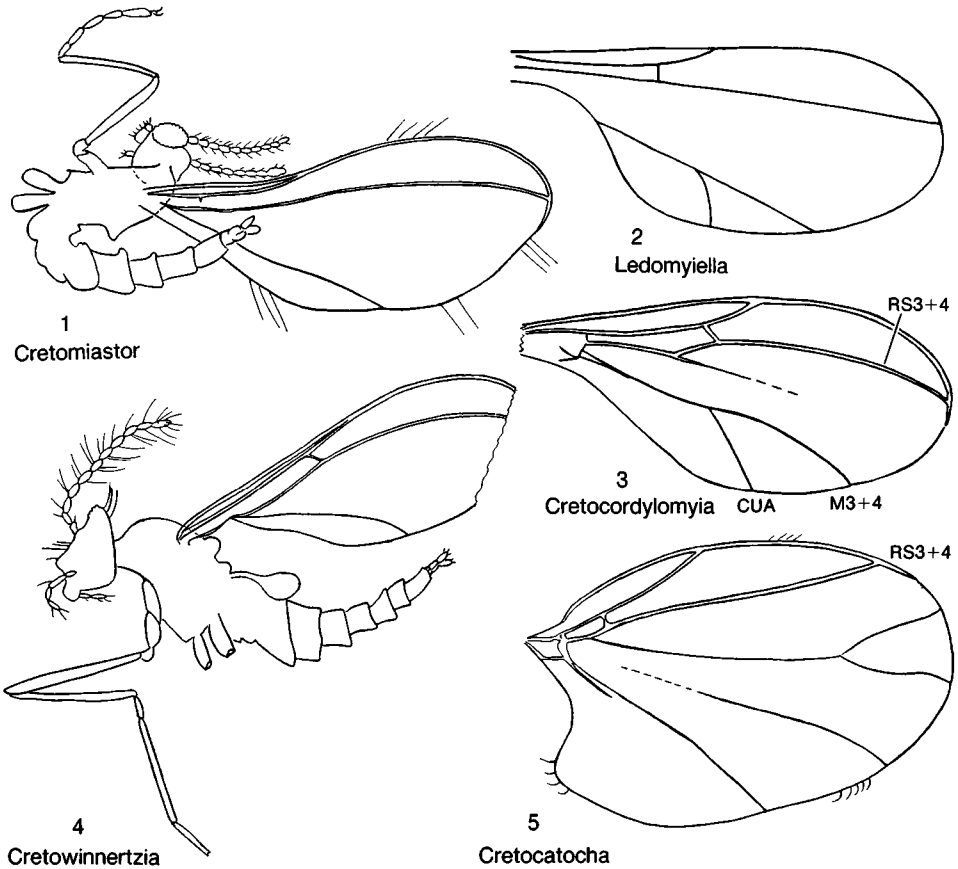


FIG. 229. Cecidomyiidae (p. 419).

tocera, are too poorly known to permit family assignment.

Amblylexis BODE, 1953, p. 330 [**A. gibberata*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Amianta BODE, 1953, p. 327 [**A. eurycephala*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Amphipromeca BODE, 1953, p. 324 [**A. acuta*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Apistogryptes BODE, 1953, p. 329 [**A. inflexa*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Chironomopsis HANDLIRSCH, 1906b, p. 631 [**Chironomus arrogans* GIEBEL, 1856, p. 250; OD]. Little-known genus. PING, 1928; KALUGINA, 1977. *Jur.*, England; *Cret.*, Mongolia, China (Liaoning).

Cormophora BODE, 1953, p. 329 [**C. arucaeformis*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Culiciscolex BODE, 1953, p. 322 [**C. gibberatus*;

OD]. Little-known genus. *Jur.*, Europe (Germany).

Cyrtomides BODE, 1953, p. 329 [**C. maculatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Ellipes BODE, 1953, p. 328 [**E. laesa*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Empidocampe BODE, 1953, p. 323 [**E. retrocrasata*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Etopychoptera HANDLIRSCH, 1910b, p. 122 [**E. tertiaria*; OD]. Little-known genus, based on incomplete wing; RS well developed, with 4 branches. [Tentatively placed by HANDLIRSCH in the family Ptychopteridae (recent).] *Eoc.*, Canada (British Columbia).

Propexis BODE, 1953, p. 327 [**P. incerta*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Rhopaloscolex BODE, 1953, p. 326 [**R. longus*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Sphallonymphites BODE, 1953, p. 330 [**S. decurtatus*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Suborder BRACHYCERA

Zetterstedt, 1842

[Brachycera ZETTERSTEDT, 1842, p. 1]

Antennae of adults shorter than thorax, commonly consisting of less than 6 segments (total) and terminating in a style or arista; maxillary palpi with 1 or 2 segments; wings often broadly oval; vein CUA diverging toward 1A and often coalescing with it. Larvae with head capsule incomplete or absent; mandibles strongly curved, not opposite, their movements vertical to plane of head. Pupae obovate or coarctate. HENNIG, 1973. *Jur.*—*Holo.*

Family PROTOBRACHYCERONTIDAE

Rohdendorf, 1962

[*nom. correct.* ROHDENDORF, 1964, p. 197, *pro* Protobracheridae ROHDENDORF, 1962a, p. 334]

Little-known family, of dubious validity. Small flies; wings with all veins equally strong; M3 and M4 converging distally; discal cell elongate. HENNIG, 1967a; KOVALEV, 1981. *Jur.*

Protobracheron HANDLIRSCH, 1920, p. 205 [**P. liasinum*; OD]. Terminations of SC, R, and RS1+2 about equally spaced; RS3+4 with a prominent terminal fork. HANDLIRSCH, 1939; ROHDENDORF, 1962a, 1964. *Jur.*, Europe (Germany).—FIG. 230, 3. **P. liasinum*; wing, $\times 12$ (Handlirsch, 1939).

Family ARCHISARGIDAE

Rohdendorf, 1962

[Archisargidae ROHDENDORF, 1962a, p. 334]

Wings long and narrow, subpetiolate; veins SC and R strong, other veins weak; RS with 3 terminal branches. KOVALEV, 1981. *Jur.*

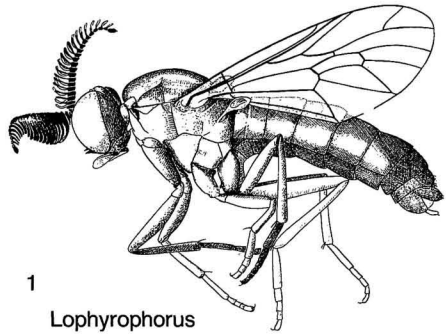
Archisargus ROHDENDORF, 1938, p. 30 [**A. pulcher*; OD]. SC extending beyond midwing; R almost straight; first fork of RS at midwing. ROHDENDORF, 1962a, 1964; KOVALEV, 1981. *Jur.*, USSR (Kazakh).

Family PALAEOSTRATIOMYIIDAE

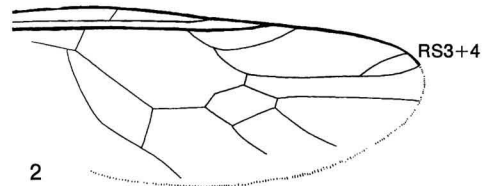
Rohdendorf, 1938

[*nom. transl.* ROHDENDORF, 1962a, p. 334, *ex* Palaestrostratiomyiinae ROHDENDORF, 1938, p. 31]

Little-known family. Small flies. Wings broadly oval, narrowed basally; veins nearly uniformly strong; discal cell present, giving

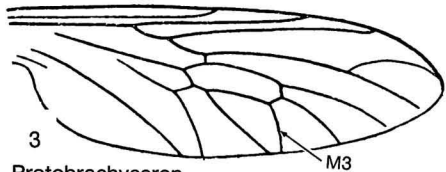


1
Lophyrophorus



2

Cretaceogaster



3

Protobracheron

FIG. 230. Protobracherontidae, Xylophagidae, and Stratiomyidae (p. 421–422).

rise to all branches of vein M. Body short and broad. KOVALEV, 1981. *Jur.*

Palaeostratiomyia ROHDENDORF, 1938, p. 32 [**P. pygmaea*; OD]. Proximal branch of RS sigmoidal; crossvein r-m at about midwing. KOVALEV, 1981. *Jur.*, USSR (Kazakh).

Family EOMYIIDAE

Rohdendorf, 1962

[Eomyiidae ROHDENDORF, 1962a, p. 334]

Wings poorly known, venation delicate; thorax strongly convex above; head and antennae small. KOVALEV, 1981. *Jur.*

Eomyia ROHDENDORF, 1962a, p. 334 [**E. veterima*; OD]. Antennae with rounded third segment. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family XYLOPHAGIDAE Fallén, 1810

[Xylophagidae FALLÉN, 1810, p. 6]

Antennal flagellum typically with 8 or 20 to 36 segments (flagellomeres), commonly subpetiolate or serrate; maxillary palpus

prominent, with two segments; legs slender; tibiae with one or two spurs; wing veins commonly uniformly strong. *Oligo.*—*Holo.*

Xylophagus MEIGEN, 1803, p. 266. [Generic assignment of fossil doubtful.] HENNIG, 1967a; KOVALEV, 1981. *Oligo.*, Europe (Baltic)—*Holo.*

Chrysothemis LOEW, 1850, p. 38 [**C. speciosa*; OD]. Little-known genus. HENNIG, 1967a. *Oligo.*, Europe (Baltic).

Lophyrophorus MEUNIER, 1902b, p. 397 [**L. flabellatus*; OD]. Similar to *Rachicerus* (recent); antennae with 33 segments in male, 15 in female. [Probably a synonym of *Chrysothemis*.] HENNIG, 1938, 1967a. *Oligo.*, Europe (Baltic).—FIG. 230, 1. **L. flabellatus*; male, $\times 7$ (Hennig, 1967a).

Trecela CARPENTER, 1986, p. 576, *nom. subst. pro Electra* LOEW, 1850, p. 38, *non* STEVENS, 1831 [**Electra formosa*; OD]. Similar to *Lophyrophorus* but with fewer antennal segments. HENNIG, 1967a. *Oligo.*, Europe (Baltic).

Family XYLOMYIDAE Verrall, 1909

[Xylomyidae VERRALL, 1909, p. 217]

Similar to Stratiomyidae, but vein M3 coalesced with M4 distally, closing cell 3m. *Oligo.*—*Holo.*

Xylomya RONDANI, 1861, p. 11. COCKERELL, 1914b; MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*
Solva WALKER, 1859, p. 98. HENNIG, 1967a. *Oligo.*, Europe (Baltic)—*Holo.*

Family STRATIOMYIDAE Newman, 1835

[Stratiomyidae NEWMAN, 1835, p. 313]

Costa extending only to about wing apex; veins R and RS crowded toward anterior margin of wing and usually stronger than other veins; RS usually arising at level of m-cu crossvein (or slightly beyond); discal cell commonly small; RS3+4 diverging anteriorly, RS4 terminating on margin before apex. Flagellum elongate, usually annulate; tibiae commonly without apical spurs. Larvae elongate, occurring in damp soil or rotting vegetation. *Cret.*—*Holo.*

Stratiomys GEOFFROY, 1762, p. 475. ENDERLEIN, 1914. *Oligo.*, England, Europe (Germany)—*Holo.*

Beris LATREILLE, 1802, p. 447. JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Cacosis WALKER, 1851, p. 83. MEUNIER, 1910b. *Oligo.*, Europe (Baltic)—*Holo.*

Cretaceogaster TESKEY, 1971, p. 1659 [**C. pygmaeus*; OD]. Similar to *Birkshiria* (recent) but with RS3+4 long and ending near wing apex. *Cret.*, Canada (Manitoba).—FIG. 230, 2. **C. pygmaeus*; wing, $\times 27$ (Teskey, 1971).

Cyphomyia WIEDEMANN, 1819, p. 54. COCKERELL, 1916c; JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Hermetiella MEUNIER, 1908d, p. 264 [**H. bifurcata*; OD]. Similar to *Campreposopa* (recent), but third antennal segment with 7 distinct divisions. *Oligo.*, Europe (Baltic).

Lasiopa BRULLÉ, 1832, p. 307. JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Moyamyia MELANDER, 1949, p. 26 [**M. limigena*; OD]. Clitellariine flies with pterostigma prominent, distal to discal cell. *Oligo.*, USA (Colorado).

Nemotelus GEOFFROY, 1762, p. 450. [Generic assignment of fossils doubtful.] COCKERELL, 1921e. *Eoc.*, USA (Colorado)—*Holo.*

Oxycera MEIGEN, 1803, p. 265. JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Protoberis COCKERELL, 1915, p. 494 [**P. oblitteratus*; OD]. Similar to *Beris* (recent); wings long; RS3 straight and slightly oblique. *Oligo.*, England.

Rhingiopsis ROEDER, 1886, p. 138. [Generic assignment of fossils doubtful.] COCKERELL, 1910c; JAMES, 1937. *Oligo.*, USA (Colorado)—*Holo.*

Sargus FABRICIUS, 1798, p. 549. [Generic assignment of fossils doubtful.] GIEBEL, 1862. *Eoc.*, USA (Colorado)—*Holo.*

Family EOSTRATIOMYIIDAE Rohdendorf, 1962

[Eostratiomyiidae ROHDENDORF, 1962a, p. 336]

Costa extending around wing apex; discal cell large; several crossveins present between veins RS3+4 and M. KOVALEV, 1981. *Jur.*

Eostratiomyia ROHDENDORF, 1962a, p. 336 [**E. avia*; OD]. Crossveins between RS3+4 and M at midwing; a single crossvein between R and base of RS1+2; anterior border of discal cell convex. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).—FIG. 231, 7. **E. avia*; wing, $\times 7.5$ (Rohdendorf, 1962a).

Family ATHERICIDAE Stuckenberg, 1973

[Athericidae STUCKENBERG, 1973, p. 669]

Similar to Rhagionidae but with RS1+2 curved anteriorly and joining costa at end of R; crossvein r-m joining discal cell near its proximal end. *Oligo.*—*Holo.*

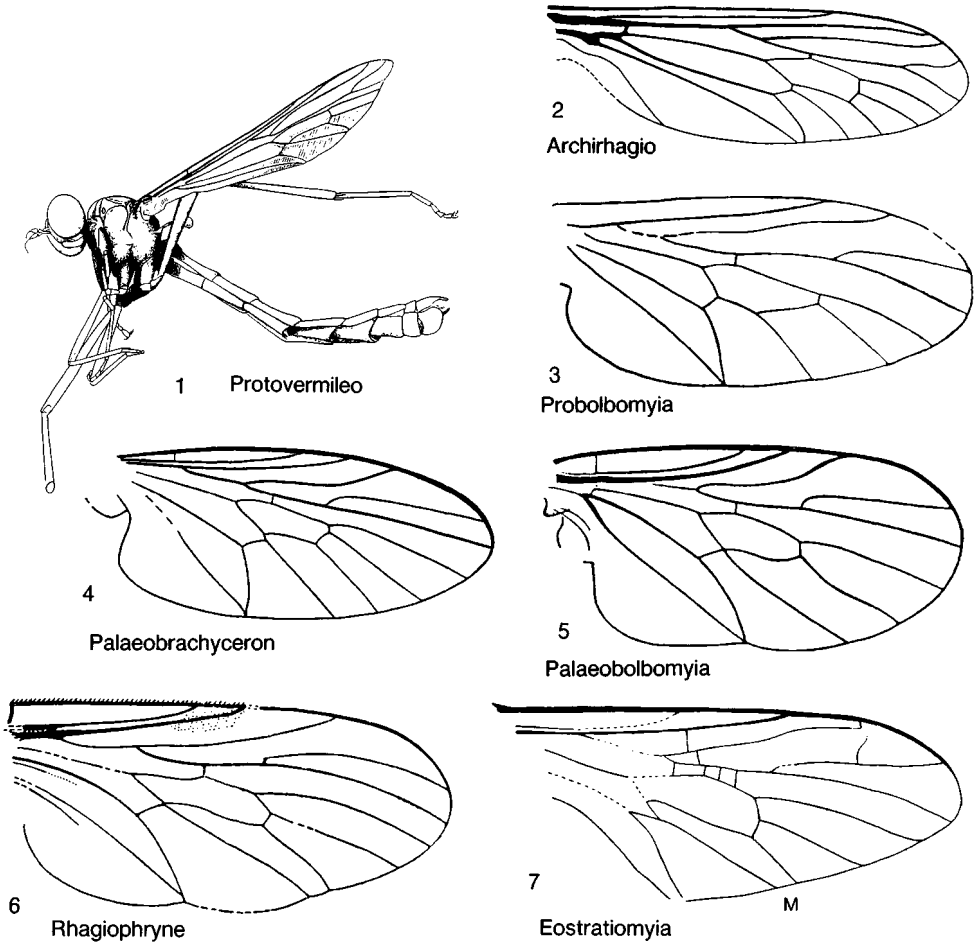


FIG. 231. Eostratiomyiidae and Rhagionidae (p. 422–424).

Atherix MEIGEN, 1803, p. 271. STUCKENBERG, 1974. *Holo.*

Succinatherix STUCKENBERG, 1974, p. 281 [**S. setifera*; OD]. Related to *Ibisia* (recent). Female: hairs on frons arranged in 2 sublateral series; third antennal segment narrowly reniform; tibial spur formula 1,2,2. Wing with discal cell remote from wing margin. *Oligo.*, Europe (Baltic).

Family RHAGIONIDAE Latreille, 1804–1805

[Rhagionidae LATREILLE, 1804–1805, p. 328] [=Rhagionempididae ROHDENDORF, 1938, *nom. transl.* ROHDENDORF, 1962a, p. 356, ex Rhagionempidinae ROHDENDORF, 1938, p. 33]

Vein SC extending at least to midwing; RS1+2 joining costa beyond end of R;

RS3+4 commonly deeply forked. Flagellum with 8 segments in generalized forms, fewer segments in more specialized species; basal flagellar segment becoming swollen and bearing a style. Larvae very diverse, occurring in damp soil, rotting wood, or sand. KOVALEV, 1982. *Jur.–Holo.*

Rhagio FABRICIUS, 1775, p. 761 [=Palaeobilari-morpha MEUNIER, 1902b, p. 400 (type, *P. bifurcata*)]. COCKERELL, 1909b; THÉOBALD, 1937b; MELANDER, 1949; HENNIG, 1967a. *Oligo.*, Europe (Baltic, France), USA (Colorado)—*Holo.*

Archirhagio ROHDENDORF, 1938, p. 35 [**A. obscurus*; OD]. Wing narrow and long; fork of RS3+4 shallow and broad; main fork of M just beyond

- midwing. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).—FIG. 231,2. **A. obscurus*; wing, $\times 4$ (Rohdendorf, 1962a).
- Atrichops** VERRALL, 1909, p. 291. COCKERELL, 1914b. *Oligo.*, USA (Colorado)—*Holo.*
- Bolbomyia** LOEW, 1850, p. 39. HENNIG, 1967a. *Oligo.*, Europe (Baltic)—*Holo.*
- Chrysopilus** MACQUART, 1826, p. 403. COCKERELL, 1921d; STATZ, 1940; HENNIG, 1967a. *Oligo.*, Europe (Baltic, Germany), England, USA (Colorado)—*Holo.*
- Dialysis** WALKER, 1850, p. 4. COCKERELL, 1908h. *Oligo.*, USA (Colorado)—*Holo.*
- Ija** KOVALEV, 1981, p. 93 [**I. problematica*; OD]. Little-known genus; vein 1A obsolescent distally, not reaching wing margin. [Family assignment doubtful.] *Jur.*, USSR (Asian RSFSR).
- Jurabrachyceron** KOVALEV, 1981, p. 92 [**J. abbreviatum*; OD]. Similar to *Palaeobrachyceron*, but wing lacking vein M3. *Jur.*, USSR (Asian RSFSR).
- Palaeobolbomyia** KOVALEV, 1982, p. 94 [**P. sibirica*; OD]. Similar to *Jurabrachyceron*. Arista of antenna not segmented; RS1+2 slightly sigmoidal; RS4 aligned with stem of RS3+4; sides of discal cell not parallel. *Jur.*, USSR (Asian RSFSR).—FIG. 231,5. **P. sibirica*; wing, $\times 20$ (Kovalev, 1982).
- Palaeobrachyceron** KOVALEV, 1981, p. 87 [**P. handlirschi*; OD]. Wing: M with 4 branches; RS3 and RS4 almost parallel; SC terminating almost at midwing. *Jur.*, USSR (Asian RSFSR).—FIG. 231,4. **P. handlirschi*; wing, $\times 17$ (Kovalev, 1981).
- Palaeoptiolina** KOVALEV, 1982, p. 89 [**P. scobloi*; OD]. Similar to *Rhagionempis* but with a much longer fork on vein RS3+4. *Jur.*, USSR (Asian RSFSR).
- Probolbomyia** USSATCHOV, 1968, p. 620 [**P. modesta*; OD]. Related to *Bolbomyia*. RS1+2 nearly straight, arising at level of middle of stem of M; stem of M well developed, not coalesced with CUA; discal cell pentagonal; CUA curving in an arc to 1A at wing margin. *Jur.*, USSR (Kazakh).—FIG. 231,3. **P. modesta*; wing, $\times 18$ (Ussatshov, 1968).
- Protorhagio** ROHDENDORF, 1938, p. 37 [**P. capitatus*; OD]. Wing moderately broad; RS forking shortly after its origin; first fork of M at midwing. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).
- Protovermileo** HENNIG, 1967a, p. 26 [**P. electrus*; OD]. Similar to *Vermileo* (recent), but arista with 6 distinct segments. *Oligo.*, Europe (Baltic).—FIG. 231,1. **P. electrus*; whole insect, $\times 5$ (Hennig, 1967a).
- Rhagionempis** ROHDENDORF, 1938, p. 34 [**R. tabanicornis*; OD]. Little-known genus, apparently similar to *Ussatchovia*. ROHDENDORF, 1962a, 1964; KOVALEV, 1982. *Jur.*, USSR (Kazakh).

- Rhagiophryne** ROHDENDORF, 1962a, p. 337 [**R. bianalis*; OD]. Wing short and broad; RS3+4 forking just beyond midwing. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).—FIG. 231,6. **R. bianalis*; wing, $\times 14$ (Rohdendorf, 1962a).
- Symphoromyia** FRAUENFELD, 1867, p. 497. PARAMONOV, 1936; THÉOBALD, 1937b; HENNIG, 1967a; STUCKENBERG, 1974. *Oligo.*, Europe (Baltic, France)—*Holo.*
- Ussatchovia** KOVALEV, 1982, p. 91 [**U. jurassica*; OD]. Similar to *Probolbomyia*; stem of RS3+4 much longer than stem of RS and nearly 3 times as long as fork of RS3+4; RS3 and RS4 diverging at a nearly symmetrical angle. Arista of antenna segmented distally. *Jur.*, USSR (Asian RSFSR).

Family TABANIDAE Leach, 1815

[Tabanidae LEACH, 1815, p. 161]

Fork of vein RS3+4 shorter than in Rhagionidae; RS3 and RS4 widely divergent distally, including wing apex between them; 1A nearly straight, usually coalesced with CUA distally. Mandibles absent in males; fore tibiae with spurs. Larvae in rotting vegetation or wood. *Eoc.*—*Holo.*

- Tabanus** LINNÉ, 1758, p. 601. COCKERELL, 1909b; DÜRRENFELDT, 1968. *Oligo.*, USA (Colorado); *Plio.*, Europe (Germany)—*Holo.*
- Chrysops** MEIGEN, 1800, p. 23. COCKERELL, 1921d; PITON, 1940a. *Eoc.*, Europe (France); *Oligo.*, England—*Holo.*
- Silvius** MEIGEN, 1820, p. 27. [Generic assignment of fossils doubtful.] MEUNIER, 1902b; MELANDER, 1946; HENNIG, 1967a. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Family ACROCERIDAE Leach, 1815

[Acroceridae LEACH, 1815, p. 162]

Venation diversely modified, often reduced. Head small; eyes holoptic in both sexes; flagellum not divided. Larvae, in early stages, parasitic on spiders. *Jur.*—*Holo.*

- Acrocera** MEIGEN, 1803, p. 266. *Holo.*
- Archocyrtus** USSATCHOV, 1968, p. 622 [**A. gibbosus*; OD]. RS1+2 absent (apparently completely coalesced with R); RS3+4 with a short distal fork; RS3 just meeting end of R; M with 3 branches. Antennae large, flagellum at least as long as first and second antennal segments combined. *Jur.*, USSR (Kazakh).—FIG. 232,4. **A.*

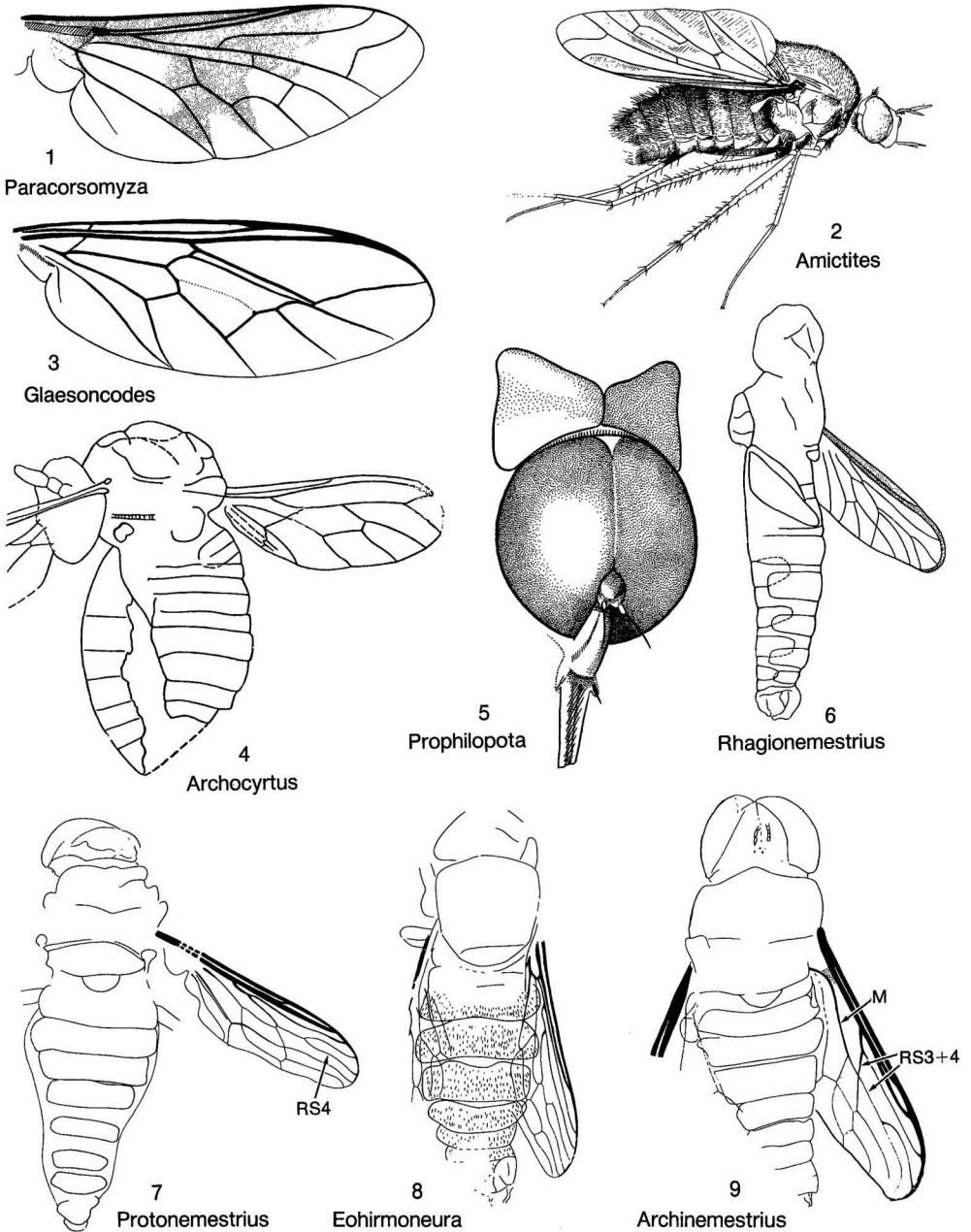


FIG. 232. Acroceridae, Nemestrinidae, and Bombyliidae (p. 424–427).

gibbosus; whole specimen, $\times 15$ (Ussatchov, 1968).

Glaesoncodes HENNIG, 1968, p. 4 [**G. completinervis*; OD]. Similar to *Ogcodes* (recent); eyes naked; wing venation more nearly complete than

in *Ogcodes. Oligo.*, Europe (Baltic). — FIG. 232,3. **G. completinervis*; wing, $\times 11$ (Hennig, 1968).

Prophilopota HENNIG, 1966e, p. 9 [**P. succinea*; OD]. Similar to *Philopota* (recent), but face

(frons) small and more nearly flat. *Oligo.*, Europe (Baltic).—FIG. 232,5. **P. succinea*; head, $\times 22$ (Hennig, 1966e).

Villalites HENNIG, 1966e, p. 19 [**V. electrica*; OD]. Similar to *Villalus* (recent), but proboscis prominent and as long as in *Holops* (recent). *Oligo.*, Europe (Baltic).

Family NEMESTRINIDAE

Macquart, 1834

[Nemestrinidae MACQUART, 1834 in MACQUART, 1834–1835, p. 370]

Wing with fork of vein RS3 + 4 very narrow; RS3 and RS4 nearly parallel and terminating on wing margin before apex; M1 and M2 also parallel and terminating on margin before apex; stem of RS3 + 4 and stem of M1 + 2 aligned to form a diagonal vein near midwing. Larvae parasitic on Orthoptera and certain coleopterous larvae. *Jur.*—*Holo.*

Nemestrina LATREILLE, 1809, p. 307. *Holo.*

Archinemestrius ROHDENDORF, 1968, p. 181 [**A. karatavicus*; OD]. Wing tip slightly falcate; M1, M2, and RS4 curved distally and terminating on hind margin of wing, below apex; RS3 + 4 briefly touching M1 + 2; M2 short. Head short, apparently lacking a long proboscis. *Jur.*, USSR (Kazakh).—FIG. 232,9. **A. karatavicus*; whole insect, $\times 5$ (Rohdendorf, 1968).

Eohirmoneura ROHDENDORF, 1968, p. 187 [**E. carpenteri*; OD]. Similar to *Hirmoneura* and belonging to subfamily Hirmoneurinae; diagonal vein incomplete, not reaching posterior wing margin. *Jur.*, USSR (Kazakh).—FIG. 232,8. **E. carpenteri*; whole insect, $\times 3.5$ (Rohdendorf, 1968).

Hirmoneura MEIGEN, 1820, p. 132 [= *Hirmoneurites* COCKERELL, 1910c, p. 283 (type, *H. willis-toni*)]. BEQUAERT & CARPENTER, 1936. *Oligo.*, USA (Colorado)—*Holo.*

Neorhynchocephalus LICHTWARDT, 1909, p. 512. COCKERELL, 1908g; BEQUAERT & CARPENTER, 1936; BERNARDI, 1974. *Oligo.*, USA (Colorado)—*Holo.*

Prohirmoneura HANDLIRSCH, 1906b, p. 633 [**P. jurassica*; OD]. Little-known genus, apparently belonging to subfamily Hirmoneurinae. BEQUAERT & CARPENTER, 1936; USSATCHOV, 1968. *Jur.*, Europe (Bavaria).

Prosoeca SCHINER, 1867, p. 311 [= *Palembolus* SCUDDER, 1878a, p. 526 (type, *P. florigerus*)]. MEUNIER, 1903a; BEQUAERT & CARPENTER, 1936. *Oligo.*, USA (Colorado)—*Holo.*

Protonemestrius ROHDENDORF, 1968, p. 182 [**P. martynovi*; OD]. Similar to *Archinemestrius*, but RS4 slightly curved and terminating on anterior margin at apex. Proboscis sometimes elongate. *Jur.*, USSR (Kazakh).—FIG. 232,7.

**P. martynovi*; whole insect, $\times 5.5$ (Rohdendorf, 1968).

Rhagionemestrius USSATCHOV, 1968, p. 621 [**R. rapidus*; OD]. SC very long, terminating slightly proximad of forking of RS3 + 4; stem of M well developed; M2 and M3 originating from a single point on discal cell. *Jur.*, USSR (Kazakh).—FIG. 232,6. **R. rapidus*; whole insect, $\times 6$ (Ussatchov, 1968).

Family BOMBYLIIDAE Latreille, 1802

[Bombyliidae LATREILLE, 1802a, p. 427]

Small to large flies, generally with a conspicuous covering of hair. Venation unusually diverse; veins RS and M usually with 3 branches; distal parts of RS1 + 2 and RS3 commonly curved anteriorly; wing apex usually between RS3 and RS4; discal cell long. Larvae parasitic on immature stages of endopterygote insects. *Oligo.*—*Holo.*

Bombylius LINNÉ, 1758, p. 606. MEUNIER, 1915a. *Oligo.*, Europe (France)—*Holo.*

Acreotrichites COCKERELL, 1917b, p. 376 [**A. scopulicornis*; OD]. Similar to *Acreotrichus* (recent), but crossvein r-m well before middle of discal cell. *Oligo.*, USA (Colorado).

Alepidophora COCKERELL, 1909d, p. 54 [**A. peali*; OD]. Similar to *Panturbes* (recent); RS1 + 2 ending on costa at a very obtuse angle; crossvein r-m located beyond midwing; discal cell long and narrow. COCKERELL, 1914c; MELANDER, 1949; LEWIS, 1972. *Oligo.*, USA (Colorado, Montana).

Alomatia COCKERELL, 1914d, p. 721 [**A. fusca*; OD]. Similar to *Lithocosmus*, but crossvein r-m at end of basal quarter of discal cell; cell between RS4 and M1 not narrowed at wing margin. COCKERELL, 1914c. *Oligo.*, USA (Colorado).

Amictites HENNIG, 1966e, p. 9 [**A. regiomontana*; OD]. Similar to *Amictus* (recent), but wing with very broad axillary area; tibiae with prominent spines. *Oligo.*, Europe (Baltic).—FIG. 232,2. **A. regiomontana*; whole insect, $\times 3$ (Hennig, 1966e).

Amphicosmus COQUILLET, 1891, p. 219. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Apolysis LOEW, 1860, p. 86. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Dischistus LOEW, 1855, p. 45. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Dolichomyia WIEDEMANN, 1830, p. 642. COCKERELL, 1917a. *Oligo.*, USA (Colorado)—*Holo.*

Exoprosopa MACQUART, 1840, p. 35. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Geron MEIGEN, 1820, p. 223. [Generic assignment of fossils doubtful.] COCKERELL, 1914f; THÉOBALD, 1937a; PARAMONOV, 1939. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*

Geronites COCKERELL, 1914c, p. 230 [**G. stig-*

- malis*; OD]. Similar to *Geron* (recent), but crossvein r-m situated well before middle of discal cell. *Oligo.*, USA (Colorado).
- Glbellula** BEZZI, 1902, p. 191. SCHLÜTER, 1976b. *Oligo./Mio.*, Dominican Republic—*Holo.*
- Glaesamictus** HENNIG, 1966f, p. 12 [**B. hafnien-sis*; OD]. Similar to *Amictites*, but vertex much broader and tibiae with fewer and weaker spines; axillary area of wing small. *Oligo.*, Europe (Baltic).
- Lithocosmus** COCKERELL, 1909b, p. 72 [**L. coquil-letti*; OD] [= *Protophthiria* COCKERELL, 1914d, p. 720 (type, *P. palpalis*)]. A cyllenine genus, with anal cell open at wing margin; distal part of R curving anteriorly toward wing margin; crossvein r-m slightly basad of middle of discal cell. MELANDER, 1949; EVENHUIS, 1984. *Oligo.*, USA (Colorado).
- Megacosmus** COCKERELL, 1909a, p. 10 [**M. miran-dus*; OD]. Similar to *Paracosmus* (recent), but RS1+2 more recurved distally. COCKERELL, 1911b, 1914c. *Oligo.*, USA (Colorado).
- Melanderella** COCKERELL, 1909b, p. 70 [**M. glos-salis*; OD]. Similar to *Dolichomyia*, but distal portion of vein M3 straight and CUA and 1A touching at wing margin. Hind femora incrassate. COCKERELL, 1911b; MELANDER, 1949. *Oligo.*, USA (Colorado).
- Pachysystropus** COCKERELL, 1909d, p. 56 [**P. roh-weri*; OD]. Similar to *Systropus*, but RS4 and M1 as well as CUA and 1A coalesced just before wing margin. COCKERELL, 1910c. *Oligo.*, USA (Colorado).
- Palaeoamictus** MEUNIER, 1916a, p. 275 [**P. spi-nosus*; OD]. Little-known genus, probably belonging to subfamily Cylleninae. HENNIG, 1966f. *Oligo.*, Europe (Baltic).
- Palaeogeron** MEUNIER, 1914a, p. 195 [**P. vetustus*; OD]. Similar to *Geron*, but cell between CUA and 1A open. *Oligo.*, Europe (France).
- Paracorsomyza** HENNIG, 1966f, p. 4 [**P. crassi-rostris*; OD]. Similar to *Callynthrophora* and *Gnumyia* (both recent) but differing by its longer proboscis and long and uniformly slender first antennal segment. RS1+2 strongly sigmoidal. *Oligo.*, Europe (Baltic).—FIG. 232, 1. **P. cras-sirostris*; wing, $\times 9$ (Hennig, 1966f).
- Phthiria** MEIGEN, 1803, p. 268. TIMON-DAVID, 1944a. *Oligo.*, Europe (France)—*Holo.*
- Praecythera** THÉOBALD, 1937b, p. 168 [**P. sardii*; OD]. Similar to *Cythera* (recent), but RS forking basad of fork of M. *Oligo.*, Europe (France).
- Proglbellula** HENNIG, 1966f, p. 15 [**P. electrica*; OD]. Similar to *Glbellula*, but short piece of M3+4 present and wing longer. *Oligo.*, Europe (Baltic).
- Proplatypygus** HENNIG, 1969b, p. 58 [**P. succin-eus*; OD]. Similar to *Platypygus* (recent) but with proboscis relatively short and occiput only slightly arched. *Oligo.*, Europe (Baltic).
- Protepacmus** COCKERELL, 1916c, p. 94 [**P. setosus*; OD]. Similar to *Alepidophora*, but wings much longer. *Oligo.*, USA (Colorado).
- Protolomatia** COCKERELL, 1914d, p. 723 [**P. anti-qua*; OD]. Similar to *Lomatia* (recent), but crossvein r-m less oblique. COCKERELL, 1914c, 1916c. *Oligo.*, USA (Colorado).
- Systropus** WIEDEMANN, 1820, p. 18. MEUNIER, 1917c; COCKERELL, 1921d. *Oligo.*, Europe (Ger-many), England—*Holo.*
- Tithonomyia** EVENHUIS, 1984, p. 160 [**Protophthi-ria atra* MELANDER, 1949, p. 33; OD]. Little-known genus, apparently close to the bomby-liines. *Oligo.*, USA (Colorado).
- Usia** LATREILLE, 1802, p. 430. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Verrallites** COCKERELL, 1913f, p. 230 [**V. cla-durus*; OD]. Somewhat similar to *Lepidophora* (recent), but CUA and 1A widely separated on wing margin. *Oligo.*, USA (Colorado).
- Villa** LIOY, 1864, p. 732. HANDLIRSCH, 1907. *Oligo.*, Europe (France); *Mio.*, Europe (Italy)—*Holo.*

Family THEREVIDAE Newman, 1835

[Therevidae NEWMAN, 1835, p. 391]

Vein M with 4 branches, all terminating on wing margin; anal cell closed; 1A and CUA meeting before wing margin. Larvae predaceous, usually found in soil. *Oligo.*—*Holo.*

- Thereva** LATREILLE, 1796, p. 167. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Glaesorthactia** HENNIG, 1967c, p. 3 [**Thereva magnicornis* MEUNIER, 1908d, p. 260; OD]. Similar to *Orthactia* (recent), but eyes of male separated. *Oligo.*, Europe (Baltic).
- Nebritus** COQUILLET, 1894, p. 98. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*
- Paraclia** ENDERLEIN, 1936, p. 88. [Generic assignment of fossils doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Psilocephala** ZETTERSTEDT, 1838, p. 525. [Generic assignment of fossils doubtful.] COCKERELL, 1909b, 1916c; HENNIG, 1967c. *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Burma—*Holo.*
- Rueppellia** KERTÉSZ, 1909, p. 148. [Generic assignment of fossils doubtful.] COCKERELL, 1927b. *Oligo.*, USA (Colorado)—*Holo.*

Family MYDIDAE Latreille, 1806

[Mydidae LATREILLE, 1806, p. 293]

All branches of veins RS, M1, and M2 terminating on wing margin before apex; antennae long and conspicuously clubbed. Larvae in rotting wood; apparently predaceous on Coleoptera. *Oligo.*—*Holo.*

Mydas FABRICIUS, 1794, p. 252. COCKERELL, 1913d. *Oligo.*, USA (Colorado)—*Holo.*

Family PROTOMPHRALIDAE Rohdendorf, 1957

[Protomphralidae ROHDENDORF, 1957, p. 91]

Little-known flies. Vein RS with 4 branches, all terminating on costal margin, its stem remote from costal margin. *Jur.*

Protomphrale ROHDENDORF, 1938, p. 39 [**P. martynovi*; OD]. Wings relatively short and narrow, with convex costal margin. ROHDENDORF, 1957, 1962a, 1964. *Jur.*, USSR (Kazakh).

Family ASILIDAE Latreille, 1804–1805

[Asilidae LATREILLE, 1804–1805, p. 305]

Wing venation generalized, close to basic pattern in Brachycera; veins RS3 and RS4 only slightly divergent distally; M3 + 4 unbranched. Vertex of head usually concave; flagellum with a terminal style; mouthparts forming a straight proboscis, commonly longer than head; thorax and legs with strong setae. Larvae in soil or rotting wood. *Eoc.*—*Holo.*

Asilus LINNÉ, 1758, p. 605. HEER, 1849; LOEW, 1850; MEUNIER, 1908c, 1915a; COCKERELL, 1909b, 1911b, 1914f, 1921d, 1921e; JAMES, 1939; MELANDER, 1946. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Europe (Germany)—*Holo.*

Asilopsis COCKERELL, 1920c, p. 250 [**A. fuscus*; OD]. Little-known genus; marginal cell (below R) closed well before wing apex. [Family assignment doubtful.] *Eoc.*, USA (Colorado).

Ceraturgus WIEDEMANN, 1824, p. 12. JAMES, 1939. *Oligo.*, USA (Colorado)—*Holo.*

Cophura OSTEN-SACKEN, 1887, p. 181. COCKERELL, 1913e; JAMES, 1939. *Oligo.*, USA (Colorado)—*Holo.*

Dioctria MEIGEN, 1803, p. 270. COCKERELL, 1909d, 1917f; JAMES, 1939. *Oligo.*, USA (Colorado)—*Holo.*

Holopogon LOEW, 1847, p. 473. [Generic assignment of fossil doubtful.] HULL, 1960. *Mio.*, USA (Montana)—*Holo.*

Leptogaster MEIGEN, 1803, p. 269. UNGER, 1841; MELANDER, 1946. *Oligo.*, USA (Colorado); *Mio.*, Europe (Croatia)—*Holo.*

Lestomyia WILLISTON, 1883, p. 19. JAMES, 1939. *Oligo.*, USA (Colorado)—*Holo.*

Machimus LOEW, 1849, p. 1. TIMON-DAVID, 1944a. *Oligo.*, Europe (France)—*Holo.*

Microstylum MACQUART, 1838, p. 26. COCKERELL, 1908h, 1909n. *Oligo.*, USA (Colorado)—*Holo.*

Nicodes JAENNICKE, 1867, p. 355. COCKERELL, 1909n. *Oligo.*, USA (Colorado)—*Holo.*

Palaeomolobra HULL, 1962, p. 23 [**Senoprosopis antiquus* JAMES, 1939, p. 43; OD]. Similar to *Lestomyia* but with only a weak spine on anterior tibia; marginal cell (below R) widely open at margin. *Oligo.*, USA (Colorado).

Philonicus LOEW, 1849, p. 144. JAMES, 1939. *Oligo.*, USA (Colorado)—*Holo.*

Proctacanthus MACQUART, 1838, p. 120. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Pseudophrisson DÜRRENFELDT, 1968, p. 45 [**P. primus*; OD]. Little-known genus, apparently similar to *Antiphrisson* (recent). *Plio.*, Europe (Germany).

Saropogon LOEW, 1847, p. 439. COCKERELL, 1914b. *Oligo.*, USA (Colorado)—*Holo.*

Senoprosopis MACQUART, 1838, p. 130. JAMES, 1939; MELANDER, 1949; HULL, 1957, 1960. *Oligo.*, USA (Colorado)—*Holo.*

Stenocinclis SCUDDER, 1878b, p. 751 [**S. anomala*; OD]. Similar to *Dioctria*; marginal cell (below R) open; RS3 + 4 arising directly from R before origin of RS1 + 2. [Family assignment doubtful.] SCUDDER, 1890. *Eoc.*, USA (Wyoming).

Taracticus LOEW, 1872, p. 64. COCKERELL, 1910c, 1911b. *Oligo.*, USA (Colorado)—*Holo.*

Family EREMOCHAETIDAE Ussatchov, 1968

[Eremochaetidae USSATCHOV, 1968, p. 617]

Costa extending along wing margin nearly to vein RS4; SC extending beyond midwing; RS1 + 2 terminating on R; middle portion of RS3 + 4 forming part of anterior side of discal cell; CUA with a strong angle at crossvein m-cu; 1A present. Antenna with a large flagellum, clearly segmented. *Jur.*

Eremochaetus USSATCHOV, 1968, p. 618 [**E. asilicus*; OD]. RS1 + 2 terminating on R near wing apex; RS3 + 4 forked distally; M with 4 branches; 1A extending to wing margin. *Jur.*, USSR (Kazakh).—FIG. 233.2. **E. asilicus*; whole specimen, $\times 7.3$ (Ussatchov, 1968).

Pareremochaetus USSATCHOV, 1968, p. 619 [**P. minor*; OD]. Similar to *Eremochaetus*, but RS1 + 2 coalesced with R shortly after origin of RS; M with 4 branches; 1A not reaching wing margin. *Jur.*, USSR (Kazakh).—FIG. 233.1. **P. minor*; whole specimen, $\times 10$ (Ussatchov, 1968).

Family PROTEMPIDIDAE Ussatchov, 1968

[Protempididae USSATCHOV, 1968, p. 623]

Wing broad, with very narrow base; vein RS3 short; discal cell present; M with 3

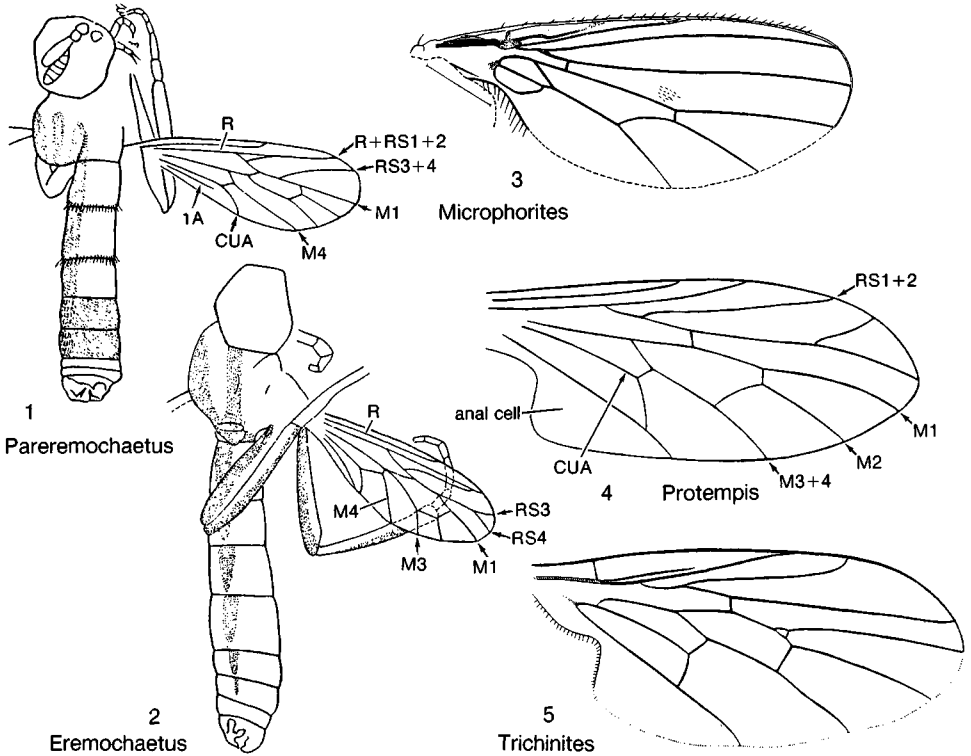


FIG. 233. Eremochaetidae, Protempidae, and Empididae (p. 428–430).

branches; anal cell closed and petiolate; antennal style with 2 segments. *Jur.*

Protempis USSATCHOV, 1968, p. 623 [**P. antennata*; OD]. M3+4 forming part of posterior margin of discal cell. HENNIG, 1970. *Jur.*, USSR (Kazakh). — FIG. 233, 4. **P. antennata*; wing, $\times 20$ (Hennig, 1970).

Family EMPIDIDAE Latreille, 1804–1805

[Empididae LATREILLE, 1804–1805, p. 310]

In generalized species veins M1+2 and RS3+4 forked, in more specialized species either or both veins may be unbranched; CUA short, commonly recurved distally and terminating on 1A. Proboscis usually straight and elongate. Larvae in decaying vegetation or aquatic. NEGROBOV, 1978. *Cret.*–*Holo.*

Empis LINNÉ, 1758, p. 603. STATZ, 1940; MELANDER, 1949. *Oligo.*, USA (Colorado), Europe (Baltic, Germany)–*Holo.*

Acallomyia MELANDER, 1927, p. 140. MELANDER, 1949. *Oligo.*, USA (Colorado)–*Holo.*

Archichrysotus NEGROBOV, 1978, p. 84 [**A. benigni*; OD]. A microphorine with 2 terminal branches on vein M. *Cret.*, USSR (Asian RSFSR).

Archiplatypalpus KOVALEV, 1974, p. 84 [**A. cretaceus*; OD]. Similar to *Platypalpus* but with holoptic eyes in male, and only a single longitudinal row of spinules on ventral surface of middle femora. *Cret.*, USSR (Asian RSFSR).

Chelifera MACQUART, 1823, p. 150. MELANDER, 1927. *Oligo.*, Europe (Baltic)–*Holo.*

Chelipoda MACQUART, 1823, p. 148. MELANDER, 1927. *Oligo.*, Europe (Baltic)–*Holo.*

Cretomicrophorus NEGROBOV, 1978, p. 82 [**C. rohdendorfi*; OD]. Similar to *Microphorites* but with antennae on apical third of head; wing with RS3+4 terminating at wing apex. *Cret.*, USSR (Asian RSFSR).

Cretoplatypalpus KOVALEV, 1978, p. 72 [**C. archaeus*; OD]. Similar to *Archiplatypalpus*, but with eyes separated and with 6 scutellar bristles. SUESS, 1979. *Cret.*, USSR (Asian RSFSR).

Drapetiella MEUNIER, 1908h, p. 97 [**D. definita*; OD]. Little-known genus, possibly close to *Euthyneura* (recent); discal cell open. MELANDER, 1927. *Oligo.*, Europe (Baltic)–*Holo.*

Drapetis MEIGEN, 1822, p. 91. MELANDER, 1927. *Oligo.*, Europe (Baltic)–*Holo.*

- Dysaletria** LOEW, 1860, p. 7. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Ecommocycromia** SCHLÜTER, 1978a, p. 103 [**E. difficilis*; OD]. Little-known genus; costa extending to end of M1+2; SC and R much reduced; RS3+4 not forked. *Cret.*, Europe (Germany).
- Electrocyrtoma** COCKERELL, 1917c, p. 22 [**E. burmanica*; OD]. Similar to *Bicellaria* (recent) but with longer arista and with slender tibiae and tarsi; discal cell open. MELANDER, 1927. *Mio.*, Burma.
- Euthyneuriella** MEUNIER, 1908h, p. 112 [**E. longirostris*; OD]. Little-known genus, possibly a synonym of *Trichina* (recent). *Oligo.*, Europe (Baltic)—*Holo.*
- Hilara** MEIGEN, 1822, p. 1. COLLADO, 1926; MELANDER, 1927. *Oligo.*, Europe (Baltic, Spain); *Mio.*, Europe (Germany)—*Holo.*
- Hybos** MEIGEN, 1803, 269. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Leptopeza** MACQUART, 1827, p. 143. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Meghyperiella** MEUNIER, 1908h, p. 112 [**M. porphyropsoides*; OD]. Related to *Leptopeza* but with more generalized arista. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Micrempis** MELANDER, 1927, p. 298. *Oligo.*, Europe (Baltic)—*Holo.*
- Microphorites** HENNIG, 1971b, p. 16 [**M. extinctus*; OD]. Similar to *Microphorus* but with anal angle of wing margin rounded. *Cret.*, Europe (Lebanon).—FIG. 233,3. **M. extinctus*; wing, $\times 46$ (Hennig, 1971b).
- Microphorus** MACQUART, 1827, p. 139. HANDLIRSCH, 1910b; HENNIG, 1971b. *Eoc.*, Canada (British Columbia); *Oligo.*, Europe (Baltic)—*Holo.*
- Oedalea** MEIGEN, 1820, p. 355. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Palaeoleptopeza** MEUNIER, 1908h, p. 111 [**P. gracilis*; OD]. Similar to *Leptopeza* but with spinose hind femora. MELANDER, 1927. *Oligo.*, Europe (Baltic).
- Palaeoparamesia** MEUNIER, 1902d, p. 98 [**P. proosti*; OD]. Little-known genus, probably a synonym of *Clinocera* (recent). MEUNIER, 1908d; MELANDER, 1927. *Oligo.*, Europe (Baltic).
- Parathalassielia** MEUNIER, 1908h, p. 106 [**P. problematica*; OD]. Little-known genus; RS3+4 forked; discal cell present; arista as long as rest of antenna. MELANDER, 1927. *Oligo.*, Europe (Baltic).
- Platypalpus** MACQUART, 1827, p. 92. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Progloma** JAMES, 1937, p. 247 [**P. rohweri*; OD]. Similar to *Gloma* (recent), but fork of RS3+4 distal to end of RS1+2 and discal cell relatively shorter. JAMES, 1939. *Oligo.*, USA (Colorado).
- Protoedalea** COCKERELL, 1920c, p. 252 [**P. brachystoma*; OD]. Similar to *Oedalea*, but R and RS1+2 longer, discal cell narrower, and M1+2 abbreviated. MELANDER, 1927. *Eoc.*, USA (Colorado).
- Ragas** WALKER, 1837, p. 229. [Generic assignment of fossils doubtful.] MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*
- Rhamphomyia** MEIGEN, 1822, p. 42. COCKERELL, 1921e; MELANDER, 1927, 1949; STATZ, 1940. *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Baltic, Germany)—*Holo.*
- Tachydromia** MEIGEN, 1803, p. 269. MELANDER, 1927; TIMON-DAVID, 1944a. *Oligo.*, Europe (Baltic, France)—*Holo.*
- Tachypeza** MEIGEN, 1830, p. 341. MELANDER, 1927, 1949. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*
- Timalphes** MELANDER, 1927, p. 97. *Oligo.*, Europe (Baltic)—*Holo.*
- Trichinities** HENNIG, 1970, p. 7 [**T. cretaceus*; OD]. Related to *Trichina* and *Trichinomyia* (recent), but with 3 branches of M arising from closed discal cell; arista longer than third antennal segment. *Cret.*, Europe (Lebanon).—FIG. 233,5. **T. cretaceus*; wing, $\times 34$ (Hennig, 1970).
- Trichopeza** RONDANI, 1856, p. 150. MELANDER, 1927. *Oligo.*, Europe (Baltic)—*Holo.*

Family DOLICHOPODIDAE

Latreille, 1809

[Dolichopodidae LATREILLE, 1809, p. 290]

Costa extending along wing margin as far as vein M1 (or M1+2); RS1+2 and RS3+4 unbranched; SC very short, ending on R, or in subcostal space; 1A very short, not reaching wing margin. Flagellum usually with long, thin arista. Larvae in rotting vegetation, under bark, etc.; mostly predaceous. *Cret.*—*Holo.*

- Dolichopus** LATREILLE, 1796, p. 159. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908, 1908i; THÉOBALD, 1937a; STATZ, 1940. *Oligo.*, Europe (France, Germany, Baltic)—*Holo.*
- Achalcus** LOEW, 1857, p. 30. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Anepsiomyia** BEZZI, 1902, p. 192. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Argyra** MACQUART, 1834, p. 456. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Campsicnemus** HALIDAY, 1832, p. 357. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Chrysotus** MEIGEN, 1824, p. 40. [Generic assignment of fossils doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic, Roumania)—*Holo.*

- Diaphorus** MEIGEN, 1824, p. 32. MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Gheynius** MEUNIER, 1907–1908, p. 8 [**G. bifurcatus*; OD]. Little-known genus; third antennal segment with a long, median arista between 2 projections from segment. *Oligo.*, Europe (Baltic).
- Gymnopternus** LOEW, 1857, p. 10. MEUNIER, 1908i. *Oligo.*, Europe (Baltic)—*Holo.*
- Hercostomus** LOEW, 1857, p. 9. QUIÉVREUX, 1938. *Oligo.*, Europe (France)—*Holo.*
- Hygroceleuthus** LOEW, 1857, p. 10. MEUNIER, 1908i. *Oligo.*, Europe (Baltic)—*Holo.*
- Lyroneurus** LOEW, 1857, p. 38. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Medetera** FISCHER VON WALDHEIM, 1819, p. 7. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Nematoproctus** LOEW, 1857, p. 40. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Neurigona** RONDANI, 1856, p. 142. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Oncopygus** LOEW, 1873, p. 44. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Palaeochrysolus** MEUNIER, 1907–1908, p. 270 [**P. horridus* MEUNIER, 1907–1908, p. 270; SD CARPENTER, herein] [= *Palaeomedeterus* MEUNIER, 1895c, p. 173, *nom. nud.*]. Little-known genus, apparently related to *Medetera*. MEUNIER, 1906c. *Oligo.*, Europe (Baltic).
- Poecilobothrus** MIK, 1878, p. 3. [Generic assignment of fossil doubtful.] MEUNIER, 1908i. *Oligo.*, Europe (Baltic)—*Holo.*
- Prochrysolus** MEUNIER, 1907–1908, p. 269. *Oligo.*, Europe (Baltic)—*Holo.*
- Prosystenus** NEGROBOV, 1976, p. 122 [**P. zherichini*; OD]. Arista of antenna apical or nearly so, with 2 segments; third antennal segment short, rounded. Wing with SC very short; CUA+1A absent. *Paleoc./Eoc.*, USSR (Asian RSFSR).
- Retinitus** NEGROBOV, 1978, p. 86 [**R. nervosus*; OD]. Wing with SC reduced, terminating on R remote from costal margin; RS3+4 terminating at wing apex; basal crossvein between RS3+4 and M1+2 absent. [Family assignment of genus doubtful.] *Cret.*, USSR (Asian RSFSR).
- Sciapus** ZELLER, 1842, p. 831. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908; STATZ, 1940. *Oligo.*, Europe (Baltic, Germany)—*Holo.*
- Systemus** LOEW, 1857, p. 34. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Thinophilus** WAHLBERG, 1844, p. 37. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*
- Thrypticus** GERSTÄCKER, 1864, p. 43. [Generic assignment of fossil very doubtful.] MEUNIER, 1907–1908; NEGROBOV, 1978. *Oligo.*, Europe (Baltic)—*Holo.*
- Wheeleromyia** MEUNIER, 1907–1908, p. 58 [**W. eocenica*; OD]. Affinities of genus uncertain; first antennal segment cylindrical; second nearly spherical; third enlarged basally, tapering distally. *Oligo.*, Europe (Baltic).
- Xanthochlorus** LOEW, 1857, p. 42. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Xiphandrium** LOEW, 1857, p. 36. [Generic assignment of fossil doubtful.] MEUNIER, 1907–1908. *Oligo.*, Europe (Baltic)—*Holo.*

Family PLATYPEZIDAE Fallén, 1815

[Platyezidae FALLÉN, 1815, p. 1]

Small flies, with covering of short hairs; wings broad; vein SC complete and separate from R; RS3+4 unbranched, the cell below open; M1+2 usually forked distally; head broad; eyes large; antennae porrect, 2 basal segments short, third with a terminal arista; thorax broad; legs short; hind tarsi with at least basal segment flattened or bearing prominent projections. Larvae fungivorous. *Eoc.—Holo.*

- Platyeza** MEIGEN, 1803, p. 272. *Holo.*
- Callomyia** MEIGEN, 1804, p. 311. [Generic assignment of fossil doubtful.] COCKERELL, 1909d. *Eoc.*, USA (Colorado)—*Holo.*
- Eucallimya** COCKERELL, 1911b, p. 82 [**E. fortis*; OD]. Similar to *Callomyia*, but R terminating on costal margin midway between ends of SC and RS1+2. *Oligo.*, USA (Colorado).

Family SCIADOCERIDAE Schmitz, 1929

[Sciadoceridae SCHMITZ, 1929, p. 3]

Similar to Platyezidae and Phoridae, but vein SC fused with R for most of its length; RS1+2 not coalesced with RS3+4; third antennal segment with a subterminal arista. Larval history unknown. *Cret.—Holo.*

- Sciadocera** WHITE, 1917, p. 218. *Holo.*
- Archiphora** SCHMITZ, 1929, p. 9. HENNIG, 1964; McALPINE & MARTIN, 1966. *Oligo.*, Europe (Baltic)—*Holo.*
- Prioriphora** McALPINE & MARTIN, 1966, p. 532 [**P. canadabra*; OD]. Costa ending near

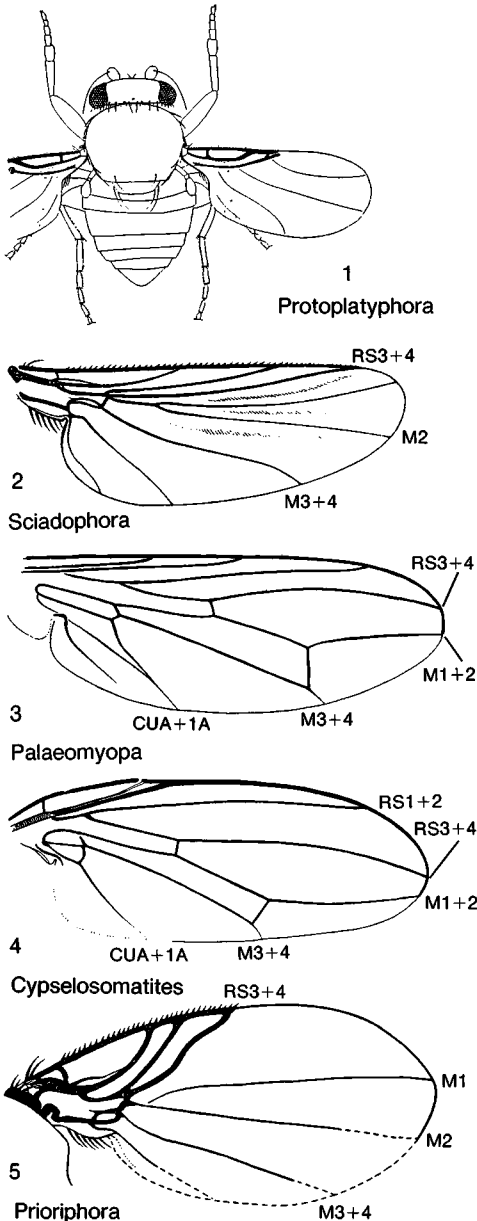


FIG. 234. Sciadoceridae, Phoridae, Conopidae, and Cypselosomatidae (p. 431–435).

midwing; branches of RS close together toward wing base; RS3+4 terminating on wing margin at about midwing. *Cret.*, Canada (Alberta). —FIG. 234.5. **P. canadambra*; wing, $\times 50$ (McAlpine & Martin, 1966).

Sciadophora McALPINE & MARTIN, 1966, p. 529 [**S. bostoni*; OD]. Costa extending almost to wing apex and branches of RS extending along most of costal margin; RS3+4 terminating almost

at wing apex; discal cell absent; mesopleuron with bristles. *Cret.*, Canada (Manitoba). —FIG. 234.2. **S. bostoni*; wing, $\times 36$ (McAlpine & Martin, 1966).

Family PALAEOPHORIDAE

Rohdendorf, 1951

[Palaeophoridae ROHDENDORF, 1951, p. 106, *nom. subst. pro* Archiphoridae ROHDENDORF, 1938, p. 40]

Little-known family, apparently related to the Phoridae. Antennae short, with 3 segments, and bearing a segmented arista; prothorax dilated anteriorly, covering the small head. Wings with vein SC apparently absent; R and RS strong and thick; RS3+4 unbranched. *Jur.*

Palaeophora ROHDENDORF, 1951, p. 106, *nom. subst. pro Archiphora* ROHDENDORF, 1938, p. 41, *non* SCHMITZ, 1929 [**Archiphora ancestris*; OD]. Discal cell present; M1+2 coalesced with RS3+4. ROHDENDORF, 1964. *Jur.*, USSR (Kazakh).

Family PHORIDAE Newman, 1835

[Phoridae NEWMAN, 1835, p. 396]

Minute to small flies. Wings relatively large, rarely greatly reduced or absent; in normal wings, veins R and RS short and thick, other veins weak; M1, M2, and M3+4 widely separated and appearing to arise from RS. Head typically small, flattened, with small eyes; thorax large and usually arched; legs short but well developed, hind femora laterally flattened. Larvae mostly scavengers, some parasitic. *Oligo.*—*Holo.*

Phora LATREILLE, 1796, p. 169. BRUES, 1908a; MEUNIER, 1912e; MELANDER, 1949. *Oligo.*, USA (Colorado), Europe (Baltic)—*Holo.*

Anevrina LIOY, 1864, p. 77. BRUES, 1939a. *Oligo.*, Europe (Baltic)—*Holo.*

Aphiochaeta BRUES, 1903, p. 337. BRUES, 1908a; MEUNIER, 1912e. *Oligo.*, Europe (Baltic)—*Holo.*

Chaetocnemistoptera BORGMEIER, 1923, p. 51. BRUES, 1939a. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Conicera MEIGEN, 1830, p. 226. MEUNIER, 1912e; BRUES, 1939a. *Oligo.*, Europe (Baltic)—*Holo.*

Diplonevra LIOY, 1864, p. 77. BRUES, 1923b, 1939a; DÜRRENFELDT, 1968. *Oligo.*, Europe (Baltic)—*Holo.*

Electrophora BRUES, 1939a, p. 426. *Oligo.*, Europe (Baltic)—*Holo.*

Hypoceridites BRUES, 1939a, p. 428 [**H. dubitatis*; OD]. Tibiae with isolated bristles near

- basal third; postantennal bristles proclinate; wing venation similar to that of *Nossibeia* (recent). *Oligo.*, Europe (Baltic).
- Megaselia** RONDANI, 1856, p. 137. BRUES, 1939a. *Oligo.*, Europe (Baltic)—*Holo.*
- Paraspiniphora** MALLOCH, 1912, p. 412. BRUES, 1939a. *Oligo.*, Europe (Baltic)—*Holo.*
- Phalacritophora** ENDERLEIN, 1912, p. 21. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Protophorites** BRUES, 1939a, p. 430 [**P. fimbriatus*; OD]. RS1 + 2 forked and bearing prominent setae over its entire length; 8 scutellar bristles present. *Oligo.*, Europe (Baltic).
- Protoplathyphora** BRUES, 1939a, p. 431 [**P. tertiaria*; OD]. Similar to *Aenigmatias* (recent), but scutellum with bristles and fore tarsus only slightly thickened. *Oligo.*, Europe (Baltic). — FIG. 234, I. **P. tertiaria*; whole specimen, $\times 15$ (Brues, 1939a).
- Triphleba** RONDANI, 1856, p. 136. BRUES, 1939a. *Oligo.*, Europe (Baltic)—*Holo.*

Family IRONOMYIIDAE McAlpine & Martin, 1966

[Ironomyiidae McALPINE & MARTIN, 1966, p. 528]

Vein SC coalesced with R for most of its length, but free basally and as it joins costal margin; RS3 + 5 terminating at wing apex; R and RS not markedly stronger than other veins. *Cret.—Holo.*

- Ironomyia** WHITE, 1917, p. 216. *Holo.*
- Cretonomyia** McALPINE, 1973, p. 106 [**C. pristina*; OD]. Similar to *Ironomyia* (recent), but mouthparts shorter and labellae apparently broader and padlike; postvertical bristles strongly developed; front and hind tibiae lacking preapical dorsal bristles. *Cret.*, Canada (Manitoba).

Family PIPUNCULIDAE Zetterstedt, 1842

[Pipunculidae ZETTERSTEDT, 1842, p. 4]

Small flies. Wings relatively long; vein M1 free from RS3 + 4 at its termination; M2 not reaching wing margin; cell below R + RS elongate. Head large, broader than thorax, and nearly spherical; eyes very large; antennae small, with dorsal arista. Larvae parasitic on Hemiptera (Homoptera). *Oligo.—Holo.*

- Pipunculus** LATREILLE, 1802, p. 463. *Holo.*
- Cephalosphaera** ENDERLEIN, 1936, p. 129. CARPENTER & HULL, 1939; ACZEL, 1948. *Oligo.*, Europe (Baltic)—*Holo.*
- Metanephrocercus** ACZEL, 1948, p. 120 [**Protonephrocercus collini* CARPENTER & HULL, 1939, p. 13; OD]. Similar to *Protonephrocercus* but with

short and fine ocellar bristles. *Oligo.*, Europe (Baltic).

- Nephrocercus** ZETTERSTEDT, 1838, p. 578. CARPENTER & HULL, 1939; ACZEL, 1948. *Oligo.*, Europe (Baltic)—*Holo.*
- Protonephrocercus** COLLIN, 1931, p. 52. CARPENTER & HULL, 1939; ACZEL, 1948. *Oligo.*, USA (Colorado)—*Holo.*
- Verrallia** MIK, 1899, p. 137. MEUNIER, 1903b; CARPENTER & HULL, 1939; ACZEL, 1948. *Oligo.*, Europe (Baltic)—*Holo.*

Family SYRPHIDAE Leach, 1815

[Syrphidae LEACH, 1815, p. 162]

Small to large flies. Wings of moderate size; vein M1 coalesced with RS3 + 4 distally; a veinlike fold present between RS and M. Head variable in shape; third antennal segment with a short dorsal arista, rarely a terminal style. Larvae in rotting vegetation or liquid media; some predaceous. *Eoc.—Holo.*

- Syrphus** FABRICIUS, 1775, p. 762. HULL, 1945, 1949, 1960. *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado), Europe (Baltic); *Mio.*, Europe (Croatia), USA (Montana)—*Holo.*
- Archalia** HULL, 1945, p. 305 [**A. femorata*; OD]. Allied to *Rhingia* (recent). Crossvein r-m situated well before middle of discal cell; apical crossvein sigmoidal, joining RS3 + 4 well back from wing apex. Hind femora massive. HULL, 1949. *Oligo.*, USA (Colorado).
- Archisyrphus** HULL, 1960, p. 270 [**A. opacus*; OD]. Similar to *Cheilosia*, but RS3 + 4 nearly straight; cell below RS3 + 4 with a sharply acute angle distally; M1 + 2 nearly straight distally, at end of discal cell. *Mio.*, USA (Montana).
- Asarcina** MACQUART, 1842, p. 77. HULL, 1945, 1949. *Eoc.*, USA (Wyoming)—*Holo.*
- Cacogaster** HULL, 1945, p. 297 [**C. novamaculata*; OD]. Related to *Rhingia*. Cell below R open; RS3 + 4 straight, ending at wing apex; crossvein r-m situated well before middle of discal cell. MEUNIER, 1908h. *Oligo.*, USA (Colorado).
- Cheilosia** MEIGEN, 1822, p. 296. COCKERELL, 1909b, 1916c; COCKERELL & LEVEQUE, 1931; THÉOBALD, 1937a; STATZ, 1940; TIMON-DAVID, 1944a; HULL, 1945, 1949; RÖDER, 1980. *Eoc.*, USA (Wyoming, Colorado); *Oligo.*, Europe (Baltic, France, Germany), USA (Colorado)—*Holo.*
- Cheilosialepta** HULL, 1945, p. 285 [**C. baltica*; OD]. Venation as in *Myiolepta*; face (frons) non-tuberculate; hind femora without spines. *Oligo.*, Europe (Baltic).
- Chrysogaster** MEIGEN, 1800, p. 32. HULL, 1945, 1949. *Oligo.*, USA (Colorado)—*Holo.*
- Doliomyia** HULL, 1945, p. 328 [**D. chalybea*; OD]. Similar to *Eumerus* (recent); hind femora slender

- and without spines; eyes bare. *Oligo.*, Europe (Baltic).
- Exylota** HULL, 1945, p. 324 [**Xylota pulchra* MEUNIER, 1904c, p. 207; OD]. Related to *Xylota*, but crossvein r-m less sigmoidal and face somewhat tuberculate. HULL, 1949. *Oligo.*, Europe (Baltic).
- Epistrophe** WALKER, 1852, p. 242. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Eristalis** LATREILLE, 1804, p. 194. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Megaxylota** HULL, 1945, p. 340 [**M. magnifemur*; OD]. Similar to *Xylota*; hind femora greatly thickened, without spines; face concave. HULL, 1949. *Oligo.*, Europe (Baltic).
- Merodon** MEIGEN, 1803, p. 274. HULL, 1945, 1949. *Oligo.*, Europe (Germany)—*Holo.*
- Metasyrphus** MATSUMURA, 1917, p. 147. HULL, 1945, 1949. *Oligo.*, USA (Colorado)—*Holo.*
- Myiolepta** NEWMAN, 1838, p. 373 [= *Arctolepta* HULL, 1945, p. 287 (type, *A. calamitans*); *Sericolepta* HULL, 1945, p. 303 (type, *S. maculata*)]. STATZ, 1940; HULL, 1945, 1949. *Oligo.*, Europe (Baltic)—*Holo.*
- Palaeoascia** MEUNIER, 1893, p. cclix [**P. uniapendiculata*; OD]. Similar to *Spheginoides* (recent); marginal crossveins straight; eyes holoptic; face (frons) tuberculate; hind femora but little thickened, without double row of spines. HANDLIRSCH, 1908b; HULL, 1945, 1949. *Oligo.*, Europe (Baltic).
- Palaeoeristalis** HULL, 1945, p. 333 [**P. tessellatus*; OD]. Similar to *Eristalis*, but RS3+4 with only slight curve. HULL, 1949. *Eoc.*, USA (Colorado).
- Palaeopipiza** MEUNIER, 1902d, p. 103 [**P. xenos*; OD]. Related to *Azpeytia* (recent); RS3+4 convex, diverging from RS1+2 apically; face flat; hind femora short and slender. HULL, 1945, 1949. *Oligo.*, Europe (Baltic).
- Palaeosphagina** MEUNIER, 1904c, p. 204 [**P. elegantula*; OD]. Venation as in *Sphagina*, but vena spuria absent; face tuberculate. HULL, 1945, 1949. *Oligo.*, Europe (Baltic).
- Pipiza** FALLÉN, 1810, p. 11. HULL, 1945, 1949. *Oligo.*, Europe (Baltic, Germany)—*Holo.*
- Platycheirus** LEPELETIER & SERVILLE, 1825, p. 513. CARPENTER & others, 1938; HULL, 1945; MELANDER, 1949. *Oligo.*, USA (Colorado); *Mio.*, Europe (Croatia)—*Holo.*
- Protochrysotoxum** HULL, 1945, p. 326 [**P. sphinx*; OD]. Similar to *Chrysotoxum* (recent); RS3+4 straight; crossvein r-m situated well before middle of discal cell. HULL, 1949. *Oligo.*, USA (Colorado).
- Protorhingia** HULL, 1945, p. 289 [**P. carpenteri*; OD]. Venation as in *Rhingia*, but face concave. HULL, 1949. *Oligo.*, Europe (Baltic).
- Pseudosphagina** HULL, 1945, p. 313 [**P. dichoptica*; OD]. Venation as in *Sphagina*, but face tuberculate; males narrowly dichoptic. HULL, 1949, 1957. *Oligo.*, Europe (Baltic).
- Ptilocephala** HULL, 1945, p. 335. HULL, 1949. *Oligo.*, Europe (Baltic)—*Holo.*
- Rhingia** SCOPOLI, 1763, p. 358. HULL, 1945, 1949. *Oligo.*, USA (Colorado)—*Holo.*
- Sphagina** MEIGEN, 1822, p. 193. THÉOBALD, 1937a; HULL, 1945, 1949. *Oligo.*, Europe (France), USA (Colorado)—*Holo.*
- Spheginascia** MEUNIER, 1904c, p. 205 [**S. biapendiculata*; OD]. Similar to *Cheilosia*. Eyes holoptic; lower face of male with broad, convex, tuberculate bulge; face of female convex, without bulge; hind femora slender, spinose. HULL, 1945, 1949; RÖDER, 1980. *Oligo.*, Europe (Baltic).
- Temnostoma** LEPELETIER & SERVILLE, 1828, p. 518. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*
- Xylotosyrphus** HULL, 1945, p. 339 [**X. pulchrafenestra*; OD]. Similar to *Xylota* (recent), but crossvein r-m well before middle of discal cell; hind femora enlarged. HULL, 1949. *Eoc.*, USA (Utah).

Family CONOPIDAE Latreille, 1802

[Conopidae LATREILLE, 1802a, p. 442]

Flies of moderate size. Wings slender; vein M1+2 close to or fused with RS3+4 near wing margin; CUA+1A extending to wing margin; cell below R+RS very long and slender; head broad; proboscis very long, often geniculate; third antennal segment with dorsal arista or terminal style. Larvae saprophagous, phytophagous, predaceous, or parasitic. *Oligo.*—*Holo.*

Conops LINNÉ, 1758, p. 604. *Holo.*

Palaeomyopa MEUNIER, 1912a, p. 177 [**P. tertiaria*; OD] [= *Palaeosicus* MEUNIER, 1916a, p. 280 (type, *P. loewi*)]. Generalized conopids, apparently close to basic stock of family; cell below RS3+4 open; third antennal segment short; arista arising dorsally and consisting of 3 segments. HENNIG, 1966c. *Oligo.*, Europe (Baltic). — FIG. 234.3. **P. tertiaria*; wing, $\times 6$ (Hennig, 1966c).

Family OTITIDAE Aldrich, 1932

[Otitidae ALDRICH, 1932, p. 7]

Small to large flies. Wings usually conspicuously marked with maculations; vein R commonly with prominent setae; cell below CUP (anal cell) usually with pointed apex; proboscis short. Larvae saprophagous. *Oligo.*—*Holo.*

Otites LATREILLE, 1804, p. 196. *Holo.*

Melieria ROBINEAU-DESVOIDY, 1830, p. 715. COCKERELL, 1917b; MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Scholastes LOEW, 1873, p. 38. COCKERELL, 1921c. ?*Plio./Pleist.*, England—*Holo.*

Stenomyites COCKERELL, 1915, p. 497 [**S. fuscipennis*; OD]. Similar to *Eumetopiella* (recent), but wings not narrow and elongate. *Oligo.*, England.

Family TEPHRITIDAE

Newman, 1835

[Tephritidae NEWMAN, 1835, p. 396]

Small to moderate-sized flies. Wings commonly spotted or banded; vein SC abruptly bent anteriorly near its distal end and joining costa at right angles; costal break commonly present, before termination of R; R setose; cell behind CUP acute distally. Larvae phytophagous. *Mio.—Holo.*

Tephrites LATREILLE, 1804, p. 196. *Holo.*

Oxyna ROBINEAU-DESVOIDY, 1830, p. 755. [Generic assignment of fossil doubtful.] DÜRRNFELDT, 1968. *Plio.*, Europe (Germany)—*Holo.*

Pseudacidia SHIRAKI, 1933, p. 216. KORNEYEV, 1982. *Mio.*, USSR (European RSFSR)—*Holo.*

Family RICHARDIIDAE

Loew, 1868

[Richardiidae Loew, 1868, p. 2]

Similar to Otitidae, but cell below vein CUP without pointed apex; costal break present. Larvae apparently saprophagous. *Oligo.—Holo.*

Richardia ROBINEAU-DESVOIDY, 1830, p. 728. *Holo.*

Pachysomites COCKERELL, 1916c, p. 95 [**P. inermis*; OD]. Venation much as in *Richardia* (recent), but R extending nearly to wing apex; RS1+2 curving anteriorly just before terminating. *Oligo.*, USA (Colorado).

Urortalis COCKERELL, 1917b, p. 378 [**U. caudatus*; OD]. Ovipositor very long and tapering; wing without markings; RS1+2 straight distally, not curved as in *Richardia* (recent). *Oligo.*, USA (Colorado).

Family CYPSELOSOMATIDAE

Hendel, 1931

[Cypselosomatidae HENDEL, 1931, p. 5]

Small flies. Wings of moderate size; costal break present at end of vein SC; CUA+1A typically short, not reaching wing margin; M3+4 not usually continuing beyond end of discal cell; third antennal segment with a short spinelike arista; vibrissae typically pres-

ent. Larvae, so far as known, developing in bat dung in caves. HENNIG, 1958. *Oligo.—Holo.*

Cypselosoma HENDEL, 1913, p. 105. *Holo.*

Cypselosomatites HENNIG, 1965, p. 38 [**C. succini*; OD]. Costa with a distinct break at end of SC; terminal parts of RS3+4 and M1+2 convergent; CUA+1A reaching wing margin; ocellar bristles stout. *Oligo.*, Europe (Baltic). — FIG. 234.4. **C. succini*; wing, ×15 (Hennig, 1965).

Family PSEUDOPOMYZIDAE

McAlpine, 1966

[Pseudopomyzidae McALPINE, 1966, p. 683]

Similar to Cypselosomatidae but with the postvertical bristles convergent. Larvae saprophagous. *Oligo.—Holo.*

Pseudopomyza STROBL, 1893, p. 284. *Holo.*

Eopseudopomyza HENNIG, 1971c, p. 7 [**E. kuehmeri*; OD]. Similar to *Pseudopomyzella* (recent) but with larger eyes and relatively smaller genae; mesopleural setae absent. *Oligo.*, Europe (Baltic).

Family MICROPEZIDAE Loew, 1862

[Micropezidae LOEW, 1862, p. 38]

Flies of moderate size, usually slender. Wings long; costal break absent; cell below vein RS3+4 at least narrowed apically, often closed; basal piece of CUA straight; fronto-orbital bristles and oral vibrissae absent; antennae short, third segment with a dorsal arista; legs long and slender. Larvae saprophagous, often in rotting wood. *Oligo.—Holo.*

Micropeza MEIGEN, 1803, p. 276. *Holo.*

Calobata MEIGEN, 1803, p. 276. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Electrobata HENNIG, 1965, p. 41 [**E. myrmecia*; OD]. Similar to *Crepidochetus* (recent) but without thickened bases of middle and hind femora; arista without long hairs; ocellar setae absent. HENNIG, 1966c, 1967b, 1969a. *Oligo.*, Europe (Baltic). — FIG. 235.1. **E. myrmecia*; head, oblique view from above, ×33 (Hennig, 1965).

Family MEGAMERINIDAE

Hendel, 1913

[Megamerinidae HENDEL, 1913, p. 90]

Similar to Psilidae; fronto-orbital bristles reduced, usually only 1 pair; hind femora thickened and spiny. *Oligo.—Holo.*

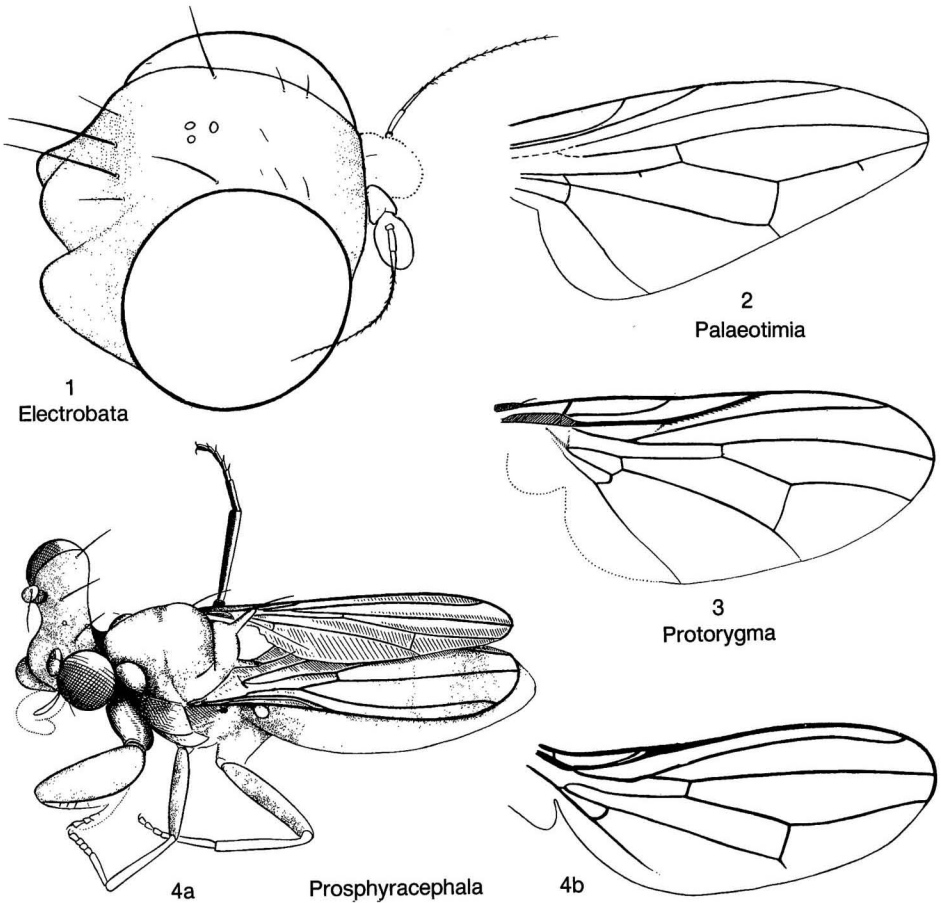


FIG. 235. Micropezidae, Diopsidae, Sepsidae, and Dryomyzidae (p. 435–437).

Megamerina RONDANI, 1861, p. 10. *Holo.*

Palaeotanypeza MEUNIER, 1917a, p. 101 [**P. spinosa*; OD]. Generalized megamerinids, with 2 pairs of fronto-orbital bristles; fore and hind femora thickened. HENNIG, 1965, 1969a. *Oligo.*, Europe (Baltic).

Family DIOPSIDAE Billberg, 1820

[Diopsidae BILLBERG, 1820, p. 115]

Small to medium-sized flies, allied to the Megamerinidae. Vein SC coalesced at least partially with R; basal crossvein between M1+2 and M3+4 absent; eyes typically stalked; fore femora thickened and spiny on ventral surface; postvertical bristles absent; only 1 pair of fronto-orbital and 1 pair of vertical bristles present. *Oligo.*—*Holo.*

Diopsis LINNÉ, 1775, p. 5. *Holo.*

Prosphyracephala HENNIG, 1965, p. 63 [**Sphyra-*

cephala succini LOEW, 1873, p. 102; OD]. Anal cell short, not narrow; CUA+1A continuing as straight line the posterior border of anal cell; notopleural bristles absent. HENNIG, 1969a; LEWIS, 1971a. *Oligo.*, Europe (Baltic), USA (Montana).—FIG. 235,4. **P. succini* (LOEW); *a*, whole insect, $\times 15$; *b*, wing, $\times 18$ (both Hennig, 1965).

Family PSILIDAE Walker, 1853

[Psilidae WALKER, 1853, p. 148]

Small to medium-sized flies; costal break prominent; vein SC incomplete, not extending beyond costal break; antennae usually long; arista pubescent; oral vibrissae absent; pleural bristles of thorax absent. Larvae phytophagous, occurring in stems or roots or under bark. *Oligo.*—*Holo.*

Psila MEIGEN, 1803, p. 278. *Holo.*

Electrochyliza HENNIG, 1965, p. 69 [**E. succini*;

OD]. Similar to *Chyliza* (recent) but more thick-set in general form; hair-covering relatively short; palpi not broadened. HENNIG, 1969a. *Oligo.*, Europe (Baltic).

Family SEPSIDAE Walker, 1833

[Sepsidae WALKER, 1833b, p. 244]

Small flies, similar to Sciomyzidae, but with at least 1 bristle on lower margin of metathoracic spiracle; palpi vestigial; abdomen elongate, constricted basally. Larvae saprophagous. *Oligo.*—*Holo.*

Sepsis FALLÉN, 1810, p. 17. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Baltic)—*Holo.*

Protorygma HENNIG, 1965, p. 83 [**P. electricum*; OD]. Generalized sepsids, close to stem of family; third antennal segment about as long as broad, decidedly oval; terminal part of M1+2 parallel to RS3+4; CUA+1A reaching hind margin of wing. *Oligo.*, Europe (Baltic).—FIG. 235,3. **P. electricum*; wing, $\times 16$ (Hennig, 1965).

Themira ROBINEAU-DESVOIDY, 1830, p. 745. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Family DRYOMYZIDAE

Schiner, 1864

[Dryomyzidae SCHINER, 1864, p. 38]

Flies of moderate size, similar to the Sciomyzidae but without femoral bristles. Larvae saprophagous or fungivorous. *Paleoc.*—*Holo.*

Dryomyza FALLÉN, 1820, p. 15. [Generic assignment of fossils doubtful.] COCKERELL, 1923b; STATZ, 1940. *Oligo.*, Europe (Germany); *Paleoc.*—*Plio.*, South America (Colombia)—*Holo.*

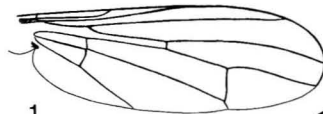
Palaeotimia MEUNIER, 1908d, p. 266 [**P. lhoesti*; OD]. Dryomyzids with 2 pairs of fronto-orbital bristles; third antennal segment short, elliptical. Wings broad basally; RS3+4 and M1+2 convergent distally. HENNIG, 1940, 1969a. *Oligo.*, Europe (Baltic). — FIG. 235,2. **P. lhoesti*; wing, $\times 9$ (Hennig, 1940).

Prodryomyza HENNIG, 1965, p. 73 [**P. electrica*; OD]. Similar to *Palaeotimia*, but terminal portions of RS3+4 and M1+2 not converging, and R with prominent setae distally. *Oligo.*, Europe (Baltic).

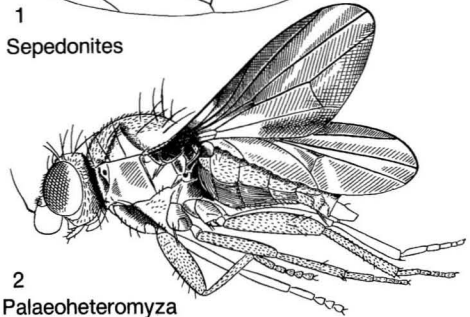
Family SCIOMYZIDAE Fallén, 1820

[Sciomyzidae FALLÉN, 1820, p. 1]

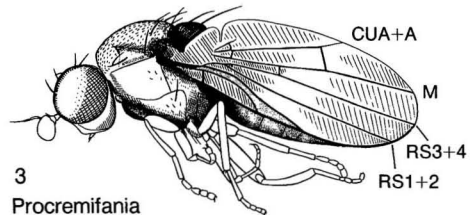
Costal break absent; vein SC independent of R and terminating on costa well before end of R; cell cup short, not produced into an acute angle distally; vibrissae absent; no bristle on lower margin of metathoracic spi-



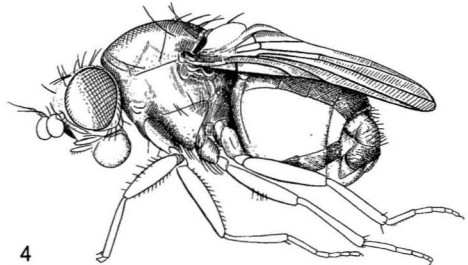
1
Sepedonites



2
Palaeoheteromyza



3
Procremifania



4
Chamaelauxania

FIG. 236. Sciomyzidae, Chamaemyiidae, and Lauxaniidae (p. 437–438).

racle. Larvae chiefly predaceous on snails. *Oligo.*—*Holo.*

Sciomyza FALLÉN, 1820, p. 11. SCUDDER, 1878d; COCKERELL, 1909a. *Eoc.*, Canada (British Columbia); *Oligo.*, USA (Colorado)—*Holo.*

Palaeoheteromyza MEUNIER, 1904f, p. 26 [**P. crassicornis*; OD]. Sciomyzines with very large third antennal segment. HENNIG, 1965, 1969a. *Oligo.*, Europe (Baltic). — FIG. 236,2. **P. crassiformis*; whole specimen, $\times 12$ (Hennig, 1965).

Prophaemyia HENNIG, 1965, p. 87 [**P. loewi*; OD]. Related to *Pelidnoptera* (recent). Middle and hind tibiae with several setae above preapical spines; terminal part of R bearing many short hairs. HENNIG, 1967b. *Oligo.*, Europe (Baltic).

Prosalticella HENNIG, 1965, p. 92 [**P. succini*; OD]. Similar to *Salticella* (recent), but propleural bris-

cles weakly developed and the sternopleura pilose. Wings with RS3+4 and M1+2 almost parallel distally. HENNIG, 1969a. *Oligo.*, Europe (Baltic). *Sepedonites* HENNIG, 1965, p. 102 [**S. baltica*; OD]. Related to *Sepedon* (recent). SC strong for its entire length, terminating well before end of R; CUA+1A reaching margin of wing. *Oligo.*, Europe (Baltic). — FIG. 236,1. **S. baltica*; wing, $\times 7.5$ (Hennig, 1965).

Tetanocera DUMÉRIL, 1800, p. 439. [Generic assignment of fossil doubtful.] THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Family CHAMAEMYIIDAE

Hendel, 1910

[Chamaemyiidae HENDEL, 1910, p. 313]

Small flies. Costa without break; vein SC complete, in some species coalesced with R for a short distance; CUA+1A not reaching wing margin; cell cup closed; postvertical bristles convergent or absent; oral vibrissae absent; fore and hind tibiae without preapical bristles. Larvae predaceous on Coccidae and other Homoptera. *Oligo.*—*Holo.*

Chamaemyia MEIGEN, 1803, p. 278. *Holo.*

Procremifania HENNIG, 1965, p. 116 [**P. electrica*; OD]. Similar to *Cremifania* (recent), but wings with cell below R relatively broader; head with larger, rounded eyes and with correspondingly narrow genae. *Oligo.*, Europe (Baltic). — FIG. 236,3. **P. electrica*; whole specimen, $\times 18$ (Hennig, 1965).

Family LAUXANIIDAE

Macquart, 1835

[Lauxaniidae MACQUART, 1835 in MACQUART, 1834–1835, p. 506]

Small flies. Wings with vein SC complete; costal break absent; cell cup closed; CUA+1A short; oral vibrissae very poorly developed or absent; postvertical bristles convergent; only 2 fronto-orbital bristles. Larvae saprophagous or phytophagous. *Oligo.*—*Holo.*

Lauxania LATREILLE, 1804, p. 196. *Holo.*

Chamaelauxania HENNIG, 1965, p. 106 [**C. succini*; OD]. Head rounded; eyes vertically elliptical; third antennal segment oval, somewhat longer than broad. *Oligo.*, Europe (Baltic). — FIG. 236,4. **C. succini*; whole specimen, $\times 10.5$ (Hennig, 1965).

Hemilauxania HENNIG, 1965, p. 109 [**H. incurviseta*; OD]. Similar to *Chamaelauxania*, but costal margin (to level of RS1+2) with short, thick spines among fine hairs; second segment of arista

relatively shorter and third with slightly longer pubescence. *Oligo.*, Europe (Baltic).

Sapromyza FALLÉN, 1810, p. 18. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Family HELEOMYZIDAE

Loew, 1862

[Heleomyzidae LOEW, 1862, p. 126]

Medium-sized flies. Costal break present, costal margin usually with short bristles; cell behind stem of vein M and cell behind vein CUP closed; vibrissae well developed; postvertical bristles convergent; antennae short, third segment usually rounded. Larvae saprophagous or phytophagous. *Oligo.*—*Holo.*

Heleomyza FALLÉN, 1810, p. 19. [Generic assignment of fossils doubtful.] MEUNIER, 1914b; THÉOBALD, 1937a; TIMON-DAVID, 1944a. *Oligo.*, Europe (Germany, France)—*Holo.*

Chaetohelomyza HENNIG, 1965, p. 148 [**C. electrica*; OD]. Little-known genus with 2 pairs of stout setae on prosternum, 3 dorsoventral setae on middle tibiae, and 3 stout sternopleural setae on thorax. *Oligo.*, Europe (Baltic).

Electroleria HENNIG, 1965, p. 150 [**Leria alacris* MEUNIER, 1904f, p. 25; OD]. Related to *Leria* (recent), but CUA+1A extending to wing margin; propleural setae absent. *Oligo.*, Europe (Baltic).

Heteromyiella HENDEL, 1910, p. 309. COCKERELL, 1914f. *Oligo.*, USA (Colorado)—*Holo.*

Heteromyza FALLÉN, 1820, p. 1. [Generic assignment of fossil doubtful.] HENNIG, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Protosuillia HENNIG, 1965, p. 143 [**Heleomyza media* MEUNIER, 1904f, p. 24; OD]. Similar to *Suillia* but with 2 fronto-orbital bristles. *Oligo.*, Europe (Baltic).

Suillia ROBINEAU-DESVOIDY, 1830, p. 642. [Generic assignment of fossil doubtful.] HENNIG, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Trixoscelis RONDANI, 1856, p. 134. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Family CHYROMYIDAE

Frey, 1921

[Chyromyidae FREY, 1921, p. 219]

Very small, stout flies. Wings with vein SC free, ending on costa; costal break typically present, though weak; cell behind stem of M closed; CUA+1A not reaching wing margin. Palpi typically reduced; postvertical bristles always present, convergent and short; alula only slightly developed. Larvae scav-

engers, in bird or rodent nests or in rotting wood. *Oligo.*—*Holo.*

Chyromya ROBINEAU-DESVOIDY, 1830, p. 621. *Holo.*
Gephyromyiella HENNIG, 1965, p. 158 [**G. electrica*; OD]. Costal break absent; costal margin evenly pubescent; SC and R parallel; RS3+4 and M1+2 nearly parallel, with slight convergence distally; crossvein r-m at about level of end of SC. *Oligo.*, Europe (Baltic).

Family PALLOPTERIDAE

Loew, 1862

[Pallopteridae LOEW, 1862, p. 56]

Similar to Lonchaeidae, but postvertical bristles present and propleural bristles commonly absent; wings with vein SC complete, terminating very close to R. Larvae saprophagous or phytophagous. *Oligo.*—*Holo.*

Palloptera FALLÉN, 1820, p. 23. *Holo.*

Pallopterites HENNIG, 1967b, p. 4 [**P. electrica*; OD]. Similar to *Palloptera* (recent) but with only 1 pair of scutellar bristles. *Oligo.*, Europe (Baltic).

Family LONCHAEIDAE

Rondani, 1856

[Lonchaeidae RONDANI, 1856, p. 118]

Stout flies, small to moderate in size. Wings with vein SC complete, ending on costal margin; oral vibrissae absent; 1 pair of fronto-orbital bristles; postocular bristles divergent; anterior and posterior tibiae without preapical bristles. Larvae saprophagous or phytophagous. *Oligo.*—*Holo.*

Lonchaea FALLÉN, 1820, p. 25. *Holo.*

Glaesolonchaea HENNIG, 1967b, p. 15 [**G. electrica*; OD]. Hind margin of mesopleura with a single bristle. *Oligo.*, Europe (Baltic).

Morgea HENNIG, 1967b, p. 11 [**M. mcalpinei*; OD]. Hind margin of mesopleura completely lacking bristles. HENNIG, 1969a. *Oligo.*, Europe (Baltic).

Family PIOPHILIDAE

Macquart, 1835

[Piophilidae MACQUART, 1835 in MACQUART, 1834–1835, p. 531]

Small flies. Wing with costal break at end of SC; cell behind stem of vein M and cell behind vein CUP complete; CUA+1A not reaching wing margin; oral vibrissae strongly developed; postvertical bristles well devel-

oped, at least slightly divergent; mesopleural bristles absent. Larvae saprophagous, usually in dead animal tissue. *Oligo.*—*Holo.*

Piophila FALLÉN, 1810, p. 20. *Holo.*

Mycetaulus LOEW, 1845, p. 37. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Family PRONEOTTIOPHILIDAE

Hennig, 1969

[Proneottiophilidae HENNIG, 1969a, p. 11]

Similar to Piophilidae but with 3 strong, reclinate fronto-orbital bristles; terminations of veins SC and R widely separated on costal margin. *Oligo.*

Proneottiophilum HENNIG, 1969a, p. 15 [**P. extinctum*; OD]. Head rounded in profile; eyes higher than long; third antennal segment elongate-oval. Costa with stout setae on dorsal surface. *Oligo.*, Europe (Baltic).—FIG. 237,2. **P. extinctum*; wings and body, ×7 (Hennig, 1969a).

Family OPOMYZIDAE

Fallén, 1810

[Opomyzidae FALLÉN, 1810, p. 10]

Small, slender flies. Costal break at end of vein SC; cell behind stem of M and cell behind CUP complete; oral vibrissae absent; only 1 pair of fronto-orbital bristles; postvertical bristles divergent. Larvae in stems of grasses. *Oligo.*—*Holo.*

Opomyza FALLÉN, 1820, p. 10. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Family CLUSIIDAE Frey, 1921

[Clusiidae FREY, 1921, p. 220]

Small flies, similar to the Agromyzidae; second antennal segment with an outer, angular projection; 2 to 4 fronto-orbital bristles. Larvae in moist, rotting wood. *Oligo.*—*Holo.*

Clusia HALIDAY, 1838, p. 188. *Holo.*

Clusiodes COQUILLET, 1904, p. 93. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Electroclusiodes HENNIG, 1965, p. 136 [**Agromyza meunieri* HENDEL, 1923, p. 145; OD]. Head with 4 pairs of fronto-orbital setae; tibiae lacking apical spines; wing with crossvein r-m not very remote from crossvein between M1+2 and

M3+4. HENNIG, 1969a. *Oligo.*, Europe (Baltic).
—FIG. 237.4. **E. meunieri* (HENDEL); whole
insect, $\times 7.8$ (Hennig, 1965).

Family ACARTOPHTHALMIDAE
Czerny, 1928

[Acartophthalmidae CZERNY, 1928, p. 3]

Similar to Clusiidae, but postvertical bristles remote from each other; eyes pubescent; arista short, only a little longer than rest of antenna. Wing with veins SC and R divergent; costa broken only near wing base. *Oligo.*—*Holo.*

Acartophthalmus CZERNY, 1902, p. 256. *Holo.*
Acartophthalmites HENNIG, 1965, p. 130 [**A. tertiaria*; OD]. Similar to *Acartophthalmus* (recent), but insects about twice as large as those of *Acartophthalmus*; thorax with a distinct color pattern. *Oligo.*, Europe (Baltic). —FIG. 237.5. **A. tertiaria*; wing, $\times 5$ (Hennig, 1965).

Family ODINIIDAE Hendel, 1918

[Odiniidae HENDEL, 1918, p. 112]

Similar to Agromyzidae. Wings with costa weakly developed or absent between terminations of veins RS3+4 and M1+2; fore and hind tibiae with short preapical bristles. Larvae saprophagous, living in galleries of wood-boring insects. *Oligo.*—*Holo.*

Odinia ROBINEAU-DESVOIDY, 1830, p. 648. *Holo.*
Protodinia HENNIG, 1965, p. 124 [**P. electrica*; OD]. Related to *Odinia* (recent). Costal break at end of SC; costa extending to termination of RS3+4; CUA+1A reaching to hind margin of wing. Eyes vertically elliptical; third antennal segment approximately square in general form. *Oligo.*, Europe (Baltic).

Family AGROMYZIDAE
Bigot, 1852

[Agromyzidae BIGOT, 1852, p. 486]

Small flies. Wings with costal break at end of vein SC; cell below stem of M complete; costa strongly developed as far as end of M1+2; preapical tibial bristles absent. Larvae leaf-miners or gall-makers. *Oligo.*—*Holo.*

Agromyza FALLÉN, 1810, p. 21. THÉOBALD, 1937a; MELANDER, 1949. *Oligo.*, Europe (France), USA (Colorado)—*Holo.*
Melanagromyza HENDEL, 1920, p. 114. MELANDER, 1949. *Oligo.*, USA (Colorado)—*Holo.*

Phytomyza FALLÉN, 1810, p. 21. HERING, 1930. *Oligo.*, Europe (France) HERING, *Oligo.*, Europe (France)—*Holo.*

Family CARNIDAE Frey, 1921

[Carnidae FREY, 1921, p. 149]

Similar to Milichiidae, but labella rounded, not elongate, and proboscis not geniculate. Larvae saprophagous. *Oligo.*—*Holo.*

Carnus NITZSCH, 1818, p. 284. *Holo.*
Meoneurites HENNIG, 1965, p. 185 [**M. enigmatica*; OD]. Similar to *Neomeoneurites* (recent), but margin of mouth not protruding; longitudinal axis of eye vertical, not oblique; distance between ends of RS1+2 and RS3+4 clearly shorter than that between ends of RS3+4 and M1+2. HENNIG, 1972a. *Oligo.*, Europe (Baltic).

Family PERISCHELIDIDAE
Oldenberg, 1914

[Periscelididae OLDENBERG, 1914, p. 41]

Costa without break and extending beyond end of vein RS3+4; SC very short, not reaching wing margin; 1 pair of fronto-orbital bristles; postvertical bristles divergent. Larvae in fermenting tree sap or in leaf mines of weevils. *Oligo./Mio.*—*Holo.*

Periscelis LOEW, 1858, p. 113. STURTEVANT, 1963. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Family NEUROCHAETIDAE
McAlpine, 1978

[Neurochaetidae McALPINE, 1978, p. 274]

Related to the Periscelididae but with 3 or more fronto-orbital bristles; vibrissae not displaced high above projecting lower ridge of face (epistoma). Wings with costal break present at end of vein SC. Larvae apparently feeding on microorganisms associated with araceous plants. *Oligo.*—*Holo.*

Neurochaeta McALPINE, 1978, p. 278. *Holo.*
Anthoclusia HENNIG, 1965, p. 165 [**A. gephyrea*; OD]. Wings unusually broad; SC weak; terminations of RS1+2 and RS3+4 nearer together than terminations of RS3+4 and M1+2; CUA+1A not reaching wing margin; third antennal segment of male oval, directed ventrally. HENNIG, 1967b, 1969a, 1971a. *Oligo.*, Europe (Baltic). —FIG. 237.6. **A. gephyrea*; *a*, whole insect, $\times 20$; *b*, male antenna, arista incomplete, $\times 150$ (both Hennig, 1965).

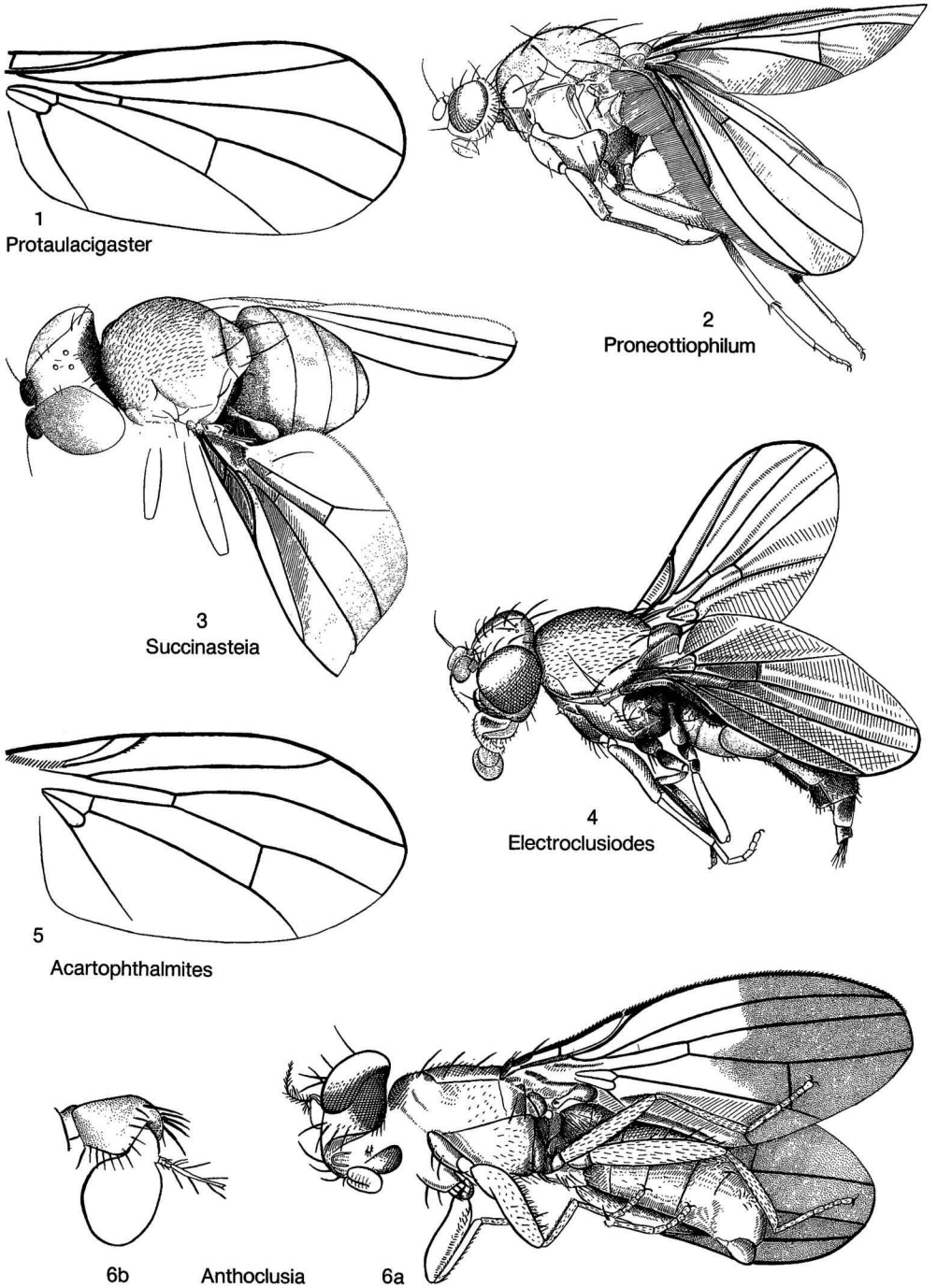


FIG. 237. Proneottiophilidae, Clusiidae, Acartophthalmidae, Neurochaetidae, Aulacigastridae, and Asteiidae (p. 439–442).

Family ANTHOMYZIDAE

Bigot, 1852

[Anthomyzidae BIGOT, 1852, p. 486]

Small, slender flies, with much structural diversity. Oral vibrissae present; frons usually desclerotized; postvertical bristles divergent when present; usually 3 pairs of fronto-orbital bristles present, at least 1 pair of which are reclinate. Larvae saprophagous, some probably phytophagous. HENNIG, 1971a. *Oligo.*—*Holo.*

Anthomyza FALLÉN, 1810, p. 20. [Generic assignment of fossil doubtful.] STATZ, 1940; HENNIG, 1971a. *Oligo.*, Europe (Germany)—*Holo.*

Protanthomyza HENNIG, 1965, p. 169 [**P. col-larti*; OD]. Costal break at end of SC absent; mesopleura with stout bristles on hind margin. *Oligo.*, Europe (Baltic).

Xenanthomyza HENNIG, 1967b, p. 19 [**X. lars-soni*; OD]. Arista of antenna with only short hairs. *Oligo.*, Europe (Baltic).

Family AULACIGASTRIDAE

Duda, 1924

[Aulacigastriidae DUDA, 1924, p. 173]

Similar to the Periscelididae, but costal break usually present; vein SC coalesced with R distally; ocellar bristles and usually post-vertical bristles absent. Larvae saprophagous, as far as known, in fermenting tree sap. *Oligo.*—*Holo.*

Aulacigaster MACQUART, 1835, p. 579. *Holo.*

Protaulacigaster HENNIG, 1965, p. 162 [**P. elec-trica*; OD]. Similar to *Aulacigaster* (recent) but without costal break at end of SC; CUA+1A extending to hind wing margin. *Oligo.*, Europe (Baltic).—FIG. 237, I. **P. electrica*; wing, $\times 22$ (Hennig, 1965).

Family ASTEIIDAE Rondani, 1856

[Asteiidae RONDANI, 1856, p. 27]

Small to minute flies. Wings long; costal break absent; vein SC incomplete, not reaching costal margin; RS1+2 diverging anteriorly shortly after its origin, usually terminating on costa before midwing; CUA+1A absent; oral vibrissae well developed; only 1 or 2 pairs of fronto-orbital bristles present. Larvae fungivorous. *Oligo.*—*Holo.*

Asteia MEIGEN, 1830, p. 88. *Holo.*

Succinasteia HENNIG, 1969a, p. 31 [**S. carpen-*

teri; OD]. Termination of RS1+2 on costa about equidistant between terminations of R and RS3+4; 2 reclinate fronto-orbital bristles present. *Oligo.*, Europe (Baltic).—FIG. 237, 3. **S. carpenteri*; whole insect, $\times 24$ (Hennig, 1969a).

Family CAMILLIDAE Frey, 1921

[Camillidae FREY, 1921, p. 65]

Small flies, similar to Drosophilidae, but vein CUA+1A very short or absent. Larvae saprophagous, usually in rodent nests. *Oligo.*—*Holo.*

Camilla HALIDAY, 1836, p. 281. *Holo.*

Protocamilla HENNIG, 1965, p. 195 [**P. succini*; OD]. Costal margin with 2 breaks; basal cross-vein present; CUA+1A absent; dorsal preapical bristles on all tibiae. *Oligo.*, Europe (Baltic).

Family DIASTATIDAE

Frey, 1921

[Diastatidae FREY, 1921, p. 220]

Similar to Ephydridae (recent) but with only 1 costal break and with convergent post-vertical bristles present. Larvae apparently saprophagous, in rotting wood. *Oligo.*—*Holo.*

Diastata MEIGEN, 1830, p. 94. *Holo.*

Pareuthychaeta HENNIG, 1965, p. 191 [**P. elec-trica*; OD]. Venation much as in *Euthychaeta* (recent); third antennal segment oval; 1 pair of reclinate and 1 pair of proclinate fronto-orbital bristles, latter fairly remote from former. HENNIG, 1967b. *Oligo.*, Europe (Baltic).

Family DROSOPHILIDAE

Rondani, 1856

[Drosophilidae RONDANI, 1856, p. 27]

Small flies. Costal break present; vein SC incomplete or coalesced with R distally; CUA+1A short. Proclinate fronto-orbital bristles located near eye margins; mesopleural bristles absent. Larvae mostly fungivorous. *Oligo.*—*Holo.*

Drosophila FALLÉN, 1823, p. 4. [Generic assignment of fossil doubtful.] COCKERELL, 1923b. *Oligo.*, South America (Colombia)—*Holo.*

Curtonotum MACQUART, 1842, p. 350. [Generic assignment of fossil doubtful.] THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Electrophortica HENNIG, 1965, p. 202 [**E. succini*; OD]. Similar to *Amiota* (recent); 3 pairs of fronto-orbital bristles; costa extending to M1+2; distal portions of RS3+4 and M1+2 nearly parallel. *Oligo.*, Europe (Baltic).

Family MILICHIIDAE Schiner, 1864

[Milichiidae SCHINER, 1864, p. 296]

Small flies. Costa with 2 breaks, 1 at end of vein SC, the other near humeral vein; cell behind stem of M and cell behind CUP closed; oral vibrissae present; postvertical bristles not divergent; labella elongate. Larvae saprophagous in various habitats. *Oligo.*—*Holo.*

Milichia MEIGEN, 1830, p. 131. *Holo.*

Phylomyza FALLÉN, 1810, p. 20. SABROSKY, 1963; HENNIG, 1967b. *Oligo.*, Europe (Baltic); *Mia.*, Mexico (Chiapas)—*Holo.*

Pseudodesmometopa HENNIG, 1971c, p. 14 [**P. succineum*; OD]. Similar to *Desmometopa* (recent), but labellae shorter and cerci of female cuspidate. *Oligo.*, Europe (Baltic).

Family CRYPTOCHAETIDAE

Brues & Melander, 1932

[Cryptochaetidae BRUES & MELANDER, 1932, p. 342]

Small flies. Costa with 2 breaks; cell behind stem of vein M open to discal cell; CUA + 1A absent; 2A well developed; third antennal segment much enlarged; fronto-orbital bristles and ocellar bristles absent. Larvae endoparasitic on certain Homoptera. *Oligo.*—*Holo.*

Cryptochaetum RONDANI, 1875, p. 167. *Holo.*

Phanerochaetum HENNIG, 1965, p. 179 [**P. tuxeni*; OD]. Similar to *Cryptochaetum* (recent) but with a distinct, though short, arista. HENNIG, 1969a. *Oligo.*, Europe (Baltic).

Family CHLOROPIDAE

Rondani, 1856

[Chloropidae RONDANI, 1856, p. 26]

Small flies. Vein CUA + 1A and cell behind CUP absent; proboscis with elongate labella; proclinate and reclinate fronto-orbital bristles absent. Larval habits very diverse: parasitic, saprophagous, or phytophagous. *Oligo.*—*Holo.*

Chloropa MEIGEN, 1803, p. 278. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Hippelates LOEW, 1863, p. 36. [Generic assignment of fossil doubtful.] COCKERELL, 1915. *Oligo.*, England—*Holo.*

Oscinella BECKER, 1910, p. 150. [Generic assignment of fossil doubtful.] STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Protoscinella HENNIG, 1965, p. 203 [**P. electricus*; OD]. Head higher than long; eyes vertically

elliptical; third antennal segment large and rounded; arista short, with short hairs; labellae of proboscis slender and long; costa extending to termination of M1 + 2. *Oligo.*, Europe (Baltic). *Protoscinis* COCKERELL, 1917b, p. 380 [**P. parvus*; OD]. Similar to *Oscinella*, but crossvein r-m nearer wing base. *Oligo.*, England.

Family SCATOPHAGIDAE

Robineau-Desvoidy, 1830

[Scatophagidae ROBINEAU-DESVOIDY, 1830, p. 614]

Similar to Anthomyiidae but with silky hairs below occiput. Larvae saprophagous or phytophagous, including a few leaf-miners. *Oligo.*—*Holo.*

Scatophaga FABRICIUS, 1803, p. 277. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Norellisoma HENDEL, 1910, p. 308. STATZ, 1940. *Oligo.*, Europe (Germany)—*Holo.*

Family GASTEROPHILIDAE

Girschner, 1896

[Gasterophilidae GIRSCHNER, 1896, p. 63]

Muscoid flies, with mouthparts vestigial in adults. Vein M1 + 2 extending nearly straight to wing margin, not curved abruptly toward RS3 + 4. Larvae parasitic in alimentary tract of mammals. *Pleist.*—*Holo.*

Gasterophilus LEACH, 1817, p. 162. *Holo.*

Cobboldia BRAUER, 1887, p. 218. [Fossils are larvae from frozen mammoth; living species of *Cobboldia* are parasites of elephants.] GRUNIN, 1973. *Pleist.*, USSR (Asian RSFSR)—*Holo.*

Family MUSCIDAE Latreille, 1802

[Muscidae LATREILLE, 1802a, p. 453]

Small to large flies. Vein M1 + 2 with an abrupt bend toward RS3 + 4 in midwing area; CUA + 1A not reaching hind margin; antennae with dorsal arista. Larvae saprophagous, phytophagous, or predaceous. *Oligo.*—*Holo.*

Musca LINNÉ, 1758, p. 589. *Holo.*

Fannia ROBINEAU-DESVOIDY, 1830, p. 567. [Fossil record is of *F. scalaris*, a widely distributed extant species.] HENNIG, 1966a. *Oligo.*, Europe (Baltic)—*Holo.*

Family GLOSSINIDAE

Malloch, 1929

[Glossinidae MALLOCH, 1929, p. 533]

Flies of moderate size, similar to Muscidae, but vein M1 + 2 nearly straight in

midwing area; proboscis in both sexes strongly sclerotized and elongate, its base bulbous. Larval development completed in abdomen of adult female. *Oligo.*—*Holo.*

Glossina WIEDEMANN, 1830, p. 253 [= *Paloestrus* SCUDDER, 1892, p. 18 (type, *P. oligocensus*); *Cockereilliiba* TOWNSEND, 1938, p. 166 (type, *Glossina osborni* COCKERELL, 1909e); *Lithoglossina* TOWNSEND, 1938, p. 166 (type, *Glossina armatipes* COCKERELL, 1917a)]. COCKERELL, 1907d, 1916b; BEQUAERT, 1930b; TOWNSEND, 1942. *Oligo.*, USA (Colorado)—*Holo.*

Family EOPHLEBOMYIIDAE Cockerell, 1925

[Eophlebomyiidae COCKERELL, 1925c, p. 230]

Little-known flies, apparently related to the Anthomyiidae. *Eoc.*

Eophlebomyia COCKERELL, 1924a, p. 4 [**E. claripennis*; OD]. Cell below vein M3 + 4 open; tibiae smooth. COCKERELL, 1925c. *Eoc.*, USA (Colorado).

Family CALLIPHORIDAE

Brauer & von Bergenstamm, 1889

[Calliphoridae BRAUER & VON BERGENSTAMM, 1889, p. 156]

Flies medium-sized to large. Similar to Sarcophagidae (recent), but arista plumose to its tip; commonly with 2 notopleural bristles. Larvae mostly scavengers, usually in carrion; some parasitic on snails or earthworms, and a few causing cutaneous myiasis in mammals. *Cret.*—*Holo.*

Calliphora ROBINEAU-DESVOIDY, 1830, p. 433. *Holo.* *Cretaphormia* McALPINE, 1970, p. 345 [**C. fowleri*; OD]. Puparium about 13 mm long; flies shaped as in *Protophormia* (recent). *Cret.*, Canada (Alberta).

Family HIPPOBOSCIDAE Samouelle, 1819

[Hippoboscidae SAMOUELLE, 1819, p. 302]

Wings long; veins SC, R, and RS strong, ending on anterior margin well before apex; M1+2, M3+4, and CUA+1A usually reaching wing margin but weakly developed; cell behind stem of M open to discal cell; body dorsoventrally flattened; proboscis porrect. Adults ectoparasites on mammals and birds. Larval development completed in abdomen of adult female. *Oligo.*—*Holo.*

Hippobosca LINNÉ, 1758, p. 607. *Holo.*

Lynchia WEYENBERGH, 1881, p. 195. STATZ, 1940; HENNIG, 1966a. *Oligo.*, Europe (Germany)—*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the order Diptera, suborder Brachycera, are too poorly known to permit assignment to families.

Acanthomyites COCKERELL, 1921e, p. 33 [**A. aldrichi*; OD]. Little-known genus of stout flies, with many large bristles on head, abdomen, and legs. [Wing unknown; probably a muscoid.] *Eoc.*, USA (Colorado).

Adipterites TOWNSEND, 1938, p. 166 [**Dipterites obovatus* HEER, 1865, fig. 323; OD]. Little-known larva. HEER, 1849; TOWNSEND, 1942. *Mio.*, Europe (Germany).

Anthracidia GERMAR, 1849, p. 64 [**A. xylozona*; OD]. Little-known genus. *Oligo.*, Europe (Germany).

Arthropiella MEUNIER, 1908d, p. 262 [**A. eocenia*; OD]. Little-known genus, possibly related to the Xylophagidae. HENNIG, 1967a. *Oligo.*, Europe (Baltic).

Burmitempis COCKERELL, 1917g, p. 367 [**B. balteralis*; OD]. Little-known genus. Discal cell open; structure of RS and M uncertain; halteres enormous. Head broad, dichoptic. MELANDER, 1927. *Mio.*, Burma.

Dipterites HEER, 1849, p. 254 [**D. obsoleta*; OD]. Little-known genus, probably belonging to suborder Brachycera. *Mio.*, Europe (Germany).

Electrotachina TOWNSEND, 1938, p. 166 [**E. smithii*; OD]. Little-known genus (adult). TOWNSEND, 1942. *Oligo.*, Europe (Baltic).

Eoasilidea BODE, 1953, p. 315 [**E. fragmentosa*; OD]. Little-known genus, based on wing fragment; placed in new family Eoasilidae, without diagnosis. *Jur.*, Europe (Germany).

Eomyza COCKERELL, 1924d, p. 200 [**E. holoptera*; OD]. Little-known genus, based on wing fragment. HENNIG, 1965. *Eoc.*, USA (Colorado).

Epidia WEYENBERGH, 1869, p. 258 [**E. wulpi*; OD]. Little-known genus. *Jur.*, Europe (Germany).

Homoeopteryx BODE, 1953, p. 317 [**H. incerta*; OD]. Little-known genus, based on wing fragment. *Jur.*, Europe (Germany).

Liassonympha BODE, 1953, p. 331 [**L. compacta*; OD]. Little-known genus, based on pupa. *Jur.*, Europe (Germany).

Lithexorista TOWNSEND, 1921, p. 133 [**L. scudleri*; OD]. Little-known genus (adult). TOWNSEND, 1942. *Eoc.*, USA (Wyoming).

Lithohypoderma TOWNSEND, 1916, p. 129 [**Musca ascarides* SCUDDER, 1877a, p. 756; OD]. Genus known only from larvae and pupae; larvae with well-developed mouth-hooks; integument setose.

- [Probably subaquatic and saprophagous.]
 SCUDDER, 1890; COCKERELL, 1907f, 1916c;
 TOWNSEND, 1942; BRADLEY, 1931. *Eoc.*, USA
 (Colorado, Utah).
- Lithotachina** TOWNSEND, 1921, p. 133 [**Echinomyia antiqua* HEER, 1849, p. 247; OD]. Little-known genus (adult). TOWNSEND, 1942. *Mio.*, Europe (Germany).
- Muscidites** HEYDEN & HEYDEN, 1866, p. 157 [**M. deperditus*; OD]. Little-known genus (larva). TOWNSEND, 1942. *Oligo.*, Europe (Germany).
- Pachyuronympa** ROHDENDORF, 1964, p. 212 [**P. karatauensis*; OD]. Little-known genus, based on fragment of pupa. *Jur.*, USSR (Kazakh).
- Protocyrus** ROHDENDORF, 1938, p. 39 [**P. jurassicus*; OD]. Little-known genus, based on wing fragment. ROHDENDORF, 1962a. *Jur.*, USSR (Kazakh).
- Remalia** GIEBEL, 1856, p. 199 [**R. sphinx*; OD]. Little-known genus, probably a muscoid. HULL, 1945. *Jur.*, England.
- Syrphopsis** ZEUNER, 1931, p. 316 [**S. globosiceps*; OD]. Little-known genus. HULL, 1945. *Mio.*, Europe (Germany).
- Vinculumusca** TOWNSEND, 1938, p. 166 [**Musca vinculata* SCUDDER, 1877a, p. 758; OD]. Little-known genus (larva). TOWNSEND, 1942. *Eoc.*, USA (Colorado).

Order HYMENOPTERA

Linné, 1758

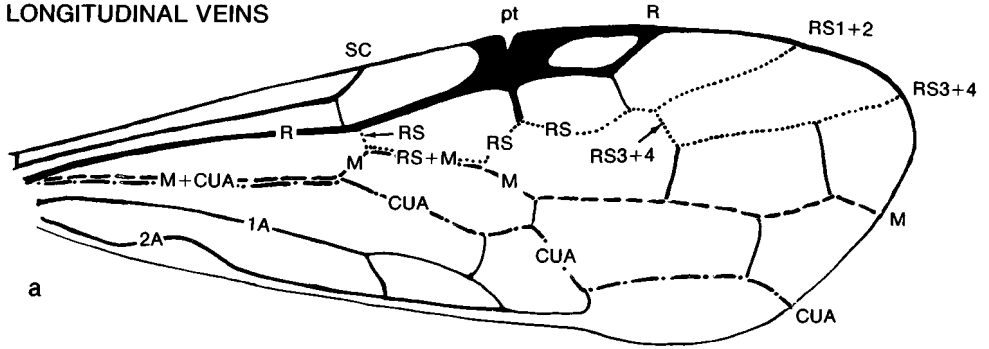
[Hymenoptera LINNÉ, 1758, p. 553]

Minute to medium-sized insects. Head free and usually very motile; compound eyes large, often holoptic in males; antennae diversely formed, especially so within the suborder Symphyta; sexual dimorphism of the antennae common in the suborder Apocrita; mouthparts of most species mandibulate and adapted for chewing, but labrum, in some Apocrita, modified to form a proboscis. Prothorax small; metathorax small and fused with the large mesothorax; abdomen broadly attached to thorax in the Symphyta, but in the Apocrita first abdominal segment fused with metathorax, with distinct constriction present between modified first abdominal segment (propodeum) and remaining segments (collectively termed the gaster, see Fig. 240), and with first gastral segment typically reduced to a narrow neck (petiole); female abdomen usually with an ovipositor. Wings membranous, hind pair much smaller than

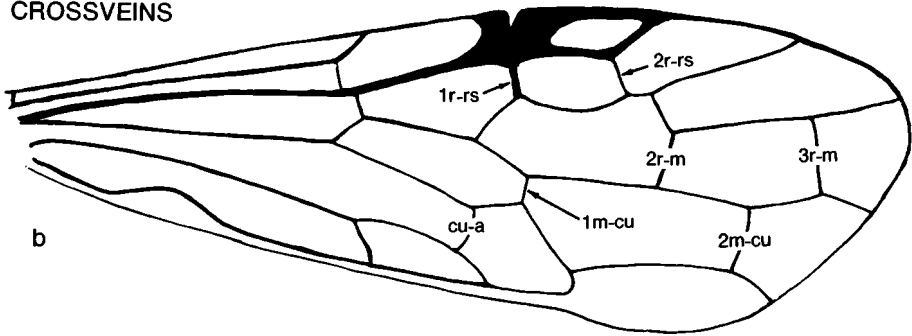
fore pair; in some species females (and more rarely males) apterous. Wing venation highly specialized, even the most generalized members of the order (Xyelidae) showing some reduction and coalescence of main veins.

Attempts to homologize the wing veins with those of other insects have resulted in several interpretations. The one proposed by Ross (1936) is now generally accepted and is used here, with slight changes in terminology suggested by RASNITSYN (1969, 1975). In the family Xyelidae (suborder Symphyta, Fig. 238), which seems to have the least specialized venation among the Hymenoptera, all main veins are present, but the basal parts of veins M and CUA are fused to near midwing, and M diverges anteriorly and coalesces with RS for a short distance; RS has two branches; CUA is long but very irregular; CUP is short, obsolescent, or absent; 1A is long and strong; 2A is irregular and close to the posterior border of the wing; R is the strongest vein in the wing and terminates at a conspicuous pterostigma; a distinct break or interruption of the sclerotization may occur just before the pterostigmal area, and the pterostigma itself may have a clear or white spot near its center. The size and shape of the pterostigma, the extent and nature of the coalescence of RS and M, and the positions of the several crossveins are structural features usually employed in the diagnoses of genera and families of the Symphyta and many of the Apocrita. Within the Apocrita, however, there is a much greater diversity of venational patterns than within the Symphyta. In the Tiphidae, for example, the venation is sufficiently similar to that of the xyelids to enable the determination of the homologies without difficulty (Fig. 239,1); but in other families of parasitic wasps the venation may be reduced to one or two veins, with stumps of a few others. In these the homologies are not clear, and different terms are usually applied to such veins (Fig. 239,2). The venation of the hind wing of the Hymenoptera is generally much more reduced than that of the fore wing, and since the hind wing is very rarely preserved

LONGITUDINAL VEINS



CROSSVEINS



CELLS OF FORE WING

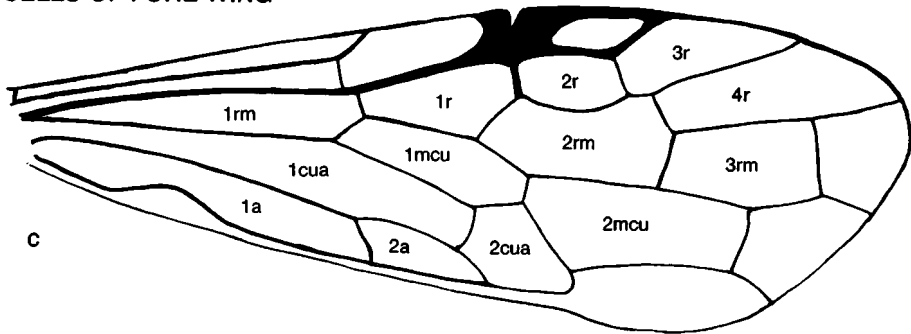


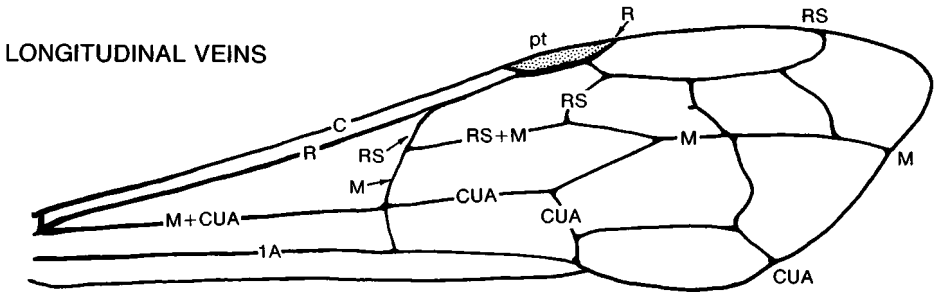
FIG. 238. Hymenoptera; suborder Symphyta, venational pattern of the fore wing of *Angaridyela vitimica* RASNITSYN, Xyelidae, from the Cretaceous of the USSR; *a*, terminology of the longitudinal veins; *b*, terminology of the crossveins; *c*, terminology of the cells. The symbols for crossveins are hyphenated to avoid confusion with those for the cells. SC, subcosta; pt, pterostigma; R, radius; RS, radial sector (dotted line); M, media (dashed line); CUA, anterior cubitus (dot-and-dash line); A, anal (adapted from Rasnitsyn, 1969).

in fossils, it is not used here in the taxonomic diagnoses.

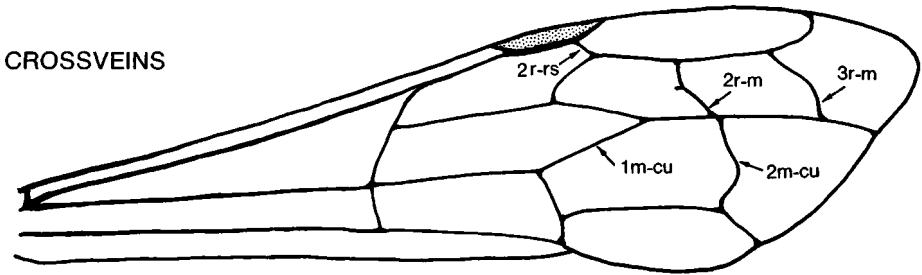
The legs of the Hymenoptera are basically cursorial, but in some, as in certain wasps, they are adapted for digging or nest building. In others, the fore tibiae and basal segments

of the fore tarsi combine to form a comblike structure, used for cleaning the antennae; and in the bees the hind legs may have structures in the form of a brush (scopa) or a basket (corbicula) for carrying pollen.

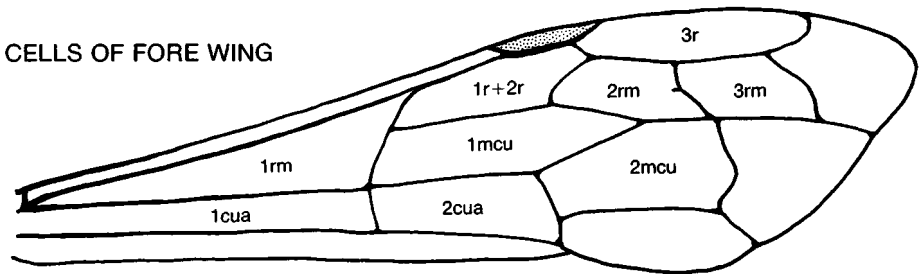
Larvae develop from eggs usually depos-



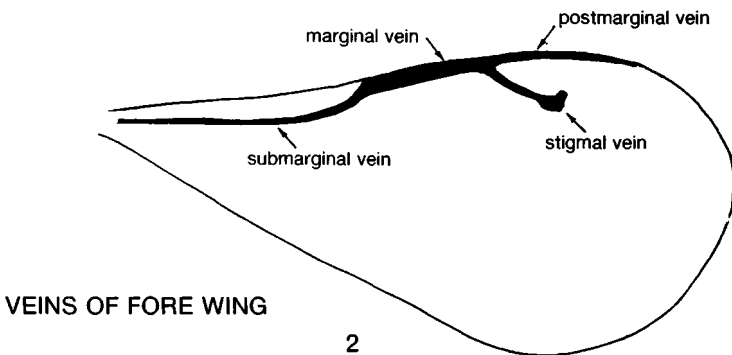
1a



1b



1c



2

FIG. 239. Hymenoptera; fore wing venation in the suborder Apocrita.—1a-c. Venational pattern of the fore wing of *Myzinum* sp., Tiphidae; a, veins; b, crossveins; c, cells. Terms are as in Figure 238 with the addition of C, costa. Note the slight reduction of the venation with the apparent loss of the subcosta, the absence of the fork in the radial sector, and the loss of crossvein 1r-rs.—2. Fore wing of *Meraporus* sp., Pteromalidae, showing the terminology of the reduced venation (from Brues, Melander, & Carpenter, 1954).

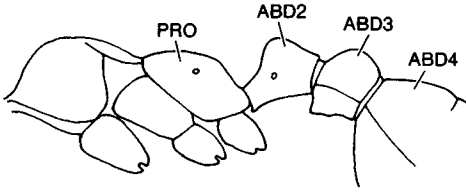


FIG. 240. Hymenoptera; lateral view of the thorax and basal abdominal segments of *Myrmica* sp., suborder Apocrita, Formicidae; PRO, propodeum or first abdominal segment; ABD2, second abdominal segment; ABD3 and ABD4, third and fourth abdominal segments (adapted from Brues, Melander, & Carpenter, 1954).

ited in specific environments and show even greater diversity of form than those of the Diptera. The larvae of the Symphyta, with a strongly sclerotized head capsule, well-developed mandibles, and three pairs of thoracic legs, resemble caterpillars (Fig. 241,*b*). These are mostly foliage feeders and apparently represent the primitive type of hymenopterous larvae. The larvae of the Apocrita, on the other hand, have at most a weakly sclerotized head and are apodous (Fig. 241,*a*). Most of them are parasitoid or predaceous; only a few are phytophagous, feeding on pollen and nectar. Pupation occurs in various environments, and in most species the pupae are exarate and encased in a cocoon.

Adults are very diverse in habitat. Most feed to some extent on nectar and are therefore important pollinators. *Trias.—Holo.*

The order Hymenoptera is at least as large and diverse as the Diptera, and probably even more of its recent species remain undescribed. Nearly 90 existing families are generally recognized. The present division of the order into two suborders, Symphyta and Apocrita, extends well back into the last century, and the general evolutionary implications of that division still seem valid. Some existing families of the Symphyta, such as the Xyelidae, are far more generalized than any family of the Apocrita. Morphological and geological evidence suggests that the Apocrita may have been derived from unknown ancestors related to the Siricidae, early in the Jurassic Period. The Apocrita is

by far the larger and more complex of the two suborders at the present time, but attempts to group its families into two categories have resulted in only informal sections. One of these includes the parasitic wasps (previously termed the Terebrantia) and the other, the ants, wasps, bees, and their relatives, collectively referred to as the aculeates. However, there are no characteristics, morphological or behavioral, that actually delimit these sections.

The families of both suborders are usually grouped into superfamilies, but there is much difference of opinion about the positions of certain families in this hierarchy and the degrees of relationship between the superfamilies. Grouping of the families becomes even more difficult when the Mesozoic genera are added, because many of the Jurassic families, often represented by few genera, do not fall into existing superfamilies as defined on recent species. The most detailed and significant account of the evolution of the Hymenoptera is that of Dr. A. P. RASNITSYN (1980b), who is responsible for most of our knowledge of the Mesozoic Hymenoptera.

The earliest appearance of the order is in the Triassic of Australia and the Soviet Union. All of these Triassic fossils appear to belong to the existing family Xyelidae (suborder Symphyta), and their diversity is remarkable, especially in comparison with the small size of the family at present. Not until the Upper Jurassic are other existing families known: the Pamphiliidae, Anaxyelidae, and Siricidae of the Symphyta and the Megalyridae and Heloridae of the Apocrita. In the Cretaceous many existing families appear, including the highly specialized chalcidoid families Trichogrammatidae, Mymaridae, and Tetracampidae among the parasitic wasps, and the family Formicidae among the aculeates. At present 78 families of the order are represented in the fossil record; 22 of them are extinct, but of that number only two are aculeates.

The diversity of the Xyelidae in the Triassic is an indication that the order probably arose in the early Triassic or possibly the very

late Permian. Study of some 40,000 Permian insects from the Soviet Union, United States, and Australia has failed to turn up any recognizable members of the order, but most of the Permian specimens are from the middle Permian or later. In the absence of evidence to the contrary, the Hymenoptera are generally assumed to have arisen from primitive neuropteroid stock, probably unknown terrestrial relatives of the sialoid Neuroptera. RASNITSYN (1980b) has recently proposed that the ancestral line was within the extinct order Miomoptera, which is known from the Upper Carboniferous and Permian. This order has previously been considered to belong to the orthopteroid complex, but RASNITSYN believes it to have been endopterygote and closely related to the Neuroptera. Whether or not the Miomoptera are in fact reasonable candidates for the ancestors of the Hymenoptera, however, will not really become clear until we have more information than we do now about the structure and life history of the members of that order.

Suborder SYMPHYTA

Gerstaecker, 1867

[Symphyta GERSTAECKER, 1867, p. 2]

Adults with abdomen broadly attached to thorax, without pronounced constriction between the first and second segments of abdomen. Larvae with thoracic legs. *Trias.*—*Holo.*

Family XYELIDAE Newman, 1835

[Xyelidae NEWMAN, 1835, p. 379]

Fore wing with vein RS usually having 2 branches; basal section of RS at least slightly slanted toward wing apex; crossveins 1r-rs always present; crossvein 2r-rs attached to RS proximally to crossvein 2r-m; crossveins 3r-m and 2m-cu always present. Antennae with many segments, third segment compound, much longer and thicker than remaining flagellar segments; fore tibiae with 2 apical spurs; ovipositor well developed, usually flat. Larvae living in plant tissues or on foliage. *Trias.*—*Holo.*

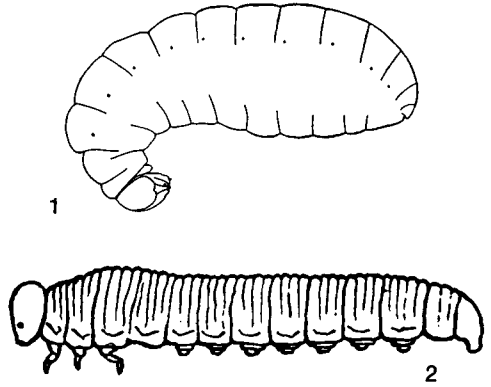


FIG. 241. Hymenoptera, larvae.—1. Apocrita, family Formicidae (from Wheeler & Wheeler, 1952).—2. Symphyta, family Tenthredinidae (from Brues, Melander, & Carpenter, 1954).

Xyela DALMAN, 1819, p. 122. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*

Angaridyela RASNITSYN, 1966, p. 75 [**A. vitimica*; OD]. Fore wing with pterostigma sclerotized basally and membranous distally; SC connected to R (by a short crossvein or branch of SC) just before origin of RS; basal section of RS slightly shorter than basal section of M. RASNITSYN, 1969. *Cret.*, USSR (Kazakh).—FIG. 242,6. **A. vitimica*; wings and body, $\times 7$ (Rasnitsyn, 1969).

Anomoxyela RASNITSYN, 1966, p. 72 [**Anaxyela incerta* RASNITSYN, 1963, p. 95; OD]. Fore wing similar to that of *Lydoxyela*, but RS3+4 only slightly curved distally and without a sharp angle at crossvein 3r-m; termination of RS1+2 closer to pterostigma than to end of RS3+4. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 242,5. **A. incerta* (RASNITSYN); wings and body, $\times 5.5$ (Rasnitsyn, 1966).

Anthoxyela RASNITSYN, 1977a, p. 99 [**S. baixensis*; OD]. Fore wing with pterostigma sclerotized basally only; SC connected to R only a very short distance beyond origin of RS; basal section of RS 1.5 times length of basal section of M; crossvein 2m-cu slightly basad of middle of cell 3rm. KRASSILOV & RASNITSYN, 1982. *Cret.*, USSR (Asian RSFSR).—FIG. 242,1. **A. baixensis*; fore wing, $\times 4$ (Rasnitsyn, 1977a).

Archxyela RIEK, 1955, p. 657 [**A. crosbyi*; OD]. Fore wing with crossvein 1r-rs running into base of pterostigma; pterostigma sclerotized at base only; crossvein 2m-cu situated slightly before apex of cell 3rm; crossvein 2r-rs meeting RS1+2 close to fork of RS. RASNITSYN, 1969. *Trias.*, Australia (Queensland).—FIG. 242,2. **A. crosbyi*; fore wing, $\times 4$ (Riek, 1955).

Asioxyela RASNITSYN, 1964, p. 92 [**A. smilodon*;

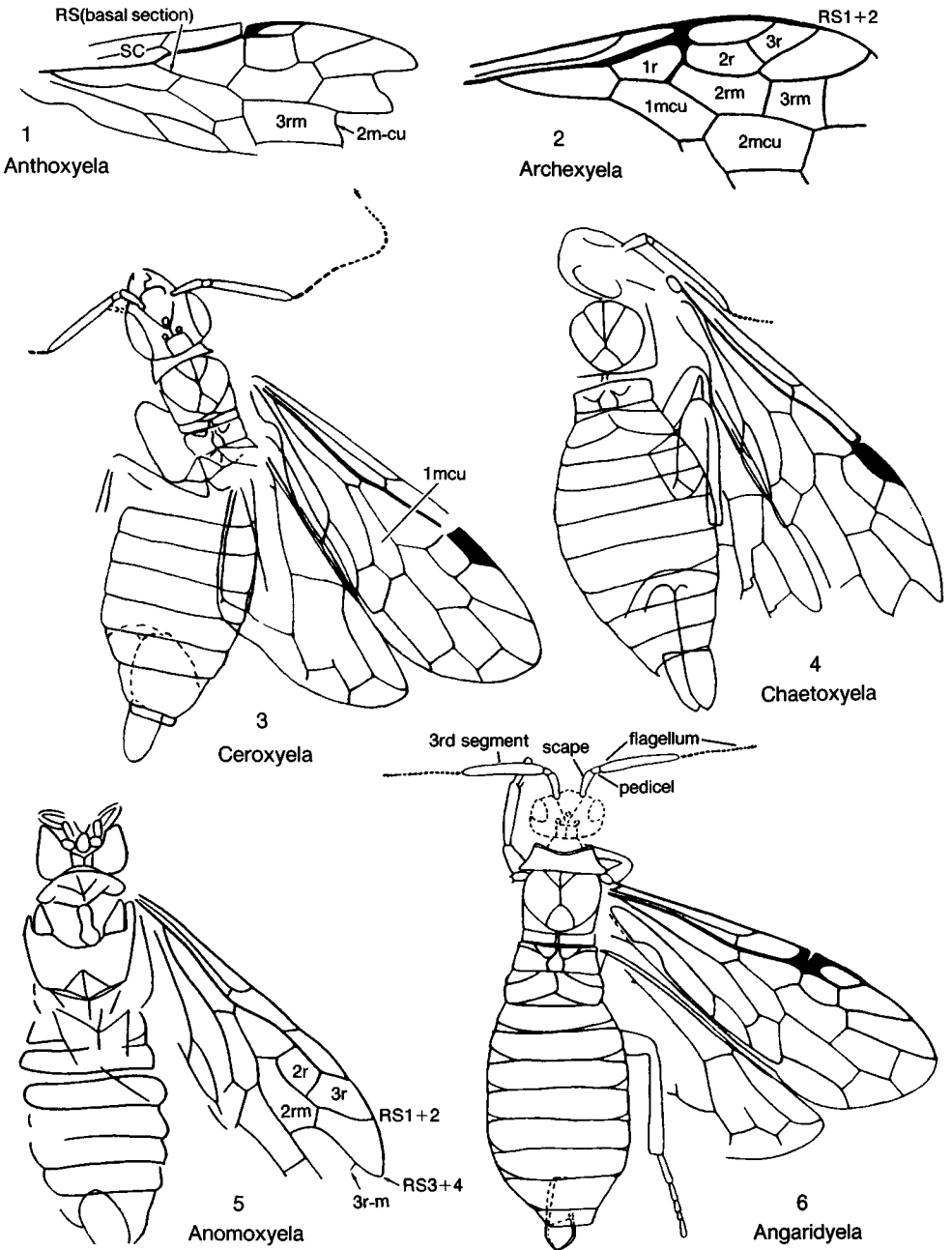


FIG. 242. Xyelidae (p. 449-451).

OD]. Fore wing with pterostigma sclerotized, but with center membranous; basal section of RS about 1.5 times length of basal section of M; crossvein 2r-rs joined to RS just beyond its fork. Head with large, crescent-shaped mandibles. RASNITSYN, 1969. *Trias.*, USSR (Kirghiz).

Baissoxyela RASNITSYN, 1969, p. 54 [**B. tarsalis*; OD]. Little-known genus. Fore wing with R almost straight; space between costal margin and R uniform. Terminal part of flagellum of antennae short but with about 16 segments. *Cret.*, USSR (Asian RSFSR).

- Ceroxyela** RASNITSYN, 1966, p. 80 [**C. dolichocera*; OD]. Fore wing with pterostigma sclerotized but with membranous area basally; SC connected to R beyond origin of RS; basal section of RS slightly shorter than basal section of M; cell 1mcu very narrow. RASNITSYN, 1969. *Cret.*, USSR (Kazakh). — FIG. 242,3. **C. dolichocera*; wings and body, $\times 6$ (Rasnitsyn, 1969).
- Chaetoxyla** RASNITSYN, 1966, p. 82 [**C. hirsuta*; OD]. Fore wing with pterostigma fully sclerotized; SC connected to R at origin of RS; basal section of RS slightly shorter than basal section of M. RASNITSYN, 1969. *Cret.*, USSR (Kazakh). — FIG. 242,4. **C. hirsuta*; wings and body, $\times 4$ (Rasnitsyn, 1969).
- Enneoxyla** RASNITSYN, 1966, p. 73 [**E. crassicauda*; OD]. Little-known genus. Fore wing with pterostigma narrow; SC connected to R beyond origin of RS; termination of RS1+2 closer to pterostigma than to end of RS3+4. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).
- Eoxyela** RASNITSYN, 1965, p. 487 [**E. scoliura*; OD]. Fore wing shorter than body; R nearly straight; basal section of RS much longer than basal section of M; cell 4r much longer than cell 3r. RASNITSYN, 1969. 1983a. *Jur.*, USSR (Kazakh). — FIG. 243,7. **E. scoliura*; fore wing, $\times 9$ (Rasnitsyn, 1969).
- Euryxyela** RASNITSYN, 1964, p. 94 [**E. euryptera*; OD]. Fore wing unusually broad; pterostigma fully sclerotized; basal section of RS longer than basal section of M; RS3+4 diverging anteriorly at crossvein 3r-m; crossvein 2r-rs joining RS at its fork. RASNITSYN, 1969. *Trias.*, USSR (Kirghiz). — FIG. 243,1. **E. euryptera*; fore wing, $\times 5.8$ (Rasnitsyn, 1969).
- Ferganoxyela** RASNITSYN, 1969, p. 47 [**F. sogdiana*; OD]. Fore wing broadly triangular; pterostigma large; RS1+2 terminating halfway between pterostigma and RS3+4. *Trias.*, USSR (Kirghiz). — FIG. 243,6. **F. sogdiana*; fore wing, $\times 8.5$ (Rasnitsyn, 1969).
- Gigantoxyla** RASNITSYN, 1966, p. 81 [**G. quadrifurcata*; OD]. Fore wing as in *Chaetoxyla*, but SC connected to R well before origin of RS. RASNITSYN, 1969. *Cret.*, USSR (Kazakh).
- Kirghizoxyla** RASNITSYN, 1966, p. 70 [**K. mirabilis*; OD]. Fore wing similar to that of *Orthoxyela*, but SC absent and R only slightly thickened at base of pterostigma. RASNITSYN, 1969. *Jur.*, USSR (Kirghiz).
- Leioxyela** RASNITSYN, 1969, p. 49 [**L. mollis*; OD]. Fore wing with pterostigma fully sclerotized; crossvein 2r-rs much nearer to apex of pterostigma than to crossvein 1r-rs; cells 1r and 2r of about same length. *Trias.*, USSR (Kirghiz).
- Liadoxyela** MARTYNOV, 1937a, p. 41 [**L. praecox*; OD]. Little-known genus. Fore wing with R strongly thickened at base of pterostigma, curved; area between R and costal margin widest near origin of RS; cell 1r only slightly longer than cell 2r. RASNITSYN, 1966, 1969, 1983a. *Jur.*, USSR (Kirghiz), Asian RSFSR. — FIG. 243,2. **L. praecox*; fore wing, $\times 4$ (Rasnitsyn, 1969).
- Lithoxyela** RASNITSYN, 1969, p. 43 [**L. fenestralis*; OD]. Fore wing with uniformly narrow costal area; pterostigma not fully sclerotized; end of RS1+2 closer to end of RS3+4 than to pterostigma. *Trias.*, USSR (Kirghiz). — FIG. 243,4. **L. fenestralis*; fore wing, $\times 5.5$ (Rasnitsyn, 1969).
- Lydoxyela** RASNITSYN, 1966, p. 71 [**L. excellens*; OD]. Fore wing with SC connected to R proximal of origin of RS; basal section of RS about half as long as basal section of M; crossvein 1r-rs longer than 2r-rs; RS3+4 with an abrupt anterior bend at crossvein 3r-m; RS1+2 apparently absent. RASNITSYN, 1969. *Jur.*, USSR (Kazakh). — FIG. 243,5. **L. excellens*; wings and body, $\times 6$ (Rasnitsyn, 1966).
- Madygella** RASNITSYN, 1969, p. 51 [**M. analoga*; OD]. Fore wing with pterostigma well sclerotized; SC distinct and well developed; R straight; basal section of RS shorter than RS+M. *Trias.*, USSR (Kirghiz). — FIG. 243,3. **M. analoga*; fore wing, $\times 12$. (Rasnitsyn, 1969).
- Madygenius** RASNITSYN, 1969, p. 45 [**M. extraradius*; OD]. Fore wing with costal area narrow; pterostigma sclerotized; end of RS1+2 much closer to RS3+4 than to pterostigma; 2 crossveins between RS1+2 and RS3+4. *Trias.*, USSR (Kirghiz). — FIG. 244,7. **M. extraradius*; fore wing, $\times 7.5$ (Rasnitsyn, 1969).
- Megaxyela** ASHMEAD, 1898, p. 206. BRUES, 1908b; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)—*Holo*.
- Microxyelecia** RASNITSYN, 1969, p. 54 [**M. brachycera*; OD]. Fore wing with R straight; distance between costal margin and R uniform but narrower than in *Baissoxyela*. Flagellum relatively longer than in *Baissoxyela*. *Jur.*, USSR (Kazakh).
- Nigrimonticola** RASNITSYN, 1966, p. 77 [**N. longicornis*; OD]. Little-known genus. Fore wing as in *Ophthalmoxyela*, but basal section of RS half as long as basal section of M; RS1+2 terminating closer to pterostigma than to end of RS3+4. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).
- Ophthalmoxyela** RASNITSYN, 1966, p. 78 [**O. brachyura*; OD]. Little-known genus. Fore wing with pterostigma sclerotized but with clear spot near center; basal section of RS almost twice as long as basal section of M. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).
- Orthoxyela** RASNITSYN, 1983a, p. 91 [**O. rectiradiata*; OD]. Related to *Kirghizoxyla*, but fore wing with SC well developed; R conspicuously thickened at base of pterostigma. *Jur.*, USSR (Asian RSFSR).
- Oryctoxyela** RASNITSYN, 1969, p. 45 [**O. anomala*; OD]. Fore wing with costal area narrow; RS1+2

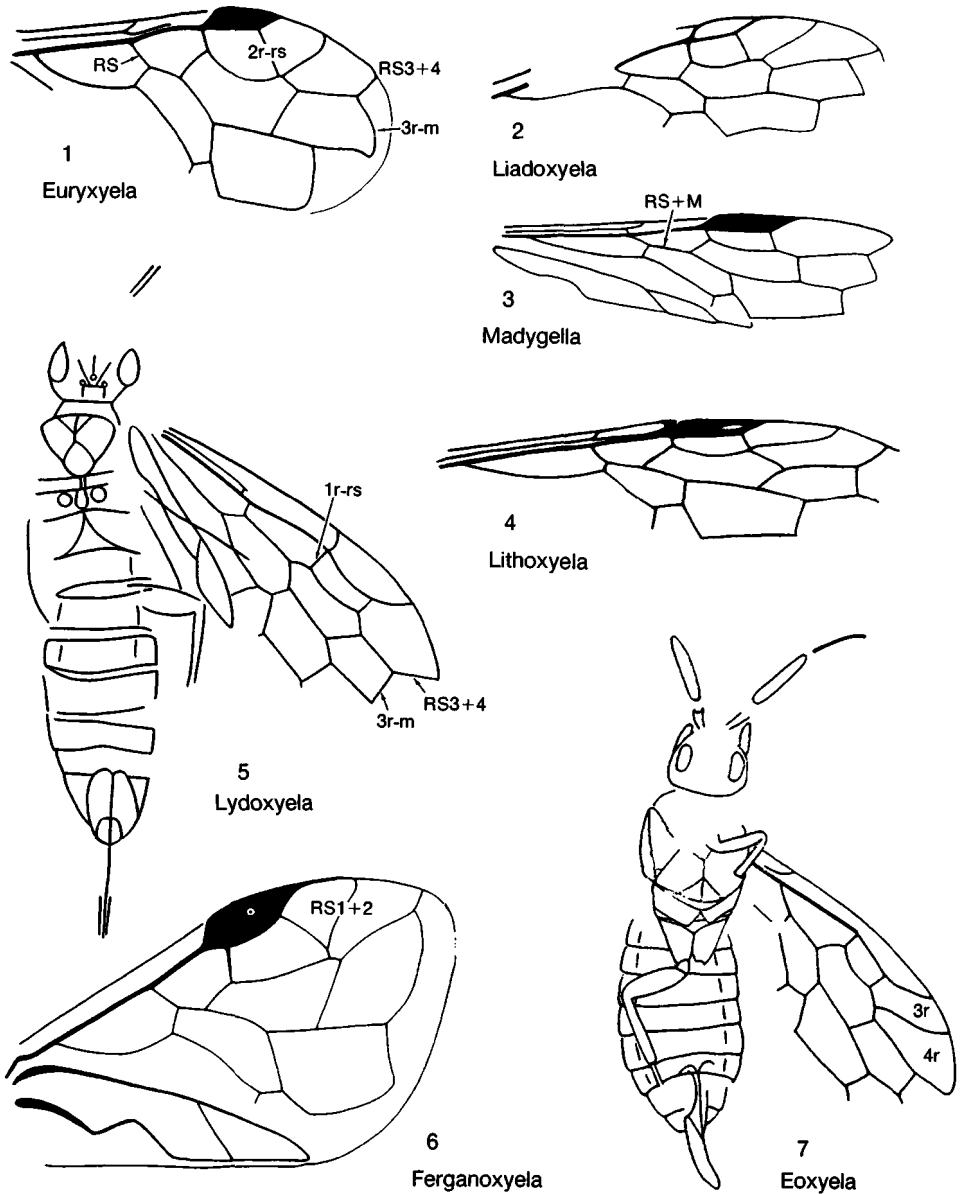


FIG. 243. Xyelidae (p. 451).

about twice as far from pterostigma as from RS3+4. *Trias.*, USSR (Kirghiz).—FIG. 244,3.

**O. anomala*; fore wing, $\times 5$ (Rasnitsyn, 1969).

Pinicolites MEUNIER, 1920c, p. 896 [**P. graciosus*; OD]. Similar to *Pleroneura* (recent), but SC in fore wing extending beyond level of origin of RS. STATZ, 1936b; RASNITSYN, 1969. *Oligo.*, Europe (Germany).

Sirecomima RASNITSYN, 1969, p. 51 [**S. xiphophora*; OD]. Fore wing with pterostigma weakly sclerotized and narrow; basal section of RS much

longer than RS+M. *Trias.*, USSR (Kirghiz).—FIG. 244,6. **S. xiphophora*; fore wing, $\times 16$ (Rasnitsyn, 1969).

Spathoxyela RASNITSYN, 1969, p. 53 [**Eoxyela fossilis* RASNITSYN, 1965, p. 487; OD]. Fore wing with R straight; distance between R and costal margin narrow and uniform; SC free from R; termination of RS1+2 slightly closer to end of RS3+4 than to pterostigma; crossvein 2r-rs distal to center of pterostigma. KRASSILOV & RASNITSYN, 1982. *Cret.*, USSR (Kazakh, Asian

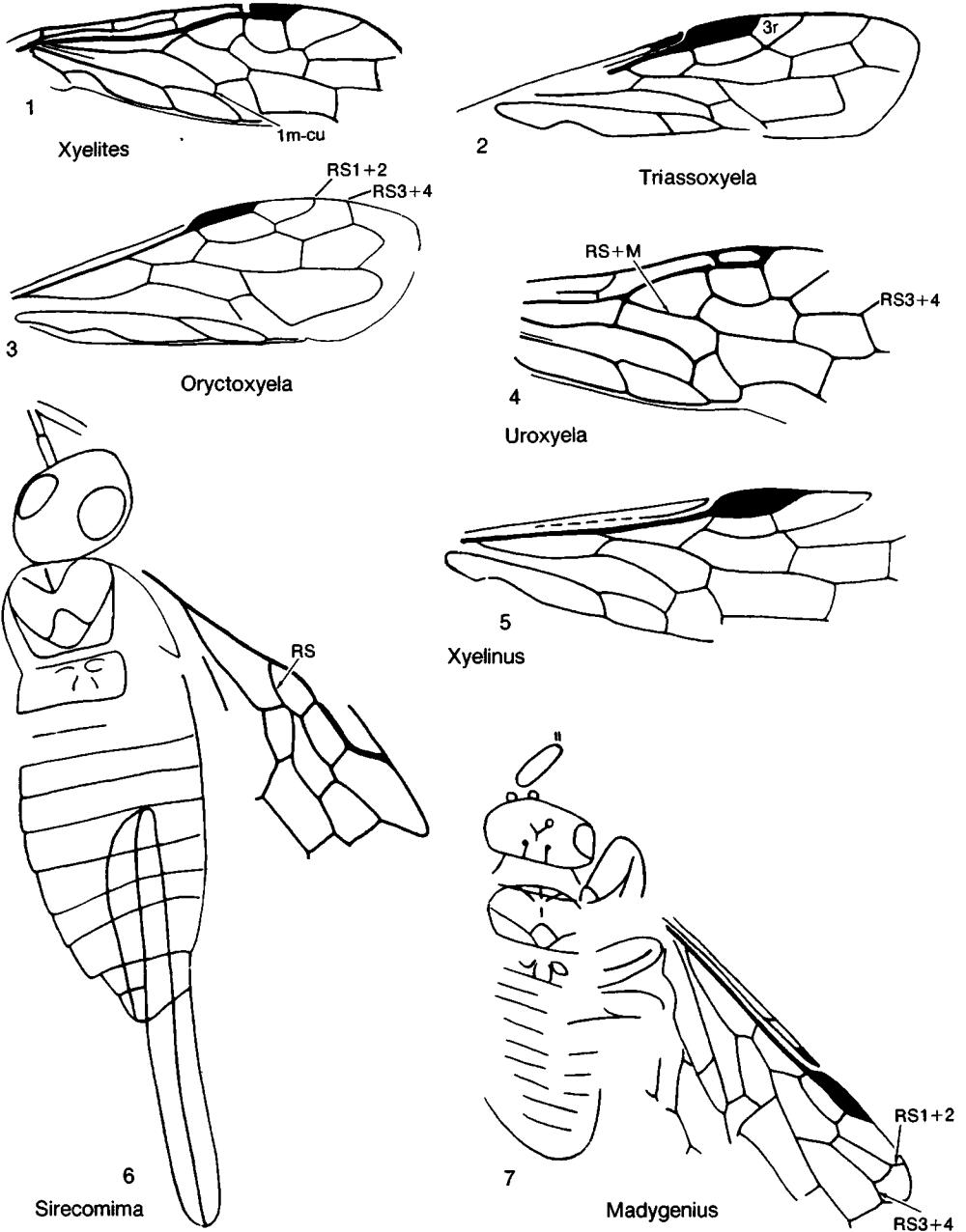
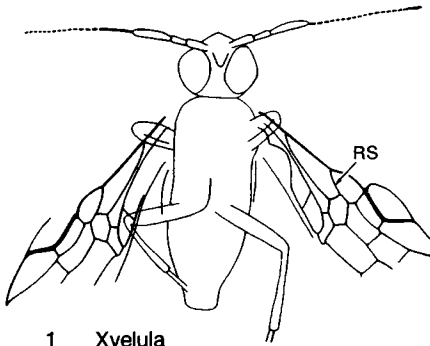


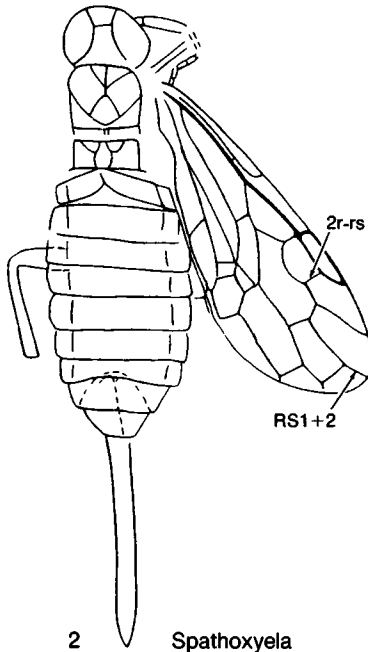
FIG. 244. Xyelidae (p. 451-454).

RSFSR).—FIG. 245,2. **S. fossilis* (RASNITSYN); wings and body, $\times 10$ (Rasnitsyn, 1977a).
Triassoxyela RASNITSYN, 1964, p. 89 [**T. foveolata*; OD]. Fore wing similar to that of *Xyelinus*, but cell 3r short. RASNITSYN, 1969. *Trias.*, USSR (Kirghiz).—FIG. 244,2. **T. foveolata*; fore wing, $\times 9.5$ (Rasnitsyn, 1969).

Uroxyela RASNITSYN, 1966, p. 84 [**U. sicicauda*; OD]. Fore wing with center of pterostigma not sclerotized; termination of SC before origin of RS; basal section of RS obsolescent; RS3+4 directed anteriorly beyond crossvein 3r-m. *Cret.*, USSR (Kazakh).—FIG. 244,4. **U. sicicauda*; fore wing, $\times 11$ (Rasnitsyn, 1966).



1 Xyelula



2 Spathoxyela

FIG. 245. Xyelidae (p. 454).

Xiphoxyela RASNITSYN, 1969, p. 46 [**X. procrusta*; OD]. Costal area narrow; pterostigma sclerotized; RS1+2 apparently absent or weak. *Trias.*, USSR (Kirghiz).

Xyelinus RASNITSYN, 1964, p. 95 [**X. angustiradius*; OD]. Fore wing slender, at least twice as long as wide; costal area narrow; basal section of RS much shorter than basal section of M; cells 2r, 3r, and 4r elongate. RASNITSYN, 1969. *Trias.*, USSR (Kirghiz).—FIG. 244.5. **X. angustiradius*; fore wing, $\times 10$ (Rasnitsyn, 1969).

Xyelisca RASNITSYN, 1969, p. 53 [**S. leptopoda*; OD]. Little-known genus. Fore wing with SC terminating at level of origin of RS. Thorax punctate. *Jur.*, USSR (Kazakh).

Xyelites RASNITSYN, 1966, p. 83 [**X. trigeminus*;

OD]. Fore wing with pterostigma fully sclerotized; SC terminating just before origin of RS; basal section of RS very short; end of RS1+2 slightly closer to end of RS3+4 than to pterostigma; RS3+4 straight or nearly so; crossvein 1m-cu very short. RASNITSYN, 1969. *Cret.*, USSR (Kazakh).—FIG. 244.1. **X. trigeminus*; fore wing, $\times 7$ (Rasnitsyn, 1969).

Xyelula RASNITSYN, 1969, p. 52 [**X. hybrida*; OD]. Fore wing with pterostigma very broad; R strongly curved; basal section of RS more than twice as long as basal section of M. *Jur.*, USSR (Kazakh).—FIG. 245.1. **X. hybrida*; head, thorax, and fore wings, $\times 10$ (Rasnitsyn, 1969).

Family XYELOTOMIDAE

Rasnitsyn, 1968

[Xyelotomidae RASNITSYN, 1968, p. 224]

Fore wing: vein RS developed between M and crossvein 1r-rs; 2r-rs present; cell 3r closed at wing apex. Antennae as in Xyelidae but with fewer (not more than 8) and thicker segments, third segment fully as large as in Xyelidae. RASNITSYN, 1969. *Jur.-Cret.*

Xyelotoma RASNITSYN, 1968, p. 225 [**X. nigricornis*; OD]. Little-known genus. Fore wing with pterostigma fully sclerotized. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Pseudoxyela RASNITSYN, 1968, p. 227 [**P. heteroclita*; OD]. Fore wing with pterostigma sclerotized basally only, mostly membranous; SC connected to R well before origin of RS; basal section of RS about half as long as basal section of M. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Undatoma RASNITSYN, 1977a, p. 100 [**U. daburica*; OD]. Fore wing with pterostigma very large and center membranous; SC apparently absent; RS not forked; basal section of RS very short, about one-eighth length of basal section of M; cell 1r very small. *Cret.*, USSR (Kazakh).—FIG. 246.1. **U. daburica*; fore wing, $\times 8.5$ (Rasnitsyn, 1977a).

Xyelocerus RASNITSYN, 1968, p. 226 [**X. admirandus*; OD]. Fore wing with pterostigma sclerotized but with clear area in center; SC weak, apparently not connected to R; basal section of M about 5 times as long as that of RS. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 246.2. **X. admirandus*; fore wing, $\times 7$ (Rasnitsyn, 1968).

Family TENTHREDINIDAE

Latreille, 1804–1805

[Tenthredinidae LATREILLE, 1804–1805, p. 109]

Fore wing: vein RS usually unbranched; crossvein 2r-rs sometimes present; M joining RS near its origin or joining directly to R

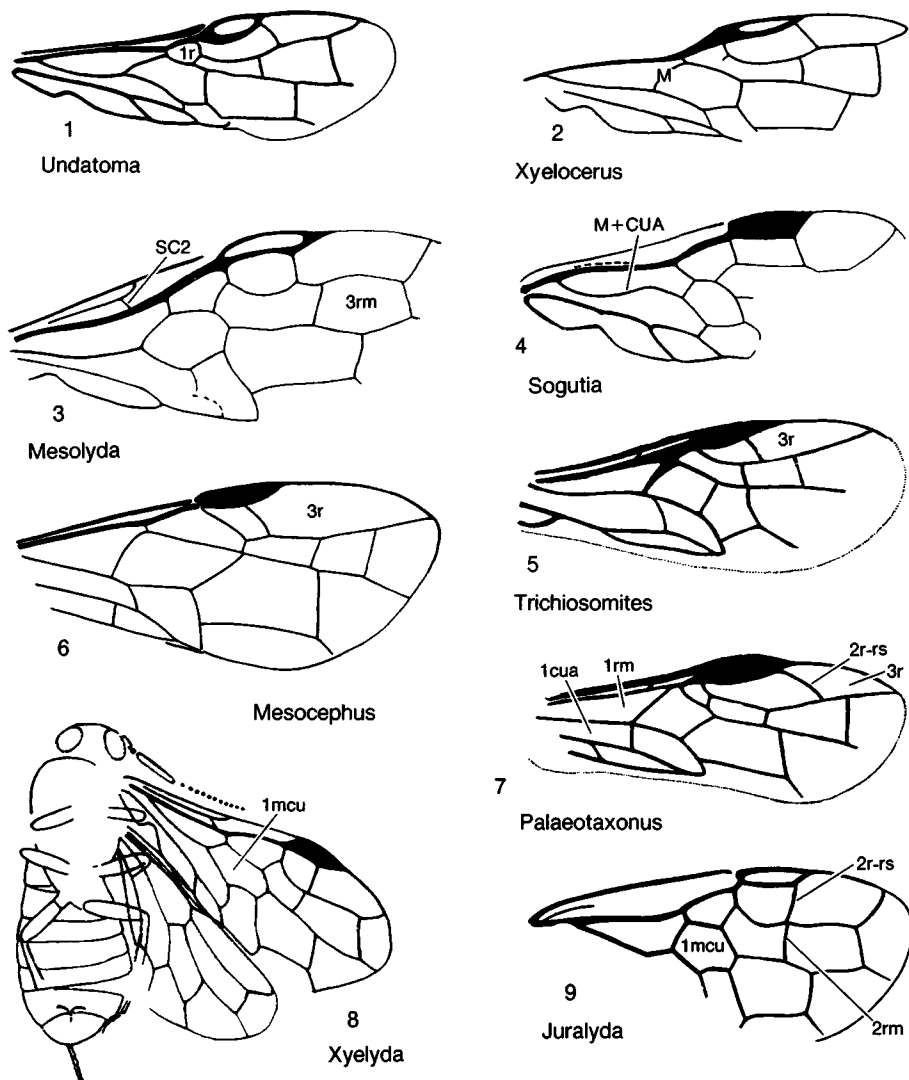


FIG. 246. Xyelotomidae, Tenthredinidae, Cimbicidae, Xyelydidae, Pamphiliidae, Cephidae, and Uncertain (p. 454–463).

near origin of RS; crossvein 2m-cu present. Antennae filiform, rarely with more than 9 segments, third segment short; pronotum with hind border deeply emarginate; fore tibiae with 2 apical spurs; ovipositor short, flat. Larvae foliage feeders. *Eoc.*–*Holo.*

Tenthredo LINNÉ, 1758, p. 555. BRUES, 1908b; ROHWER, 1908c; COCKERELL, 1914a, 1917f, 1927d; MEUNIER, 1923c; STATZ, 1936b; PITON, 1940a. *Oligo.*, USA (Colorado); Europe (Germany, France)–*Holo.*

Athalia LEACH, 1817, p. 126. [Generic assignment of fossil doubtful.] COCKERELL, 1906c, 1927d; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)–*Holo.*

Caliroa COSTA, 1859, p. 59. COCKERELL, 1909n, 1916b, 1917f. *Oligo.*, USA (Colorado)–*Holo.*

Cladius ILLIGER, 1807, p. 190. COCKERELL, 1914f. *Oligo.*, USA (Colorado)–*Holo.*

Dineura DAHLBOM, 1835, p. 5. BRUES, 1908b; ROHWER, 1908b, 1908c. *Oligo.*, USA (Colorado)–*Holo.*

Dolerus PANZER, 1801, pl. 11. MEUNIER, 1923b.

- Oligo.*, Europe (Germany); *Mio.*, Europe (France)—*Holo.*
- Eohemichroa** ZHELOCHOVTZEV & RASNITSYN, 1972, p. 323 [**Hemichroa eophila* COCKERELL, 1906d, p. 501; OD]. Similar to *Hemichroa* but with a short distance between anal cells of fore wing, stouter antennae, and longer first segment of hind tarsus. ADAMS, 1967. *Oligo.*, USA (Colorado).
- Eriocampa** HARTIG, 1837, p. 279. BRUES, 1908b; COCKERELL, 1910c, 1911b, 1914f, 1922d; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*
- Fenusa** LEACH, 1817, p. 126 [= *Lithoryssus* BRUES, 1906, p. 491 (type, *L. parvus*)]. ROHWER, 1908b; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)—*Holo.*
- Florissantinus** ZHELOCHOVTZEV & RASNITSYN, 1972, p. 320 [**F. angulatus*; OD]. Similar to *Hemichroa*, but M of fore wing straight, not bent at crossveins 2r-m and 3r-m. *Oligo.*, USA (Colorado).
- Hemichroa** STEPHENS, 1835, p. 55. COCKERELL, 1906d, 1916b. *Oligo.*, USA (Colorado)—*Holo.*
- Hoplocampa** HARTIG, 1837, p. 276. COCKERELL, 1927c; STATZ, 1936b. *Oligo.*, Europe (Germany), USA (Colorado)—*Holo.*
- Leucempria** ENSLIN, 1913, p. 187. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*
- Mesoneura** HARTIG, 1837, p. 228 [= *Lisconeura* ROHWER, 1908b, p. 529 (type, *Scolioneura vexabilis* BRUES, 1908b, p. 263)]. RASNITSYN, 1969; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)—*Holo.*
- Nortonella** ROHWER, 1908c, p. 592 [**N. typica*; OD]. Fore wing as in *Macrophya* (recent) but SC absent. *Oligo.*, USA (Colorado).
- Palaeotaxonus** BRUES, 1908b, p. 266 [**P. typicus*; OD]. Fore wing as in *Taxonus*, but cell 1cua not longer than cell 1rm; cell 3r long, pointed apically; crossvein 2r-rs strongly oblique. ROHWER, 1908b; COCKERELL, 1917f. *Oligo.*, USA (Colorado). — FIG. 246, 7. **P. typicus*; fore wing, $\times 5.2$ (Brues, 1908b).
- Pseudosiobla** ASHMEAD, 1898, p. 308. [Generic assignment of fossil doubtful.] ROHWER, 1908b. *Oligo.*, USA (Colorado)—*Holo.*
- Rhogogaster** KONOW, 1884, p. 338. [Generic assignment of fossil doubtful.] BRUES, 1908b; GIBSON, 1980. *Oligo.*, USA (Colorado)—*Holo.*
- Selandria** LEACH, 1817, p. 126. COCKERELL, 1910c. *Oligo.*, USA (Colorado)—*Holo.*
- Taeniurites** COCKERELL, 1917b, p. 382 [**T. fortis*; OD]. Fore wing as in *Macrophya* (recent), but body structure as in *Strongylogaster* (recent). COCKERELL, 1927d. *Oligo.*, USA (Colorado).
- Taxonus** HARTIG, 1837, p. 297. HEER, 1849; KONOW, 1897; PONGRÁČZ, 1928. *Eoc.*, USA (Wyoming); *Mio.*, Europe (Germany)—*Holo.*
- Tenthredinites** MEUNIER, 1915a, p. 11 [**T. bifasciata*; OD]. Little-known genus. Fore wing with 2 dark transverse bands. [Possibly a junior synonym of *Tentredo*.] LOEW, 1850. *Oligo.*, Europe (France).

Family ELECTROTOMIDAE Rasnitsyn, 1977

[Electrotomidae RASNITSYN, 1977b, p. 1304]

Little-known family, apparently related to the Argidae, and based on mature larva (pre-pupa). Head relatively large, as in Blasticotomidae; tenth abdominal tergite conical, as in Xyelidae; antennae not contiguous with ocelli; false legs absent from ninth abdominal segment. *Oligo.*

Electrotoma RASNITSYN, 1977b, p. 1307 [**E. succini*; OD]. Head capsule with 15 to 20 long setae; body with short pubescence. *Oligo.*, Europe (Baltic).

Family ARGIDAE Konow, 1890

[Argidae KONOW, 1890, p. 229]

Fore wing with crossvein 2r-rs absent; vein M joined to R before origin of RS; RS joined or nearly joined to R distally near wing apex. Antennae with 3 segments, the last compound and very long; fore tibiae with 2 apical spurs. Larvae foliage feeders. *Oligo.*—*Holo.*

Arge SCHRANK, 1802, p. 209. *Holo.*

Sterictiphora BILLBERG, 1820, p. 99. ROHWER, 1908c; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)—*Holo.*

Family CIMBICIDAE Kirby, 1837

[Cimbicidae KIRBY in RICHARDSON, SWANSON, & KIRBY, 1837, p. 254]

Fore wing with crossvein 2r-rs present. Antennae clubbed but third segment not enlarged; pronotum with hind border deeply emarginate. Larvae foliage feeders. *Eoc.*—*Holo.*

Cimbex OLIVIER, 1790, p. 762. COCKERELL, 1922d. *Oligo.*, USA (Colorado)—*Holo.*

Eopachylosticta MALAISE, 1945, p. 14 [**Amasis byrami* COCKERELL, 1924a, p. 10; OD]. Similar to *Pseudopachylosticta* (recent), but head strongly enlarged behind eyes and mesonotal lobes separated by deep furrows. ZHELOCHOVTZEV & RASNITSYN, 1972. *Eoc.*, USA (Colorado).

Trichiosomites BRUES, 1908b, p. 259 [**T. obliuiosus*; OD]. Similar to *Zeraea* (recent); cell 3r long; cell 1cua only a little longer than cell 1rm. Antennae with 6 segments. *Oligo.*, USA (Colo-

rado).—FIG. 246,5. **T. obliviosus*; fore wing, $\times 5.5$ (Brues, 1908b).

Family BLASTICOTOMIDAE

Thomson, 1871

[Blasticotomidae THOMSON, 1871, p. 131]

Fore wing with vein R close to and nearly coalesced with costa; M extending distally beyond crossvein 3r-m; CUA extending distally beyond crossvein 2m-cu. Antennae with 3 or 4 segments, third very long, fourth short or absent. Larvae stem borers. *Oligo.*—*Holo.*

Blasticotoma KLUG, 1834, p. 251. *Holo.*

Paremphytus BRUES, 1908b, p. 265. ZHELOCHOVITZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado)—*Holo.*

Family DIPRIONIDAE Rohwer, 1911

[Diprionidae ROHWER, 1911, p. 220]

Fore wing with crossvein 2r-rs absent. Antennae with at least 13 segments and almost always serrate or pectinate; third segment not elongate, shorter than total length of all other flagellar segments. Larvae on coniferous foliage. *Oligo.*—*Holo.*

Diprion SCHRANK, 1802, p. 209. BRUES, 1908b. *Oligo.*, USA (Colorado)—*Holo.*

Family XYELYDIDAE

Rasnitsyn, 1968

[Xyelydidae RASNITSYN, 1968, p. 192]

Fore wing: vein SC with 2 branches, posterior branch joining R basad of origin of RS; crossvein 1m-cu much shorter than half length of section of M distal to it; cell 1m-cu large; M+CUA only slightly curved. Antennae multisegmented; third segment commonly much enlarged and elongate, more than a third length of antenna. *Jur.*

Xyelyda RASNITSYN, 1968, p. 193 [**X. excellens*; OD]. Fore wing with posterior branch of SC strongly oblique; cells 1r and 1m-cu narrow and long; cell 1r longer than cell 2rm; length of cell 1m-cu more than twice its width; pterostigma fully sclerotized; crossvein 1m-cu much shorter than the section of CUA adjoining it distally. RASNITSYN, 1969, 1983b. *Jur.*, USSR (Kazakh).—FIG. 246,8. **X. excellens*; fore wing, $\times 5.6$ (Rasnitsyn, 1969).

Ferganolyda RASNITSYN, 1983b, p. 61 [**F. cubitalis*; OD]. Similar to *Xyelyda*, but cell 1r shorter

than cell 2rm; anterior border of cell 1m-cu almost straight. *Jur.*, USSR (Kazakh).

Mesolyda RASNITSYN, 1963, p. 86 [**M. jurassica*; OD]. Fore wing with basal section of RS very short and almost perpendicular to longitudinal axis of wing; posterior branch of SC only slightly oblique; cell 3rm not widened distally, shorter than cell 2m-cu. RASNITSYN, 1969, 1983b. *Jur.*, USSR (Kazakh).—FIG. 246,3. **M. jurassica*; fore wing, $\times 6$ (Rasnitsyn, 1969).

Prolyda RASNITSYN, 1968, p. 194 [**P. karatavica*; OD]. Fore wing with posterior branch of SC very short; basal section of RS oblique and relatively long; cell 3rm widened distally. RASNITSYN, 1963, 1983b. *Jur.*, USSR (Kazakh).

Sagulyda RASNITSYN, 1983b, p. 57 [**S. ferganica*; OD]. Similar to *Xyelyda*. Fore wing with crossvein 1m-cu about as long as section of CUA adjoining it distally. *Jur.*, USSR (Kirghiz).

Strophandria RASNITSYN, 1968, p. 195 [**S. grossa*; OD]. Similar to *Mesolyda*. Fore wing with basal section of RS more than half as long as basal section of M; cell 3rm widened distally and longer than cell 2m-cu. RASNITSYN, 1969, 1983b. *Jur.*, USSR (Kazakh).

Family PARAPAMPHILIIDAE

Rasnitsyn, 1968

[Parapamphiliidae RASNITSYN, 1968, p. 191]

Fore wing with vein SC apparently absent; area between R and costal margin broad, widest at origin of RS; basal section of RS much longer than basal section of M; cell 3r very narrow and long. *Jur.*

Parapamphilius RASNITSYN, 1968, p. 192 [**P. confusus*; OD]. Fore wing with pterostigma sclerotized at base. Head considerably wider than pronotum. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Family PAMPHILIIDAE

Cameron, 1890

[Pamphiliidae CAMERON, 1890, p. 84]

Fore wing with vein SC absent or obsolescent; RS unbranched; crossvein 2r-rs present. Antennae with at least 13 segments, third not elongate; pronotum with hind margin straight or only slightly concave; fore tibiae with 2 apical spurs; ovipositor short. Larvae foliage feeders, usually in rolled leaves. *Jur.*—*Holo.*

Pamphilius LATREILLE, 1802, p. 303. *Holo.*

Atocus SCUDDER, 1892, p. 25 [**A. defessus*; OD]. Similar to *Neurotoma* (recent), but antennae very

short and with a small number of segments; basal section of RS in fore wing longer than in *Neurotoma*. BRUES, 1908b; COCKERELL, 1908c; ZHELOCHOVTZEV & RASNITSYN, 1972; RASNITSYN, 1983b. *Oligo.*, USA (Colorado).

Juralyda RASNITSYN, 1977a, p. 102 [**J. udensis*; OD]. Fore wing with pterostigma narrow, only margins sclerotized; basal section of RS about equal in length to crossvein 1r-rs; crossvein 3r-m nearly perpendicular to longitudinal axis of wing; cell 1mcu very short. *Jur.*, USSR (Kazakh). —FIG. 246,9. **J. udensis*; fore wing, $\times 5$ (Rasnitsyn, 1977a).

Tapholyda RASNITSYN, 1983b, p. 65 [**Cephaleia captani*; OD]. Apparently related to *Acantholyda* (recent). Antennae with less than 20 segments, third segment only a little longer than fourth; head transverse. Fore wing with cells 1r and 1mcu twice as long as their width. COCKERELL, 1933a, 1940b; ZHELOCHOVTZEV & RASNITSYN, 1972. *Oligo.*, USA (Colorado); *Mio.*, USSR (Asian RFSFR).

Family CEPHIDAE Newman, 1835

[Cephidae NEWMAN, 1835, p. 411]

Fore wing with vein SC absent; RS unbranched; basal section of RS very short; crossvein 2r-rs joined to RS proximally to 2r-m; cell 2r short; cell 1mcu large. Antennal segments little differentiated; prothorax large; fore tibiae with 1 apical spur; abdomen somewhat constricted between first and second segments; ovipositor flat. Larvae stem or twig borers. *Jur.*—*Holo.*

Cephus LATREILLE, 1802, p. 303. *Holo.*

Electrocephus KONOW, 1897, p. 37 [**E. stralendorffi*; OD]. Similar to *Janus*, but 18-segmented antennae much shorter and thicker; third antennal segment almost a third longer than fourth, penultimate segment shorter than broad. *Oligo.*, Europe (Baltic).

Janus STEPHENS, 1835, p. 107. COCKERELL, 1913b. *Oligo.*, USA (Colorado)—*Holo.*

Mesocephus RASNITSYN, 1968, p. 196 [**M. sibiricus*; OD]. Similar to *Pachycephus* (recent), but cell 3r of fore wing wide and cell 2rm nearer wing apex. RASNITSYN, 1963. *Jur.*, USSR (Kazakh). —FIG. 246,6. **M. sibiricus*; fore wing, $\times 7$ (Rasnitsyn, 1969).

Family GIGASIRICIDAE Rasnitsyn, 1968

[Gigasiricidae RASNITSYN, 1968, p. 197]

Fore wing: vein SC well developed; basal section of RS slanted toward apex of wing,

longer than basal section of M; crossveins 2r-m, 3r-m, and 2m-cu well developed. Antennae with third segment enlarged and elongate. *Jur.*

Gigasirex RASNITSYN, 1968, p. 197 [**G. longipes*; OD]. Fore wing with pterostigma fully sclerotized; SC free from R; RS + M shorter than basal section of RS. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Liasirex RASNITSYN, 1968, p. 198 [**L. sogdianus*; OD]. Fore wing with pterostigma incompletely sclerotized; section of R between base of RS and pterostigma strongly arched; basal section of RS more than twice as long as basal section of M. RASNITSYN, 1969. *Jur.*, USSR (Kazakh). —FIG. 247,2. **L. sogdianus*; fore wing, $\times 4$ (Rasnitsyn, 1969).

Protosirex RASNITSYN, 1969, p. 62 [**P. xyelopterus*; OD]. Fore wing with SC contiguous with R; pterostigma narrow, strongly sclerotized; basal section of RS less than twice as long as basal section of M; RS + M longer than basal section of RS. *Jur.*, USSR (Kazakh). —FIG. 247,1. **P. xyelopterus*; fore wing, $\times 6$ (Rasnitsyn, 1969).

Family KARATAVITIDAE Rasnitsyn, 1963

[Karatavitidae RASNITSYN, 1963, p. 96]

Fore wing with vein SC apparently absent; basal section of RS directed toward wing apex and longer than basal section of M; crossvein 2r-rs situated before center of pterostigma. Antennae setaceous; ovipositor very slender. *Jur.*

Karatavites RASNITSYN, 1963, p. 97 [**K. angustus*; OD]. Fore wing with basal section of RS 1.5 times as long as basal section of M; cell 2rm longer than cell 1r but shorter than cell 3rm. Antennae thin, setaceous, with long segments. RASNITSYN, 1968, 1969. *Jur.*, USSR (Kazakh). —FIG. 247,4. *K. medius* RASNITSYN; fore wing, $\times 6$ (Rasnitsyn, 1969).

Family SEPULCIDAE Rasnitsyn, 1968

[*nom. transl.* RASNITSYN, 1969, p. 63, ex Sepulcinae RASNITSYN, 1968, p. 210]

Fore wing with basal section of vein RS slanting toward wing apex; cell 1mcu large, with basal-posterior margin sigmoidal. *Jur.*

Sepulca RASNITSYN, 1968, p. 210 [**S. mirabilis*; OD]. Fore wing with pterostigma completely sclerotized; SC coalesced with R, only distal end of SC free, appearing like a crossvein. RASNITSYN,

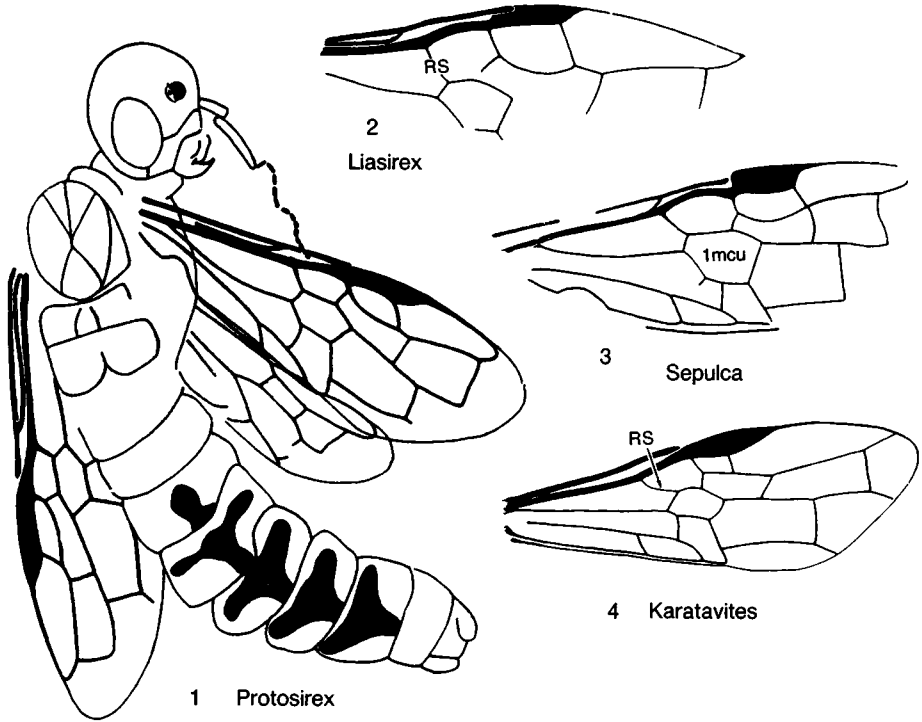


FIG. 247. Gigasiricidae, Karatavidae, and Sepulcidae (p. 458–459).

1969. *Jur.*, USSR (Kazakh).—FIG. 247,3. **S. mirabilis*; fore wing, $\times 7$ (Rasnitsyn, 1969).

Sepulenia RASNITSYN, 1968, p. 210 [**S. syriacta*; OD]. Similar to *Sepulca*, but SC completely coalesced with R. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Family ANAXYELIDAE

Martynov, 1925

[Anaxyelidae MARTYNOV, 1925d, p. 754] [=Syntexidae BENSON, 1935, p. 539]

Fore wing: vein SC coalesced with R, at most appearing as a crossvein proximal to origin of RS; basal section of RS slanted toward wing apex and longer than basal section of M; crossveins 3r-m and 2m-cu present; cell 1m-cu with 5 or 6 corners. No recent genera of the family are known as fossils. *Jur.*—*Holo.*

Anaxyela MARTYNOV, 1925d, p. 754 [**A. gracilis*; OD]. Fore wing with pterostigma weakly sclerotized, extending only slightly beyond basal margin of cell 3r; RS+M distinct. Basal half of antennae dark; ovipositor sheaths thin. RASNITSYN, 1963, 1968. *Jur.*, USSR (Kazakh).

—FIG. 248,3. **A. gracilis*; wings and body, $\times 5$ (Rasnitsyn, 1969).

Anasyntexis RASNITSYN, 1968, p. 208 [**A. strophandra*; OD]. Fore wing with pterostigma sclerotized; basal section of RS 1.5 times longer than basal section of M; RS+M shorter than basal section of M. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 249,5. **A. strophandra*; fore wing, $\times 6.5$ (Rasnitsyn, 1969).

Brachysyntexis RASNITSYN, 1969, p. 70 [**Syntexyela brachyura* RASNITSYN, 1968, p. 202; OD]. Fore wing with pterostigma sclerotized, not extending to middle of cell 3r; RS+M shorter than section of CUA between its divergence from M and its union with crossvein cu-a; basal section of RS more than twice as long as basal section of M. Antennae broad basally, much narrowed distally. *Jur.*, USSR (Kazakh).—FIG. 248,2. **B. brachyura* (RASNITSYN); wings and body, $\times 8$ (Rasnitsyn, 1969).

Dolichostigma RASNITSYN, 1968, p. 200 [**D. tenuipes*; OD]. Fore wing with pterostigma sclerotized, extending at least to center of cell 3r; RS and M joined at a single point of contact; cell 1m-cu narrowed distally. RASNITSYN, 1969. *Cret.*, USSR (Kazakh).—FIG. 249,4. **D. tenuipes*; wings and body, $\times 4.5$ (Rasnitsyn, 1969).

Kempendaja RASNITSYN, 1968, p. 207 [**K. jacu-*

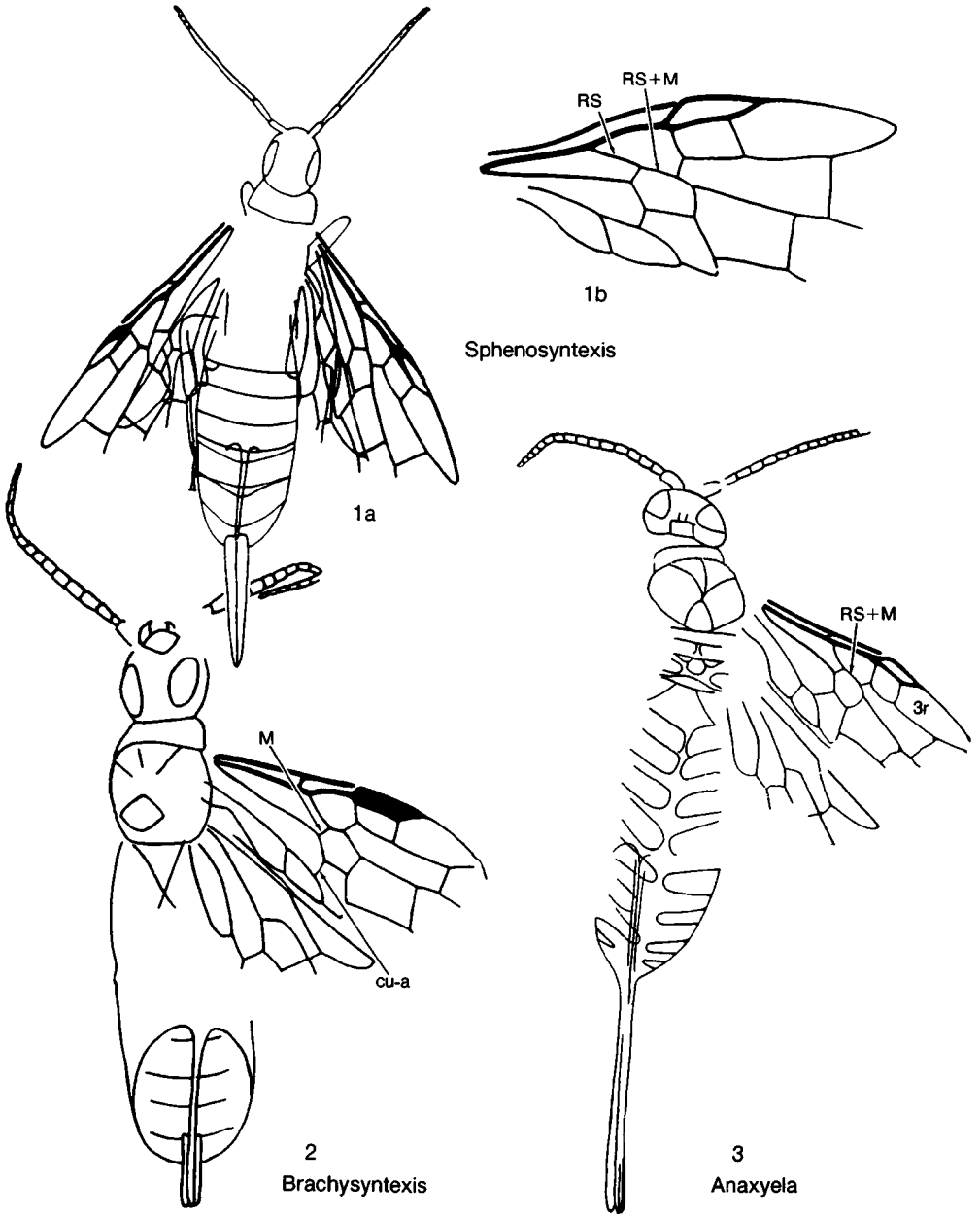


FIG. 248. Anaxyelidae (p. 459–461).

ensis; OD]. Similar to *Brachysyntexis*, but pterostigma not sclerotized. RASNITSYN, 1969. *Cret.*, USSR (Kazakh). — FIG. 249, 2. **K. jacutensis*; fore wing, $\times 7.3$ (Rasnitsyn, 1969).

Kulbastavia RASNITSYN, 1968, p. 207 [**Anaxyela macrura* RASNITSYN, 1963, p. 92; OD]. Fore wing with pterostigma sclerotized; basal section of RS more than twice as long as basal section of M and slightly longer than RS+M; crossvein cu-a

nearly at level of center of cell 1mcu. Ovipositor longer than body. RASNITSYN, 1969. *Jur.*, USSR (Kazakh). — FIG. 249, 1. **K. macrura* (RASNITSYN); wings and body, $\times 4$ (Rasnitsyn, 1969).

Sphenosyntexis RASNITSYN, 1969, p. 67 [**Anaxyela antonovi* RASNITSYN, 1963, p. 90; OD]. Fore wing with pterostigma weakly sclerotized; basal section of RS aligned with RS+M, forming a straight line. Antennae filiform, with dark basal

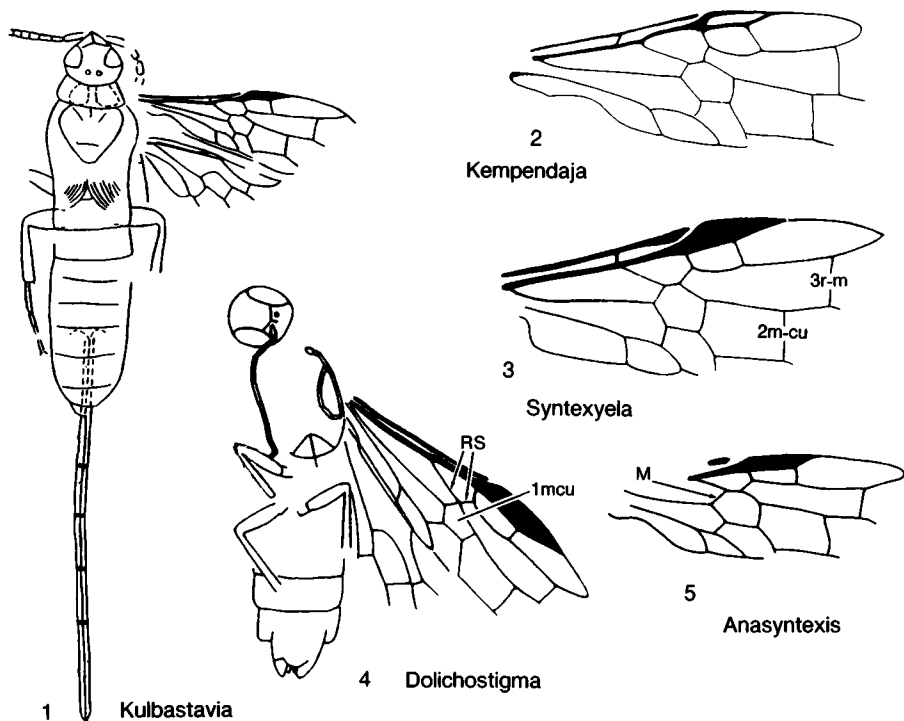


FIG. 249. Anaxyelidae (p. 459–461).

and apical segments. RASNITSYN, 1968. *Jur.*, USSR (Kazakh).—FIG. 248, 1a. *S. pallicornis* RASNITSYN; wings and body, $\times 6$ (Rasnitsyn, 1969).—FIG. 248, 1b. **S. antonovi* (RASNITSYN); fore wing, $\times 10$ (Rasnitsyn, 1969).

Syntexyela RASNITSYN, 1968, p. 201 [**Anaxyela media* RASNITSYN, 1963, p. 94; OD]. Fore wing with pterostigma sclerotized; section of M between crossveins 2m-cu and 3r-m about equal in length to crossvein 2m-cu. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 249, 3. **S. media* (RASNITSYN); fore wing, $\times 7$ (Rasnitsyn, 1969).

Urosyntexis RASNITSYN, 1969, p. 71 [**Syntexyela magna* RASNITSYN, 1968, p. 201; OD]. Similar to *Syntexyela*, but section of M between crossveins 2m-cu and 3r-m about half length of crossvein 2m-cu. RASNITSYN, 1963. *Jur.*, USSR (Kazakh).

Family PRAESIRICIDAE Rasnitsyn, 1968

[*nom. transl.* RASNITSYN, 1983b, p. 62, *ex Praesiricinae* RASNITSYN, 1968, p. 216]

Antennal segmentation nearly homonomous, third segment usually slightly longer than following segments; head large, mandibles long and narrow. Fore wing with vein SC apparently absent; origin of RS remote

from pterostigma; cell 3r not broadened distally; M + CUA arcuate. *Jur.—Cret.*

Praesirex RASNITSYN, 1968, p. 216 [**P. hirtus*; OD]. Fore wing with basal section of RS short, inclined toward wing base; cell 1m-cu large; crossvein 1m-cu much shorter than section of CUA adjoining it distally. RASNITSYN, 1969, 1983b. *Cret.*, USSR (Asian RSFSR).

Aulidontes RASNITSYN, 1983b, p. 64 [**A. mandibulatus*; OD]. Similar to *Praesirex*. Fore wing with basal section of RS long; cell 1m-cu relatively large and long. *Jur.*, USSR (Kazakh).

Xyelydones RASNITSYN, 1983b, p. 64 [**X. sculpturatus*; OD]. Similar to *Praesirex*. Fore wing with basal section of RS short and inclined toward wing apex; cell 1m-cu small. *Cret.*, USSR (Mongolia).

Family PSEUDOSIRICIDAE Handlirsch, 1906

[Pseudosiricidae HANDLIRSCH, 1906b, p. 574] [=Myrmiciidae MAA, 1949, p. 17; Megapteritidae MAA, 1949, p. 77]

Fore wing with venation reduced; crossveins 3r-m and 2m-cu absent; vein SC either present or obsolescent; basal section of RS slanted toward wing apex or wing base. *Jur.—Eoc.*

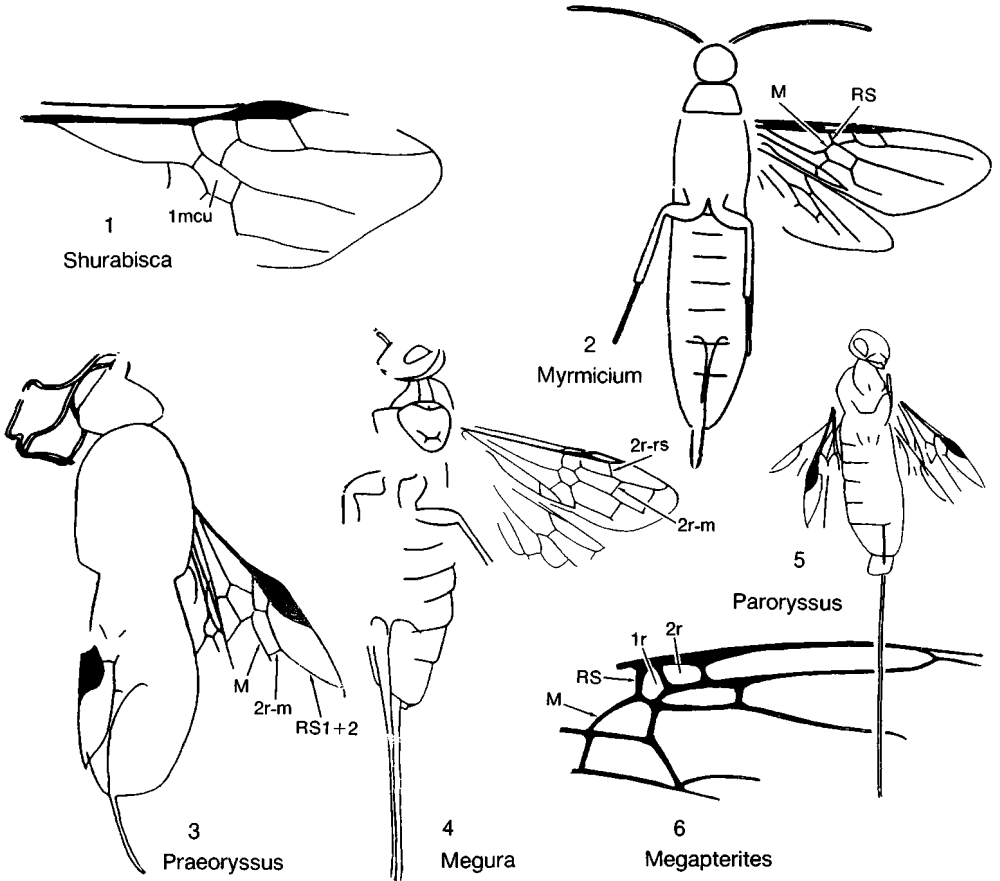


FIG. 250. Pseudosiricidae, Siricidae, and Paroryssidae (p. 462–463).

Myrmicium WESTWOOD, 1854, p. 396 [**M. beeri*; OD] [= *Hagenia* WEYENBERGH, 1869, p. 250 (type, *Sphinx schroeteri* GERMAR, 1839, p. 193); *Pseudostrex* WEYENBERGH, 1873, p. 238 (type, *P. darwini*); *Rhipidorhabdus* OPPENHEIM, 1885, p. 344 (type, *Sphinx schroeteri* GERMAR, 1839, p. 193); *Fabellovena* OPPENHEIM, 1885, p. 344 (type, *F. karschi*)]. Fore wing with basal section of RS strongly slanted toward wing apex and only slightly longer than basal section of M; RS+M very short, touching only a corner of cell 1m-cu. MAA, 1949; RASNITSYN, 1968, 1969; SMITH, 1978. *Jur.*, England, Europe (Germany). — FIG. 250,2. *M. schroeteri* (GERMAR); wings and body, ventral view, $\times 1$ (Rasnitsyn, 1969).

Eoponera CARPENTER, 1929b, p. 301 [**E. berryi*; OD]. Little-known genus, apparently related to *Myrmicium*; basal section of M much longer than basal section of RS; crossvein 2r-rs absent. BARONI URBANI, 1980d; RASNITSYN, 1980b. *Eoc.*, USA (Tennessee).

Formicium WESTWOOD, 1854, p. 388 [**F. brodeii*; OD]. Little-known genus. Fore wing with basal

section of RS arising from R at an acute angle and about one-quarter as long as basal section of M. COCKERELL, 1921b; RASNITSYN, 1969, 1980b. *Jur.*, England.

Megapterites COCKERELL, 1920a, p. 278 [**M. mirabilis*; OD]. Fore wing with basal section of RS perpendicular to R and about half as long as basal section of M; cell 1r shorter than cell 2r. COCKERELL, 1921b; MAA, 1949; RASNITSYN, 1969, 1980b. *Eoc.*, England. — FIG. 250,6. **M. mirabilis*; fore wing, $\times 1$ (Cockerell, 1921b).

Shurabisca RASNITSYN, 1968, p. 217 [**S. liassica*; OD]. Fore wing with basal section of RS almost twice as long as basal section of M; cell 1m-cu much wider distally than basally. RASNITSYN, 1969. *Jur.*, USSR (Kazakh). — FIG. 250,1. **S. liassica*; fore wing, $\times 3.8$ (Rasnitsyn, 1969).

Family SIRICIDAE Billberg, 1820

[Siricidae BILLBERG, 1820, p. 98]

Fore wing with vein SC short or absent; crossveins 1r-rs, 3r-m, and 2m-cu present;

basal section of RS perpendicular to R or slanted toward wing base. Antennae with many segments, not markedly differentiated; pronotum with hind margin deeply emarginate; fore tibiae with 1 of the 2 apical spurs small or absent; abdomen terminating in a spine or horn. Larvae wood boring. *Jur.*—*Holo.*

Sirex LINNÉ, 1761, p. 396 [= *Urocerites* HEER, 1867, p. 36 (type, *U. spectabilis*)]. KONOW, 1898; MAA, 1949; SMITH, 1978. *Mio.*, Europe (Yugoslavia)—*Holo.*

Aulisca RASNITSYN, 1968, p. 212 [**A. odontura*; OD]. Fore wing with basal section of RS about equal in length to RS+M and directed posteriorly; crossvein 2r-rs more distal than crossvein 2r-m. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Eosirex PITON, 1940a, p. 229 [**E. ligniticus*; OD]. Little-known genus. Fore wing with cell 2rm broad; crossvein 2r-m sigmoidal. *Eoc.*, Europe (France).

Eoxeris MAA, 1949, p. 78 [**Urocerus klebsi* BRUES, 1926, p. 168; OD]. Similar to *Urocerus* (recent). Fore wing with apical angle of cell 1rm obtuse; cell 2r relatively short and below proximal part of pterostigma; cell 2cua very long. MAA, 1949. *Oligo.*, Europe (Baltic).

Megaulisca RASNITSYN, 1968, p. 213 [**M. grossa*; OD]. Fore wing as in *Megura*, but basal section of RS much longer than RS+M. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Megura RASNITSYN, 1968, p. 214 [**M. magnifica*; OD]. Fore wing with basal section of RS about as long as RS+M and curved posteriorly or apically; crossvein 2r-rs situated proximally to 2r-m. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 250.4. **M. magnifica*; wings and body, $\times 2.4$ (Rasnitsyn, 1969).

Family PARORYSSIDAE

Martynov, 1925

[Paroryssidae MARTYNOV, 1925d, p. 755]

Fore wing with reduced venation; crossveins 2m-cu and 3r-m absent; vein RS distinct between cells 1r and 2rm. Ovipositor well developed. *Jur.*

Paroryssus MARTYNOV, 1925d, p. 756 [**P. extensus*; OD]. Little-known genus, similar to *Praeoryssus*. Fore wing with R sharply curved between origin of RS and pterostigma. Prothorax elongate; ovipositor straight and longer than body. RASNITSYN, 1963, 1968. *Jur.*, USSR (Kazakh).—FIG. 250.5. **P. extensus*; wings and body, $\times 5.5$ (Rasnitsyn, 1969).

Microoryssus RASNITSYN, 1968, p. 221 [**M. brachyurus*; OD]. Similar to *Praeoryssus*, but crossvein

2r-m absent. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).

Praeoryssus RASNITSYN, 1968, p. 219 [**P. venosus*; OD]. R straight between origin of RS and pterostigma; crossvein 2r-m present. Prothorax short; ovipositor shorter than body, curved forward. RASNITSYN, 1969. *Jur.*, USSR (Kazakh).—FIG. 250.3. **P. venosus*; wings and body, $\times 8$ (Rasnitsyn, 1969).

Family UNCERTAIN

The following genera, apparently belonging to the order Hymenoptera, suborder Symphyta, are too poorly known to permit assignment to families.

Phenacoperga COCKERELL, 1908c, p. 113 [**Perga coloradensis* COCKERELL, 1907f, p. 446; OD]. Little-known genus, probably related to the Cimbicidae; cell 3r of fore wing with very smoothly curved posterior margin. ROHWER, 1908b. *Oligo.*, USA (Colorado).

Pseudocimbex ROHWER, 1908b, p. 526 [**P. clavata*; OD]. Similar to *Phenacoperga*, but cell 3r with very irregular posterior margin. *Oligo.*, USA (Colorado).

Sogutia RASNITSYN, 1977a, p. 101 [**S. liassica*; OD]. Fore wing with pterostigma fully sclerotized; basal section of vein RS slightly longer than RS+M, which is about as long as basal section of M; M+CUA sigmoidally curved. [Probably related to Xyelidae.] *Jur.*, USSR (Kirghiz).—FIG. 246.4. **S. liassica*; fore wing, $\times 17$ (Rasnitsyn, 1977a).

Suborder APOCRITA

Gerstaecker, 1867

[Apocrita GERSTAECKER, 1867, p. 1]

Adults: first abdominal segment (propodeum) fused to metathorax and structurally a part of it (see Fig. 240); deep constriction between propodeum and second abdominal segment; gaster often petiolate. Larvae apodous. *Jur.*—*Holo.*

Family EPHIALTITIDAE

Handlirsch, 1906

[Ephialtitidae HANDLIRSCH, 1906b, p. 577]

Fore wing with crossvein 2r-m present; crossvein 1r-rs obsolescent, occasionally reaching pterostigma; cell 2a often closed. Antennae diverse, setaceous or clubbed, with 12 to 30 segments; propodeum commonly large, flat or weakly convex, often not ele-

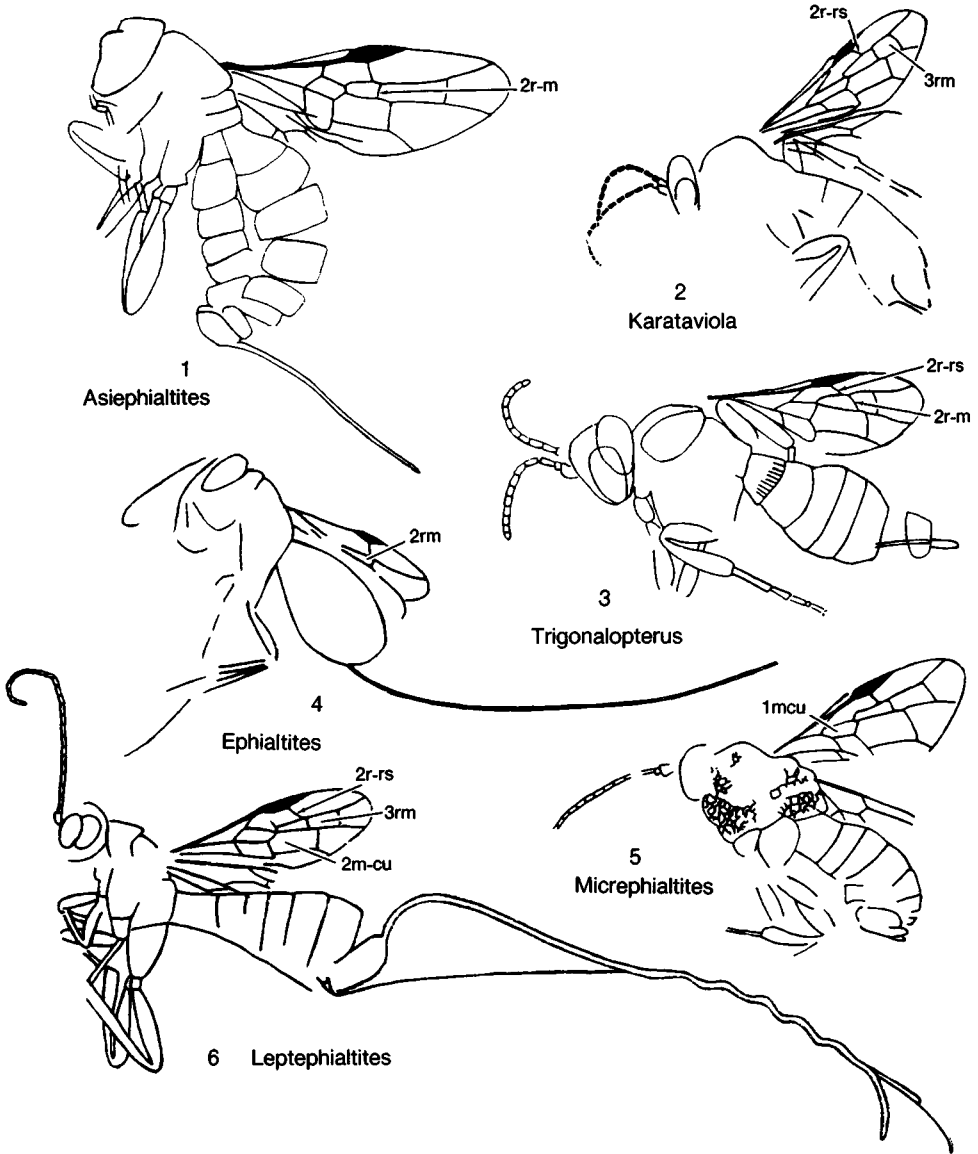


FIG. 251. Ephialtitidae (p. 464-466).

vated over base of second abdominal segment. *Jur.*

Ephialtites MEUNIER, 1903c, p. 4 [**E. jurassicus*; OD]. Little-known genus. Fore wing with pterostigma short; crossvein cu-a situated at origin of M from CUA+M; cell 2r-m very narrow and long. Ovipositor twice length of body, strongly curved. HANDLIRSCH, 1906b; RASNITSYN, 1975. *Jur.*, Europe (Spain). — FIG. 251,4. **E. jurassicus*; wings and body, ×4 (Rasnitsyn, 1975).

Asiephialtites RASNITSYN, 1975, p. 29 [**A. niger*; OD]. Fore wing similar to that of *Stephanogaster* but not more than 4 mm long. Gaster widest at middle. *Jur.*, USSR (Kazakh). — FIG. 251,1. **A. niger*; wing and body, ×9 (Rasnitsyn, 1975).

Karataviola RASNITSYN, 1975, p. 51 [**K. micruva*; OD]. Fore wing with basal section of RS arising near pterostigma and directed toward wing base; crossvein 1r-rs absent; crossvein 2r-m not slanted and situated distally to 2r-rs; cell 3rm shorter than cell 2r-m. Antennae setaceous, with at least

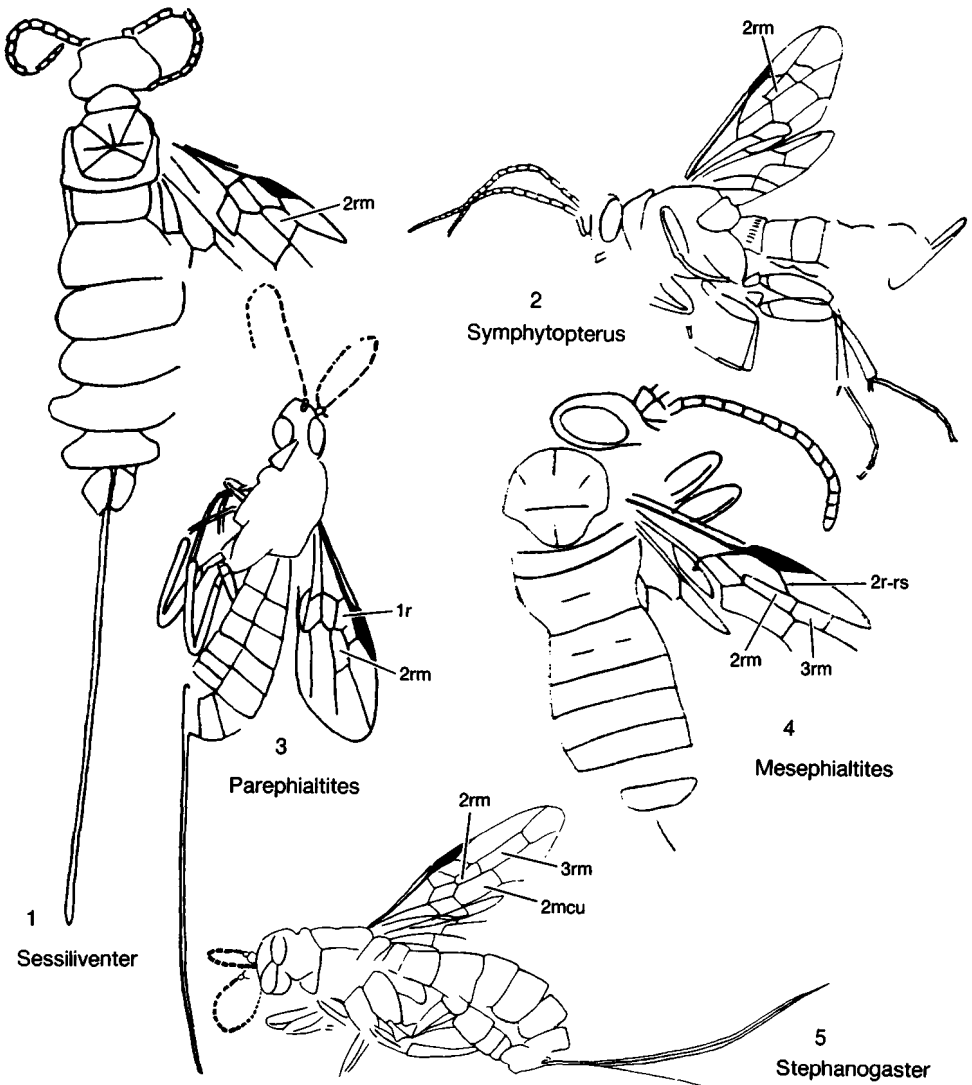


FIG. 252. Ephialtitidae (p. 465–466).

15 segments; ovipositor very short. *Jur.*, USSR (Kazakh). — FIG. 251,2. **K. micrura*; wings and body, $\times 3.6$ (Rasnitsyn, 1975).

Leptepialtites RASNITSYN, 1975, p. 33 [**L. caudatus*; OD]. Fore wing with basal section of RS arising close to pterostigma and directed toward wing base; proximal border of cell 2rm distal of base of pterostigma; cell 3rm shorter than 2mcu; crossvein 1r-rs missing in some species. Antennae with from 16 to 30 segments; ovipositor longer than gaster, often much longer than body; gaster usually broadest distally. *Jur.*, USSR (Kazakh). — FIG. 251,6. **L. caudatus*; body and wings, $\times 6$ (Rasnitsyn, 1975).

Mesepialtites RASNITSYN, 1975, p. 32 [**M. paurocerus*; OD]. Fore wing with basal section of RS arising close to base of pterostigma and directed obliquely toward wing base; proximal border of cell 2rm slightly distal to base of pterostigma; cell 3rm shorter than cells 2rm and 2mcu; crossvein 1r-rs absent. Antennae with 15 segments; gaster widest along middle. *Jur.*, USSR (Kazakh). — FIG. 252,4. **M. paurocerus*; wings and body, $\times 9$ (Rasnitsyn, 1975).

Microepialtites RASNITSYN, 1975, p. 48 [**M. minor*; OD]. Fore wing with basal section of RS remote from pterostigma and directed toward wing base; crossvein 1r-rs absent; cells 2rm and 3rm long.

Ovipositor very short, barely projecting beyond end of gaster. *Jur.*, USSR (Kazakh).—FIG. 251,5. **M. minor*; wings and body, $\times 8$ (Rasnitsyn, 1975).

Parephialtites RASNITSYN, 1975, p. 32 [**P. reductus*; OD]. Fore wing with basal section of RS very short, directed slightly toward wing apex; crossveins 3r-m and 2m-cu absent; cell 2a closed; cell 2rm with proximal border distal to base of pterostigma. Antennae with 20 segments; propodeum barely extending over base of second abdominal segment; gaster widest at level of segments 6 and 7; ovipositor only slightly longer than body. *Jur.*, USSR (Kazakh).—FIG. 252,3. **P. reductus*; wings and body, $\times 6.7$ (Rasnitsyn, 1975).

Sessiliventer RASNITSYN, 1975, p. 39 [**S. temporalis*; OD]. Fore wing with basal section of RS very short and slanted toward wing base; proximal border of cell 2rm distal to base of pterostigma; crossveins 1r-rs and 3r-rm absent. Antennae with 15 to 17 segments; gaster broadest near middle; ovipositor longer than abdomen, but not longer than body. *Jur.*, USSR (Kazakh).—FIG. 252,1. **S. temporalis*; wings and body, $\times 7.8$ (Rasnitsyn, 1975).

Stephanogaster RASNITSYN, 1975, p. 27 [**S. magna*; OD]. Fore wing at least 5 mm long; pterostigma long; basal section of RS arising near base of pterostigma and nearly perpendicular to R; proximal border of cell 2rm distal to base of pterostigma; cell 3rm longer than cell 2mcu; crossvein cu-a situated at origin of M from M+CUA. Antennae setaceous, with at least 20 segments; gaster broad posteriorly; ovipositor long, but not as long as body. *Jur.*, USSR (Kazakh).—FIG. 252,5. **S. magna*; wing and body, $\times 3.5$ (Rasnitsyn, 1975).

Symphogaster RASNITSYN, 1975, p. 49 [**S. cylindrica*; OD]. Similar to *Micrephialtites*, but crossvein 3r-m absent in fore wing. Antennae with 19 segments. *Jur.*, USSR (Kazakh).

Symphypterus RASNITSYN, 1975, p. 42 [**S. nigricornis*; OD]. Fore wing with basal section of RS strongly slanted toward base of wing; proximal border of cell 2rm at about level of base of pterostigma. Antennae apparently with from 12 to 24 segments; gaster narrowed toward apex, widest near middle. *Jur.*, USSR (Kazakh).—FIG. 252,2. **S. nigricornis*; wings and body, $\times 5$ (Rasnitsyn, 1975).

Trigonalopterus RASNITSYN, 1975, p. 51 [**T. brachycerus*; OD]. Fore wing with basal section of RS close to pterostigma and directed toward wing base; crossvein 1r-rs absent; crossvein 2r-m oblique, close to crossvein 2r-rs. Antennae with 12 segments; ovipositor short. *Jur.*, USSR (Kazakh).—FIG. 251,3. **T. brachycerus*; wing and body, $\times 7.7$ (Rasnitsyn, 1975).

Family STEPHANIDAE Leach, 1815

[Stephanidae LEACH, 1815, p. 142]

Fore wing with costal space broad; distal veins weak or obsolescent. Antennae multi-segmented, with at least 20 segments; head spherical, with a circular row of 5 teeth around median ocellus; cervix long; hind coxae long, hind femora swollen. Larvae parasitic on wood-boring insects, mostly Coleoptera. *Oligo.*—*Holo.*

Stephanus PANZER, 1805, p. 77. *Holo.*

Electrostephanus BRUES, 1933, p. 12 [**E. brevicornis*; OD]. Fore wing similar to that of *Stephanus* (recent), but basal section of M directed slightly anteriorly. Antennae with not more than 23 segments. *Oligo.*, Europe (Baltic).—FIG. 253,6. **E. brevicornis*; wings and body, $\times 10$ (Brues, 1933).

Protostephanus COCKERELL, 1906b, p. 57 [**P. ashmeadi*; OD]. Little-known genus. Hind femora toothed. [Family assignment doubtful.] BRUES, 1933; RASNITSYN, 1963. *Oligo.*, USA (Colorado).

Family MEGALYRIDAE

Schletterer, 1890

[Megalyridae SCHLETTERER, 1890, p. 198]

Similar to the Stephanidae, but antennae commonly with fewer segments, segments long and narrow; gaster sessile. Larvae apparently parasitic on certain wood-boring beetles. *Jur.*—*Holo.*

Megalyra WESTWOOD, 1832, p. 790. *Holo.*

Brachycleistogaster RASNITSYN, 1975, p. 64 [**B. karatavica*; OD]. Fore wing with basal section of RS shorter than basal section of M; crossveins 3r-m and 2m-cu absent; crossvein 2r-m present. Antennae filiform, with 13 to 15 segments; ovipositor short. *Jur.*, USSR (Kazakh).—FIG. 253,1. **B. karatavica*; wings and body, $\times 13$ (Rasnitsyn, 1975).

Cleistogaster RASNITSYN, 1975, p. 53 [**C. buriatica*; OD]. Fore wing with pterostigma slender; basal section of RS shorter than basal section of M; crossveins 2r-m and 3r-m present. *Jur.*, USSR (Kazakh); *Cret.*, USSR (Asian RSFSR).—FIG. 253,5. **C. buriatica*, *Jur.*; wings and body, $\times 6$ (Rasnitsyn, 1975).

Cretocleistogaster RASNITSYN, 1975, p. 72 [**C. vitimica*; OD]. Fore wing with pterostigma very short and broad at middle; basal section of RS longer than basal section of M; crossveins 2r-m, 3r-m, and 2m-cu absent. Antennae with about 15 segments; ovipositor short. *Cret.*, USSR (Asian RSFSR).

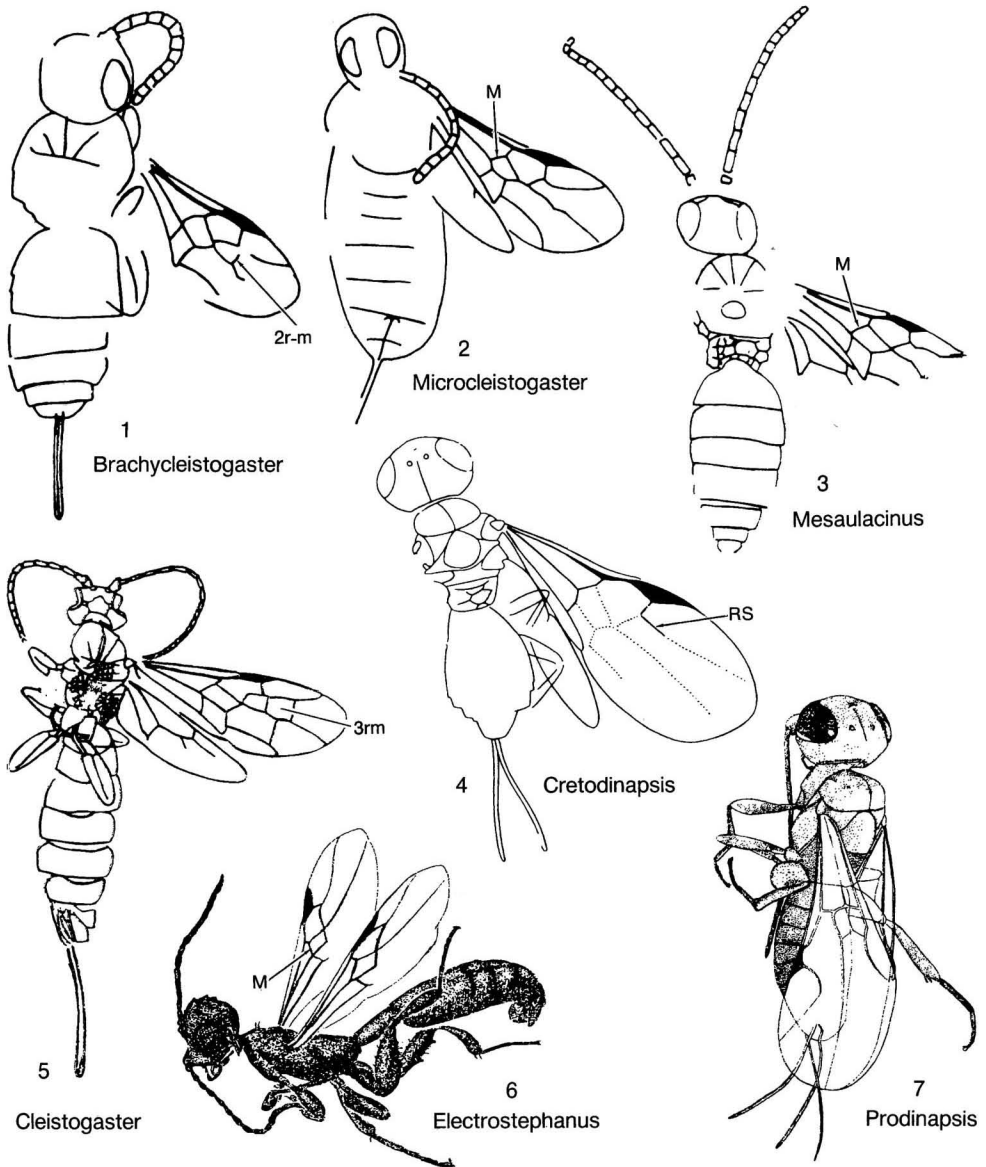


FIG. 253. Stephanidae and Megalyridae (p. 466–468).

Cretodinapsis RASNITSYN, 1977a, p. 106 [**C. caucasica*; OD]. Fore wing with RS, as it connects to crossvein 2r-rs, perpendicular to it; RS obsolete, but distinct between cells 1r+2r and 3r; R curved at origin of RS. Head broader than thorax; ovipositor shorter than body. *Cret.*, USSR (Azerbaijan). — FIG. 253,4. **C. caucasica*; wings and body, $\times 24$ (Rasnitsyn, 1977a).

Leptocleistogaster RASNITSYN, 1975, p. 57 [**L. pallida*; OD]. Fore wing as in *Cleistogaster*, but

crossvein 2m-cu absent or reduced to only stubs. Antennae with 10 to 21 segments. *Jur.*, USSR (Kazakh).

Mesaulacinus MARTYNOV, 1925d, p. 757 [**M. oviformis*; OD]. Fore wing with basal section of RS shorter than basal section of M; crossvein 3r-m absent or obsolete, with stubs present. Antennae apparently with 12 to 20 segments, distal ones shortened. RASNITSYN, 1975. *Jur.*, USSR (Kazakh). — FIG. 253,3. *M. areolatus*

RASNITSYN; wings and body, $\times 11$ (Rasnitsyn, 1975).

Microcleistogaster RASNITSYN, 1975, p. 69 [**M. parvula*; OD]. Fore wing with pterostigma narrow; basal section of RS shorter than basal section of M; crossveins 2r-m, 3r-m, and 2m-cu absent. Body stout; antennae with less than 15 segments; distal segment shorter than others. *Jur.*, USSR (Kazakh).—FIG. 253,2. **M. parvula*; wings and body, $\times 18$ (Rasnitsyn, 1975).

Prodinapsis BRUES, 1923c, p. 31 [**P. succinalis*; OD]. Similar to *Dinapsis* (recent). Fore wing with pterostigma small, elongate; RS short, curved. Antennae filiform, with 14 segments; antennal grooves (scrobes) present; hind coxae very large; ovipositor long. BRUES, 1923a, 1933. *Oligo.*, Europe (Baltic).—FIG. 253,7. **P. succinalis*; wings and body, $\times 16$ (Brues, 1933).

Family TRIGONALIDAE

Cresson, 1887

[Trigonalidae CRESSON, 1887, p. 37]

Fore wing: venation generalized, with pterostigma, veins RS2 and RS3 (usually), RS+M, and cells 2rm and 3rm present; costal space open. Antennae multisegmented. Larvae mostly hyperparasites on other Hymenoptera or Diptera. *Cret.*—*Holo.*

Trigonalys WESTWOOD, 1835, p. 52. [Generic assignment of fossils doubtful.] COCKERELL, 1917e; STATZ, 1938b. *Oligo.*, Europe (Germany); *Mio.*, Burma—*Holo.*

Cretogonalyis RASNITSYN, 1977a, p. 106 [**C. tai-myricus*; OD]. Fore wing with basal section of RS nearly perpendicular to R; cell 1mcu very short, much shorter than cell 2rm. Head narrow, with large, protruding eyes; antennae with 16 segments. *Cret.*, USSR (Asian RSFSR).

Family MAIMETSHIDAE

Rasnitsyn, 1975

[Maimetshidae RASNITSYN, 1975, p. 73]

Fore wing with costal area distinct; pterostigma narrow; basal section of vein RS slanted slightly toward wing base; distal part of RS (beyond crossvein 2r-rs) curved, closing cell 3r; crossvein 2r-m present. Hind wing with venation reduced; RS very short; abdomen with second segment short and narrow; ovipositor well developed. *Cret.*

Maimetsha RASNITSYN, 1975, p. 74 [**M. arctica*; OD]. Fore wing with basal section of RS arising far from pterostigma; cell 3r short, broad; cross-

veins 3r-m and 2m-cu obsolescent. Gaster broadly oval. *Cret.*, USSR (Asian RSFSR).—FIG. 254,4. **M. arctica*; a, body, lateral view, b, wings and body, dorsal view, both $\times 22$ (Rasnitsyn, 1975).

Family STIGMAPHRONIDAE

Kozlov, 1975

[Stigmaphronidae Kozlov, 1975, p. 75]

Fore wing widest distally, venation greatly reduced; veins C and R thick; pterostigma long. Antennae with 11 segments; posterior ocelli almost contiguous with compound eyes; hind tibiae broad and flattened; tibial spurs long; tarsi long, with 5 segments. *Cret.*

Stigmaphron KOZLOV, 1975, p. 77 [**S. orphne*; OD]. Fore wing with RS absent. Antennae clubbed; tibial spur formula 1,2,3; spurs long and thin; hind coxae as long as wide; all femora strongly broadened; hind legs twice as long as forelegs. *Cret.*, USSR (Asian RSFSR).—FIG. 254,1. **S. orphne*; wings and body, $\times 50$ (Kozlov, 1975).

Allocotidus MUESEBECK, 1963, p. 129 [**A. bruesi*; OD]. Female similar to those of *Stigmaphron*, but antenna short, not clubbed, and flagellar segments (except the last) broader than long. RASNITSYN, 1975. *Cret.*, USA (Alaska).

Elasmomorpha KOZLOV, 1975, p. 78 [**E. melpomene*; OD]. Fore wing with RS almost reaching wing apex. Tibial spur formula 2,2,2. Antennal scape 3 times as long as maximum width and as long as following 5 segments combined. *Cret.*, USSR (Asian RSFSR).—FIG. 254,3. **E. melpomene*; wings and body, $\times 38$ (Kozlov, 1975).

Hippocoon KOZLOV, 1975, p. 80 [**H. evadne*; OD]. Fore wing with RS almost reaching wing margin. Tibial spur formula 2,2,2. Antennae not clubbed, length of antennal scape only about 1.3 times its greatest width and equal to 2 following segments combined. *Cret.*, USSR (Asian RSFSR).—FIG. 254,5. **H. evadne*; wings and body, $\times 50$ (Kozlov, 1975).

Family MEGASPILIDAE

Ashmead, 1888

[Megaspilidae ASHMEAD, 1888, p. 49]

Fore wing with pterostigma large, linear, or absent. Antennae with same number of segments in both sexes; middle tibiae with 2 spurs; sixth gastric tergite lacking a net-like area Larvae parasitic on braconids and chalcids. MASNER & DESSART, 1967. *Cret.*—*Holo.*

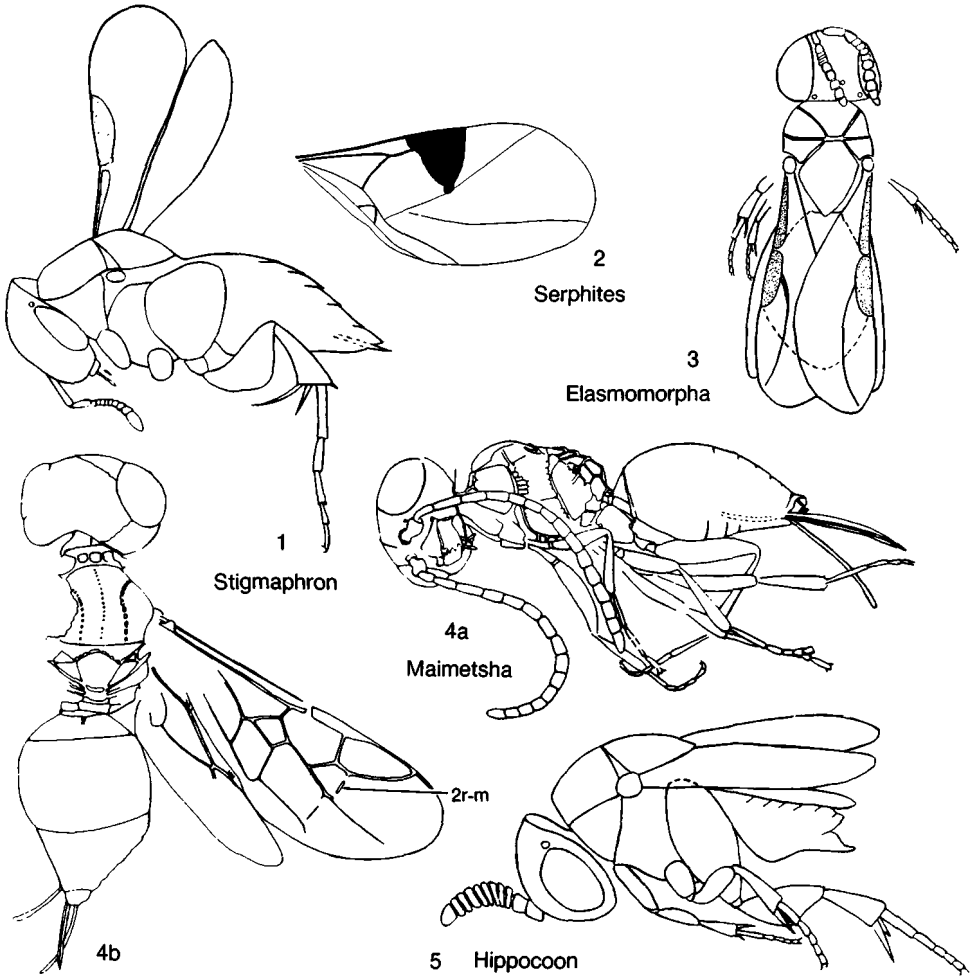


FIG. 254. Maimetshidae, Stigmaphronidae, and Serphitidae (p. 468–470).

Megaspilus WESTWOOD, 1829, p. 37. *Holo.*

Conostigmus DAHLBOM, 1858, p. 291. BRUES, 1940a; DESSART, 1977; ALEKSEYEV & RASNITSYN, 1981. *Cret.*, USSR (Asian RSFSR); *Oligo.*, Europe (Baltic)—*Holo.*

Lagynodes FÖRSTER, 1841, p. 46. BRUES, 1940a; DESSART, 1976. *Oligo.*, Europe (Baltic)—*Holo.*

Lygocerus FÖRSTER, 1856, p. 97. [Generic assignment of fossils doubtful.] CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*

Prolagynodes ALEKSEYEV & RASNITSYN, 1981, p. 127 [**P. penniger*; OD]. Related to *Lagynodes*. Female: wings fully developed; marginal vein of fore wing forming a slightly conical pterostigma; mesonotum with 3 complete furrows. *Cret.*, USSR (Asian RSFSR).

Family MESOSERPHIDAE

Kozlov, 1970

[*nom. transl.* Kozlov, 1975, p. 82, ex Mesoserphinae Kozlov, 1970, p. 205]

Similar to Proctotrupidae, but cells 1mcu and 2cua present in fore wing; gaster of female with 7 visible tergites; antennae of female with 15 or more segments. *Jur.*

Mesoserphus KOZLOV, 1968, p. 239 [**M. karatavicus*; OD]. Cell 1mcu of fore wing nearly rectangular; M curved distally. KOZLOV, 1970, 1975. *Jur.*, USSR (Kazakh).

Mesohelorus MARTYNOV, 1925d, p. 758 [**M. muchini*; OD]. Similar to *Mesoserphus*, but cell

1m-cu nearly triangular in fore wing; M straight distally. RASNITSYN, 1975. *Jur.*, USSR (Kazakh).
Udaserphus RASNITSYN, 1983a, p. 91 [**U. transbaicalicus*; OD]. Similar to *Mesoserphus*, but much smaller; antennal segments broadened apically. Fore wing with RS+M, basal section of RS, and crossvein 1m-cu complete; basal section of M reduced. *Jur.*, USSR (Asian RSFSR).

Family SERPHITIDAE Brues, 1937

[Serphitidae BRUES, 1937, p. 33]

Male: fore wing with pterostigma very large, extending to center of wing; vein SC remote from C; other veins reduced; M and CU nearly obsolescent. Antennae with 10 segments and long scape; flagellum clavate; mandibles large; prothorax short. *Cret.*

Serphites BRUES, 1937, p. 33 [**S. paradoxus*; OD]. Right mandible with 3 long, curved teeth directed inward; antennae inserted below middle of frons; femora slightly thickened near middle. *Cret.*, Canada (Manitoba).—FIG. 254,2. **S. paradoxus*; fore wing, $\times 33$ (Brues, 1937).

Family PROCTOTRUPIDAE Leach, 1815

[Proctotrupidae LEACH, 1815, p. 145]

Fore wing with venation reduced; distal veins obsolescent or absent; pterostigma usually prominent; cell $2r+3r$ small to very small, closed; cells 1m-cu and 2cua absent. Antennae with 13 segments, inserted at middle of frons, not on a projection; gaster of female terminating in a series of fused plates; ovipositor appearing to arise from apex of gaster. *Oligo.*—*Holo.*

Proctotrupes LATREILLE, 1796, p. 108. BRUES, 1910, 1923a. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Cryptoserphus KIEFFER, 1907, p. 288. BRUES, 1940a. *Oligo.*, Europe (Baltic)—*Holo.*

Family HELORIDAE Förster, 1856

[Heloridae FÖRSTER, 1856, p. 20]

Fore wing with pterostigma present, sometimes small; costal space open, commonly narrow; cell $2r+3r$ small, triangular; several closed cells usually present. Antennae not arising from a projection, commonly with 15 segments. Larvae parasitic on diverse types of insects. *Jur.*—*Holo.*

Helorus LATREILLE, 1802, p. 309. STATZ, 1938b. *Oligo.*, Europe (Baltic)—*Holo.*

Protohelorus KOZLOV, 1968, p. 237 [**P. mesozoicus*; OD]. Fore wing with cell 1m-cu more than 3 times as long as its maximum width. Antennae with 20 segments. *Jur.*, USSR (Kazakh).

Family DIAPRIIDAE Haliday, 1833

[Diapriidae HALIDAY, 1833, p. 274]

Fore wing venation usually reduced to a compound vein extending along anterior border of wing and consisting of the submarginal and marginal veins and a very small stigmal vein. Antennae with 11 to 15 segments, usually arising on a frontal projection. *Oligo.*—*Holo.*

Diapria LATREILLE, 1796, p. 110. *Holo.*

Aclista FÖRSTER, 1856, p. 128. BRUES, 1906; THÉOBALD, 1937a; STATZ, 1938b. *Oligo.*, USA (Colorado), Europe (Germany, France)—*Holo.*

Aneurhynchus WESTWOOD, 1832, p. 129. COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Archabelyta MEUNIER, 1923b, p. 84 [**A. superba*; OD]. Little-known genus, apparently related to *Lithobelyta*; pterostigma absent in fore wing. [Family assignment doubtful.] MEUNIER, 1923c. *Oligo.*, Europe (Germany).

Cinetus JURINE, 1807, p. 310. BRUES, 1910; MANEVAL, 1938. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Galesimorpha BRUES, 1910, p. 12 [**G. wheeleri*; OD]. Similar to *Psilus* (recent); compound vein of fore wing submarginal, ending at pterostigma near midwing. *Oligo.*, USA (Colorado).

Lithobelyta COCKERELL, 1921a, p. 22 [**L. reducta*; OD]. Similar to *Cinetus*, but pterostigma absent. *Oligo.*, England.

Miota FÖRSTER, 1856, p. 13. [Generic assignment of fossils doubtful.] COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Pantolyta FÖRSTER, 1856, p. 128. MANEVAL, 1938. *Oligo.*, Europe (Baltic)—*Holo.*

Paramesius WESTWOOD, 1832, p. 129. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Zygota FÖRSTER, 1856, p. 128. [Generic assignment of fossils doubtful.] COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Family JURAPRIIDAE Rasnitsyn, 1983

[Jurapriidae RASNITSYN, 1983a, p. 92]

Similar to Diapriidae; venation much reduced. Antennal scape relatively small, only slightly longer than twice its width; cells $1r+2r+1m-cu$ forming an undivided compound cell. *Jur.*

Jurapria RASNITSYN, 1983a, p. 93 [**J. sibirica*; OD]. Antennae of female with 15 segments and slightly thickened distally but not forming a club; RS arising from R close to pterostigma. *Jur.*, USSR (Asian RSFSR).

Family PELECINOPTERIDAE

Brues, 1933

[Pelecinopterae BRUES, 1933, p. 17]

Fore wing similar to that of Pelecinidae (recent). Antennae with 13 segments; hind tibiae clavate; hind tarsus with fourth segment short; female abdomen with 6 tubular segments, male abdomen with 7 tubular segments. [Probably a synonym of Pelecinidae.] *Oligo.*

Pelecinopteron BRUES, 1933, p. 19 [**P. tubuliforme*; OD]. Fore wing with pterostigma very narrow, acute apically; cell 1mcu small; cell 2rm larger. KOZLOV, 1974. *Oligo.*, Europe (Baltic).—FIG. 255.8. **P. tubuliforme*; a, male, wings and body, $\times 6$; b, female, wings and body, $\times 5$ (both Brues, 1933).

Family SCELIONIDAE

Thomson, 1858

[Scelionidae THOMSON, 1858, p. 417]

Fore wing with venation much reduced, without closed cells, and with a distinct compound vein along anterior margin of wing; costal space often open; stigmal vein usually present, but often thin or obsolescent. Antennae with 10 to 12 segments, rarely the distal 4 or 5 segments fused to form a club; middle tibia with 1 spur. Larvae parasitic on eggs of diverse insects. *Cret.*—*Holo.*

Scelio LATREILLE, 1805, p. 226. *Holo.*

Aneurobaeus KIEFFER, 1912, p. 87. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Archaeoscelio BRUES, 1940b, p. 88 [**A. rugosus*; OD]. Male: fore wing with SC apparently remote from costal margin, several thickenings associated with its termination. Body very short and stout; antennae with 14 segments, geniculate and filiform; legs slender, femora and tibiae clavate. Female: similar to male, but segments of flagellum thick, forming a long club. [Family assignment doubtful.] *Oligo.*, Europe (Baltic).—FIG. 255.5. **A. rugosus*, female; wings and body, $\times 17$ (Brues, 1940b).

Baryconus FÖRSTER, 1856, p. 101. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba)—*Holo.*

Brachyscelio BRUES, 1940b, p. 76 [**B. cephalotes*; OD]. Female: fore wing with venation present;

basal section of M strong, nearly perpendicular to costal margin of wing; pterostigma absent; SC free from C. Head about twice as wide as long; antennae with 12 segments, geniculate; legs slender. [Family assignment doubtful.] *Oligo.*, Europe (Baltic).—FIG. 255.1. **B. cephalotes*; wings and body, $\times 23$ (Brues, 1940b).

Ceratobaecoides DODD, 1913, p. 337. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Chromoteleia ASHMEAD, 1893, p. 209. MANEVAL, 1938; BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Dissolcus ASHMEAD, 1893, p. 164. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Electroteleia BRUES, 1940b, p. 80 [**E. stigmatica*; OD]. Female: fore wing with pterostigma forming a thick ridge on wing margin; RS terminating on wing margin just beyond pterostigma but well before wing apex. Antennae long, with 12 segments, terminal 7 or 8 segments shorter and thicker than others. Male: similar to female, but antennae filiform, distal segments not thickened. *Oligo.*, Europe (Baltic).—FIG. 255.2. **E. stigmatica*; male, wings and body, $\times 11$ (Brues, 1940b).

Hadronotoides DODD, 1913, p. 171. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Hadronotus FÖRSTER, 1856, p. 101. COCKERELL, 1909k. *Oligo.*, Europe (Baltic)—*Holo.*

Hoploteleia ASHMEAD, 1893, p. 227. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Macroteleia WESTWOOD, 1835, p. 70. COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Microtenomus DODD, 1913, p. 173. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Palaeogron MASNER, 1969, p. 398. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Palaeoteleia COCKERELL, 1914f, p. 637 [**P. oxyura*; OD]. Similar to *Chromoteleia*, but SC well developed; antennae inserted very close to middle line of frons; gaster broader. *Oligo.*, USA (Colorado).

Parabaeus KIEFFER, 1910, p. 294. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Proplatyscelio BRUES, 1940b, p. 85 [**P. depressus*; OD]. Female: similar to those of *Platyscelio* (recent), but fore wing with SC submarginal and extending beyond midwing; pterostigma reduced to a thickening beyond end of SC. *Oligo.*, Europe (Baltic).—FIG. 255.3. **P. depressus*, female; wings and body, $\times 13$ (Brues, 1940b).

Proteroscelio BRUES, 1937, p. 39 [**P. antennalis*; OD]. Apparently a scelionine genus, but antennae with 14 segments, scape reaching vertex of head; scape and flagellum flattened. *Cret.*, Canada (Manitoba).

Pseudobaeus PERKINS, 1910, p. 620. BRUES, 1940b. *Oligo.*, Europe (Baltic)—*Holo.*

Sembilanocera BRUES, 1940b, p. 70 [**S. clavata*; OD]. Related to *Baeus* (recent), but antennae of female with 9 segments and strongly clubbed. Wing veins present but reduced. *Oligo.*, Europe

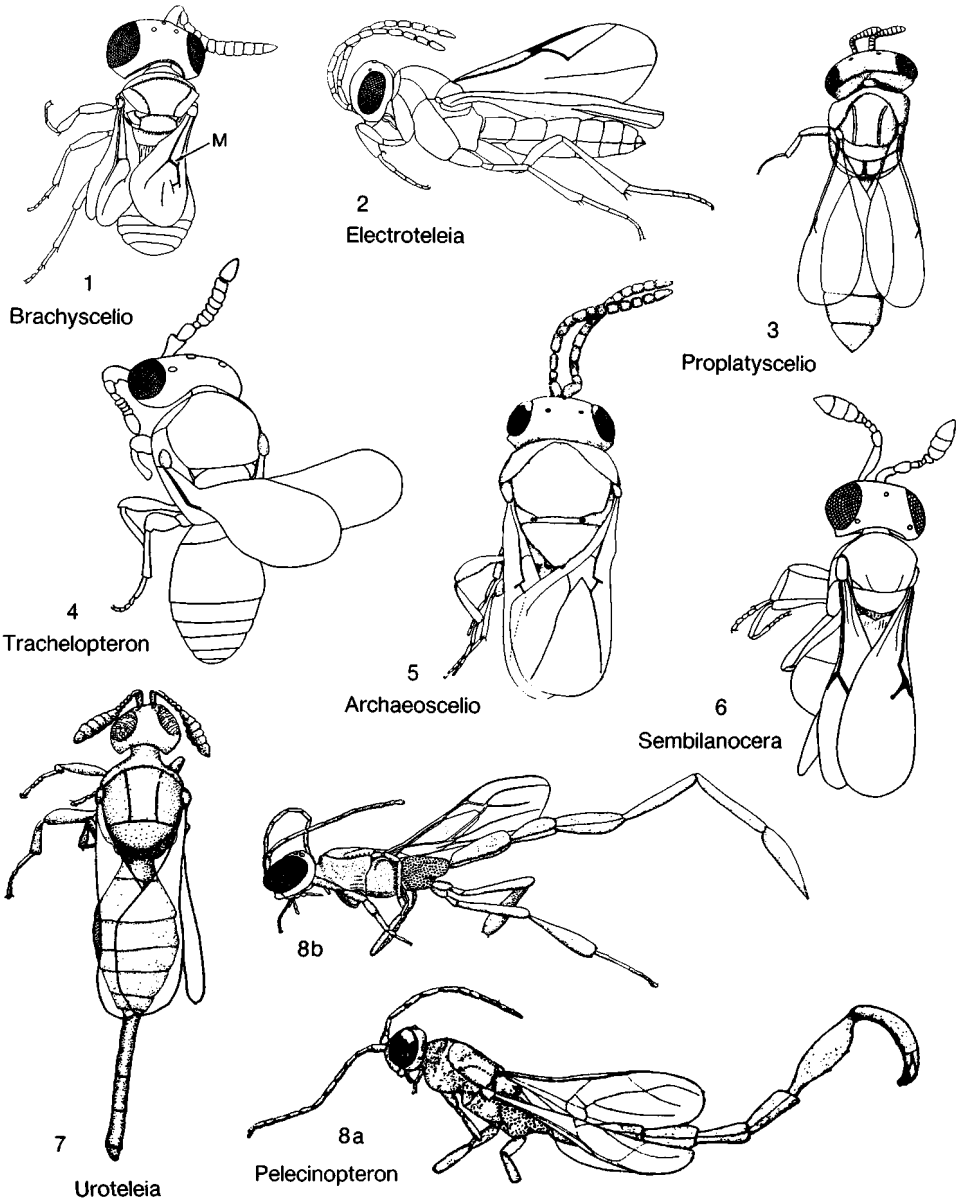


FIG. 255. Pelecinopteridae and Scelionidae (p. 471–473).

(Baltic). — FIG. 255,6. **S. clavata*; female, wings and body, $\times 40$ (Brues, 1940b).

Sparasion LATREILLE, 1802, p. 316. BRUES, 1940b.

Oligo., Europe (Baltic)—*Holo.*

Trachelopteron BRUES, 1940b, p. 86 [**T. angulipenne*; OD]. Male: fore wing apparently bent sharply upward near base, basal part narrow and strap-shaped. Head, thorax, and abdomen flattened; antennae with 10 segments; scape short.

[Family assignment doubtful.] *Oligo.*, Europe (Baltic). — FIG. 255,4. **T. angulipenne*; male, wings and body, $\times 57$ (Brues, 1940b).

Uroteleia BRUES, 1940b, p. 87 [**U. synthetica*; OD].

Female: SC of fore wing extending beyond midwing; prestigma reduced to a thickened marginal vein extending well beyond end of SC; part of basal section of RS apparently present. Antennae with 12 segments; scape long and slen-

der, 6 terminal segments forming a large club; prothorax long; gaster narrowed basally; apical segments also narrow, tip with a tubular process extending straight backward. [Family assignment doubtful.] *Oligo.*, Europe (Baltic).—FIG. 255,7. **U. synthetica*; wings and body, $\times 17$ (Brues, 1940b).

Family PRAEAULACIDAE

Rasnitsyn, 1972

[Praeaulacidae RASNITSYN, 1972, p. 70]

Related to Aulacidae but with fuller venation, especially of hind wing. Fore wing: basal section of vein RS long, about equal to basal section of M; crossvein 1r-rs obsolescent or absent; crossveins 2r-m, 3r-m, and 2m-cu always present; crossvein 1m-cu reaching cell 2rm. Hind wing: costa not developed but R strong, extending to level of end of RS as a distinct vein. Antennae with 14 to 27 segments; ovipositor long. *Jur.*

Praeaulacus RASNITSYN, 1972, p. 72 [**P. ramosus*; OD]. Fore wing with basal section of RS at least half its length from pterostigma; crossvein 2r-rs about as long as maximum width of cell 2rm. *Jur.*, USSR (Kazakh).—FIG. 256,4. **P. ramosus*; wings and body, $\times 5$ (Rasnitsyn, 1972).

Aulacogastrinus RASNITSYN, 1983c, p. 103, *nom. subst. pro Aulacogaster* RASNITSYN, 1972, p. 85, *non* AGASSIZ, 1846 [**Aulacogaster ater* RASNITSYN, 1972, p. 85; OD]. Fore wing with basal section of RS separated from pterostigma by less than half its length; crossvein 2r-rs distinctly longer than width of cell 2rm; crossvein 3r-m not slanted. Distal part of first gastral segment dilated. *Jur.*, USSR (Kazakh).

Evanigaster RASNITSYN, 1972, p. 85 [**E. petiolatus*; OD]. Similar to *Aulacogastrinus*, but first gastral segment narrow, tubular. *Jur.*, USSR (Kazakh).

Evanioops RASNITSYN, 1972, p. 85 [**E. rostratus*; OD]. Fore wing with basal segment of RS separated from pterostigma by a distance greater than its length; crossvein 2r-rs much longer than width of cell 2rm; crossvein 3r-m not oblique; gaster broad; second segment of abdomen forming a cylindrical petiole. *Jur.*, USSR (Kazakh).

Praeaulacinus RASNITSYN, 1972, p. 77 [**P. parvus*; SD RASNITSYN, 1973, p. 122, *nom. subst. pro minus* RASNITSYN, 1972, p. 77, *non minor* RASNITSYN, 1972]. Similar to *Praeaulacus*, but crossvein 2r-rs longer than width of cell 2rm; base of gaster broadly rounded. *Jur.*, USSR (Kazakh).

Praeaulacites RASNITSYN, 1972, p. 83 [**P. pachygaster*; OD]. Similar to *Praeaulacops*, but crossvein 3r-m slightly oblique. *Jur.*, USSR (Kazakh).

Praeaulacon RASNITSYN, 1972, p. 79 [**P. elongatum*; OD]. Similar to *Praeaulacus*, but base of gaster broadly rounded, nearly sessile. *Jur.*, USSR (Kazakh).

Praeaulicops RASNITSYN, 1972, p. 83 [**P. lucidus*; OD]. Fore wing with basal section of RS separated from pterostigma by a distance less than its length; crossvein 3r-m strongly slanted. *Jur.*, USSR (Kazakh).

Family CRETEVANIIDAE

Rasnitsyn, 1975

[Cretevaniidae RASNITSYN, 1975, p. 83]

Similar to Aulacidae and Evaniidae. Fore wing with costal area relatively broad; basal section of vein RS remote from pterostigma, very short and perpendicular to R; cell 3r very narrow. Hind wing very short, about half as long as fore wing. Antennae with 12 segments; hind tibiae thickened. *Cret.*

Cretevania RASNITSYN, 1975, p. 84 [**C. minor*; OD]. Head without sculpturing; mandibles with 4 teeth; maxillary palpi apparently with 5 segments; labial palpi with 3 segments. *Cret.*, USSR (Asian RSFSR).

Family ANOMOPTERELLIDAE

Rasnitsyn, 1975

[Anomopterellidae RASNITSYN, 1975, p. 88]

Fore wing with costal area broad; basal section of vein RS directed toward base of wing; crossvein 2r-rs situated at apex of pterostigma; crossvein 2r-m present; cells 1m-cu and 2m-cu narrow. Antennae with at least 15 segments. *Jur.*

Anomopterella RASNITSYN, 1975, p. 90 [**A. mirabilis*; OD]. Fore wing with basal section of RS very close to pterostigma; cell 3r very broad; gaster widest beyond its middle; ovipositor short. *Jur.*, USSR (Kazakh). — FIG. 256,6. **A. mirabilis*; wing and body, $\times 9$ (Rasnitsyn, 1975).

Family EVANIIDAE Leach, 1815

[Evaniidae LEACH, 1815, p. 142]

Fore wing with pterostigma present, commonly small; costal space open and wide; crossveins 2r-m, 3r-m, and 1m-cu commonly present; crossvein 2m-cu absent; venation greatly reduced in some species. Antennae with 13 or 14 segments; gaster short, oval, with long petiole, arising abruptly just pos-

terior to scutellum. Larvae parasitic on eggs of Blattaria. *Oligo.*—*Holo.*

Evania FABRICIUS, 1775, p. 345. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

Family AULACIDAE Shuckard, 1841

[Aulacidae SHUCKARD, 1841, p. 115] [=Gasteruptionidae ASHMEAD, 1901, p. 7; Kotujellidae RASNITSYN, 1975, p. 87; Baissidae RASNITSYN, 1975, p. 90]

Gaster attached very high on propodeum; first and second segments of gaster partially or completely fused; male with 13 antennal segments, female with 14. Venation of fore wing very diverse, relatively complete in some genera, apically reduced in others. Larvae mostly parasitic on wood-boring Coleoptera or bees and wasps nesting in wood. TOWNES, 1950; RASNITSYN, 1980b. *Cret.*—*Holo.*

Aulacus JURINE, 1807, p. 89. *Holo.*

Aulacostethus PHILIPPI, 1873, p. 302 [= *Aulacites* COCKERELL, 1916c, p. 102 (type, *A. secundus*)]. BRUES, 1910, 1923a, 1933. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Baissa RASNITSYN, 1975, p. 91 [**B. anomala*; OD]. Fore wing with cell 1mcu small and narrow; cell 2cua with a small distal projection. RASNITSYN, 1980b. *Cret.*, USSR (Asian RSFSR).

Electrofoenus COCKERELL, 1917g, p. 364 [**E. gracilipes*; OD]. Similar to *Gasteruption* (recent). Fore wing with basal section of RS very long, directed toward wing base; cell 3r large, its face on cell 2rm about equal in length to crossvein 2r-rs. Head large and broad, with prominent eyes; legs very long and slender. *Mio.*, Burma. —FIG. 256, 1. **E. gracilipes*; fore wing, $\times 10$ (Cockerell, 1917g).

Hyptiogastries COCKERELL, 1917c, p. 19 [**H. electrinus*; OD]. Similar to *Hyptiogaster* (recent), but crossvein 2r-rs in fore wing perpendicular to front margin of wing. Antennae long, filiform; hind tibiae thickened. *Mio.*, Burma.

Kotujella RASNITSYN, 1975, p. 87 [**K. crucis*; OD]. Fore wing with pterostigma triangular; apex of cell 3r pointed; crossvein 3r-m absent; cell 2rm long. RASNITSYN, 1980b. *Cret.*, USSR (Asian RSFSR).

Protofoenus COCKERELL, 1917c, p. 19 [**P. swinhoi*; OD]. Similar to *Gasteruption* (recent). Gaster of female thick and short, with a long, slender ovipositor, directed obliquely upward. Fore wing with pterostigma shallow; cell 1r+2rm very broad. *Mio.*, Burma.

Vectevania COCKERELL, 1922b, p. 33 [**V. vetula*; OD]. Similar to *Protofoenus*, but cell 1r+2rm of fore wing narrow; pterostigma broadly triangular. BRUES, 1933. *Oligo.*, England.

Family PRAEICHNEUMONIDAE Rasnitsyn, 1983

[Praeichneumonidae RASNITSYN, 1983d, p. 259]

Related to Ichneumonidae, but fore wing with vein RS+M present; crossveins 2r-m, 3r-m, and 2m-cu equally well developed; cells 2rm and 3rm large. *Cret.*

Praeichneumon RASNITSYN, 1983d, p. 259 [**P. townesi*; OD]. Female with head transverse, eyes moderately large; pronotum short centrally; mesonotum transverse; legs apparently short. *Cret.*, Asia (Mongolia). —FIG. 257. **P. townesi*; fore wing and body, $\times 9$ (Rasnitsyn, 1983d).

Family ICHNEUMONIDAE Latreille, 1802

[Ichneumonidae LATREILLE, 1802b, p. 309]

Fore wing with pterostigma distinct, usually triangular; vein R marginal; costal space closed; RS+M typically absent; cell 2rm commonly very small or absent; cell 2mcu usually present. Body generally slender; antennae long, with at least 16 segments; trochanters with 2 segments; ovipositor long, often longer than body. Larvae parasitic on diverse groups of insects and a few other arthropods. *Cret.*—*Holo.*

Ichneumon LINNÉ, 1758, p. 343. BRUES, 1910; COCKERELL, 1921a; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), England, Europe (France)—*Holo.*

Absyrtus HOLMGREN, 1858, p. 32. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Acoenites LATREILLE, 1810, p. 300. GIEBEL, 1856; BRUES, 1906; MEUNIER, 1923b. *Oligo.*, USA (Colorado), Europe (Germany); *Mio.*, Europe (Yugoslavia)—*Holo.*

Acourtia COCKERELL, 1921a, p. 11 [**A. perplexa*; OD]. Little-known genus. Fore wing with pterostigma triangular; RS+M apparently absent; cell 2rm absent. [Family assignment doubtful.] *Oligo.*, England. —FIG. 256, 2. **A. perplexa*; fore wing, $\times 8$ (Cockerell, 1921a).

Amblyteles WESMAEL, 1845, p. 114. COCKERELL, 1927e. *Oligo.*, USA (Colorado)—*Holo.*

Anomalon PANZER, 1804, pl. 15. BRUES, 1910; COCKERELL, 1919b; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*

Astiphromma FÖRSTER, 1868, p. 170. BRUES, 1923a. *Oligo.*, Europe (Baltic)—*Holo.*

Barylypa FÖRSTER, 1868, p. 146. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Campoplex GRAVENHORST, 1829, p. 453. [Generic assignment of fossil doubtful.] STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*

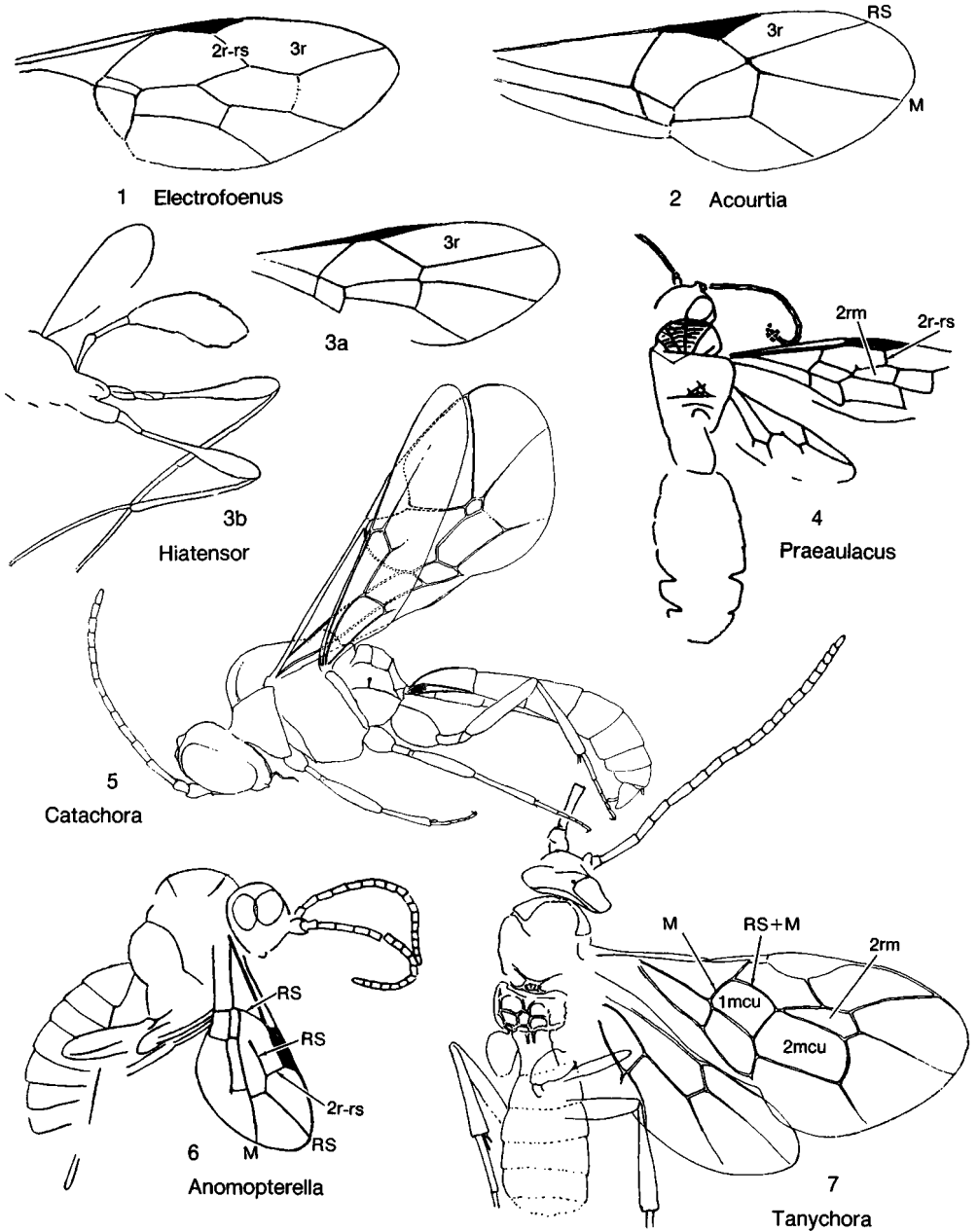


FIG. 256. Praeaulacidae, Anomopterellidae, Aulacidae, and Ichneumonidae (p. 473–477).

Catachora TOWNES, 1973b, p. 284 [**C. minor*; OD]. Related to *Grypocentrus* (recent), but cell 3r very broad. *Cret.*, USSR (Asian RSFSR). — FIG. 256, 5. **C. minor*; wings and body, $\times 28$ (Townes, 1973b).
Coleocentrus GRAVENHORST, 1829, p. 437. COCKERELL, 1921a. *Oligo.*, England–Holo.
Cremastus GRAVENHORST, 1829, p. 730. [Generic assignment of fossils doubtful.] COCKERELL,

1921a; THÉOBALD, 1937a. *Oligo.*, England, Europe (France)–Holo.
Cubocephalus RATZEBURG, 1848, p. 121. STATZ, 1936b. *Oligo.*, Europe (Germany)–Holo.
Demophorus THOMSON, 1890, p. 1457. [Generic assignment of fossils uncertain.] BRUES, 1910; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)–Holo.
Eopimpla COCKERELL, 1920c, p. 257 [**E. grandis*;

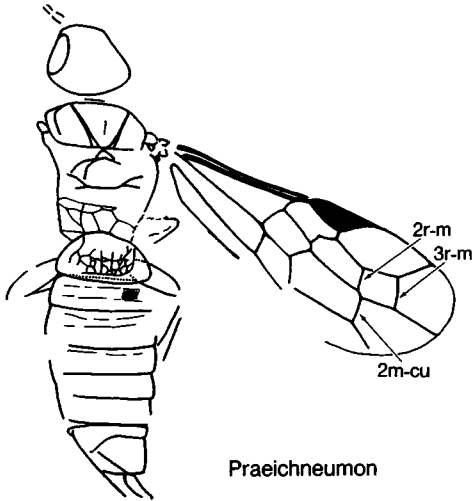


FIG. 257. Praeichneumonidae (p. 474).

- OD]. Little-known genus, apparently related to *Pimpla*. Large species; fore wing with crossvein 2r-rs connected to middle of pterostigma; cells 1r+2r and 1m-cu combined to form a large cell projecting distally well beyond pterostigma. *Eoc.*, USA (Colorado).
- Eubaeus** TOWNES, 1973b, p. 287 [**E. leiponeura*; OD]. Fore wing lacking crossvein 2m-cu; cell 2rm absent. *Cret.*, USSR (Asian RSFSR).
- Exacrodus** FÖRSTER, 1868, p. 210. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Exenterus** HARTIG, 1837, p. 156. COCKERELL, 1924c. *Oligo.*, USA (Colorado)—*Holo.*
- Exetastes** GRAVENHORST, 1829, p. 395. BRUES, 1910; NAORA, 1933a; STATZ, 1936b. *Oligo.*, USA (Colorado), Europe (Germany); *Pleist.*, Asia (Mongolia)—*Holo.*
- Exochus** GRAVENHORST, 1829, p. 328. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Glypta** GRAVENHORST, 1829, p. 3. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Hellwigia** GRAVENHORST, 1823, p. 318 [= *Prothellwigia* BRUES, 1910, p. 66 (type, *P. obsoleta*)]. TOWNES, 1966. *Oligo.*, USA (Colorado)—*Holo.*
- Hemiteles** GRAVENHORST, 1829, p. 780. BRUES, 1910; STATZ, 1936b. *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*
- Hiatensor** BRUES, 1910, p. 73 [**H. semirutus*; JD]. Apparently related to *Campoplex* (recent). Fore wing with pterostigma elongate, nearly linear; cell 3r long. Hind legs elongate, tip of femora extending beyond end of abdomen. TOWNES, 1966. *Oligo.*, USA (Colorado).—FIG. 256, 3. **H. semirutus*; a, fore wing, $\times 10$; b, hind leg and abdomen, $\times 5$ (Brues, 1910).
- Holomeristus** FÖRSTER, 1868, p. 171. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Horogenes** FÖRSTER, 1868, p. 152. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*
- Hypsicera** LATREILLE, 1829, p. 288. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Itopelectis** FÖRSTER, 1868, p. 164. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Labrorychus** FÖRSTER, 1868, p. 146. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Lampronota** CURTIS, 1832, p. 407. BRUES, 1910; COCKERELL, 1921a. *Oligo.*, USA (Colorado)—*Holo.*
- Lapton** NEES, 1815, p. 46. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Lithotorus** SCUDDER, 1890, p. 609 [**L. cressoni*; OD]. Little-known genus, possibly within the subfamily Diplazontinae. [Family assignment doubtful.] TOWNES, 1966. *Eoc.*, USA (Wyoming).
- Megatryphon** COCKERELL, 1924c, p. 9 [**M. morififerus*; OD]. Little-known genus, apparently similar to *Tryphon*. Fore wing with pterostigma very long, narrowly lanceolate; cell 2rm very small, triangular. Metathorax truncate posteriorly, but dorsal surface straight in lateral view. *Oligo.*, USA (Colorado).
- Melanichneumon** THOMSON, 1893, p. 1954. [Generic assignment of fossil doubtful.] BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Mesochorus** GRAVENHORST, 1829, p. 960. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Mesoleptus** GRAVENHORST, 1829, p. 3. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Mesopimpla** COCKERELL, 1919b, p. 376 [**M. sequoiarum*; OD]. Little-known genus, apparently related to *Thebonia* (recent). Fore wing with basal section of M slightly curved, joined to very base of pterostigma; pterostigma narrow, elongate. Hind femora very stout. *Oligo.*, USA (Colorado).
- Mesostenus** GRAVENHORST, 1829, p. 750. BRUES, 1906. *Oligo.*, USA (Colorado)—*Holo.*
- Nemeritis** HOLMGREN, 1858, p. 105. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Netelia** GRAY, 1860, p. 341. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Olesicampe** FÖRSTER, 1868, p. 153. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Ophion** FABRICIUS, 1798, p. 210. PONGRÁČZ, 1928; THÉOBALD, 1937a. *Oligo.*, Europe (France); *Mio.*, Europe (Yugoslavia)—*Holo.*
- Orthocentrus** GRAVENHORST, 1829, p. 358. BRUES, 1906, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Orthopelma** TASCHENBERG, 1865, p. 137. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*
- Parapimpla** THÉOBALD, 1937a, p. 191 [**P. rhenana*; OD]. Little-known genus. Similar to *Apechthis* (recent), but crossvein 1m-cu close to posterior margin of wing. *Oligo.*, Europe (France).
- Phaenolobus** FÖRSTER, 1868, p. 168. PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*
- Phygadeuon** GRAVENHORST, 1829, p. 635.

- COCKERELL, 1920c; STATZ, 1936b. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany)—*Holo.*
- Pimpla** FABRICIUS, 1804, p. 112. BRUES, 1906, 1910; COCKERELL, 1919c; HENRIKSEN, 1922b; STATZ, 1936b; THÉOBALD, 1937a. *Eoc.*, USA (Colorado), Europe (Denmark); *Oligo.*, USA (Colorado)—*Holo.*
- Plectiscidea** VIERECK, 1914, p. 118. *Eoc.*, USA (Colorado)—*Holo.*
- Polysphincta** GRAVENHORST, 1829, p. 112. BRUES, 1910; COCKERELL, 1921a; STATZ, 1936b. *Oligo.*, USA (Colorado), England—*Holo.*
- Porizon** FALLÉN, 1813, p. 18. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Promethes** FÖRSTER, 1868, p. 162. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Protarchus** FÖRSTER, 1868, p. 201. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*
- Rhyssa** GRAVENHORST, 1829, p. 260. BRUES, 1906. *Oligo.*, USA (Colorado)—*Holo.*
- Scambus** HARTIG, 1838, p. 267. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Spudaeus** GISTEL, 1848, p. 11. BRUES, 1910; COCKERELL, 1941. *Oligo.*, USA (Colorado)—*Holo.*
- Stenomacrus** FÖRSTER, 1868, p. 160. BRUES, 1910; STATZ, 1936b. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*
- Stilpnus** GRAVENHORST, 1829, p. 664. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Tanychora** TOWNES, 1973a, p. 216 [**T. petiolata*; OD]. Fore wing with RS+M present, separating cells 1r+2r from 1mcu; cell 2rm relatively large. *Cret.*, USSR (Asian RSFSR), Asia (Mongolia). —FIG. 256.7. **T. petiolata*; wings and body, $\times 11$ (Townes, 1973a).
- Tanychorella** RASNITSYN, 1975, p. 91 [**T. parvula*; OD]. Similar to *Tanychora*, but cell 2rm of fore wing shorter. *Cret.*, USSR (Asian RSFSR).
- Theronia** HOLMGREN, 1859, p. 123. [Generic assignment of fossil doubtful.] BRUES, 1910; COCKERELL, 1919b. *Oligo.*, USA (Colorado)—*Holo.*
- Tilgidopsis** COCKERELL, 1921e, p. 37 [**T. baestans*; OD]. Little-known genus. Fore wing with pterostigma lanceolate, narrow; cell 3r pointed posteriorly; crossvein 2r-rs slightly sigmoidal. *Eoc.*, USA (Colorado).
- Trachysphyrus** HALIDAY, 1836, p. 317. BRUES, 1910; MEUNIER, 1920a; STATZ, 1936b, 1938b. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*
- Trogus** PANZER, 1806, p. 80. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Tryphon** FALLÉN, 1813, p. 16. BRUES, 1910; GRISSELL, 1976. *Eoc.*, USA (Colorado); *Oligo.*, USA (Colorado)—*Holo.*
- Urottryphon** TOWNES, 1973b, p. 286 [**U. pusillus*; OD]. Related to *Idiogramma* (recent), but propodeum nearly completely areate. *Cret.*, USSR (Asian RSFSR).
- Xorides** LATREILLE, 1809, p. 4. BRUES, 1910; HANDLIRSCH, 1910b. *Eoc.*, Canada (British Columbia); *Oligo.*, USA (Colorado)—*Holo.*

Family ICHNEUMONOMIMIDAE Rasnitsyn, 1975

[Ichneumonomimidae RASNITSYN, 1975, p. 92]

Fore wing with costal space broad; vein R+M weak; crossveins 2r-m and 3r-m present; cell 2rm longer than 3rm; cell 3rm short and high. *Cret.*

Ichneumonomima RASNITSYN, 1975, p. 92 [**I. paradoxa*; OD]. Fore wing with crossvein 2r-rs short; cell 3rm higher than its width. Antennae apparently with 13 to 14 segments. SCHMIDT, 1963. *Cret.*, USSR (Asian RSFSR). —FIG. 258.2. **I. paradoxa*; wings and body, $\times 4.3$ (Rasnitsyn, 1975).

Family BRACONIDAE Latreille, 1829

[Braconidae LATREILLE, 1829, p. 289]

Adults small. Fore wing with costal area obsolescent or closed; basal sections of vein RS and RS+M usually present; crossveins 2m-cu and sometimes 1m-cu absent; veins in distal part of wing often obsolescent. Body stout; antennae usually long. Larvae parasitic on diverse types of insects. *Cret.*—*Holo.*

Bracon FABRICIUS, 1805, p. 102. [Generic assignment of fossils doubtful.] HEYDEN, 1858; FÖRSTER, 1891; BRUES, 1910; MEUNIER, 1915b; COCKERELL, 1919b. *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*

Agathis LATREILLE, 1804, p. 173. BRUES, 1910; COCKERELL, 1927b. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Alysia LATREILLE, 1804, p. 173. BRUES, 1910; THÉOBALD, 1937a; STATZ, 1938b. *Oligo.*, Europe (Germany, France), USA (Colorado)—*Holo.*

Anacanthobracon BRUES, 1939b, p. 251 [**A. femorator*; OD]. Apparently related to *Doryctes*. Male with hind legs greatly thickened; coxae large; tibiae stout and thickened distally; gastral tergites forming a dorsal shield. *Oligo.*, USA (Colorado).

Apanteles FÖRSTER, 1862, p. 245. STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*

Aphidius NEES, 1818, p. 302. BRUES, 1933; PÉREZ, 1940. *Oligo.*, Europe (Baltic, France)—*Holo.*

Ascogaster WESMAEL, 1835, p. 226. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

Aspicolpus WESMAEL, 1838, p. 155. BRUES, 1933; STATZ, 1936b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Aspilota FÖRSTER, 1862, p. 268. STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*

Austrohelcon TURNER, 1918, p. 166. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

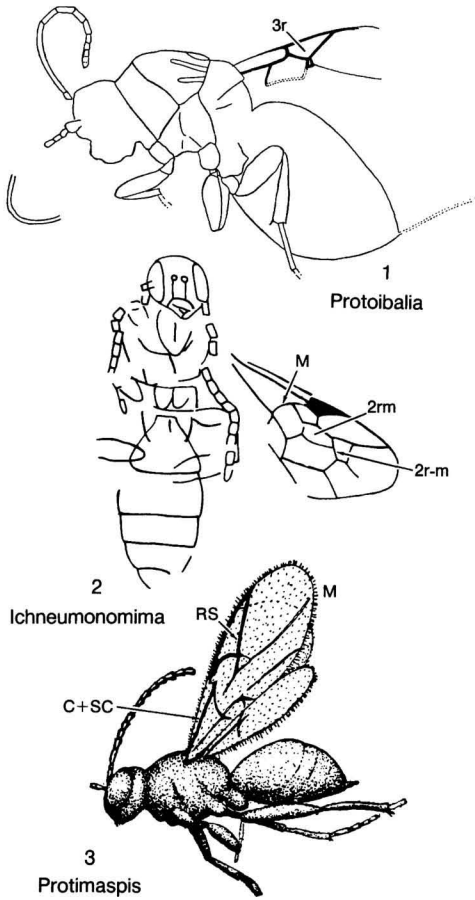


FIG. 258. Ichneumonomimidae, Cynipidae, Iba-liidae (p. 477–482).

Blacus NEES, 1818, p. 306 [= *Electroblacus* BRUES, 1933, p. 85 (type, *E. facialis*)]. BRUES, 1923a, 1939b; ACHTERBERG, 1982. *Oligo.*, Europe (Baltic)–*Holo.*

Calyptoides COCKERELL, 1921a, p. 13 [**C. veterinus*; OD]. Little-known genus, apparently related to *Eubazus*. Fore wing with pterostigma large and triangular; gaster slender basally. *Oligo.*, England.

Cantharoctonus VIERECK, 1912, p. 617. BRUES, 1933; STATZ, 1936b. *Oligo.*, Europe (Baltic, Germany)–*Holo.*

Chelonehelcon BRUES, 1933, p. 61 [**C. mirabundus*; OD]. Fore wing with RS terminating on costa before wing apex; crossvein 2r-rs situated slightly distal of middle of pterostigma; basal section of RS less than half as long as basal section of M. Eyes large, extending nearly to base of mandibles; mandibles long, curved, and bidentate; antennae with 21 segments, as long as body; basal segment of flagellum enlarged; gaster narrow, elongate; tergites fused to form carapace;

fore and hind femora stout. *Oligo.*, Europe (Baltic).—FIG. 259,6. **C. mirabundus*; wings and body, $\times 6.5$ (Brues, 1933).

- Chelonus** PANZER, 1806, p. 99. BRUES, 1910. *Oligo.*, USA (Colorado)–*Holo.*
- Clinocentrus** HALIDAY, 1833, p. 266. BRUES, 1933; STATZ, 1938b. *Oligo.*, Europe (Baltic, Germany)–*Holo.*
- Coeloreuteus** ROMAN, 1910, p. 112. BRUES, 1933. *Oligo.*, Europe (Baltic)–*Holo.*
- Colastes** HALIDAY, 1833, p. 266. BRUES, 1910. *Oligo.*, USA (Colorado)–*Holo.*
- Cremnops** FÖRSTER, 1862, p. 246. COCKERELL, 1919b; BRUES, 1933. *Oligo.*, USA (Colorado)–*Holo.*
- Dacnuses** COCKERELL, 1921a, p. 19 [**D. sepultus*; OD]. Similar to *Polemon* (recent), but RS of fore wing bent posteriorly just beyond its contact with crossvein 2r-rs; cells 2rm and 3rm absent. *Oligo.*, England.—FIG. 260,1. **D. sepultus*; fore wing, $\times 17$ (Cockerell, 1921a).
- Diaeretus** FÖRSTER, 1862, p. 249. PÉREZ, 1940. *Oligo.*, Europe (France)–*Holo.*
- Digastrotheca** BRUES, 1933, p. 39 [**D. mirabilis*; OD]. Related to the Rhogadininae (recent), but basal abdominal tergites fused into long plates, forming carapace over abdomen; basal plate with 2 pairs of longitudinal ridges, second pair widely separated. *Oligo.*, Europe (Baltic).—FIG. 260,6. **D. mirabilis*; body, $\times 9$ (Brues, 1933).
- Diodontogaster** BRUES, 1933, p. 59 [**D. bidentata*; OD]. Related to *Chelonus*. Fore wing with cell 3r acute apically; cells 1r + 2r and 1mcu present. Head large; eyes bare, oval; antennae with about 30 segments; abdomen elongate, with apex rounded above but ventrally projecting posteriorly to form a pair of prolongations. *Oligo.*, Europe (Baltic).—FIG. 259,4. **D. bidentata*; wings and body, $\times 6$ (Brues, 1933).
- Diospilites** BRUES, 1933, p. 81 [**D. brevicornis*; OD]. Related to *Diospilus*. Small species, with stout body. Fore wing with pterostigma broad, triangular; crossvein 2r-rs at middle of pterostigma; RS terminating almost at wing apex. Antennae less than half length of body, with 11 segments; propodeum rugose; gaster short and broad, smooth above. *Oligo.*, Europe (Baltic).—FIG. 259,5. **D. brevicornis*; wings and body, $\times 15$ (Brues, 1933).
- Diospiloides** COCKERELL, 1921a, p. 14 [**D. hooleyi*; OD]. Little-known genus, apparently related to *Diospilus*. Fore wing with pterostigma of moderate size, its posterior border smoothly curved; crossvein 2r-rs slightly distal of middle of pterostigma; basal section of M distinctly curved. *Oligo.*, England.
- Diospilus** HALIDAY, 1833, p. 262. BRUES, 1910; COCKERELL, 1921a; CARPENTER & others, 1937; MASON, 1976. *Cret.*, Canada (Manitoba); *Oligo.*, USA (Colorado), England–*Holo.*

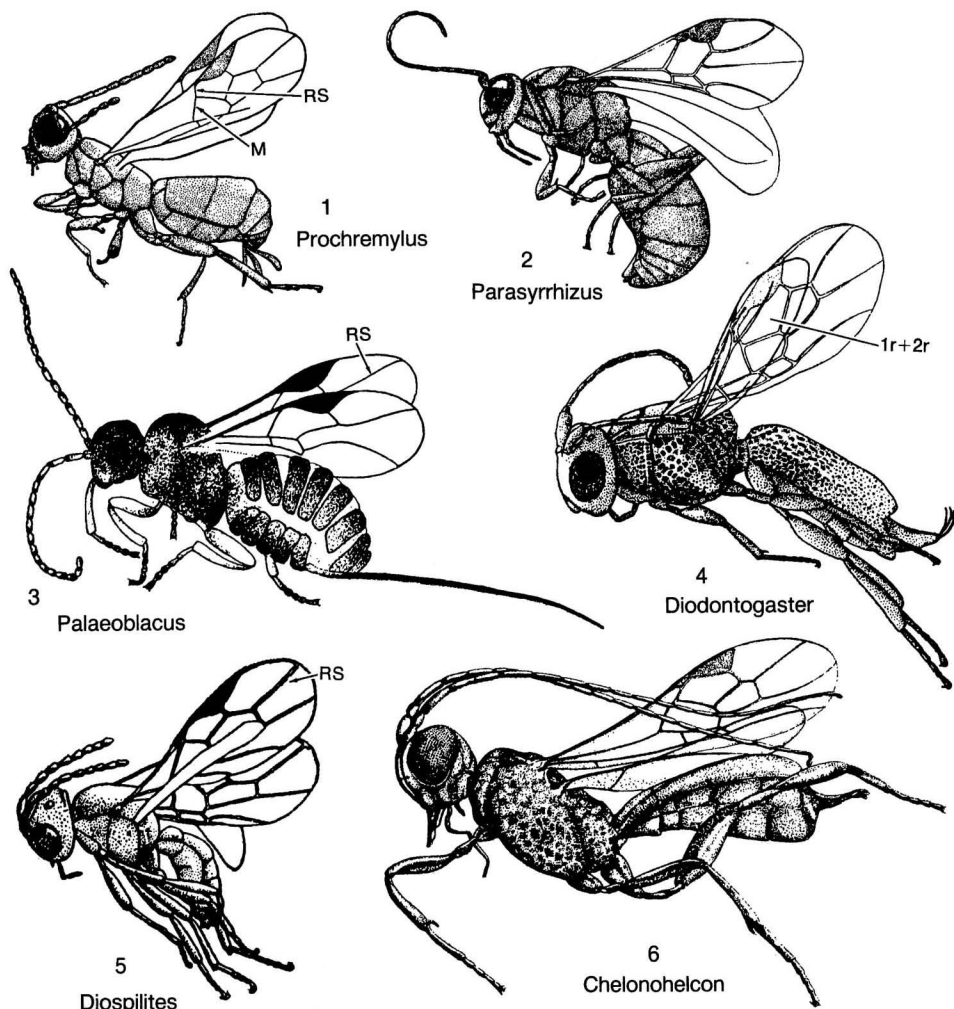


FIG. 259. Braconidae (p. 477–482).

Doryctes HALIDAY, 1836, p. 45. BRUES, 1933; STATZ, 1938b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*

Doryctomorpha ASHMEAD, 1901, p. 144. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

Ecphylus FÖRSTER, 1862, p. 237. MUESEBECK, 1960. ?*Mio.*, Mexico (Chiapas)—*Holo.*

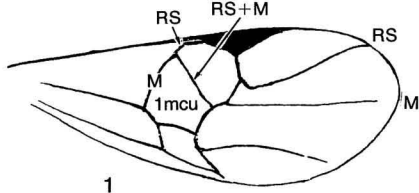
Elasmosomites BRUES, 1933, p. 97 [**E. primordialis*; OD]. Related to *Elasmosoma* (recent). Female: antennae with 14 segments, as long as head and thorax; flagellum tapering, its first segment as long as scape; maxillary palpus with 4 segments; propodeum abruptly truncate, its posterior face nearly vertical; legs very stout; ovipositor short. *Oligo.*, Europe (Baltic).

Electrohelcon BRUES, 1933, p. 62 [**E. grandis*; OD]. Similar to *Chelonohelcon*, but gastral tergites separated and articulated. *Oligo.*, Europe (Baltic).

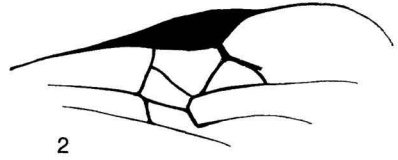
Eobracon COCKERELL, 1920c, p. 258 [**E. cladurus*; OD]. Fore wing as in *Diopspilites*, but gaster as in *Chelonus*; wing base sessile but narrow, apex enlarged. *Eoc.*, USA (Colorado).

Eobraconus RASNITSYN, 1985, p. 163, *nom. subst. pro Eobracon* RASNITSYN, 1983d, p. 263, *non* COCKERELL, 1920c [**Eobracon inopinatus* RASNITSYN, 1983d; OD]. Fore wing with R extending only a short distance beyond pterostigma and without a distinct break at base of pterostigma; basal section of RS only slightly shorter than basal section of M; M and CU almost reaching wing margin; crossvein 1m-cu reduced apically; cell 3rm closed. Antennae with about 16 segments. *Cret.*, Mongolia.

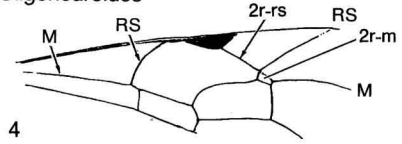
Eocardiochiles BRUES, 1933, p. 92 [**E. fritschi*; OD]. Similar to *Cardiochiles* (recent), but antennae with only 18 segments, first 12 flagellar seg-



1
Dacnusites



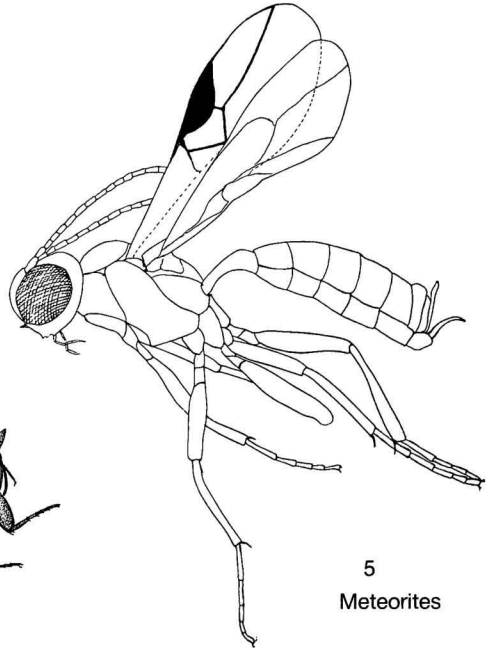
2
Oligoneuroides



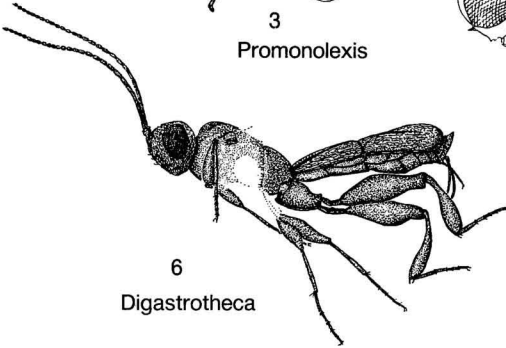
4
Lithapeptis



3
Promonolexis



5
Meteorites



6
Digastrotheca

FIG. 260. Braconidae (p. 478–481).

ments at least twice as long as thick; cell 2r_m very short. *Oligo.*, Europe (Baltic).
Ephedrus HALIDAY, 1833, p. 261. BRUES, 1933; TIMON-DAVID, 1944b. *Oligo.*, Europe (Baltic, France)–*Holo.*
Eubazus NEES, 1814, p. 214. BRUES, 1910, 1923a; BURKS, 1979; ACHTERBERG, 1982. *Oligo.*, Europe (Baltic), USA (Colorado)–*Holo.*
Eumacrocentrus ASHMEAD, 1901, p. 120. BRUES, 1933. *Oligo.*, Europe (Baltic)–*Holo.*
Euphorus NEES, 1834, p. 360. BRUES, 1910. *Oligo.*, USA (Colorado)–*Holo.*
Hecabolus HALIDAY, 1834, p. 127. STATZ, 1936b. *Oligo.*, Europe (France)–*Holo.*

Helcon NEES, 1814, p. 216. BRUES, 1933. *Oligo.*, Europe (Baltic)–*Holo.*
Holocnomus PÉREZ, 1940, p. 50 [**H. braconiformis*; OD]. Fore wing with RS extending to wing apex. Antennae with 13 or 14 segments, all almost equal in length and thickness. *Oligo.*, Europe (France).
Hormiellus ENDERLEIN, 1912, p. 20. BRUES, 1933. *Oligo.*, Europe (Baltic)–*Holo.*
Hormiopterus GIRAUD, 1869, p. 478. BRUES, 1910, 1933. *Eoc.*, USA (Colorado)–*Holo.*
Ichneutes NEES, 1816, p. 275. BRUES, 1933. *Oligo.*, Europe (Baltic)–*Holo.*
Iphiaulax FÖRSTER, 1862, p. 234. BRUES, 1910;

- COCKERELL, 1919b, 1921a. *Oligo.*, USA (Colorado); England—*Holo.*
- Lithapechtis** COCKERELL, 1921a, p. 6 [**L. fumosus*; OD]. Little-known genus, apparently related to *Apechtis* (recent). Fore wing with basal section of M nearly straight; crossvein 2r-rs straight; crossvein 2r-m very short. *Oligo.*, England. — FIG. 260,4. **L. fumosus*; fore wing, $\times 6$ (Cockerell, 1921a).
- Meteorites** BRUES, 1939b, p. 258 [**M. inopinata*; OD]. Similar to *Meteorus*, but fore wing lacking crossveins 2r-m and 3r-m. *Oligo.*, Europe (Baltic). — FIG. 260,5. **M. inopinata*; wings and body, $\times 20$ (Brues, 1939b).
- Meteorus** HALIDAY, 1835, p. 24. [Generic assignment of fossils doubtful.] BRUES, 1933; STATZ, 1936b. *Oligo.*, Europe (Baltic, Germany)—*Holo.*
- Microctonus** WESMAEL, 1835, p. 54. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Microgaster** LATREILLE, 1804, p. 175. BRUES, 1906, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Microplitis** FÖRSTER, 1862, p. 245. BRUES, 1910; TIMON-DAVID, 1944b. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*
- Microtypus** RATZBURG, 1848, p. 47. BRUES, 1933, 1939b. *Oligo.*, Europe (Baltic)—*Holo.*
- Miracoides** BRUES, 1933, p. 98 [**M. proteus*; OD]. Fore wing; cell 1rm slightly longer than cell 1cua; RS obsolescent beyond pterostigma and diverging posteriorly. Antennae with 16 or 17 segments, shorter than body; 6 basal segments of flagellum long; head large, twice as broad as thick; legs slender. *Oligo.*, Europe (Baltic).
- Neoblacus** ASHMEAD, 1901, p. 122. BRUES, 1933; CARPENTER & others, 1937; ACHTERBERG, 1982. *Cret.*, Canada (Manitoba); *Oligo.*, Europe (Baltic)—*Holo.*
- Oligoaphidius** PÉREZ, 1940, p. 52 [**O. sannoniensis*; OD]. Little-known genus. Fore wing with RS almost reaching wing margin. Funicula of antennae with 9 thick segments. *Oligo.*, Europe (France).
- Oligoneuroides** BRUES, 1910, p. 103 [**O. destructus*; OD]. Similar to *Oligoneurus* (recent), but cell 2rm nearly triangular, its posterior side about as long as RS+M. Antennae with about 25 segments. *Oligo.*, USA (Colorado). — FIG. 260,2. **O. destructus*; fore wing, $\times 17$ (Brues, 1910).
- Onychoura** BRUES, 1933, p. 105 [**O. petiolata*; OD]. Fore wing with pterostigma triangular. Eyes large, extending to base of mandibles; antennae short, with oval segments; gaster petiolate, swollen; ovipositor short, stout, terminating in very slender hook. *Oligo.*, Europe (Baltic).
- Opius** WESMAEL, 1835, p. 115. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Orgilus** HALIDAY, 1833, p. 262. BRUES, 1939b; ACHTERBERG, 1982. *Oligo.*, Europe (Baltic)—*Holo.*
- Palaeoblacus** STATZ, 1936b, p. 277 [**P. aculeatus*; OD]. Little-known genus. Fore wing with RS+M apparently absent; pterostigma broad; ovipositor about as long as body; antennae with 17 segments. *Oligo.*, Europe (Germany). — FIG. 259,3. **P. aculeatus*; wings and body, $\times 18$ (Statz, 1936b).
- Palaeorhysalus** BRUES, 1933, p. 37 [**P. dubitosis*; OD]. Probably related to the Rhodadinae. First 4 gastral segments irregularly striated, second much longer than third and separated from it by a deep furrow. *Oligo.*, Europe (Baltic).
- Parasyrrhizus** BRUES, 1933, p. 91 [**P. ludens*; OD]. Similar to *Syrrhizus* (recent) but with deep grooves on lateral parts (parapsides) of scutum. *Oligo.*, Europe (Baltic). — FIG. 259,2. **P. ludens*; wings and body, $\times 13$ (Brues, 1933).
- Pentapleura** FÖRSTER, 1862, p. 264. [Generic assignment of fossil doubtful.] STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*
- Phanerotoma** WESMAEL, 1838, p. 165. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Phanomeris** FÖRSTER, 1862, p. 235. [Generic assignment of fossil doubtful.] COCKERELL, 1921a. *Oligo.*, USA (Colorado), England—*Holo.*
- Polystenus** FÖRSTER, 1862, p. 237. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Praon** HALIDAY, 1833, p. 261. PÉREZ, 1940. *Oligo.*, Europe (France)—*Holo.*
- Prochremylus** BRUES, 1933, p. 26 [**P. brevicornis*; OD]. Similar to *Chremylus* (recent). Fore wing with basal section of RS at least half as long as basal section of M. Antennae with 11 segments; legs stout, especially femora; ovipositor less than half length of gaster. *Oligo.*, Europe (Baltic). — FIG. 259,1. **P. brevicornis*; wings and body, $\times 20$ (Brues, 1933).
- Promonolexis** BRUES, 1933, p. 34 [**P. klebsi*; OD]. Similar to *Monolexis* (recent), but RS arising at very base of pterostigma; cell 1mcu triangular; ovipositor thick and strongly curved. *Oligo.*, Europe (Baltic). — FIG. 260,3. **P. klebsi*; wings and body, $\times 20$ (Brues, 1933).
- Propraon** BRUES, 1933, p. 108 [**P. cellularis*; OD]. Fore wing: venation as in *Praon*. Antennae longer than body; eyes small; legs slender, hind coxae long; gaster lanceolate. *Oligo.*, Europe (Baltic).
- Protephedrus** PÉREZ, 1940, p. 55 [**P. tertiaris*; OD]. Fore wing as in *Epbedrus*, but RS obsolescent, not reaching wing apex. Antennal segments thick; 13 funicular segments. *Oligo.*, Europe (France).
- Pygostolus** HALIDAY, 1833, p. 263. BRUES, 1933; CARPENTER & others, 1937. *Cret.*, Canada (Manitoba); *Oligo.*, Europe (Baltic)—*Holo.*
- Rhaconotus** RUTHE, 1854, p. 349. [Generic assignment of fossil doubtful.] SCUDDER, 1890; BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Rhysiopolis** DALLA TORRE, 1898, p. 4. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

- Rhysipolis** FÖRSTER, 1862, p. 235. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Rhysalus** HALIDAY, 1833, p. 266. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Rogas** NEES, 1818, p. 306. BRUES, 1906, 1910, 1933; STATZ, 1938b. *Oligo.*, Europe (Baltic, Germany), USA (Colorado)—*Holo.*
- Semirhytus** SZÉPLIGETI, 1902, p. 55. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Sigalphus** LATREILLE, 1802, p. 327. [Generic assignment of fossil doubtful.] COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Sinobracon** HONG, 1974, p. 135 [**S. speciosus*; OD]. Fore wing as in *Dacnusa*, but cell 1mcu much larger, and vein M ending well beyond wing apex. Antennae of female with 12 segments. *Eoc.*, China (Liaoning).
- Snellenius** WESTWOOD, 1882, p. 19. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*
- Spathius** NEES, 1818, p. 301. STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*
- Tanycarpa** FÖRSTER, 1862, p. 265. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*
- Taphaeus** WESMAEL, 1835, p. 189. BRUES, 1906. *Oligo.*, Europe (Baltic)—*Holo.*
- Triaspis** HALIDAY, 1835, p. 124. COCKERELL, 1921a; BRUES, 1933, 1939b. *Oligo.*, Europe (Baltic), England—*Holo.*
- Trioxys** HALIDAY, 1833, p. 261. PÉREZ, 1940. *Oligo.*, Europe (France)—*Holo.*
- Urosigalphus** ASHMEAD, 1889, p. 637. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Xenarcha** FÖRSTER, 1862, p. 235. [Generic assignment of fossil doubtful.] COCKERELL, 1921a. *Oligo.*, England—*Holo.*

Family CYNIPIDAE Leach, 1815

[Cynipidae LEACH, 1815, p. 142]

Fore wing (sometimes absent): pterostigma and basal part of costa absent; venation much reduced, but cell 2r+3r usually present and closed. Antennae filiform, with from 13 to 19 segments; second gastral tergite usually at least half as long as entire gaster. Larvae mainly gall makers; a few parasitic on other Hymenoptera and Diptera. *Cret.*—*Holo.*

- Cynips** LINNÉ, 1758, p. 553. *Holo.*
- Andricus** HARTIG, 1840, p. 185. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Aulacidea** ASHMEAD, 1897, p. 68. KINSEY, 1919. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*
- Diplolepis** GEOFFROY, 1762, p. 308. COCKERELL, 1921a. *Oligo.*, England—*Holo.*
- Protimaspis** KINSEY, 1937, p. 22 [**P. costalis*; OD]. Similar to *Timaspis* (recent) and *Aulacidea* (recent), but abdomen more lenticulate in profile

and its second segment larger; R and SC fused and submarginal, lacking a terminal process leading to C; costal margin much thickened near termination of RS; distal part of RS very straight. *Cret.*, Canada (Manitoba).—FIG. 258,3. **P. costalis*; wings and body, ×22 (Carpenter & others, 1937).

Family FIGITIDAE Förster, 1869

[Figitidae FÖRSTER, 1869, p. 329]

Similar to Cynipidae, but second gastral tergite less than half as long as gaster. Larvae parasitic on certain Diptera and Neuroptera. *Oligo.*—*Holo.*

- Figites** LATREILLE, 1802, p. 307. BRUES, 1910; STATZ, 1938b. *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*

Family IBALIIDAE Förster, 1869

[Ibaliidae FÖRSTER, 1869, p. 329]

Similar to Cynipidae, but cell 2r+3r very narrow, at least 9 times as long as wide; sixth gastral tergite larger than others. *Oligo.*—*Holo.*

- Ibalia** LATREILLE, 1802, p. 306. *Holo.*
- Protoibalia** BRUES, 1910, p. 15 [**P. convexa*; OD]. Similar to *Ibalia* (recent), but fore wing with cell 3r much shorter and broader. *Oligo.*, USA (Colorado).—FIG. 258,1. **P. convexa*; wings and body, ×10 (Brues, 1910).

Family AGAONTIDAE Walker, 1871

[Agaontidae WALKER, 1871, p. 58]

Adults with marked sexual dimorphism. Males usually wingless; antennae with 3 to 9 segments. Females with fore wing broadened distally; venation much reduced; submarginal vein weak and very close to wing margin, or entirely absent; pterostigma and postmarginal vein absent. Females with 11 or 12 antennal segments; front and hind legs stout; fore tibiae short, without spurs; middle tibiae with a single spur. Larvae developing in figs. *Oligo.*—*Holo.*

- Agaon** DALMAN, 1818, p. 69. *Holo.*
- Tetrapus** MAYR, 1885, p. 156. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Family TORYMIDAE Walker, 1833

[Torymidae WALKER, 1833a, p. 115]

Minute insects. Venation of fore wing much reduced; submarginal vein weakly developed

and commonly short; stigmal vein usually small; pterostigma obsolescent or absent. Mandibles well developed, with 3 or 4 teeth; hind coxae very large, at least 5 times length of fore coxae; tarsi with 5 segments; ovipositor usually long and exserted. Larvae mostly parasitic on gall-making Diptera and Hymenoptera. *Oligo.*—*Holo.*

- Torymus** DALMAN, 1820, p. 135. FÖRSTER, 1891; BRUES, 1910, 1923a; GRISSELL, 1976. *Oligo.*, Europe (Baltic, France), USA (Colorado)—*Holo.*
- Monodontomerus** WESTWOOD, 1833, p. 443. BRUES, 1923a. *Oligo.*, Europe (Baltic)—*Holo.*
- Neopalachia** BOUČEK, 1978, p. 104. GRISSELL, 1980. *Oligo./Mio.*, Dominican Republic—*Holo.*
- Palaeotorymus** BRUES, 1910, p. 18 [**P. typicus*; OD]. Similar to *Torymus*, but costa extending nearly to apex of wing. *Oligo.*, USA (Colorado).
- Zophodetus** GRISSELL, 1980, p. 253 [**Z. woodruffi*; OD]. Similar to *Microdontomerus* (recent), but propodeum carinate; metanotum more than half length of propodeum. *Oligo./Mio.*, Dominican Republic.

Family CHALCIDAE Leach, 1815

[Chalcidae LEACH, 1815, p. 144]

Similar to Torymidae, but ovipositor usually short and stout; hind coxae cylindrical in cross section; hind femora much swollen, denticulate. *Oligo.*—*Holo.*

- Chalcis** FABRICIUS, 1789, p. 272. COCKERELL, 1907c; BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*
- Eterochalcis** BURKS, 1939, p. 184. *Oligo.*, USA (Colorado)—*Holo.*

Family EURYTOMIDAE Walker, 1833

[Eurytomidae WALKER, 1833a, p. 12]

Similar to Chalcidae, but hind coxae not enlarged and hind femora without teeth; thorax usually coarsely punctate. Larvae parasitic on diverse types of insects; some phytophagous, on grasses. *Oligo.*—*Holo.*

- Eurytoma** ILLIGER, 1807, p. 192. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Family PTEROMALIDAE Haliday, 1833

[Pteromalidae HALIDAY, 1833, p. 267]

Very small insects. Fore wing as in Chalcidae, with much diversity; thorax usually not coarsely punctate; hind coxae normal, not

enlarged; hind femora without teeth; tarsi with 5 segments. Larvae parasitic on diverse types of insects. *Oligo.*—*Holo.*

- Pteromalus** SWEDERUS, 1795, p. 201. [Generic assignment of fossils doubtful.] BRUES, 1910; COCKERELL, 1921a; STATZ, 1938b. *Oligo.*, England, Europe (Germany), USA (Colorado)—*Holo.*
- Bruesisca** HEQUIST, 1961, p. 93 [**Cleonymus submersus* BRUES, 1910, p. 27; OD]. Little-known genus, resembling *Cleonymus* (recent), but head shape and venation of fore wing different. *Oligo.*, USA (Colorado).
- Ferrierelus** THÉOBALD, 1937a, p. 311 [**F. bernardi*; OD]. Similar to *Lamprotatus* (recent), but antennae much shorter. *Oligo.*, Europe (France).
- Heydeniopsis** HEQUIST, 1961, p. 94 [**H. cleonymoides*; OD]. Similar to *Heydenia* (recent). Wings unknown. Head subglobular; antennae with 12 segments, inserted near clypeus; ocelli in an equilateral triangle; propodeum long, with median carina. *Oligo.*, Europe (Baltic).
- Ormyrodes** BRUES, 1907, p. 46. BRUES, 1910. *Oligo.*, USA (Colorado)—*Holo.*

Family ENCIRTIDAE Förster, 1856

[Encyrtidae FÖRSTER, 1856, p. 18]

Very small insects. Fore wing with submarginal vein usually short; stigmal vein near midwing. Middle tibia modified for jumping, with enlarged spur and commonly with patch of modified setae on ventral surface; hind tibiae usually with 2 spurs, 1 often reduced. Larvae parasitic on diverse insects. *Oligo.*—*Holo.*

- Encyrtus** LATREILLE, 1809, p. 31. [Generic assignment of fossils doubtful.] STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*
- Propelma** TRJAPITZIN, 1963, p. 89 [**P. rohdendorfi*; OD]. Similar to *Metapelma* (recent), but hind tibiae normal, not flattened and broad. *Oligo.*, Europe (Baltic).

Family EULOPHIDAE Haliday, 1833

[Eulophidae HALIDAY, 1833, p. 268]

Fore wing with submarginal vein close to wing margin and commonly concurrent with it; stigmal vein present but often very short and situated well toward wing apex. Fore tibial spur short and straight; fore basitarsus with an oblique comb basally. Larvae parasitic on diverse types of insects. *Oligo.*—*Holo.*

- Eulophus** GEOFFROY, 1762, p. 312. [Generic assignment of fossils doubtful.] STATZ, 1938b. *Oligo.*, Europe (Germany)—*Holo.*

Family TRICHOGRAMMATIDAE

Förster, 1856

[Trichogrammatidae FÖRSTER, 1856, p. 20]

Minute insects. Fore wing broad and fringed with hairs; venation greatly reduced, the veins not developed beyond midwing; proximal veins forming a short marginal compound vein; stigmal vein absent. Larvae parasitic on insect eggs. *Cret.—Holo.*

Trichogramma WESTWOOD, 1833, p. 444. *Holo.*

Enneagmus YOSHIMOTO, 1975, p. 512 [**E. pristinus*; OD]. Fore wing long and narrow, as long as body and hyaline; longest cilia at distal end of wing; cilia on anterior and posterior margins gradually shorter toward base of wing. Antennae with 9 segments, funicle with 4; tarsi with 3 segments; all tibiae with a single spur; gaster short, broadly sessile. *Cret.*, Canada (Manitoba).

Family MYMARIDAE Haliday, 1833

[Mymaridae HALIDAY, 1833, p. 269]

Minute insects. Fore wing usually with a long marginal fringe, venation commonly limited to basal third of wing; basal portion of wing often reduced to a single, thin vein, forming a stalk for the broader distal part. Hind wings linear, often threadlike. Larvae parasitic on eggs of insects. *Cret.—Holo.*

Mymar CURTIS, 1832, p. 411. *Holo.*

Alaptus WESTWOOD, 1839, p. 79. [Fossils are specimens of *A. globosicornis* and *A. psocidivorus*, both recent.] DOUTT, 1973b. ?*Mio.*, Mexico—*Holo.*

Anaphes HALIDAY, 1833, p. 269. MEUNIER, 1901b. *Oligo.*, Europe (Baltic)—*Holo.*

Archaeromma YOSHIMOTO, 1975, p. 503 [**Ooctonus minutissimus* BRUES, 1937, p. 44; OD]. Similar to *Palaeomymar*. Fore wing not reticulate; antennal club with 4 segments in both sexes; scape short. CARPENTER & others, 1937. *Cret.*, Canada (Manitoba, Alberta).

Areson WALKER, 1846, p. 50. MEUNIER, 1901b, 1905a; DOUTT, 1973b. *Oligo.*, Europe (Baltic)—*Holo.*

Carpenteriana YOSHIMOTO, 1975, p. 510 [**C. tumida*; OD]. Female as in *Ooctonus*, but antennae with 10 segments, funicle with 7 segments; gaster elongate-oval. Pterostigma of fore wing well defined. *Cret.*, Canada (Manitoba).

Galloromma SCHLÜTER, 1978a, p. 74 [**G. bezonaisensis*; OD]. Little-known genus, similar to *Archaeromma*. Antennae with 14 segments, 4 terminal segments forming a club. [Probably a synonym of *Archaeromma*.] *Cret.*, Europe (Germany).

Gonatocerus NEES, 1834, p. 192. MEUNIER, 1905a; DOUTT, 1973b; BURKS, 1979. *Oligo.*, Europe (Baltic)—*Holo.*

Litus HALIDAY, 1833, p. 269. MEUNIER, 1901b; DOUTT, 1973b. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Macalpinia YOSHIMOTO, 1975, p. 527 [**M. canadensis*; OD]. Fore wing elongate, about 3.5 times as long as broad; stigmal vein very large, subtriangular; anterior marginal setae about half as long as posterior ones; gaster conical at base, elongate-oval in dorsal view; antennae with 13 segments, pedicel enlarged, about twice as long as broad. *Cret.*, Canada (Alberta).

Malfattia MEUNIER, 1901b, p. 285 [**M. molitorae*; OD]. Little-known genus. Tarsi with 5 segments, antennae with 9 segments. DOUTT, 1973b; YOSHIMOTO, 1975. *Oligo.*, Europe (Baltic).

Ooctonus HALIDAY, 1833, p. 269. CARPENTER & others, 1937; DOUTT, 1973b; YOSHIMOTO, 1975. *Oligo.*, Europe (Baltic)—*Holo.*

Palaeomymar MEUNIER, 1901b, p. 289 [**Mymar duisburgi* STEIN, 1877, p. 30; OD] [= *Mymaromma* GIRAULT, 1920, p. 38 (type, *M. goethei*, recent); *Petiolaria* BLOOD & KRYGER, 1922, p. 229 (type, *P. anomala*, recent); *Mymaromella* GIRAULT, 1931, p. 4 (type, *M. mira*, recent)]. STEIN, 1877; BAKKENDORF, 1948; DOUTT, 1973b. *Oligo.*, Europe (Baltic)—*Holo.*

Polynemoidea GIRAULT, 1913, p. 116. DOUTT, 1973a, 1973b. ?*Mio.*, Mexico—*Holo.*

Protooctonus YOSHIMOTO, 1975, p. 511 [**D. masneri*; OD]. Similar to *Carpenteriana*, but antennae of female with 13 segments; gaster subpetiolate. Antennae of male with 12 segments. *Cret.*, Canada (Manitoba).

Triadomerus YOSHIMOTO, 1975, p. 508 [**T. bulbosus*; OD]. Fore wing elongate-spatulate, about 3 times as long as broad. Antennae of female with 13 segments; scape not greatly elongate, unusually swollen and flattened; tarsi with 5 segments; gaster elongate-oval. *Cret.*, Canada (Manitoba, Alberta).

Family TETRACAMPIDAE

Förster, 1856

[Tetracampidae FÖRSTER, 1856, p. 79]

Minute insects. Antennae with 11 or 12 segments, often clubbed; pronotum usually large, bell-shaped; anterior tibiae with a single furcate spur or with 2 small spurs. Legs slender and long. Larvae endoparasites of eggs or larvae of Coleoptera, Hymenoptera, or Diptera. *Cret.—Holo.*

Tetracampe FÖRSTER, 1841, p. 34. *Holo.*

Baeomorpha BRUES, 1937, p. 41 [**B. dubitata*; OD]. Antennae with 12 segments, scape broad

except at base; tarsi 5-segmented in female, 4-segmented in male. Fore wing broad and spatulate; submarginal and marginal veins nearly equal in length; stigmal vein large; postmarginal vein long, extending nearly to apical margin. YOSHIMOTO, 1975. *Cret.*, Canada (Manitoba, Alberta).

Bouceklytus YOSHIMOTO, 1975, p. 516 [**B. arcuodens*; OD]. Antennae with 12 segments; tarsi with 5 segments; petiole consisting of a single segment; mandibles concave, protruding downward. *Cret.*, Canada (Manitoba).

Distylopus YOSHIMOTO, 1975, p. 514 [**D. bisegmentus*; OD]. Antennae with 11 segments; scape short; tarsi with 5 segments; petiole 2-segmented, first segment very short. *Cret.*, Canada (Manitoba).

Family KARATAIDAE Rasnitsyn, 1977

[Karataidae RASNITSYN, 1977a, p. 103]

Fore wing as in Ephialtitidae, but vein 2A complete or nearly complete and reaching base of wing. *Jur.*

Karataus RASNITSYN, 1977a, p. 103 [**K. pedalis*; OD]. Fore wing with basal segment of RS long, directed toward wing base; crossvein 1r-rs absent; crossvein 2r-m closer to 2m-cu than to 2r-rs; cell 2rm very long. Antennae with many segments; hind femora very thick. *Jur.*, USSR (Kazakh). —FIG. 261,1. **K. pedalis*; wings and body, $\times 5$ (Rasnitsyn, 1977a).

Family BETHYLONYMIDAE Rasnitsyn, 1975

[Bethylonymidae RASNITSYN, 1975, p. 94]

Fore wing with costal area broad; basal section of vein RS directed slightly basally; antennae filiform, with 8 to 27 segments; legs short; abdomen spindle-shaped, segments nearly alike. *Jur.*

Bethylonymus RASNITSYN, 1975, p. 94 [**B. curtipes*; OD]. Fore wing with crossvein 2m-cu present; cell 2a absent. Antennae with 11 to 13 segments; pronotum short. *Jur.*, USSR (Kazakh, Asian RSFSR). —FIG. 261,5. **B. curtipes*, Kazakh; body and base of wing, $\times 10$ (Rasnitsyn, 1975).

Arthrogaster RASNITSYN, 1975, p. 103 [**A. seticornis*; OD]. Fore wing with pterostigma broad; basal section of RS short; cell 2a absent. Antennae setaceous, with more than 25 segments; pronotum short. *Jur.*, USSR (Kazakh). —FIG. 261,6. **A. seticornis*; wing and body, $\times 5.5$ (Rasnitsyn, 1975).

Bethylonymellus RASNITSYN, 1975, p. 98 [**B. cervicalis*; OD]. Fore wing with crossveins 2r-m and 2m-cu absent or obsolescent; cell 2a absent. Antennae with 8 to 12 segments; pronotum long. *Jur.*, USSR (Kazakh). —FIG. 261,8. **B. cervicalis*; wing and body, $\times 12$ (Rasnitsyn, 1975).

Leptogastrella RASNITSYN, 1975, p. 103 [**L. leptogastra*; OD]. Fore wing with crossveins 1r-rs and 3r-m absent; crossveins 2r-m and 2m-cu and cell 2a present. Antennae with 17 to 19 segments. *Jur.*, USSR (Kazakh).

Family CHRYSIDIDAE Latreille, 1802

[Chrysididae LATREILLE, 1802b, p. 316]

Antennae elbowed, with 12 or 13 segments; pronotum short and broad; hind tibial spurs and basitarsus not modified for grooming; fore wing with reduced venation; hind wing without closed cells; gaster with 2 to 4 exposed tergites and with dorsal surface convex and ventral surface concave. Larvae parasitic on immature stages of certain aculeate Hymenoptera and occasionally on Lepidoptera and Phasmatodea. *Cret.—Holo.*

Chrysis LINNÉ, 1761, p. 414. COCKERELL, 1907c; ROHWER, 1909c. *Oligo.*, USA (Colorado)—*Holo.*

Hypocleptes EVANS, 1973, p. 175 [**H. rasnitsyni*; OD]. Female similar to those of *Procleptes*, but lacking dentiform processes on propodeum and apical processes on front coxae; scapes short. *Cret.*, USSR (Asian RSFSR). —FIG. 261,3. **H. rasnitsyni*; body, $\times 20$ (Evans, 1973).

Omalus PANZER, 1801, no. 13. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

Procleptes EVANS, 1969, p. 257 [**P. carpenteri*; OD]. Similar to *Cleptes* (recent), but mandibles broad and with 3 or 4 teeth apically; scape long and slender. *Cret.*, Canada (Manitoba). —FIG. 261,4. **P. carpenteri*; dorsal view, $\times 15$ (Evans, 1969).

Protamisega EVANS, 1973, p. 176 [**P. khatanga*; OD]. Female similar to those of *Hypocleptes*, but venation less reduced and scape longer. *Cret.*, USSR (Asian RSFSR).

Protochrysidis CARPENTER, 1986, p. 577, *nom. subst. pro Protochrysis* BISCHOFF, 1917, p. 139, *non* PASCHER, 1911 [**Protochrysis succinalis*; OD]. Little-known genus. Head flattened; postscutellum extending as a horizontal lamella as long as scutellum and mesonotum combined; 6 visible gastral tergites present; all legs very short; femora flattened and very broad; coxae excavated for femora. [Family assignment doubtful.] BRUES, 1933. *Oligo.*, Europe (Baltic). —FIG. 261,7. **P. succinalis* (BISCHOFF); body and wings, $\times 5.5$ (Brues, 1933).

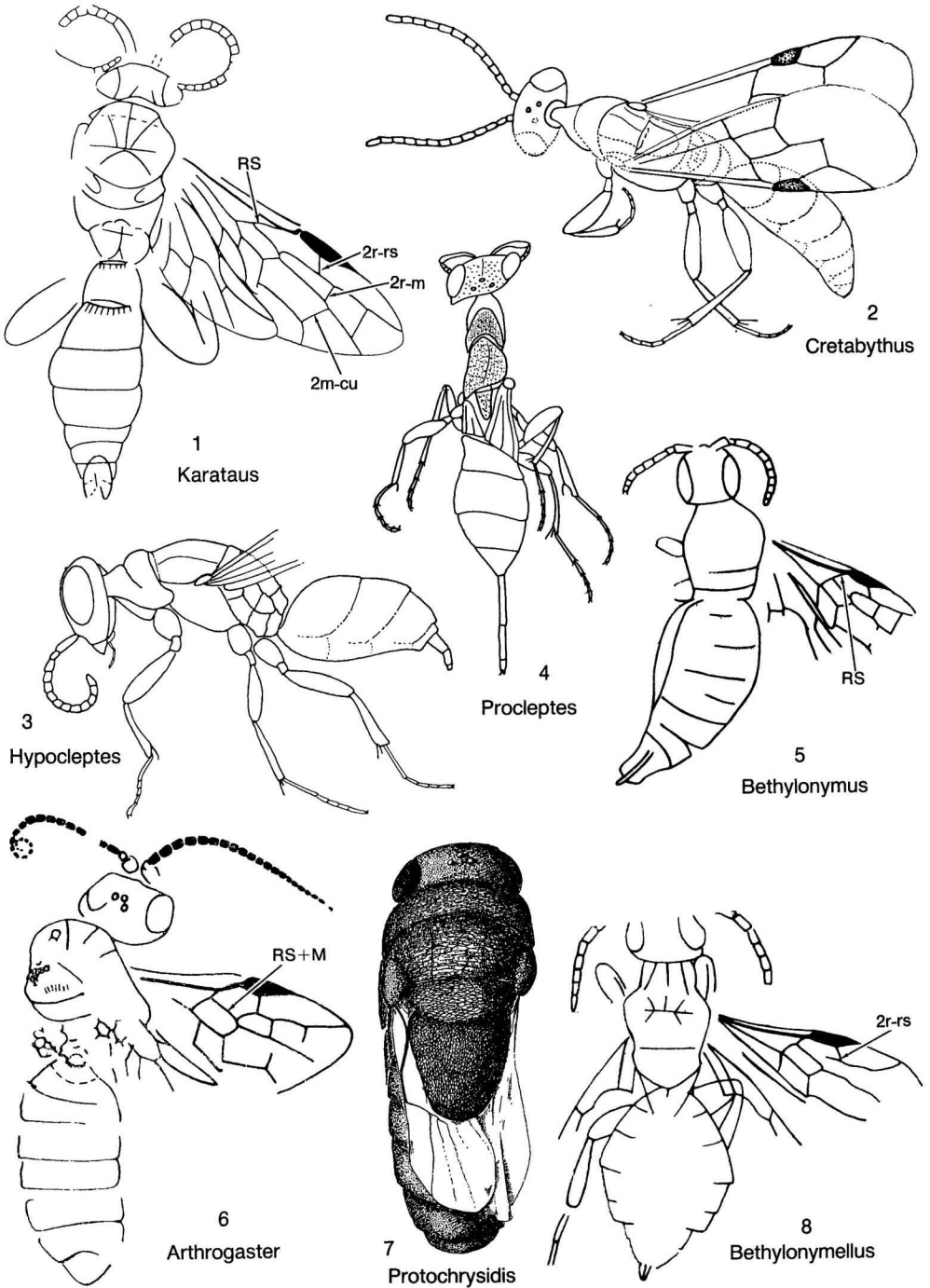


FIG. 261. Karataidae, Bethlyonymidae, Chrysididae, and Scolebythidae (p. 485–487).

Family SCOLEBYTHIDAE Evans, 1963

[Scolebythidae H. E. EVANS, 1963, p. 71]

Small wasps, without marked sexual dimorphism. Labial palpi short, with 4 segments; maxillary palpi with 6 segments; antennae with 13 segments, scape flattened; hind wing without closed cells; no constriction between first and second gastral segments. *Cret.*—*Holo.*

Scolebythus H. E. EVANS, 1963, p. 9. *Holo.*

Cretabythus EVANS, 1973, p. 171 [**C. sibiricus*; OD]. Male with fore wing similar to that of pemphredomines (Sphecidae), but mandibles broad and with 4 teeth; 2 midtibial spurs present. [Family position doubtful.] *Cret.*, USSR (Asian RSFSR). — FIG. 261,2. **C. sibiricus*; wings and body, $\times 16$ (Evans, 1973).

Family BETHYLIDAE Förster, 1856

[Bethylidae FÖRSTER, 1856, p. 95]

Antennae with 11 to 13 segments; pronotum extending back to tegulae; gaster with 7 or 8 exposed segments; wings present in some species but reduced or absent in others, especially in females. Larvae parasitic on immature stages of Coleoptera and Lepidoptera. *Cret.*—*Holo.*

Bethylus LATREILLE, 1802, p. 315. *Holo.**Apenesia* WESTWOOD, 1874, p. 170. COCKERELL, 1917d. *Mio.*, Burma—*Holo.*

Archaeopyris EVANS, 1973, p. 174 [**A. minutus*; OD]. Male with antennae simple, with 13 segments; eyes large, protruding; mandibles short, broad, with apical teeth; legs not spinose. Fore wing with RS+M present only as short, basal stub. *Cret.*, USSR (Asian RSFSR). — FIG. 262,1. **A. minutus*; fore wing, $\times 35$ (Evans, 1973).

Artiepyris KIEFFER, 1913, p. 108. BRUES, 1933. *Oligo.*, Europe (Baltic)—*Holo.*

Bethylitella COCKERELL, 1917g, p. 365 [**B. cylindrella*; OD]. Fore wing as in *Mesitius* (recent); head elongate; eyes very small; mandibles large, with 5 small teeth on apical margin; antennae with 13 segments, scape stout; petiole short. *Mio.*, Burma.

Bethylopteron BRUES, 1933, p. 121 [**B. ambiguum*; OD]. Head large, globose; antennae with 13 segments; compound eyes large, ocelli very large; propodeum very short, truncate posteriorly; petiole lacking; legs stout. [Family position doubtful.] *Oligo.*, Europe (Baltic).

Calyzoa WESTWOOD, 1837, p. 56. BRUES, 1923a. *Oligo.*, Europe (Baltic)—*Holo.*

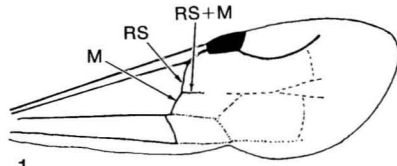
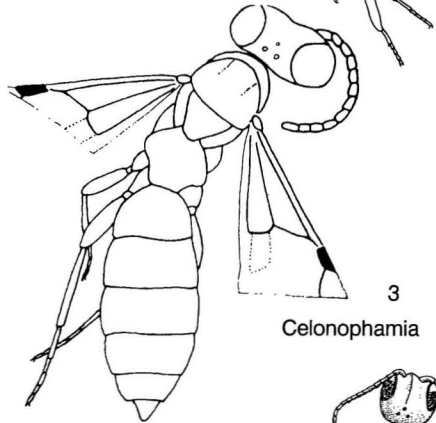
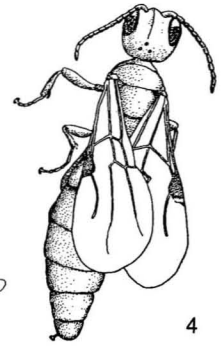
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Archaeopyris2
Ctenobethylus3
Celonophamia5
Palaeobethylus4
Pristapenesia

FIG. 262. Bethylidae (p. 487–488).

Celonophamia EVANS, 1973, p. 175 [**C. taimyria*; OD]. Similar to *Cephalonomia* (recent), but female having broader wings with fuller venation. *Cret.*, USSR (Asian RSFSR). — FIG. 262,3. **C. taimyria*; wings and body, $\times 25$ (Evans, 1973).

Ctenobethylus BRUES, 1939b, p. 261 [**C. succinialis*; OD]. Female apterous; thorax nearly normal. Similar to *Apenesia*, but mandibles with at

- least 7 teeth. *Oligo.*, Europe (Baltic). — FIG. 262.2. **C. succinialis*; body, $\times 14$ (Brues, 1939b).
- Epyris** WESTWOOD, 1832, p. 129. BRUES, 1910, 1923a; COCKERELL, 1920a, 1921a. *Oligo.*, Europe (Baltic), England, USA (Colorado); *Mio.*, Burma-Holo.
- Eupsenella** WESTWOOD, 1874, p. 168. BRUES, 1923a, 1933; RASNITSYN, 1975. *Oligo.*, Europe (Baltic)-Holo.
- Holepyris** KIEFFER, 1904, p. 390. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Homoglenus** KIEFFER, 1904, p. 388. BRUES, 1939b. *Oligo.*, Europe (Baltic)-Holo.
- Isobrachium** FÖRSTER, 1856, p. 96. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Laelius** ASHMEAD, 1893, p. 50. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Misepyrus** KIEFFER, 1913, p. 108. BRUES, 1933, 1939b. *Oligo.*, Europe (Baltic)-Holo.
- Palaeobethyloides** BRUES, 1933, p. 119 [**P. longiceps*; OD]. Similar to *Palaeobethylus*, but head of female much longer and narrower. *Oligo.*, Europe (Baltic).
- Palaeobethylus** BRUES, 1923a, p. 334 [**P. longicollis*; OD]. Body flattened; head width about 8 times dorsoventral thickness; thorax width about 4 times thickness; mandibles long and straight, with edentate margins; antennae with 13 segments, scape long; pterostigma lanceolate. BRUES, 1933. *Oligo.*, Europe (Baltic). — FIG. 262.5. **P. longicollis*, male; wings and body, $\times 10$ (Brues, 1923a).
- Parapristocera** BRUES, 1933, p. 122 [**P. skewarrae*; OD]. Similar to *Pristocera* (recent), but integument of head and thorax smooth. *Oligo.*, Europe (Baltic).
- Perisierola** KIEFFER, 1914, p. 533. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Pristapenesia** BRUES, 1933, p. 131 [**P. primaeva*; OD]. Related to *Apenesia*. Male with prothorax produced anteriorly, as in *Holepyris*; hind femora without a tooth; mandibles long, enlarged apically; antennae with 13 segments. Female with wings present; RS and M almost reaching wing margin; pterostigma present. *Oligo.*, Europe (Baltic). — FIG. 262.4. **E. primaeva*; wings and body, $\times 10$ (Brues, 1933).
- Prosierola** KIEFFER, 1905, p. 243. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Protopristocera** BRUES, 1923a, p. 337 [**P. succini*; OD]. Related to *Pristocera* (recent), but female with wings fully developed. BRUES, 1933. *Oligo.*, Europe (Baltic).
- Pseudisobrachium** KIEFFER, 1904, p. 368. THÉOBALD, 1937a. *Oligo.*, Europe (France)-Holo.
- Rhabdepyris** KIEFFER, 1904, p. 32. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.
- Scleroderma** LATREILLE, 1809, p. 118. COCKERELL, 1917d. *Mio.*, Burma-Holo.
- Uromesitius** BRUES, 1933, p. 116 [**U. caudatus*; OD]. Similar to *Mesitius* (recent), but female

with gastral segments beyond fourth drawn out into long slender tube; gaster of male short, consisting of 5 visible segments; fore wing with cell 3r very short; RS terminating on front margin of wing before apex; antennae of female with 13 segments. *Oligo.*, Europe (Baltic).

Family DRYINIDAE Haliday, 1833

[Dryinidae HALIDAY, 1833, p. 272]

Antennae diverse in form, with 10 segments in both sexes and inserted on prominence near dorsal margin of clypeus; fore tarsi of female usually chelate; fore wing with reduced venation; females of some species apterous. Larvae endoparasites of Hemiptera (Homoptera). *Cret.*-Holo.

Dryinus LATREILLE, 1804, p. 176. BRUES, 1923a. *Oligo.*, Europe (Baltic)-Holo.

Ampulicomorpha ASHMEAD, 1893, p. 79. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.

Avodryinus PONOMARENKO, 1981, p. 139 [**A. canadensis*; OD]. Female with well-developed wings; pterostigma narrow; prothorax longer than broad, narrower than mesothorax; propodeum with distinct areolation. *Cret.*, Canada (Alberta).

Cretodryinus PONOMARENKO, 1975c, p. 104 [**C. zberichini*; OD]. Similar to *Thaumadryinus* but with well-developed parapsidal furrows, short trochanters, and coarse rugosity of propodeum; tibial spur formula 1,1,2. Wings well developed. *Cret.*, USSR (Asian RSFSR). — FIG. 263.4. **C. zberichini*; thorax and abdomen, $\times 11$ (Ponomarenko, 1975c).

Dicondylus CURTIS, 1829, p. 110. PONOMARENKO, 1981. *Cret.*, USSR (European RSFSR)-Holo.

Electrodryinus PONOMARENKO, 1975a, p. 126 [**E. areolatus*; OD]. Similar to *Hesperodryinus* (recent), but enlarged claw of fore tarsus unarmed and pronotum short. *Oligo.*, Europe (Baltic). — FIG. 263.6. **E. areolatus*; wing and body, $\times 10$ (Ponomarenko, 1975a).

Embolemus WESTWOOD, 1833, p. 444. BRUES, 1933. *Oligo.*, Europe (Baltic)-Holo.

Thaumadryinus PERKINS, 1905, p. 58. BRUES, 1923a, 1933; PONOMARENKO, 1975a. *Oligo.*, Europe (Baltic)-Holo.

Family BAISSODIDAE Rasnitsyn, 1975

[Baissodidae RASNITSYN, 1975, p. 122]

Little-known family, possibly related to the Sphecidae. Female: antennae with 12 segments; mesonotum with prominent sutures; legs without special modifications, grooming structures absent from hind legs; abdomen short, weakly sclerotized; ovipos-

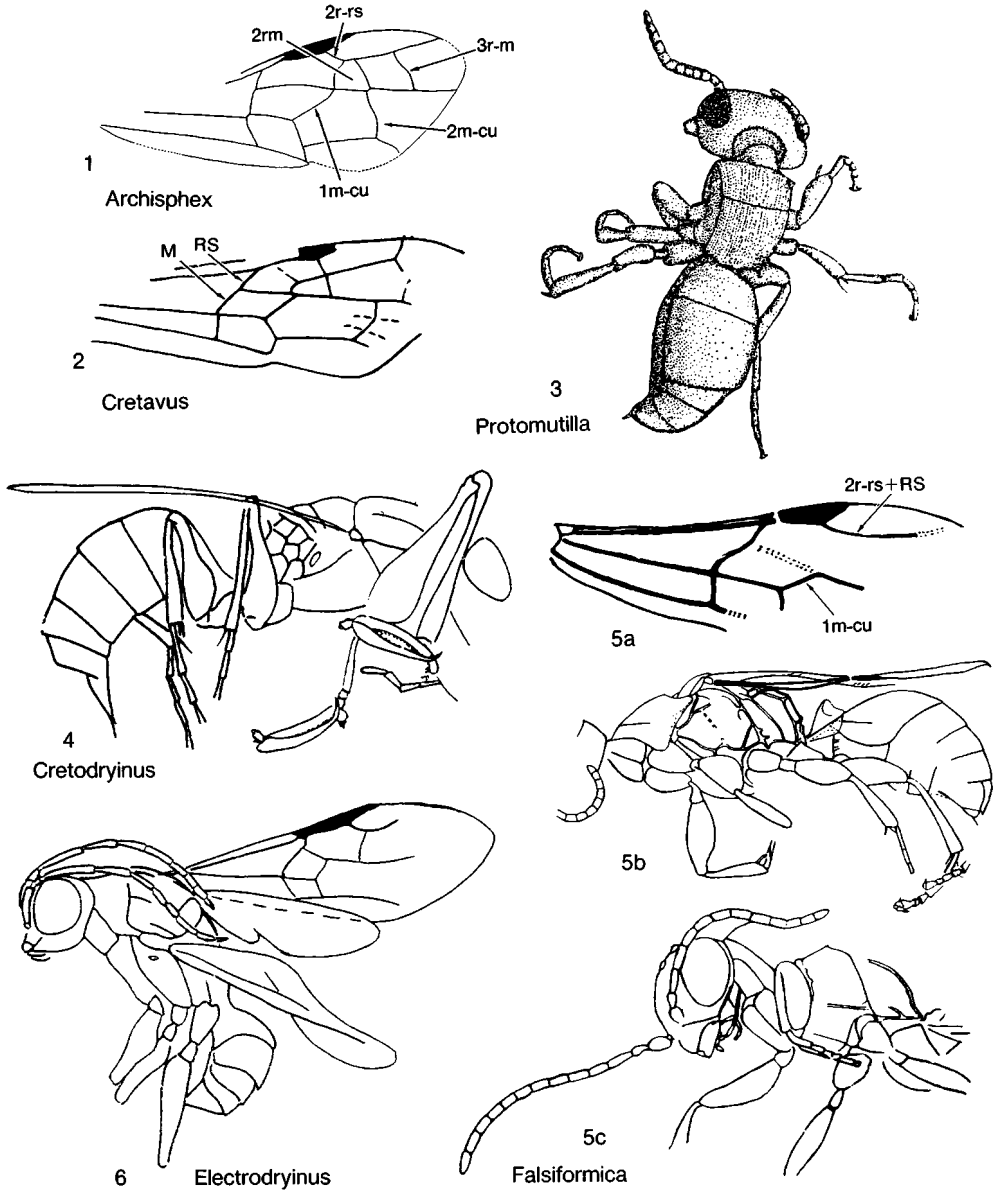


FIG. 263. Dryinidae, Baissodidae, Tiphidae, Mutillidae, and Falsiformicidae (p. 488–490).

itor short. Fore wing venation relatively primitive; crossvein 1m-cu close to end of vein RS + M. *Cret.*

Baissodes RASNITSYN, 1975, p. 123 [**B. robustus*; OD]. Fore wing with cell 2rm longer than broad; cell 3r with pointed apex. *Cret.*, USSR (Asian RSFSR).

ArchispheX EVANS, 1969, p. 252 [**A. crowsoni*; OD]. Similar to *Baissodes*, but crossvein 1m-cu

close to base of cell 2rm; crossvein 2m-cu close to apex of cell 2rm; crossvein 3rm sigmoidal. RASNITSYN, 1975. *Cret.*, England.—FIG. 263, 1. **A. crowsoni*; fore wing, $\times 9$ (Evans, 1969).

Oryctobaissodes RASNITSYN, 1975, p. 125 [**O. armatus*; OD]. Fore wing with cell 3r truncate apically; femora thick. *Cret.*, USSR (Asian RSFSR).

Trichobaissodes RASNITSYN, 1975, p. 126 [**T. antennatus*; OD]. Similar to *Baissodes*, but cell

3r rounded apically; femora not thickened. *Cret.*, USSR (Asian RSFSR).

Family TIPHIIDAE Leach, 1815

[Tiphidae LEACH, 1815, p. 118]

Similar to Mutillidae but second gastral tergite without lateral bands of dense, appressed hairs; thorax and propodeum not fused into a single plate; females often apterous. Larvae ectoparasites of immature insects, usually Coleoptera, Orthoptera, or Hymenoptera. *Oligo.*—*Holo.*

Tiphia FABRICIUS, 1775, p. 353. *Holo.*

Anthobosca GUÉRIN-MÉNEVILLE, 1838, p. 236 [= *Geotiphia* COCKERELL, 1906b, p. 49 (type, *G. foxiana*)]. TURNER, 1912; COCKERELL, 1926a; ILLIES, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Myrmosa LATREILLE, 1796, p. 118. [Generic assignment of fossils doubtful.] PITON, 1940a. *Oligo.*, Europe (France)—*Holo.*

Myzinum LATREILLE, 1803, p. 326. PITON, 1940a. *Oligo.*, Europe (France)—*Holo.*

Protomutilla BISCHOFF, 1917, p. 142 [**P. succinialis*; OD]. Little-known genus, apparently related to *Myrmosa*. Thoracic dorsum with a single transverse suture; first gastral sternite with a median carina; front femora strongly thickened. All known specimens apterous. BRUES, 1933. *Oligo.*, Europe (Baltic).—FIG. 263,3. **P. succinialis*; dorsal view, $\times 6.5$ (Brues, 1933).

Family MUTILLIDAE Latreille, 1802

[Mutillidae LATREILLE, 1802b, p. 347] [= Cretavidae SHAROV, 1957a, p. 943]

Second gastral tergite with lateral bands of dense, appressed hairs; thorax and propodeum usually fused to form a single plate; body with prominent pubescence; females apterous. Larvae mostly ectoparasites of larvae and pupae of other Hymenoptera. *Cret.*—*Holo.*

Mutilla LINNÉ, 1802, p. 582. *Holo.*

Cretavus SHAROV, 1957a, p. 943 [**C. sibiricus*; OD]. Little-known genus. Fore wing with basal sections of RS and of M forming a straight, oblique line. RASNITSYN, 1975. *Cret.*, USSR (Asian RSFSR).—FIG. 263,2. **C. sibiricus*; fore wing, $\times 6$ (Rasnitsyn, 1975).

Family FALSIFORMICIDAE Rasnitsyn, 1975

[Falsiformicidae RASNITSYN, 1975, p. 111]

Female: fore wing venation reduced as in bethyloids; hind wing without veins, but

apparently with jugal lobe. Head prognathous; pronotum very long, with several small humeral protuberances; metapleural gland apparently absent; abdomen apparently shorter than head and thorax combined; gaster shorter than head and thorax combined, second tergite forming a high triangle, resembling a formicid node. Male: head hypognathous; antennae with 13 segments, not elbowed; pronotum relatively short. *Cret.*

Falsiformica RASNITSYN, 1975, p. 112 [**F. cretacea*; OD]. Fore wing (known in female only) with pterostigma relatively narrow; crossvein 2r-rs and distal section of RS forming a single, curved vein; basal section of RS about half as long as basal section of M; RS+M obsolescent; crossvein 1m-cu present. Male with antennae filiform, scape short; maxillary palpi apparently with 6 segments. *Cret.*, USSR (Asian RSFSR).—FIG. 263,5. **F. cretacea*; a, wing of female, $\times 20$; b, thorax and abdomen of female, $\times 19$; c, head and thorax of male, $\times 22$ (all Rasnitsyn, 1975).

Family FORMICIDAE Latreille, 1802

[Formicidae LATREILLE, 1802b, p. 352] [= Armaniidae DLUSSKY, 1983, p. 65]

Antennae distinctly elbowed in females and workers, often less so in males; first gastral segment (and sometimes second) a nodiform or scalelike petiole (and postpetiole) separated from rest of gaster; males and females usually winged, but wings shed by females after nuptial flight; workers apterous. Social insects (ants); nests diverse, usually in ground. [The subfamily Sphecomyrminae is included in the Formicidae as originally proposed by WILSON, CARPENTER, and BROWN (1967a).] *Cret.*—*Holo.*

Formica LINNÉ, 1758, p. 579. WHEELER, 1914; MEUNIER, 1915b, 1917c; COCKERELL, 1920a, 1923c; CARPENTER, 1930a; PITON & THÉOBALD, 1935; THÉOBALD, 1937a; DLUSSKY, 1981. *Eoc.*, USA (Texas), England; *Oligo.*, Europe (Baltic, France, Germany), USA (Colorado); *Mio.*, Europe (France), USSR (European RSFSR)—*Holo.*

Agroecomyrmex WHEELER, 1910a, p. 265 [**Myrmica duisburgi* MAYR, 1868; OD]. Worker and female: similar to those of *Lachnomyrmex* (recent), but funiculus of antennae without a 2-segmented club, eyes near posterior corners of head, and tip of gaster directed forward. WHEELER, 1914. *Oligo.*, Europe (Baltic).

Ameghinoia VIANA & HAEDO ROSSI, 1957, p. 109 [**A. piatnitskyi*; OD]. Little-known genus, pos-

sibly related to Myrmeciinae; tibiae apparently without spurs. *Oligo./Mio.*, Argentina.

Aphaenogaster MAYR, 1853, p. 107. WHEELER, 1914; CARPENTER, 1930a; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Europe (France)—*Holo.*

Archaeopone DLUSSKY, 1975, p. 120 [**A. kyzylzharica*; OD]. Male: third antennal segment about 5 times as long as second; thorax distinctly segmented. [Family assignment doubtful.] DLUSSKY, 1983. *Cret.*, USSR (Kazakh).

Archimyrmex COCKERELL, 1923a, p. 51 [**A. rostratus*; OD]. Little-known genus, possibly a myrmicine. WHEELER, 1928; CARPENTER, 1930a. *Eoc.*, USA (Colorado).

Archiponera CARPENTER, 1930a, p. 27 [**A. wheeleri*; OD]. Closely related to *Gnamptogenys*. Worker: head large, with convex sides; mandibles linear; anterior margin of clypeus with a median incision, posterior margin with large median lobe; ocelli absent; antennae with 12 segments; petiole cuneiform. WHEELER, 1930; BROWN, 1958. *Oligo.*, USA (Colorado).—FIG. 264. **A. wheeleri*; worker, $\times 4.6$ (Carpenter, 1930a).

Armania DLUSSKY, 1983, p. 67 [**A. robusta*; OD]. Similar to *Sphecomyrma*. Female: petiole large, its width about equal to its length, its posterior part elevated and forming a node. *Cret.*, USSR (Asian RSFSR).

Armaniella DLUSSKY, 1983, p. 71 [**A. curiosa*; OD]. Similar to *Armania*, but petiole not forming a node. *Cret.*, USSR (Asian RSFSR).

Asymphyomyrmex WHEELER, 1914, p. 96 [**A. balticus*; OD]. A dolichoderine genus. Worker: head suborbicular, slightly flattened anteriorly; thorax short and compact; spurs absent on middle and hind tibiae. *Oligo.*, Europe (Baltic).

Brachyponera EMERY, 1901, p. 43. [Generic assignment of fossil doubtful.] THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Bradoponera MAYR, 1868, p. 73 [**B. meieri*; OD]. A ponerine genus, closely related to *Discothrea* (recent). Worker: antennae with 9 segments; eyes minute. WHEELER, 1914. *Oligo.*, Europe (Baltic).

Camponotites DLUSSKY, 1981, p. 76 [collective group]. Little-known species; fore wing lacking cells 2_{rm} and 3_{rm}; cell 2r + 3r closed. *Mio.*, USSR (European RSFSR).

Camponotus MAYR, 1861, p. 25. MAYR, 1868; WHEELER, 1914; DONISTHORPE, 1920; CARPENTER, 1930a; NAORA, 1933a; PITON & THÉOBALD, 1935; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France), England, USA (Colorado); *Mio.*, Europe (France); *Paleoc.*—*Plio.*, China (Fushun)—*Holo.*

Cephalomyrmex CARPENTER, 1930a, p. 37 [**C. rotundatus*; OD]. Little-known genus, apparently a myrmicine. Female: head exceedingly large; thorax short; gaster small; funiculus of antennae apparently with only 5 or 6 segments;



Archiponera

FIG. 264. Formicidae (p. 491).

petiole pedunculate; venation unknown. *Oligo.*, USA (Colorado).

Cerapachys SMITH, 1857, p. 74 [= *Procerapachys* WHEELER, 1914, p. 27 (type, *P. annosus*)]. BROWN, 1975. *Oligo.*, Europe (Baltic)—*Holo.*

Cretomyrma DLUSSKY, 1975, p. 115 [**C. arnoldii*; OD]. Worker: similar to that of *Sphecomyrma* but with a short, median epinotal spine and a short sting. *Cret.*, USSR (Asian RSFSR).

Dolichoderus LUND, 1831, p. 130. MAYR, 1868; COCKERELL, 1915; WHEELER, 1914; DONISTHORPE, 1920; CARPENTER, 1930a; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France), England, USA (Colorado)—*Holo.*

Dolichomyrma DLUSSKY, 1975, p. 121 [**D. longiceps*; OD]. Little-known genus. Female: head elongate; thorax similar to that of *Sphecomyrma*; petiole short. [Family assignment doubtful.] DLUSSKY, 1983. *Cret.*, USSR (Kazakh).

Drymomyrmex WHEELER, 1914, p. 135 [**D. fuscipennis*; OD]. Related to *Aphomyrmex* (recent), but female with 11-segmented antennae. THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France).

Elaeomyrmex CARPENTER, 1930a, p. 48 [**E. gracilis*; OD]. Related to *Iridomyrmex*. Female: head much longer than broad, lateral margins nearly straight; mandibles prominent; posterior margin of clypeus with a prominent median prolongation; clypeus striated. Worker: smaller but very similar. *Oligo.*, USA (Colorado).

- Electromyrmex** WHEELER, 1910b, p. 167 [**E. klebsi*; OD]. A myrmicine genus, close to *Podomyrma* (recent). Worker: mandibles very long, sublinear; antennae with 12 segments; thorax narrower than head; prothorax greatly elongated; petiole slender, cylindrical, with only a faint indication of a node. WHEELER, 1914. *Oligo.*, Europe (Baltic).
- Electroponera** WHEELER, 1914, p. 34 [**E. dubia*; OD]. A ponerine genus, apparently related to *Ectatomma* (recent). Worker: head subrectangular, with rounded sides, and weakly excised posterior border; antennae with 12 segments; thorax constricted in mesoepinotal region; petiole with a concave anterior face. *Oligo.*, Europe (Baltic).
- Emplastus** DONISTHORPE, 1920, p. 86 [**E. emeryi*; OD]. Little-known ponerine genus, apparently close to *Pachycondyla*. Female: eyes small, close to base of mandibles; mandibles without teeth. *Oligo.*, England.
- Eoformica** COCKERELL, 1921e, p. 38 [**E. eocenica*; OD; =*Liometopum pingue* SCUDDER, 1877a, p. 742]. Little-known genus of uncertain relationships. SCUDDER, 1890; WHEELER, 1928; CARPENTER, 1930a. *Eoc.*, USA (Colorado, Wyoming, Utah).
- Eomyrmex** HONG, 1974, p. 138 [**E. quchengziensis*; OD]. Worker (subfamily position uncertain): antennae with 13 segments; scape of moderate length; mandibles relatively small, with 3 denticles, the terminal one being longest; petiole slender; gaster with pronounced constriction between first and second segments; legs long; middle and hind tibiae with prominent spurs. *Eoc.*, China (Liaoning).
- Eulithomyrmex** CARPENTER, 1935b, p. 91, *nom. subst. pro Lithomyrmex* CARPENTER, 1930a, p. 34, *non* CLARK, 1928 [**Lithomyrmex rugosus* CARPENTER, 1930a, p. 35; OD]. A myrmicine genus, related to *Agroecomyrmex*, but all castes with smaller mandibles and a larger antennal club. *Oligo.*, USA (Colorado).
- Gesomyrmex** MAYR, 1868, p. 50. EMERY, 1905; WHEELER, 1914; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)–*Holo.*
- Glaphyromyrmex** WHEELER, 1914, p. 131 [**G. oligocenicus*; OD]. Close to *Formica* (recent), but worker with large, flat eyes; elliptical head; short, thickset thorax; and large, convex pronotum. THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France).
- Gnamptogenys** ROGER, 1863, p. 174. WHEELER, 1914; BROWN, 1958; BARONI URBANI, 1980d. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Dominican Republic–*Holo.*
- Iridomyrmex** MAYR, 1862, p. 702. WHEELER, 1914; CARPENTER, 1930a; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France), USA (Colorado)–*Holo.*
- Kotshkorkia** DLUSSKY, 1981, p. 71 [**K. laticeps*; OD]. Similar to *Dolichoderus*. Female: head broad; front margin of clypeus convex; propodeum and petiole extended dorsally. *Mio.*, USSR (Kirghiz).
- Lasius** FABRICIUS, 1805, p. 415. WHEELER, 1914; COCKERELL, 1927b; PONGRÁČZ, 1928; CARPENTER, 1930a; POPOV, 1933; PITON & THÉOBALD, 1935; THÉOBALD, 1937a; ZALESSKY, 1949; WILSON, 1955; DLUSSKY, 1981. *Oligo.*, Europe (Baltic, France), USA (Colorado); *Mio.*, Europe (France, Croatia), USSR (European RSFSR)–*Holo.*
- Leptomymex** MAYR, 1862, p. 695. BARONI URBANI, 1980c. *Oligo./Mio.*, Dominican Republic–*Holo.*
- Leptomymex** EMERY, 1912, p. 16 [**Leptomymex maravignae* EMERY, 1891, p. 578; OD]. Similar to *Leptomymex*, but cell 3r of fore wing much larger. *Mio.*, Europe (Italy).
- Leptothorax** MAYR, 1855, p. 431. WHEELER, 1914. *Oligo.*, Europe (Baltic)–*Holo.*
- Leucotaphus** DONISTHORPE, 1920, p. 89 [**Leptothorax gurnetensis* COCKERELL, 1915, p. 485; OD]. Similar to *Formica* (recent), but cell 1mcu very small. *Oligo.*, England.
- Liometopum** MAYR, 1861, p. 25. WHEELER, 1914; PONGRÁČZ, 1928; CARPENTER, 1930a; DLUSSKY, 1981. *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Europe (Croatia), USSR (European RSFSR)–*Holo.*
- Mianeuretus** CARPENTER, 1930a, p. 38 [**M. mirabilis*; OD]. Close to *Paraneuretus*. Worker: eyes large, ocelli present; mandibles triangular, with blunt teeth; antennae slender, with 11 subequal segments; petiole much longer than broad, with a small node. *Oligo.*, USA (Colorado).
- Miomyrmex** CARPENTER, 1930a, p. 51 [**Formica impactus* COCKERELL, 1927b, p. 165; OD]. Apparently a dolichoderine. Female: antennae inserted close to clypeus, exceedingly short, but 12-segmented; scape not over half length of head; funiculus only a little longer than scape. *Oligo.*, USA (Colorado).
- Monomorium** MAYR, 1855, p. 452. WHEELER, 1914. *Oligo.*, Europe (Baltic)–*Holo.*
- Myrmica** LATREILLE, 1804, p. 179. WHEELER, 1914; MEUNIER, 1915b. *Oligo.*, Europe (Baltic, Germany)–*Holo.*
- Nothomyrmica** WHEELER, 1910b, p. 171 [**Macromischa rudis* MAYR, 1868, p. 85; OD]. Related to *Tetramorium* (recent). Worker: head and thorax coarsely rugose; antennae with 12 segments; middle and hind tibiae without spurs. *Oligo.*, Europe (Baltic).
- Odontomachus** LATREILLE, 1804, p. 179. BARONI URBANI, 1980b. *Oligo./Mio.*, Dominican Republic–*Holo.*
- Oecophylla** F. SMITH, 1860, p. 101. COCKERELL, 1915, 1920a; WHEELER, 1914; EMERY, 1921; THÉOBALD, 1937a. *Eoc.*, England; *Oligo.*, Europe (Baltic, France); *Mio.*, Europe (Italy)–*Holo.*
- Oligomyrmex** MAYR, 1867, p. 110. WHEELER, 1914; PITON & THÉOBALD, 1935; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France); *Mio.*, Europe (France)–*Holo.*

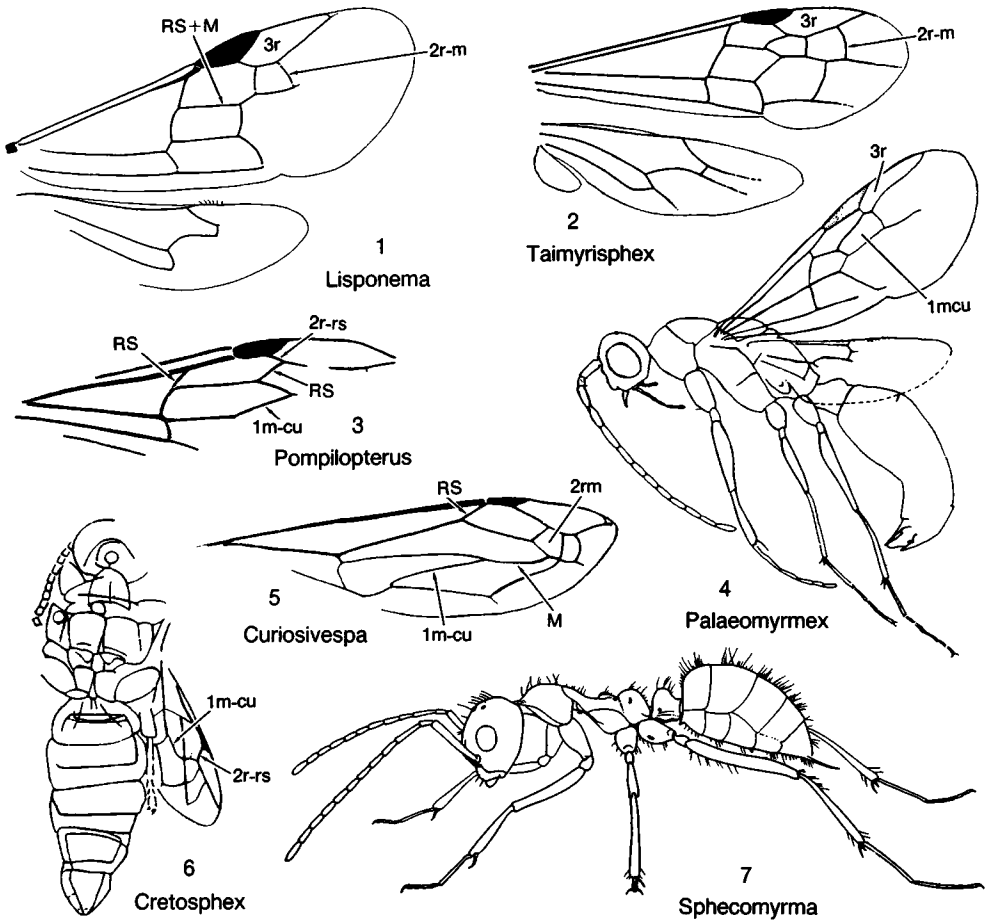


FIG. 265. Formicidae, Pompilidae, Sphecidae, and Uncertain (p. 493–498).

Pachycondyla F. SMITH, 1858, p. 105. MAYR, 1868; WHEELER, 1914; DONISTHORPE, 1920; THÉOBALD, 1937a; TAYLOR, 1964; DLUSSKY, 1981. *Oligo.*, Europe (Baltic, France), England; *Mio.*, USSR (European RSFSR)—*Holo.*

Palaeomyrmex DLUSSKY, 1975, p. 118 [**P. zberichini*; OD]. Apparently related to *Sphecomyrma*. Male: fore wing with cells 1r+2r, 3r, 2rm, and 1m-cu closed; mandibles narrow, without teeth; antennae with 13 segments; scape very short; middle and hind tibiae with 2 spurs. *Cret.*, USSR (Asian RSFSR).—FIG. 265, 4. **P. zberichini*; male, wing and body, $\times 12$ (Dlussky, 1975).

Parameranoplus WHEELER, 1914, p. 69 [**P. primaevus*; OD]. Apparently similar to *Meranoplus* (recent), but worker with much shallower antennal scrobes. *Oligo.*, Europe (Baltic).

Paraneuretus WHEELER, 1914, p. 73 [**P. tornquisti*; OD]. Similar to *Aneuretus* (recent) but worker much more slender; petiole with peduncle very short and with anterior slope of node

more gradual than posterior slope. *Oligo.*, Europe (Baltic).

Paraphaenogaster DLUSSKY, 1981, p. 68 [**P. microphthalmus*; OD]. Similar to *Aphaenogaster* but male with unusually small eyes. *Mio.*, USSR (European RSFSR).

Petraeomyrmex CARPENTER, 1930a, p. 55 [**P. minimus*; OD]. Little-known genus, probably a dolichoderine, possibly close to *Forelius* (recent). Female small, head quadrate, scape short and thick, petiole very small. *Oligo.*, USA (Colorado).

Petropona DLUSSKY, 1975, p. 119 [**P. petiolata*; OD]. Little-known genus. Mandibles large, curved; petiole narrow and long. [Family assignment doubtful.] DLUSSKY, 1983. *Cret.*, USSR (Kazakh).

Pheidole WESTWOOD, 1840, p. 87. CARPENTER, 1930a. *Oligo.*, USA (Colorado)—*Holo.*

Pityomyrmex WHEELER, 1914, p. 98 [**P. tornquisti*; OD]. Little-known genus, apparently a dolichoderine. Worker: body slender, with very

- long legs and antennae; eyes large; mandibles inserted far apart, with numerous denticles; petiole much longer than broad, with a small node; middle and hind tibiae with pectinated spurs. *Oligo.*, Europe (Baltic).
- Plagiolepis** MAYR, 1861, p. 26. MAYR, 1868; WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*
- Platythyrea** ROGER, 1863, p. 172. WHEELER, 1914; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)—*Holo.*
- Pogonomymex** MAYR, 1868, p. 169. CARPENTER, 1930a. *Oligo.*, USA (Colorado)—*Holo.*
- Ponera** LATREILLE, 1804, p. 179. MAYR, 1868; EMERY, 1891; WHEELER, 1914; OKE, 1956; TAYLOR, 1964. *Oligo.*, Europe (Baltic); *Mio.*, Europe (Italy); *Pleist.*, Australia (Victoria)—*Holo.*
- Poneropsis** HEER, 1867, p. 19 [collective group] [= *Ponerites* DLUSSKY, 1981, p. 67 (collective group)]. Little-known species, based mainly on fore wings. Cell 2r+3r open or closed; cells 2rm and 3rm always closed. [A diverse group of species probably belonging to the subfamily Ponerinae.] COCKERELL, 1915; MEUNIER, 1917c, 1923c; TAYLOR, 1964; DLUSSKY, 1981. *Oligo.*, England, Europe (Germany); *Mio.*, USSR (European RSFSR).
- Poneropterus** DLUSSKY, 1983, p. 73 [**P. sphaecoides*; OD]. Male: second antennal segment elongate, third segment nearly 3 times as long as second; posterior part of petiole forming a distinct node. *Cret.*, USSR (Asian RSFSR).
- Prenolepis** MAYR, 1861, p. 26. WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*
- Prionomyrmex** MAYR, 1868, p. 77 [**P. longiceps*; OD]. Closely related to *Myrmecia* (Myrmecinae). Mandibles of worker elongate and with a distinct, uniformly denticulate, masticatory border; clypeus triangular, well developed; petiole and gaster resembling those of the Ponerinae. WHEELER, 1914; TAYLOR, 1978. *Oligo.*, Europe (Baltic).
- Prodimorphomyrmex** WHEELER, 1914, p. 112 [**P. primigenius*; OD]. Related to *Aphomomyrmex* (recent), but antennae with 10 segments; eyes small. *Oligo.*, Europe (Baltic).
- Protamblyopone** DLUSSKY, 1981, p. 65 [**P. inversa*; OD]. Little-known genus, related to *Concoctio* (recent), but antennae longer, apparently with 12 segments. KUKALOVÁ-PECK & PECK, 1976. *Mio.*, USSR (Kirghiz).
- Protanuretus** WHEELER, 1914, p. 71 [**P. succineus*; OD]. Related to *Aneuretus* (recent), but worker with less cordate head and with large eyes; antennae and legs much less slender. *Oligo.*, Europe (Baltic).
- Protazteca** CARPENTER, 1930a, p. 41 [**P. elongata*; OD]. Related to *Azteca* (recent), but worker with eyes small and more posteriorly situated; node of petiole less inclined. *Oligo.*, USA (Colorado).
- Pseudoarmania** DLUSSKY, 1983, p. 69 [**P. rasnitsyni*; OD]. Similar to *Armania*, but petiole small, somewhat broader than long, and not forming a node. *Cret.*, USSR (Asian RSFSR).
- Pseudocamponotus** CARPENTER, 1930a, p. 22 [**P. elcoanus*; OD]. Little-known genus, apparently related to *Camponotus*, but female with eyes and antennal insertions farther forward on head and antennae with 12 segments. *Mio.*, USA (Nevada).
- Pseudolasius** EMERY, 1887, p. 244. WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*
- Pseudomyrmex** LUND, 1831, p. 137. CARPENTER, 1930a. *Oligo.*, USA (Colorado)—*Holo.*
- Rhopalomyrmex** MAYR, 1868, p. 41 [**R. pygmaeus*; OD]. Similar to *Plagiolepis*, but worker with 10-segmented antennae, the 4 terminal segments forming a club. WHEELER, 1914. *Oligo.*, Europe (Baltic).
- Sicilomyrmex** WHEELER, 1914, p. 111 [**Gesomyrmex corniger* EMERY, 1891, p. 581; OD]. A formicine genus of uncertain affinities; worker with bicornuate head and 2-spined propodeum. WHEELER, 1926; BROWN & CARPENTER, 1978. *Mio.*, Europe (Italy).
- Solenopsis** WESTWOOD, 1840, p. 86. PONGRÁČZ, 1928; THÉOBALD, 1937a. *Oligo.*, Europe (France); *Mio.*, Europe (Croatia)—*Holo.*
- Sphecomyrma** WILSON & BROWN in WILSON, CARPENTER, & BROWN, 1967a, p. 8 [**S. freyi*; OD]. Worker: mandibles wasplike, short, narrow, bidentate; antennae 12-segmented; scape relatively short, funiculus long; eyes large, convex, near middle of sides of head; ocelli present; distinct sutures between thoracic segments; petiole with a distinct node; gaster without a constriction behind first segment; middle and hind tarsi with 2 spurs; sting exsertile. TAYLOR, 1978. *Cret.*, USA (New Jersey). — FIG. 265, 7. **S. freyi*; worker, ×14 (Wilson, Carpenter, & Brown, 1967b).
- Stenammas** WESTWOOD, 1840, p. 83. WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*
- Stigmomyrmex** MAYR, 1868, p. 95. WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*
- Stiphromyrmex** WHEELER, 1914, p. 67 [**S. robustus*; OD]. Similar to *Pristomyrmex* (recent), but worker with 12-segmented antennae, terminal 3 segments forming a club; middle and hind tibiae with spurs; mandibles short and convex. MAYR, 1868. *Oligo.*, Europe (Baltic).
- Syntaphus** DONISTHORPE, 1920, p. 84 [**S. wheeleri*; OD]. Little-known genus. Female: apparently similar to that of *Ectatomma* (recent) but with epinotal spines. CARPENTER & others, 1937. *Oligo.*, England.
- Tetraoponera** F. SMITH, 1852, p. 44. WHEELER, 1914; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)—*Holo.*
- Trachomyrmex** FOREL, 1893, p. 600. BARONI

URBANI, 1980a. *Oligo./Mio.*, Dominican Republic—*Holo.*
Vollenhovia MAYR, 1865, p. 21. WHEELER, 1914. *Oligo.*, Europe (Baltic)—*Holo.*

Family EUMENIDAE Leach, 1815

[Eumenidae LEACH, 1815, p. 153]

Similar to Vespidae, but tarsal claws bifid and middle tibiae with 1 apical spur. Solitary wasps, mostly fossorial or mud-daubers. Larvae predaceous on larvae of other insects. *Eoc.*—*Holo.*

Eumenes LATREILLE, 1802, p. 360. HANDLIRSCH, 1910c; PITON, 1940a. *Oligo.*, Europe (France, Germany)—*Holo.*

Alastor LEPELETIER, 1841, p. 668. [Generic assignment of fossils doubtful.] SCUDDER, 1890; MEUNIER, 1915b; STATZ, 1936b; EVANS, 1966. *Eoc.*, USA (Wyoming); *Oligo.*, Europe (Germany)—*Holo.*

Ancistrocerus WESMAEL, 1836, p. 45. PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*

Eunortonia CARPENTER, 1986, p. 576, *nom. subst. pro Pseudonortonia* TIMON-DAVID, 1944b, p. 41, *non* SOIKA, 1936 [**Pseudonortonia sepulta* TIMON-DAVID, 1944b, p. 41; OD]. Similar to *Nortonia* (recent) but with very different abdominal markings. *Oligo.*, Europe (France).

Odynerus LATREILLE, 1802, p. 362. COCKERELL, 1909n, 1914f; THÉOBALD, 1937a; PITON, 1940a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*

Rygiichium SPINOLA, 1806, p. 84. THÉOBALD, 1937a; PITON, 1940a. *Eoc.*, Europe (France)—*Holo.*

Family VESPIDAE Leach, 1815

[Vespidae LEACH, 1815, p. 153]

Pronotum extending back to tegulae; antennae with 11 to 13 segments; middle tibiae with 2 apical spurs; tarsal claws simple; mandibles short and broad; fore wing with cell 1m-cu very long; hind wing with closed cells. Social wasps, with queens, workers, and males; larvae mostly predaceous on other insects. *Eoc.*—*Holo.*

Vespa LINNÉ, 1758, p. 343. BRUES, 1926. *Oligo.*, Europe (Germany)—*Holo.*

Palaeovespa COCKERELL, 1906b, p. 54 [**P. baltica*; OD]. Little-known genus, apparently related to *Vespa* but with differences in venational details. [Family assignment doubtful.] COCKERELL, 1907c, 1909o, 1911b, 1914f, 1923e; BEQUAERT, 1930a. *Oligo.*, Europe (Baltic), USA (Colorado).

Polistes LATREILLE, 1802, p. 363. [Generic assignment of fossils doubtful.] COCKERELL, 1914f;

STATZ, 1936b; THÉOBALD, 1937a; PITON, 1940a. *Eoc.*, Europe (Germany); *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Germany)—*Holo.*
Polybia LEPELETIER, 1836, p. 533. COCKERELL, 1921a, 1923e. *Oligo.*, England—*Holo.*

Family POMPILIDAE Leach, 1815

[Pompilidae LEACH, 1815, p. 149]

Pronotum produced back to tegulae, forming a lobe over anterior thoracic spiracle; mesopleuron with an oblique groove; legs long, especially posterior pair; fore wings not longitudinally folded; hind wing with at least 1 closed cell and with a small anal lobe; first segment of gaster not forming a node or scale. Solitary, fossorial wasps; larvae predaceous on spiders. *Cret.*—*Holo.*

Pompilus FABRICIUS, 1798, p. 212. MEUNIER, 1917b; THÉOBALD, 1937a. *Oligo.*, Europe (Baltic, France)—*Holo.*

Anoplius DUFOUR, 1834, p. 484. STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*

Cryptocheilus PANZER, 1806, p. 120. COCKERELL, 1906b, 1914d; ROHWER, 1909a; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*

Dipogon FOX, 1897, p. 241. COCKERELL, 1908e; ROHWER, 1909a. *Oligo.*, USA (Colorado)—*Holo.*

Pepsis FABRICIUS, 1805, p. 207. COCKERELL, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Pompilopterus RASNITSYN, 1975, p. 106 [**P. ciliatus*; OD]. Fore wing thickly pubescent, especially in costal area; origin of RS remote from pterostigma; basal section of RS and M aligned to form a slightly curved oblique vein; crossvein 3r-m apparently present; crossvein 2r-rs slanted toward wing apex; crossvein 1m-cu strongly slanted; cell 3r narrow and long. [Family position doubtful.] *Cret.*, USSR (Asian RSFSR).—FIG. 265.3. **P. ciliatus*; fore wing, $\times 6$ (Rasnitsyn, 1975).

Priocnemis SCHIÖDTE, 1837, p. 324. BRUES, 1926; STATZ, 1936b. *Oligo.*, Europe (Germany)—*Holo.*

Family SPHECIDAE Leach, 1815

[Sphecidae LEACH, 1815, p. 148] [=Angarosphecidae RASNITSYN, 1975, p. 109]

Pronotum not extending as far back as tegulae; males with 13 antennal segments, females with 12; hind wing with an anal lobe and closed cells. Solitary, fossorial wasps; larvae predaceous on various insect larvae and on spiders. *Cret.*—*Holo.*

- Sphex** LINNÉ, 1758, p. 569. PONGRÁ CZ, 1928; ZEUNER, 1931; STATZ, 1936b. *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany, Yugoslavia)—*Holo.*
- Angarosphex** RASNITSYN, 1975, p. 110 [**A. myrmicopterus*; OD]. Fore wing with vestiges of crossvein 1r-rs very short; crossvein 2r-rs shorter than width of pterostigma; cells 2rm and 3rm elongate. Head quadrangular; pronotum moderately long. RASNITSYN, 1980b. *Cret.*, USSR (Asian RSFSR).
- Cerceris** LATREILLE, 1802, p. 367. TIMON-DAVID, 1944b. *Oligo.*, Europe (France)—*Holo.*
- Chalybion** DAHLBOM, 1844, p. 21. HAGEN, 1858a. *Oligo.*, USA (Colorado)—*Holo.*
- Ectemnius** DAHLBOM, 1845, p. 389. MEUNIER, 1912e; COCKERELL, 1910a; BOHART & MENKE, 1976. *Oligo.*, Europe (Germany), USA (Colorado)—*Holo.*
- Gallosphex** SCHLÜTER, 1978a, p. 83 [**G. cretaceus*; OD]. Apparently an ampulicine. Fore wing with pterostigma very small, triangular; basal section of M slightly longer than basal section of RS; crossvein 2r-rs very short; crossveins 2r-m and 3r-m well developed; cell 2rm larger than cell 3rm. *Cret.*, Europe (Germany).
- Gorytes** LATREILLE, 1804, p. 180. [Generic assignment of fossil doubtful.] COCKERELL, 1922h, 1924a; EVANS, 1966; BOHART & MENKE, 1976. *Oligo.*, Europe (Germany)—*Holo.*
- Harpactostigma** ASHMEAD, 1899, p. 299. COCKERELL, 1922h, 1924a; EVANS, 1966; BOHART & MENKE, 1976. *Eoc.*, USA (Colorado)—*Holo.*
- Larrophanes** HANDLI RSCH, 1907, p. 888 [**L. ophthalmicus*; OD]. Little-known genus, possibly belonging to the Larrinae. [Family assignment doubtful.] *Mio.*, Europe (Italy).
- Lisponema** EVANS, 1969, p. 255 [**L. singularis*; OD]. Similar to *Spilomena* (recent) but with pterostigma slightly longer and veins 3-rm and 2m-cu absent; tibial spur formula 1,1,2; legs very slender, smooth. *Cret.*, Canada (Manitoba). — FIG. 265.1. **L. singularis*; fore and hind wings, $\times 3$ (Evans, 1969).
- Mellinus** FABRICIUS, 1790, p. 226. ROHWER, 1908d. *Oligo.*, USA (Colorado)—*Holo.*
- Passaloeus** SHUCKARD, 1837, p. 188. ROHWER, 1909b. *Oligo.*, USA (Colorado)—*Holo.*
- Philanthus** FABRICIUS, 1790, p. 224. ROHWER, 1909c; THÉOBALD, 1937a. *Oligo.*, USA (Colorado), Europe (France)—*Holo.*
- Philoponites** COCKERELL, 1915, p. 482 [**P. clarus*; OD]. Little-known genus. Cells 1r+2r and 1mcu almost as wide as long; cell 2rm nearly triangular. *Oligo.*, England.
- Pison** JURINE, 1808, p. 255. ROHWER, 1908a; COCKERELL, 1909o. *Oligo.*, USA (Colorado), Europe (Baltic)—*Holo.*
- Pittoecus** EVANS, 1973, p. 170 [**P. pauper*; OD]. Male similar to *Passaloeus*. Head broad, with large eyes; antennae short, with 12 segments; mandibles straight, not dentate; tibial spur formula 1,1,2; claws dentate. *Cret.*, USSR (Asian RSFSR).
- Prophilanthus** COCKERELL, 1906b, p. 46 [**P. destructus*; OD]. Similar to *Philoponites*, but cells 1r+2r and 1mcu at least twice as long as wide. *Oligo.*, USA (Colorado).
- Psammaecius** LEPELETIER, 1832, p. 72. COCKERELL, 1906b; EVANS, 1966; PULAWSKI & RASNITSYN, 1980. *Oligo.*, USA (Colorado)—*Holo.*
- Sceliphron** KLUG, 1801, p. 561. [Generic assignment of fossils doubtful.] MEUNIER, 1915a; COCKERELL, 1921a. *Oligo.*, England; *Mio.*, Europe (France)—*Holo.*
- Taimyrisphex** EVANS, 1973, p. 167 [**T. pristinus*; OD]. Male: antennae short, with 13 segments; scape only slightly longer than thick; eyes and ocelli large; pronotum with small, rounded posterior lobes nearly reaching tegulae; venation more generalized than in *Archisphex* (recent). [Family position uncertain, possibly related to Falsifomicidae.] RASNITSYN, 1980b. *Cret.*, USSR (Asian RSFSR). — FIG. 265.2. **T. pristinus*; fore and hind wings, $\times 20$ (Evans, 1973).
- Tracheliodes** MORAWITZ, 1866, p. 249. COCKERELL, 1909o, 1910a; BOHART & MENKE, 1976. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Family ANDRENIDAE Latreille, 1802

[Andrenidae LATREILLE, 1802b, p. 369]

Glossa pointed; labial palpi with all segments similar, or first segment elongate and flattened; 2 subantennal sutures below each antennal socket. Solitary bees, nests sometimes colonial. *Oligo.*—*Holo.*

Andrena FABRICIUS, 1775, p. 376. COCKERELL, 1906b, 1908n, 1911b, 1914f. *Oligo.*, Europe (Baltic), USA (Colorado); *Mio.*, Europe (Germany)—*Holo.*

Libellulapis COCKERELL, 1906b, p. 42 [**L. anti-quorum*; OD]. Apparently close to *Panurgus* (recent), but eyes very prominent. COCKERELL, 1909c, 1913b; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado).

Lithandrena COCKERELL, 1906b, p. 44 [**L. sax-arum*; OD]. Close to *Andrena* but differing in shape of cells 1r and 2rm. ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado).

Pelandrena COCKERELL, 1909f, p. 159 [**P. reducta*; OD]. Close to *Andrena*, but fore wing with cell 3rm apparently absent. ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado).

Family HALICTIDAE Ashmead, 1899

[Halictidae ASHMEAD, 1899, p. 90]

Labial palpi with 4 equal segments; glossa pointed; mesepisternum with anterior-dorsal

groove; fore wing with basal section of vein M strongly arched and crossvein 2m-cu slightly arched. Mostly solitary, fossorial bees, some social. *Oligo.*—*Holo.*

Halictus LATREILLE, 1804, p. 182 [= *Prohalictus* ARMBRUSTER, 1938, p. 48 (type, *P. schemppi*)]. TIMON-DAVID, 1944b; ZEUNER & MANNING, 1976. *Oligo.*, Europe (France), USA (Colorado); *Mio.*, Europe (Germany)—*Holo.*

Cyrtapis COCKERELL, 1908f, p. 339 [**C. anomalus*; OD]. Crossvein 3r-m sigmoidal, anterior end closer to apex than posterior end. [Family assignment doubtful.] *Oligo.*, USA (Colorado).

Family MELITTIDAE Schenk, 1860

[Melittidae SCHENK, 1860, p. 136]

Segments of labial palpi similar and cylindrical; glossa acute, often elongate; dorsal mesoepisternal groove absent; fore wing with 2 or 3 submarginal cells. Solitary bees. *Oligo.*—*Holo.*

Melitta KIRBY, 1802, p. 130. COCKERELL, 1909k. *Oligo.*, USA (Colorado)—*Holo.*

Ctenoplectrella COCKERELL, 1909o, p. 13 [**C. viridiceps*; OD]. Similar to *Glyptapis* but eyes bare. KELNER-PILLAULT, 1970a. *Oligo.*, Europe (Baltic).

Glyptapis COCKERELL, 1909o, p. 13 [**G. mirabilis*; OD]. Apparently related to *Ctenoplectra* (recent); eyes hairy, thorax strongly sculptured; metathorax divided by ridges into large quadrangular areas. KELNER-PILLAULT, 1970a; ZEUNER & MANNING, 1976. *Oligo.*, Europe (Baltic).

Family MEGACHILIDAE Kirby, 1837

[Megachilidae KIRBY in RICHARDSON, SWAINSON, & KIRBY, 1837, p. 270]

Labrum longer than broad; labial palpi with segments 1 and 2 very elongate and flattened; a single suture below each antennal socket; pollen brush (scopa), when present, on gastral sternites. Solitary bees; nests small, diversely situated. *Oligo.*—*Holo.*

Megachile LATREILLE, 1802, p. 434. COCKERELL, 1908b, 1925g; SALT, 1931; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado); *Mio.*, USSR (Asian RSFSR)—*Holo.*

Anthidium FABRICIUS, 1805, p. 364. [Generic assignment of fossils doubtful.] COCKERELL, 1906b; STATZ, 1936b; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado), Europe (Germany)—*Holo.*

Dianthidium COCKERELL, 1900, p. 412. COCKERELL, 1906b. *Oligo.*, USA (Colorado)—*Holo.*

Heriades SPINOLA, 1808, p. 7. COCKERELL, 1906b,

1913f, 1917b, 1923e, 1925d; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado)—*Holo.*

Lithanthidium COCKERELL, 1911a, p. 225 [**L. pertriste*; OD]. Apparently related to *Anthidium*. Fore wing with cells 1r and 2rm present; basal part of M strongly arched. *Oligo.*, USA (Colorado).

Lithurge LATREILLE, 1825, p. 463. HEER, 1865, 1867; COCKERELL, 1909m; ZEUNER & MANNING, 1976. *Mio.*, Europe (Germany)—*Holo.*

Osmia PANZER, 1806, p. 230. HEER, 1849; HEYDEN, 1862; STATZ, 1936b; ZEUNER & MANNING, 1976. *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany)—*Holo.*

Family ANTHOPHORIDAE

Kirby, 1837

[Anthophoridae KIRBY in RICHARDSON, SWAINSON, & KIRBY, 1837, p. 271]

Glossa long; labrum broader than long; clypeus protuberant; fore coxae slightly broader than long; hind tibia with a scopa and 2 apical spurs; pollen basket (corbicula) absent. Solitary bees, nesting in ground. *Eoc.*—*Holo.*

Anthophora LATREILLE, 1803, p. 167. COCKERELL, 1908m, 1908n; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado)—*Holo.*

Anthophorites HEER, 1849, p. 97 [**A. mellona*; SD COCKERELL, 1909m, p. 315]. Little-known genus, apparently related to *Anthophora*. HEER, 1867; ZEUNER & MANNING, 1976. *Oligo.*, Europe (France); *Mio.*, Croatia.

Celliforma BROWN, 1934, p. 532 [**C. spirifer*; OD]. Little-known genus. Larval chambers, with spiral apex. BROWN, 1935. *Eoc.*, USA (Wyoming).

Protomelecta COCKERELL, 1908f, p. 341 [**P. brevipennis*; OD]. Apparently related to *Melecta* (recent). Fore wings short, not reaching tip of gaster; cell 2r+3r long; cells 1r, 2rm, and 3rm present. [Family assignment doubtful.] TILLYARD, 1926d; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado).

Family APIDAE

Leach, 1815

[Apidae LEACH, 1815, p. 160]

Similar to Anthophoridae, but workers and most females with a corbicula on hind tibiae; spurs absent (except in Bombicinae). Mostly social bees. *Eoc.*—*Holo.*

Apis LINNÉ, 1758, p. 343. COCKERELL, 1907e; STATZ, 1931; ZEUNER, 1931; THÉOBALD, 1937a; ROUSSY, 1960; KELNER-PILLAULT, 1969; ZEUNER & MANNING, 1976. *Oligo.*, Europe (Germany, France); *Mio.*, Europe (Germany, Sicily)—*Holo.*

- Bombus** LATREILLE, 1802, p. 437 [= *Calyptapis* COCKERELL, 1906b, p. 41 (type, *C. florissantiensis*). HEER, 1867; NOVÁK, 1877; CARPENTER, 1931d; COCKERELL, 1931b; MILLIRON, 1971; ZEUNER & MANNING, 1976. *Oligo.*, USA (Colorado), Europe (Czechoslovakia); *Mio.*, Europe (Germany), USA (Washington)—*Holo.*
- Ceratina** LATREILLE, 1802, p. 380. COCKERELL, 1906b; DALY, 1973. *Oligo.*, USA (Colorado)—*Holo.*
- Chalcobombus** COCKERELL, 1909o, p. 11 [**C. humilis*; OD]. Small bees of uncertain relationships but probably close to the Bombini. Vertex usually with coarse, erect bristles, sparingly plumose; eyes not usually hairy; ocelli large, close together, forming a slight curve; antennal cleaner with exceptionally long hairs. ZEUNER & MANNING, 1976. *Oligo.*, Europe (Baltic).
- Electrapis** COCKERELL, 1909o, p. 7 [**Apis meliponoides* BUTTEL-REEPEN, 1906, p. 158; OD]. Similar in general appearance to *Apis*; hind basitarsus about twice as long as broad; posterior tibiae with a single short spur or none; eyes with little or no hair. COCKERELL, 1908n; MANNING, 1961; KELNER-PILLAULT, 1969, 1970a, 1974; ZEUNER & MANNING, 1976. *Oligo.*, Europe (Baltic).
- Kelnermelia** MOURE in MOURE & CAMARGO, 1978, p. 565 [**Trigona eocenica* KELNER-PILLAULT, 1970b, p. 437; OD]. Similar to *Trigona*. Scutellum strongly projected and swollen, with scutocutellar suture deeply depressed. *Oligo.*, Europe (Baltic).
- Plebeia** SCHWARZ, 1938, p. 480. WILLE & CHANDLER, 1964; MOURE & CAMARGO, 1978. *Oligo.*, Dominican Republic—*Holo.*
- Probombus** PITON, 1940a, p. 218 [**P. hirsutus*; OD]. Little-known genus, apparently similar to *Bombus*. KELNER-PILLAULT, 1969. *Eoc.*, Europe (France).
- Sophrobombus** COCKERELL, 1909p, p. 21 [**S. fatalis*; OD]. Similar to *Chalcobombus*. Mandibles with a convex cutting edge; ocelli large and arranged in a curve; basitarsus flattened, short; inner hind tibial spur present. ZEUNER & MANNING, 1976. *Oligo.*, Europe (Baltic).
- Tetralonia** SPINOLA, 1839, p. 538. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*
- Trigona** JURINE, 1807, p. 245 [= *Meliponorytes* TOSI, 1896, p. 352 (type, *M. succini*). COCKERELL, 1922e; WILLE, 1959, 1977; KELNER-PILLAULT, 1970b; KERR & DA CUNHA, 1976; ZEUNER & MANNING, 1976; MOURE & CAMARGO, 1978; MICHENER, 1982. *Oligo.*, Europe (Baltic); *Oligo./Mio.*, Mexico (Chiapas); *Mio.*, Europe (Sicily), Burma—*Holo.*
- Xylocopa** LATREILLE, 1802, p. 379. HEER, 1849; COCKERELL, 1909m; STATZ, 1936b; ZEUNER, 1938; ZEUNER & MANNING, 1976. *Oligo.*, Europe (Germany); *Mio.*, Europe (Germany)—*Holo.*

Family UNCERTAIN

The following genera, apparently belonging to the order Hymenoptera, suborder Apocrita, are too poorly known to permit assignment to families.

- Baissobius** RASNITSYN, 1975, p. 128 [**B. parvus*; OD]. Fore wing with venation much reduced; no closed cells distal to level of basal sections of RS and M, except for cell 3r; pterostigma elongate. Head large and wide, with small eyes. *Cret.*, USSR (Asian RSFSR).
- Cenomanscelio** SCHLÜTER, 1978a, p. 78 [**C. pulcher*; OD]. Little-known genus, based on body; venation unknown. Antennae with 11 segments, apical 5 enlarged and forming a club; lateral ocelli relatively close to compound eyes. [Possibly related to Scelionidae.] *Cret.*, Europe (Germany).
- Cretopone** DLUSSKY, 1975, p. 119 [**C. magna*; OD]. Little-known genus, possibly a formicid. Female: middle and hind tarsi with single spurs; petiole apparently very large. *Cret.*, USSR (Kazakh).
- Cretophax** RASNITSYN, 1975, p. 106 [**C. incertus*; OD]. Fore wing with basal sections of RS and M aligned to form straight, oblique line; crossvein 1r-rs obsolescent; crossvein 2r-rs directed toward wing apex; apex of cell 3r acute; crossvein 1m-cu at base of cell 2rm. Pronotum of moderate length, projecting at sides; legs short; femora very short and thick; first segment of hind tarsus not broadened; abdomen long, strongly sclerotized. [Possibly related to the Sphecoidea.] RASNITSYN, 1980a, 1980b. *Cret.*, USSR (Asian RSFSR).—FIG. 265,6. **C. incertus*; wings and body, ×25 (Rasnitsyn, 1975).
- Curiosivespa** RASNITSYN, 1975, p. 113 [**C. curiosa*; OD]. Fore wing with RS arising from R at base of pterostigma; pterostigma narrow; apex of cell 3r submarginal; crossvein 1m-cu far basad of cell 2rm. [Possibly related to Masaridae.] *Cret.*, USSR (Kazakh).—FIG. 265,5. **C. curiosa*; fore wing, ×5.5 (Rasnitsyn, 1975).
- Diapriites** STATZ, 1938b, p. 104 [**D. insignicornis*; OD]. Little-known genus, possibly a proctotrupoid. Antennae with 12 segments. *Oligo.*, Europe (Germany).
- Iscopinus** KOZLOV, 1974, p. 145 [**I. baissicus*; OD]. Antennae with at least 15 segments; cell 3r closed; segments of gaster short, transverse. [Possibly related to Pelecinidae.] *Cret.*, USSR (Asian RSFSR).
- Platygasterites** CARPENTER, herein [**P. femoralis* STATZ, 1938b, p. 106; OD]. Little-known genus; wing venation apparently absent. [The original generic name, *Platygasterites*, was a *nomen nudum* (STATZ, 1938b).] *Oligo.*, Europe (Germany).

- Proctotrypites** MEUNIER, 1918, p. 145 [**P. rothen-sis*; OD]. Little-known genus. Antennae with 11 segments; venation much reduced. *Oligo.*, Europe (Germany).
- Scelionites** STATZ, 1938b, p. 107 [**S. capitatus*; OD]. Little-known genus, possibly a proctotrupoid. *Oligo.*, Europe (Germany).
- Vitimosphex** RASNITSYN, 1975, p. 127 [**V. incompletus*; OD]. Little-known genus, probably related to *Baissodes*. Fore wing with cell 3r narrowly rounded apically; RS extending beyond apex of cell 3r; cell 2rm short. *Cret.*, USSR (Asian RSFSR).

Suborder UNCERTAIN

The following genera, apparently belonging to the order Hymenoptera, are too poorly known to permit assignment to suborders.

- Proopocritus** RASNITSYN, 1975, p. 22 [**P. praecursor*; OD]. Little-known genus, based on fore wing fragment; SC absent; area between R and costal margin narrow; basal section of RS straight and shorter than basal section of M, with slight slope toward wing apex; crossvein 1r-rs weakly developed; crossvein 2r-rs situated at center of preostigma; cell 1mcu long. [Possibly related to Karataviidae, suborder Symphyta.] *Jur.*, USSR (Kirghiz).
- Protenthredo** PONGRÁ CZ, 1928, p. 156 [**P. transylvanicus*; OD]. Little-known genus; venation unknown. *Mio.*, Europe (Croatia).

Infraclass NEOPTERA

Order UNCERTAIN

The following genera, apparently belonging to the infraclass Neoptera, are too poorly known to permit assignment to orders.

- Aleuronympha** RIEK, 1974b, p. 272 [**A. bibulla*; OD]. Little-known genus, based on small nymph with wing buds. [Originally placed in the Hemiptera (Homoptera, family Permaleurodidae) but probably belonging to the Blattaria. The supposed eyes are cuticular protuberances on pronotum; see ROTH, 1982, figs. 16–20. Also see note under *Permaleurodes*.] *Perm.*, South Africa.
- Apheloneura** CARPENTER, 1976, p. 365 [**A. minutissima*; OD]. Little-known genus, based on complete wings and parts of body. [Type of the family Apheloneuridae CARPENTER, 1976.] *Perm.*, USA (Kansas).
- Aphryganoneura** TILLYARD, 1926e, p. 276 [**A. anormala*; OD]. Little-known genus. [Placed in the Mecoptera by TILLYARD (1926e) and MARTYNOVA (1962e) but considered by HANDLIRSCH (1939) to belong to the Neuroptera.] RIEK, 1953; WILLMANN, 1978. *Perm.*, Australia (New South Wales).
- Archipanorpa** TILLYARD, 1917a, p. 191 [**A. magnifica*; OD]. Little-known genus, based on wing fragments. [Type of the family Archipanorpidae TILLYARD, 1917a; assigned by TILLYARD (1917a) to a new order, Protomecoptera.] RIEK, 1953; WILLMANN, 1978. *Trias.*, Australia (Queensland).
- Austroidelia** RIEK, 1954c, p. 161 [**A. perplexa*; OD]. Little-known genus, based on proximal fragment of wing. [Originally placed in the Proorthoptera (family Ideliidae).] *Trias.*, Australia (New South Wales).
- Choristosialis** TILLYARD, 1932a, p. 19 [**C. enigmatica*; OD]. Little-known genus, based on wing fragment. [Type of the family Choristosialidae TILLYARD, 1932a. Originally placed by TILLYARD in the Neuroptera, but transferred to the Mecoptera by CARPENTER (1943a); ordinal position considered by WILLMANN (1978) to be uncertain.] *Perm.*, USA (Kansas).
- Climaconeura** PRUVOST, 1912, p. 327 [**C. remauxi*; OD]. Little-known genus, based on fragment of wing. [Type of the family Climaconeuridae HANDLIRSCH, 1919b. Originally placed in the Protorthoptera by PRUVOST (1912, 1919); transferred by HANDLIRSCH (1919b, 1922) to the order Mixotermitoidea, by HAUPT (1952) to the Mecoptera, and by SHAROV (1962d) to the Proorthoptera (Paraplecoptera).] WILLMANN, 1978. *U. Carb.*, Europe (France).
- Crosaphis** EVANS, 1971, p. 146 [**C. anomala*; OD]. Little-known genus, based on wing. [Placed in the Hemiptera (Aphidoidea) by EVANS (1971) and in the Hemiptera (Coccoidea) by HEIE (1981); transferred to Diptera by KOVALEV (1983).] *Trias.*, Australia (Queensland).
- Ctenostematopteryx** HAUPT, 1952, p. 253 [**C. thuringiaca*; OD]. Little-known genus. [Originally placed in the Mecoptera, but transferred to Insecta, *incertae sedis* by HENNIG (1969c).] WILLMANN, 1978. *Perm.*, Europe (Germany).
- Elmothone** CARPENTER, 1976, p. 353 [**E. martynovae*; OD]. Little-known genus, based on incomplete fore wing. [Originally placed in the order Neuroptera.] *Perm.*, USA (Kansas).
- Eopanorpella** SCHMIDT, 1962, p. 849 [**E. ernsti*; OD]. Little-known genus, based on incomplete wing. [Originally placed in the Mecoptera (family Permochoristidae), but assignment to that order has been seriously questioned by HENNIG (1969c) and WILLMANN (1978).] *U. Carb.*, Europe (Germany).

- Eukuloja** ROHDENDORF, 1962a, p. 72 [**Kuloja cubitalis* MARTYNOV, 1932, p. 5; OD] [= *Parakuloja* ROHDENDORF, 1962a, p. 72 (type, *Kuloja paurovenosa* MARTYNOV, 1932, p. 3)]. Little-known genus, based on isolated wings. [Originally placed by ROHDENDORF (1962a) in the order Diaphanopteroidea, but transferred to the order Hypoperlida (allied to the Psocoptera) by SINITSHENKOVA (1981b).] *Perm.*, USSR (European RSFSR).
- Gelasopteron** CARPENTER, 1976, p. 372 [**G. gracile*; OD]. Little-known genus, based on a very elongate wing. [Type of the family Gelasopteridae CARPENTER, 1976.] *Perm.*, USA (Kansas).
- Geroneura** MATTHEW, 1889, p. 57 [**G. wilsoni*; OD]. Little-known genus. [Originally placed in the order Uncertain; transferred to the new order Mixotermiotoidea by HANDLIRSCH (1906a, 1919b).] PRUVOST, 1919. *U. Carb.*, Canada (New Brunswick).
- Glessaria** KOCH & BERENDT, 1854, p. 117 [**G. rostrata*; OD]. Little-known genus. [Originally placed in Thysanura, but considered by HANDLIRSCH (1906b) to be a coleopterous larva.] *Oligo.*, Europe (Baltic).
- Hypoperlia** MARTYNOV, 1928b, p. 57 [**H. elegans*; OD]. Little-known genus, based on isolated wings. [Type of the family Hypoperlidae MARTYNOV, 1928b. Included in the Protorthoptera by MARTYNOV (1928b); transferred to the superorder Perloidea, *incertae sedis* by ROHDENDORF (1962a); and placed in a new order, Hypoperlida (allied to the Psocoptera), by RASNITSYN (1980f).] SINITSHENKOVA, 1981b. *Perm.*, USSR (European RSFSR).
- Hypoperlopsis** ZALESSKY, 1948b, p. 1042 [**H. splendens*; OD]. Little-known genus. [Originally placed in the order Perlaria; transferred to the superorder "Plecopteroidea," order Uncertain by SHAROV (1962d).] *Perm.*, USSR (Asian RSFSR).
- Ignotala** RIEK, 1973, p. 522 [**I. mirifica*; OD]. Little-known genus, based on wing fragment. [Type of the family Ignotalidae and the superfamily Ignotaloidea RIEK, 1973. Originally placed in the Hemiptera (Homoptera), although the genus is considered to be "intermediate in many attributes between the Protoblattodea and the Homoptera."] *Perm.*, South Africa.
- Kamopanorpa** MARTYNOV, 1928b, p. 101 [**K. lata*; OD]. Based on a series of well-preserved wings. [Originally placed in the Mecoptera by MARTYNOV (1928b) and MARTYNOVA (1962e); transferred to the Trichoptera by SUKATSCHEVA (1976) and to the Trichoptera-Mecoptera complex by WILLMANN (1978).] *Perm.*, USSR (European and Asian RSFSR).
- Kliveria** HANDLIRSCH, 1906b, p. 325 [**Termes incertus* KLIVER, 1886, p. 104; OD]. Little-known genus, based on isolated wing. [Placed by KLIVER (1886) in the Isoptera; transferred by GÜTHORL (1939) to the order Mixotermiotoidea, by HAUPT (1952) to the Mecoptera, and by SHAROV (1962d) to the Protorthoptera (Paraplecoptera).] WILLMANN, 1978. *U. Carb.*, Europe (Germany).
- Lemmatophoropsis** ZALESSKY, 1935, p. 691 [**L. sibirica*; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the Protorthoptera.] *Trias.*, USSR (Asian RSFSR).
- Marimerobius** ZALESSKY, 1946b, p. 543 [**M. splendens*; OD]. Little-known genus, based on fore wing. [Placed in the Neuroptera by ZALESSKY (1946b) and MARTYNOV (1952b, 1962d), but transferred to the Mecoptera by WILLMANN (1978), in the new family Marimerobiidae.] *Perm.*, USSR (Asian RSFSR).
- Megoniella** RIEK, 1973, p. 526 [**M. multinerva*; OD]. Little-known genus, based on a wing fragment. [Originally placed in the Hemiptera (Homoptera), family Ignotalidae.] *Perm.*, South Africa.
- Mesacridites** RIEK, 1954c, p. 163 [**M. elongata*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Protorthoptera, family Sthenaropodidae.] *Trias.*, Australia (New South Wales).
- Metropatorites** KELLER, 1934, p. 45 [**M. kassenbergensis*; OD]. Little-known genus, based on fragment of wing. [Considered by KELLER to be closely related to *Metropator* (Miomoptera, Metropatoridae), but placed by SCHMIDT (1962) and HENNIG (1969c) in *incertae sedis* at the ordinal level.] WILLMANN, 1978. *U. Carb.*, Europe (Germany).
- Micropalentomum** SCHMIDT, 1962, p. 833 [**M. minisculum*; OD]. Little-known genus, based on a very small, nymphal wing, probably from an orthopteroid species. [Type of the family Micropalentomidae SCHMIDT, 1962. Not assigned to an order.] *U. Carb.*, Europe (Germany).
- Mixotermes** STERZEL, 1881, p. 273 [**M. lagauensis*; OD]. Little-known genus. [Originally placed in the existing order Isoptera and considered to be a subgenus of *Termes*; transferred to the Orthoptera by BRONGNIART (1885a), to the new order Mixotermiotoidea by HANDLIRSCH (1906a, 1919b, 1920), and to the extinct order Hapalopteroidea by PRUVOST (1919).] *U. Carb.*, Europe (Germany).
- Mononeura** BECKER-MIGDISOVA, 1951, p. 1208 [**M. angustipennis*; OD]. Little-known genus, based on incomplete wing. [Placed in the family Uninervidae, order Uncertain.] BECKER-MIGDISOVA, 1962b. *Trias.*, USSR (Kirghiz).
- Nugonioneura** TILLYARD, 1937a, p. 92 [**N. problematica*; OD]. Little-known genus, based on isolated wings. [Type of the family Nugonioneuridae CARPENTER, 1976. Originally placed

- in the Psocoptera by TILLYARD (1937a); transferred to the Protorthoptera by CARPENTER (1976).] *Perm.*, USA (Kansas).
- Ocellia** OLFERS, 1907, p. 7 [**O. articularicornis*; OD]. Little-known genus. [Originally placed in order Zygentoma, but considered by SILVESTRI (1913a) to be based on an immature specimen of the order Dermaptera.] *Oligo.*, Europe (Baltic).
- Palaeomantina** RASNITSYN, 1977c, p. 75 [**P. peniamera*; OD]. Little-known genus. [Originally placed in the Miomoptera, family Palaeomantiscidae. See discussion under the order Miomoptera.] *Perm.*, USSR (Asian RSFSR).
- Palaeomantisca** MARTYNOV, 1940, p. 34 [**P. lata*; OD]. Little-known genus, based on wing fragment. [Placed in the order Miomoptera (family Palaeomanteidae) by MARTYNOV (1940) and MARTYNOVA (1962a); transferred to the new family Palaeomantiscidae by RASNITSYN (1977c). See discussion under the order Miomoptera.] *Perm.*, USSR (Asian RSFSR).
- Paraulacus** PING, 1928, p. 17 [**P. sinicus*; OD]. Little-known genus, based on fragments of body and wings. [Originally placed in the order Hymenoptera, family Aulacidae.] *Cret.*, China (Jehol).
- Perielytron** ZALESSKY, 1943, p. 70 [**P. mirabilis*; OD]. Little-known genus, based on incomplete specimen. [Type of family Perielytridae ZALESSKY and originally placed in a new order, Perielytrodea ZALESSKY (1943, 1948c). Possibly related to the Psocoptera.] SHAROV, 1962a; RASNITSYN, 1980f. *Perm.*, USSR (Asian RSFSR).
- Permaleurodes** BECKER-MIGDISOVA, 1959a, p. 108 [**P. rotundatus*; OD]. Little-known genus, based on small nymph with wing buds. [Type of family Permaleurodidae BECKER-MIGDISOVA, 1959a. Originally placed in Hemiptera (Homoptera), but transferred to Blattaria by MOUND and HALSEY (1978). See note under *Aleuromypha*.] *Perm.*, USSR (Asian RSFSR).
- Permarrhaphus** MARTYNOV, 1931c, p. 211 [**P. venosus*; OD]. Little-known genus, based on incomplete wing. [Type of the family Permarrhaphidae MARTYNOV, 1931c. Placed in the Coleoptera by MARTYNOV (1931c) and by ROHDENDORF and PONOMARENKO (in ROHDENDORF, 1962b); transferred to the order Paracoleoptera by LAURENTIAUX (1953), and to the order Hypoperlida by RASNITSYN (1980f).] ZALESSKY, 1947. *Perm.*, USSR (European RSFSR).
- Permembia** TILLYARD, 1928f, p. 479 [**P. delicatula*; OD]. Little-known genus, based on poorly preserved wing. [Type of the family Permembiiidae TILLYARD, 1937a. Originally placed by TILLYARD (1928f, 1937a) in the family Delopteridae, then considered to belong to the order Psocoptera; subsequently transferred with some uncertainty by MARTYNOVA (1962a) to the Miomoptera. CARPENTER (1976), following study of the type specimen of *Permembia*, placed the genus in *incertae sedis* at the ordinal level.] CARPENTER, 1935a; RIEK, 1973, 1976a. *Perm.*, USA (Kansas).
- Permomerope** TILLYARD, 1926e, p. 275 [**P. australis*; OD]. Little-known genus. [Type of the family Permomeropidae HANDLIRSCH, 1937. Originally placed in the Mecoptera by TILLYARD (1926e); transferred to the Trichoptera by SUKATSHEVA (1976); and assigned by WILLMANN (1978) to the Mecoptera-Trichoptera complex, order Unknown.] *Perm.*, Australia (New South Wales); USSR (Kazakh).
- Permonia** KUKALOVÁ, 1963a, p. 43 [**P. permonii*; OD]. Little-known genus, based on several isolated wings. [Originally placed in the order Miomoptera (family Permembiiidae); transferred to the order Uncertain by CARPENTER (1976).] *Perm.*, Europe (Czechoslovakia).
- Permonikia** KUKALOVÁ, 1963a, p. 41 [**P. permoniki*; OD]. Little-known genus, based on isolated wings. [Originally placed in the order Miomoptera, family Permembiiidae. See discussion under *Permembia*.] CARPENTER, 1976; RASNITSYN, 1977c. *Perm.*, Europe (Czechoslovakia).
- Permonka** RIEK, 1973, p. 520 [**P. bifida*; OD]. Genus based on specimens of fore and hind wings. [Type of the family Permonkiidae RASNITSYN, 1977c. Placed by RIEK (1973) and RASNITSYN (1977c) in the Miomoptera. See discussion under the order Miomoptera.] *Perm.*, South Africa (Natal); *Trias., Jur.*, USSR (Asian RSFSR).
- Permonympa** SHAROV, 1957b, p. 1107 [**P. gracilis*; OD]. Little-known genus, based on nymph with long antennae and legs, prominent cerci, and slender wing pads. [Originally placed in the order Miomoptera.] ROHDENDORF & RASNITSYN, 1980. *Perm.*, USSR (Asian RSFSR).
- Permosialis** MARTYNOV, 1928b, p. 94 [**P. paucinervis*; OD]. Little-known genus. [Type of the family Permosialidae MARTYNOV (1928b). Placed in the order Neuroptera by MARTYNOV (1928b) and MARTYNOVA (1962a), but transferred to the Miomoptera by RASNITSYN (1977c, and in ROHDENDORF & RASNITSYN, 1980).] *Perm.*, USSR (European RSFSR).
- Platychorista** TILLYARD, 1926c, p. 154 [**P. venosa*; OD] [= *Protomerope* TILLYARD, 1926c, p. 157 (type, *P. permiana*)]. Little-known genus. [Type of the family Protomeropidae TILLYARD, 1926c. Placed in the Mecoptera by TILLYARD (1926c), MARTYNOVA (1962e), and HENNIG (1969c). Transferred to the Trichoptera by SUKATSHEVA (1976) and to the Trichoptera-Lepidoptera complex by WILLMANN (1978).] CARPENTER, 1930b. *Perm.*, USA (Kansas).
- Protoblattinopsis** LAURENTIAUX, 1953, p. 447 [**P. stubblefeldi*; OD]. Little-known genus, based on

- proximal fragment of wing. [Type of the family Protoblattinopsidae LAURENTIAUX, 1966. Originally placed in the order Protorthoptera, but transferred by RASNITSYN (1980f) to the order Blattinopseida, considered to be related to the order Caloneurodea.] KUKALOVÁ, 1959b; CARPENTER, 1966. *U. Carb.*, England.
- Recula** HANDLIRSCH, 1906b, p. 128 [**R. parva*; OD]. Little-known genus, based on incomplete wing. [Placed by HANDLIRSCH (1906b) in a new order, Reculoidea.] SCHLECHTENDAL, 1913; HANDLIRSCH, 1919b, 1920, 1922. *U. Carb.*, Europe (Germany).
- Redactineura** RIEK, 1973, p. 529 [**R. acuminata*; OD]. Little-known genus, based on apical fragment of wing. [Not assigned to an order, but placed in the family Uninervidae, order Uncertain.] *Perm.*, South Africa.
- Reprehensa** BODE, 1953, p. 292 [**R. acuminata*; OD]. Little-known genus, based on poorly preserved wing. [Originally placed in the Mecoptera.] *Jur.*, Europe (Germany).
- Saurophthirus** PONOMARENKO, 1976, p. 103 [**S. longipes*; OD]. Little-known genus, based on wingless specimen, with long, slender legs. [Originally placed in the order Siphonaptera.] RASNITSYN, 1980c. *Cret.*, USSR (Asian RSFSR).
- Scalaeoptera** BOLTON, 1922, p. 88 [**S. recta*; OD]. Little-known genus, based on small fragment of wing. [Originally placed, with some doubt, in the Protorthoptera.] *U. Carb.*, England.
- Sheimia** MARTYNOVA, 1958, p. 69 [**S. sojanensis*; OD]. Little-known genus, based on wing fragment and part of body. [Type of the family Sheimiidae MARTYNOVA (1958). Placed in the Embioptera by MARTYNOVA (1958, 1962a) and RIEK (1970); transferred to the order Uncertain by CARPENTER (1976).] RASNITSYN in ROHDENDORF & RASNITSYN, 1980. *Perm.*, USSR (European RSFSR).
- Sindomiomoptera** RASNITSYN, 1977c, p. 71 [**S. sojanensis*; OD]. Little-known genus. [Originally placed in the family Permosialidae, order Mioptera. See discussion under *Permosialis*.] *Perm.*, USSR (Asian RSFSR).
- Sphalmatoblattina** HANDLIRSCH, 1906b, p. 392 [**Blattina latinervis* HEER, 1864, p. 288; OD]. Little-known genus, based on isolated wing. [Considered by HANDLIRSCH to be orthopteroid, but placed by HAUPT (1952) in the Mecoptera; assigned by WILLMANN (1978) to the category of order Uncertain.] *Perm.*, Europe (Germany).
- Stereochorista** TILLYARD, 1919a, p. 196 [**S. frustata*; OD]. Little-known genus, based on wing fragment. [Placed in the Mecoptera by TILLYARD (1919a) and LAURENTIAUX (1953), but considered by RIEK (1956) and WILLMANN (1978) to be more closely related to the Trichoptera.] *Trias.*, Australia (Queensland).
- Sycopteron** BOLTON, 1917a, p. 6 [**S. symmetricum*; OD]. Little-known genus. [Originally placed in the Mecoptera by BOLTON (1917a), but transferred to the Psocoptera by TILLYARD (1918f) and to the Caloneurodea by LAMEERE (1917c).] HANDLIRSCH, 1922; WILLMANN, 1978. *U. Carb.*, Europe (France).
- Tillyardites** HANDLIRSCH, 1937, p. 110 [**Archipanorpa bairda* TILLYARD, 1922a, p. 284; OD]. Little-known genus, based on wing fragment. [Type of the family Tillyarditidae HANDLIRSCH, 1937. Placed in the Mecoptera by TILLYARD (1922a, 1926e), MARTYNOVA (1948a), and HANDLIRSCH (1937); ordinal position considered uncertain by CARPENTER (1954b) and WILLMANN (1978).] *Perm.*, Australia (New South Wales).
- Trachopteryx** CARPENTER, 1976, p. 356 [**T. martynovi*; OD]. Little-known genus, based on well-preserved wing. [Type of the family Trachopterygidae CARPENTER, 1976]. *Perm.*, USA (Kansas).
- Trichorthophlebia** HANDLIRSCH, 1939, p. 89 [**T. pilifera*; OD]. Little-known genus. [Placed by HANDLIRSCH (1939), with some doubt, in the Trichoptera and by BODE (1953) and WILLMANN (1978) in the Mecoptera.] *Jur.*, Europe (Germany).
- Uninervus** BECKER-MIGDISOVA, 1951, p. 1207 [**U. zorapteroides*; OD]. Little-known genus, based on incomplete wing. [Type of the family Uninervidae BECKER-MIGDISOVA, 1951; not assigned to an order, but probably belonging to the Neoptera]. BECKER-MIGDISOVA, 1962c. *Perm.*, USSR (Asian RSFSR).
- Xeroptera** BOLTON, 1922, p. 85 [**X. obtusata*; OD]. Little-known genus, based on small fragment of a wing. [Originally placed in the Protorthoptera, with some doubt, but not assigned to any family.] *U. Carb.*, England.

Subclass PTERYGOTA Order UNCERTAIN

The following genera, apparently belonging to the subclass Pterygota, are too poorly known to permit assignment to orders.

- Merlebachia** WATERLOT, 1934, p. 162 [**M. grimaldi*; OD]. Little-known genus, based on wing fragment. [Originally placed in the Megasecoptera (family Mecynopteridae), but transferred to order Uncertain by KUKALOVÁ-PECK (1975).] *U. Carb.*, Europe (France).
- Pteronepionites** BOLTON, 1921, p. 27 [collective group]. Includes nymphal wings that cannot be assigned to a known genus of Pterygota. *U. Carb.*, England.

Class INSECTA
Subclass UNCERTAIN

The genus described below, apparently belonging to the class Insecta, is too poorly known to permit assignment to subclasses.

Xiphenax COCKERELL, 1931a, p. 96 [**X. jurassicus*; OD]. Little-known genus, based on a very poorly preserved specimen; possibly an immature insect, but not assigned to any order. *Jur.*, USA (New Mexico).

Superclass HEXAPODA
Class UNCERTAIN

The genus described below, apparently belonging to the superclass Hexapoda, is too poorly known to allow assignment to classes.

Onycholepisma PIERCE, 1951, p. 45 [**O. arizonae*; OD]. Little-known genus, based on poorly preserved specimen. [Originally placed in the class Insecta (*Zygentoma*), but transferred to the class Diplura by P_{ACL}T (1967).] *Tert.*, USA (Arizona).

THE SUPERCLASS HEXAPODA

OUTLINE OF CLASSIFICATION

The following outline of the superclass Hexapoda summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera of fossils in each supra-familial group.

Superclass Hexapoda, 5188, *Dev.*–*Holo.*

Class and Order Collembola, 14, *Dev.*–*Holo.*

Class and Order Protura, 0, *Holo.*

Class and Order Diplura, 4, *Paleoc.*–*Holo.*

Class Insecta, 5169, *U. Carb.*–*Holo.*

Subclass Apterygota, 8, *U. Carb.*–*Holo.*

Order Archaeognatha, 5, *U. Carb.*–*Holo.*

Order Zygentoma, 3, *Oligo.*–*Holo.*

Subclass Pterygota, 5160, *U. Carb.*–*Holo.*

Infraclass Palaeoptera, 502, *U. Carb.*–*Holo.*

Order Ephemeroptera, 59, *U. Carb.*–*Holo.*

Order Palaeodictyoptera, 125, *U. Carb.*–*Perm.*

Order Megasecoptera, 34, *U. Carb.*–*Perm.*

Order Diaphanopterodea, 20, *U. Carb.*–*Perm.*

Order Protodonata, 13, *U. Carb.*–*Perm.*

Order Odonata, 204, *Perm.*–*Holo.*

Infraclass Palaeoptera, Order Uncertain, 47

Infraclass Neoptera, 4656, *U. Carb.*–*Holo.*

Division Exopterygota, 1393, *U. Carb.*–*Holo.*

Order Perlaria, 28, *Perm.*–*Holo.*

Order Protorthoptera, 236, *U. Carb.*–*Trias.*

Order Blattaria, see p. 134, *U. Carb.*–*Holo.*

Order Isoptera, 33, *Cret.*–*Holo.*

Order Manteodea, 4, *Oligo.*–*Holo.*

Order Protelytroptera, 29, *Perm.*–*Cret.*

Order Dermaptera, 16, *Jur.*–*Holo.*

Order Orthoptera, 166, *U. Carb.*–*Holo.*

Order Grylloblattodea, 0, *Holo.*

Order Titanoptera, 8, *Trias.*

Order Phasmatodea, 13, *Trias.*–*Holo.*

Order Embioptera, 5, *Oligo.*–*Holo.*

Order Psocoptera, 58, *Perm.*–*Holo.*

Order Zoraptera, 0, *Holo.*

Order Mallophaga, 0, *Holo.*

Order Anoplura, 0, *Holo.*

Order Caloneurodeae, 16, *U. Carb.*–*Perm.*

Order Miomoptera, 10, *U. Carb.*–*Perm.*

Order Thysanoptera, 43, *Perm.*–*Holo.*

Order Hemiptera, 728, *Perm.*–*Holo.*

Division Endopterygota, 3203, *Perm.*–*Holo.*

Order Coleoptera, 1397, *Perm.*–*Holo.*

Order Strepsiptera, 4, *Oligo.*–*Holo.*

Order Neuroptera, 125, *Perm.*–*Holo.*

Order Glosselytrodeae, 11, *Perm.*–*Jur.*

Order Trichoptera, 112, *Perm.*–*Holo.*

Order Lepidoptera, 111, *Cret.*–*Holo.*

Order Mecoptera, 82, *Perm.*–*Holo.*

Order Siphonaptera, 1, *Oligo.*–*Holo.*

Order Diptera, 708, *Trias.*–*Holo.*

Order Hymenoptera, 652, *Trias.*–*Holo.*

Infraclass Neoptera, Order Uncertain, 60

Subclass Pterygota, Order Uncertain, 2

Class Insecta, Subclass Uncertain, 1

Superclass Hexapoda, Class Uncertain, 1

RANGES OF TAXA

The stratigraphic distribution of classes, orders, and families of Hexapoda recognized in this volume of the *Treatise* is shown graphically in Table 2, which follows (compiled by JACK D. KEIM, computer software by KENNETH C. HOOD and DAVID W. FOSTER).

TABLE 2. Stratigraphic Distribution of the Hexapoda.

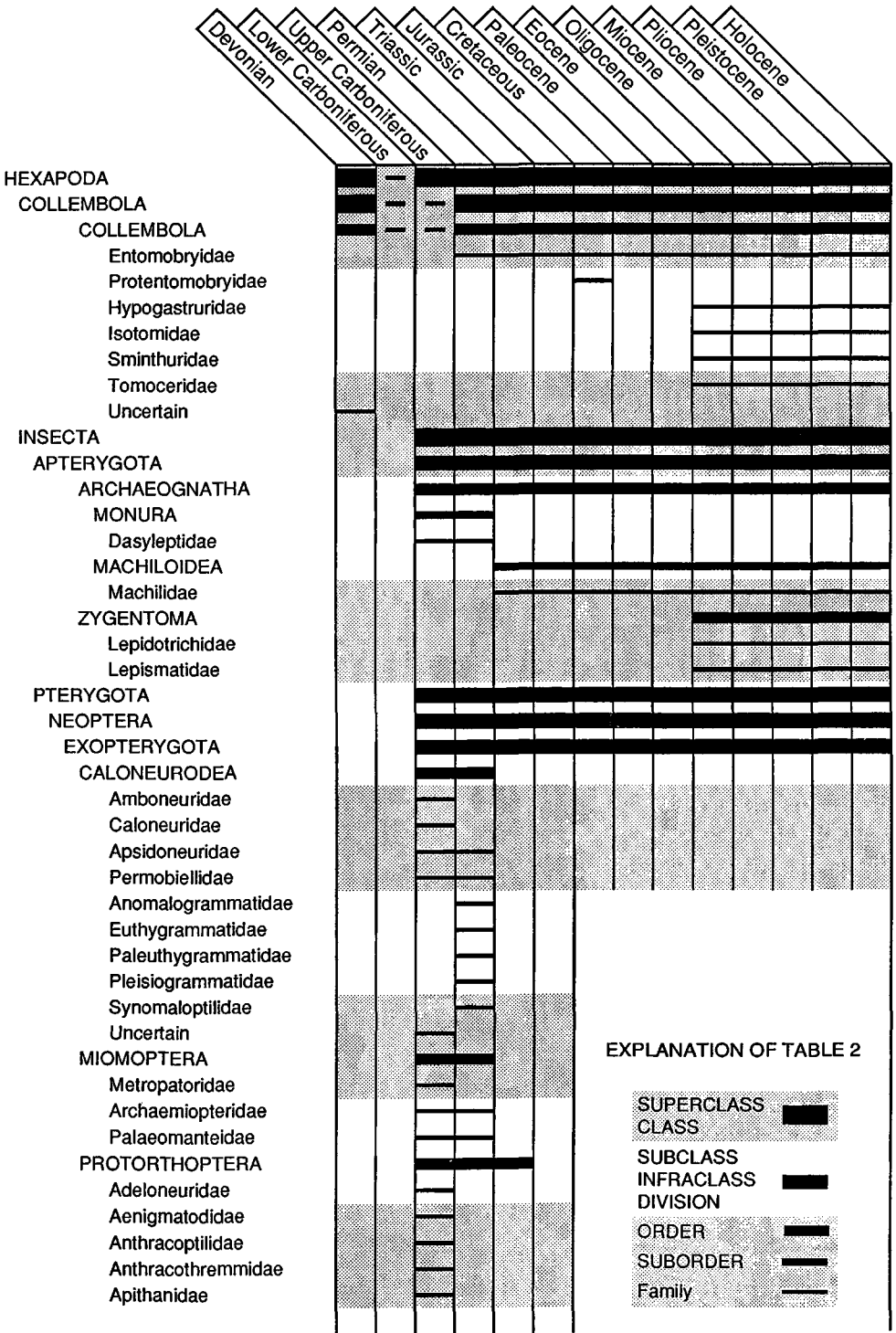


TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Cacurgidae														
Cnemidolestidae														
Epideigmatidae														
Eucaenidae														
Geraridae														
Hadentomidae														
Hapalopteridae														
Herbstiidae														
Herdinidae														
Homalophlebiidae														
Ischnoneuridae														
Narkemidae														
Omaliiidae														
Pachytylopsidae														
Paoliidae														
Protokollariidae														
Protophasmatidae														
Spanioideridae														
Stenoneuridae														
Stenoneuritidae														
Stygnidae														
Thoronysididae														
Blattinopsidae														
Ideliidae														
Strephocladidae														
Archiprobnidae														
Atactophlebiidae														
Camptoneuritidae														
Chelopteridae														
Cymbopsidae														
Demopteridae														
Epimastacidae														
Euremiscidae														
Euryptilonidae														
Havlatiidae														
Heteroptilidae														
Homoeodictyidae														
Jabloniidae														
Lemmatophoridae														
Liomopteridae														
Megakhosaridae														
Permotermopsidae														
Phenopteridae														
Probnidae														

TABLE 2. (Continued.)

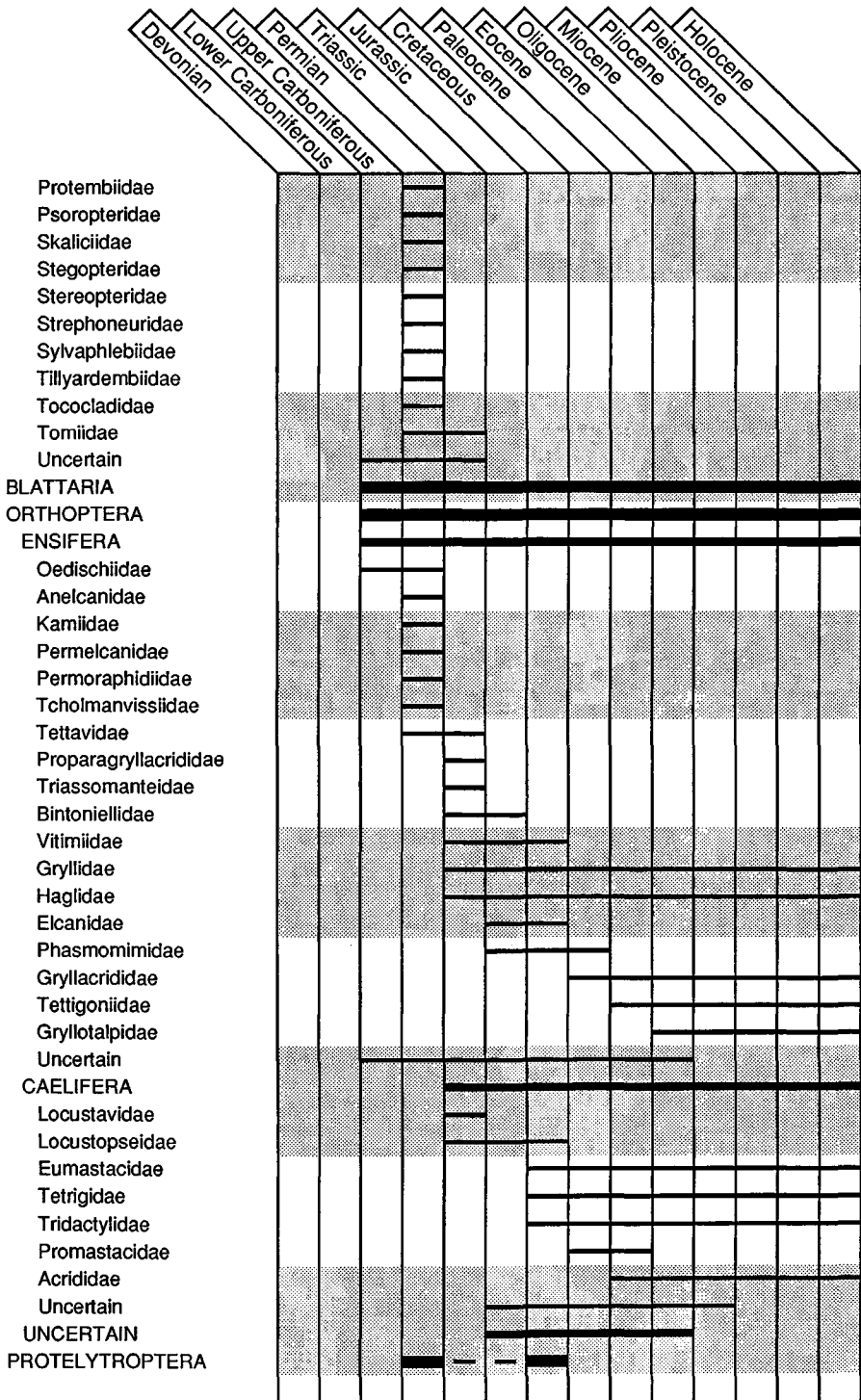


TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Apachelytridae														
Archelytridae														
Dermelytridae														
Elytroneuridae														
Labidelytridae														
Megelytridae														
Permelytridae														
Permophilidae														
Planelytridae														
Protelytridae														
Protocoleidae														
Umenocoleidae														
Uncertain														
THYSANOPTERA														
TEREBRANTIA														
Permothripidae														
Aeolothripidae														
Heterothripidae														
Merothripidae														
Thripidae														
Uncertain														
TUBULIFERA														
Phlaeothripidae														
UNCERTAIN														
Liassohipidae														
HEMIPTERA														
HETEROPTERA														
Progonocimicidae														
Archegocimicidae														
Cuneocoridae														
Mesopentacoridae														
Pachymeridiidae														
Scaphocoridae														
Shurabellidae														
Alydidae														
Belostomatidae														
Coreidae														
Corixidae														
Lygaeidae														
Miridae														
Nabidae														
Naucoridae														
Notonectidae														
Saldidae														

TABLE 2. (Continued.)

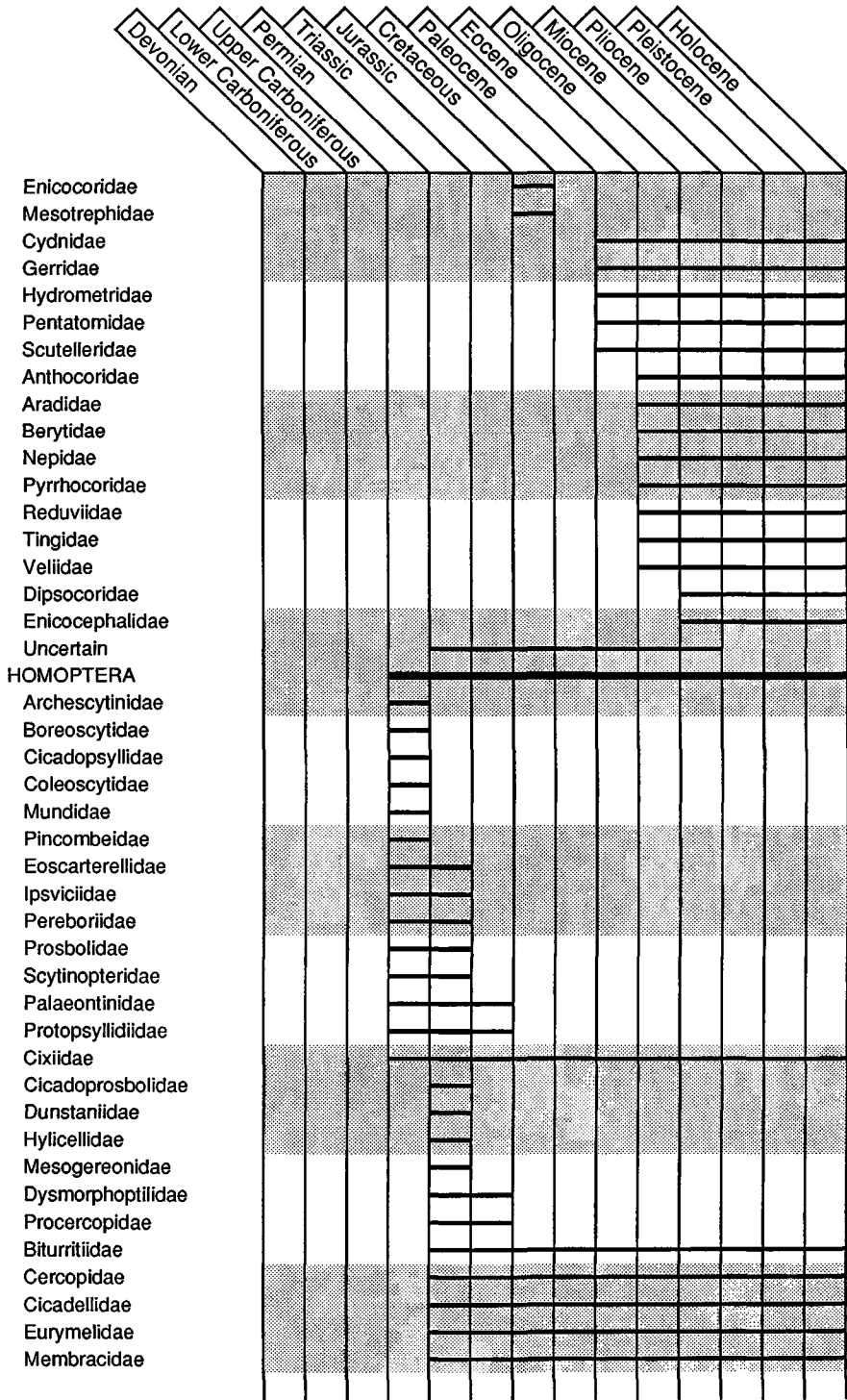


TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Ricaniidae														
Archijassidae														
Fulgoridiidae														
Genaphididae														
Issidae														
Lophopidae														
Psyllidae														
Canadaphididae														
Oviparasiphidae														
Palaeoaphididae														
Shaposhnikovidae														
Tajmyraphididae														
Elektraphididae														
Aphididae														
Dictyopharidae														
Drepanosiphidae														
Margarodidae														
Mindaridae														
Cicadidae														
Araeopidae														
Flatidae														
Fulgoridae														
Nogodinidae														
Tettigarctidae														
Achilidae														
Aetalionidae														
Aleyrodidae														
Anoeciidae														
Coccidae														
Hormaphididae														
Ortheziidae														
Pemphigidae														
Pseudococcidae														
Thelaxidae														
Lachnidae														
Uncertain														
UNCERTAIN														
Paraknightiidae														
Uncertain														
PERLARIA														
Palaeoperlidae														
Perloipseidae														
Eustheniidae														
Taeniopterygidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Platyperlidae														
Siberoperlidae														
Notonemouridae														
Perlidae														
Leuctridae														
Perlodidae														
Uncertain														
PSOCOPTERA														
Lophioneuridae														
Martynopsocidae														
Permopsocidae														
Psocidiidae														
Surijokopsocidae														
Zygopsocidae														
Archipsyllidae														
Asienthomidae														
Amphientomidae														
Epipsocidae														
Liposcelidae														
Mesopsocidae														
Pachytroctidae														
Polypsocidae														
Pseudocaeciliidae														
Psocidae														
Trogiidae														
Psyllipsocidae														
Lepidopsocidae														
Uncertain														
TITANOPTERA														
Gigatitanidae														
Mesotitanidae														
Paratitanidae														
PHASMATODEA														
Aeroplanidae														
Prochresmodidae														
Xiphopteridae														
Aerophasmatidae														
Cretophasmatidae														
Phasmatidae														
Phylliidae														
Uncertain														
DERMAPTERA														
ARCHIDERMAPTERA														
Protodiplatyidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
FORFICULINA														
Pygidicranidae														
Labiduridae														
Forficulidae														
UNCERTAIN														
ISOPTERA														
Hodotermitidae														
Kalotermitidae														
Mastotermitidae														
Rhinotermitidae														
Termitidae														
Uncertain														
EMBIOPTERA														
Embiidae														
Notoligotomidae														
MANTEODEA														
Chaeteessidae														
Manteidae														
ANOPLURA														
GRYLLOBLATTODEA														
MALLOPHAGA														
ZORAPTERA														
ENDOPTERYGOTA														
GLOSSELYTRODEA														
Archoglossopteridae														
Glosselytridae														
Jurinidae														
Permoberothidae														
Uskatelytridae														
Uncertain														
COLEOPTERA														
ARCHOSTEMATA														
Asiocolleidae														
Oborocoleidae														
Permocupedidae														
Rhombocoleidae														
Tshekardocoleidae														
Taldycupidae														
Catiniidae														
Schizophoridae														
Tricoleidae														
Ademosynidae														
Cupedidae														
Labradorocoleidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Micromalthidae														
ADEPHAGA														
Triaplidae														
Carabidae														
Liadytidae														
Parahygrobiidae														
Coptoclavidae														
Dytiscidae														
Gyrinidae														
POLYPHAGA														
Buprestidae														
Chrysomelidae														
Curculionidae														
Tenebrionidae														
Eobelidae														
Praelateriidae														
Alleculidae														
Dascillidae														
Elateridae														
Hydrophilidae														
Mordellidae														
Nitidulidae														
Oedemeridae														
Scarabaeidae														
Silphidae														
Staphylinidae														
Trogossitidae														
Acanthocnemidae														
Attelabidae														
Cerophytidae														
Cryptophagidae														
Lathridiidae														
Melandryidae														
Scraptiidae														
Anobiidae														
Cerambycidae														
Dryopidae														
Eucnemidae														
Circaeidae														
Electrapatidae														
Anthicidae														
Anthribidae														
Apionidae														
Artematopidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Bostrychidae														
Cantharidae														
Cleridae														
Colydiidae														
Cucujidae														
Dermestidae														
Endomychidae														
Helodidae														
Lucanidae														
Lycidae														
Melyridae														
Mycetophagidae														
Passalidae														
Pselaphidae														
Ptiliidae														
Ptilodactylidae														
Pyrochroidae														
Pythidae														
Salpingidae														
Scydmaenidae														
Trixagidae														
UNCERTAIN														
Uncertain														
MECOPTERA														
Agetopanorpidae														
Choristopsychidae														
Cyclopteridae														
Cycloristidae														
Kaltanidae														
Lithopanorpidae														
Permocentropidae														
Permopanorpidae														
Permotipulidae														
Tomiochoristidae														
Tychtopsychidae														
Mesopanorpodidae														
Permochoristidae														
Nannochoristidae														
Mesopsychidae														
Laurentipteridae														
Neorthophlebiidae														
Orthophlebiidae														
Pseudopolycentropidae														
Bittacidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Choristidae														
Eomeropidae														
Panorpidae														
Panorpididae														
Dinopanorpidae														
Uncertain														
NEUROPTERA														
RAPHIDIODEA														
Sojanoraphidiidae														
Baissorpterae														
Mesoraphidiidae														
Alloraphidiidae														
Inocelliidae														
Raphidiidae														
Uncertain														
PLANIPENNIA														
Palaemerobiidae														
Permithonidae														
Sialidopsidae														
Archeosmylidae														
Mesoberothidae														
Osmylopsychopidae														
Nymphitidae														
Psychopsidae														
Brongniartiellidae														
Kalligrammatidae														
Mesochrysopidae														
Mesopolystoechotidae														
Osmylitidae														
Prohemerobiidae														
Solenoptilidae														
Coniopterygidae														
Nymphidae														
Berothidae														
Mantispidae														
Osmylidae														
Hemerobiidae														
Ascalaphidae														
Chrysopidae														
Myrmeleontidae														
Nemopteridae														
Sisyridae														
Uncertain														
SIALODEA														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Corydalidae														
Uncertain														
TRICHOPTERA														
Microptysmatidae														
Cladochoristidae														
Prorhyacophilidae														
Dysoneuridae														
Liassophilidae														
Necrotauliidae														
Prosepididentidae														
Electralbertidae														
Taymyrelectronidae														
Hydrobiosidae														
Leptoceridae														
Philopotamidae														
Polycentropodidae														
Rhyacophilidae														
Limnophilidae														
Phryganeidae														
Beraeidae														
Brachycentridae														
Calamoceratidae														
Glossosomatidae														
Goeridae														
Helicopsychidae														
Hydropsychidae														
Hydroptilidae														
Lepidostomatidae														
Molannidae														
Odontoceridae														
Psychomyidae														
Stenopsychidae														
Uncertain														
DIPTERA														
ARCHIDIPTERA														
Dictyodipteridae														
Dyspolyneuridae														
Hyperpolyneuridae														
NEMATOCERA														
Architendipedidae														
Diplopolyneuridae														
Eopolyneuridae														
Musidoromimidae														
Oligophryneidae														

TABLE 2. (Continued.)

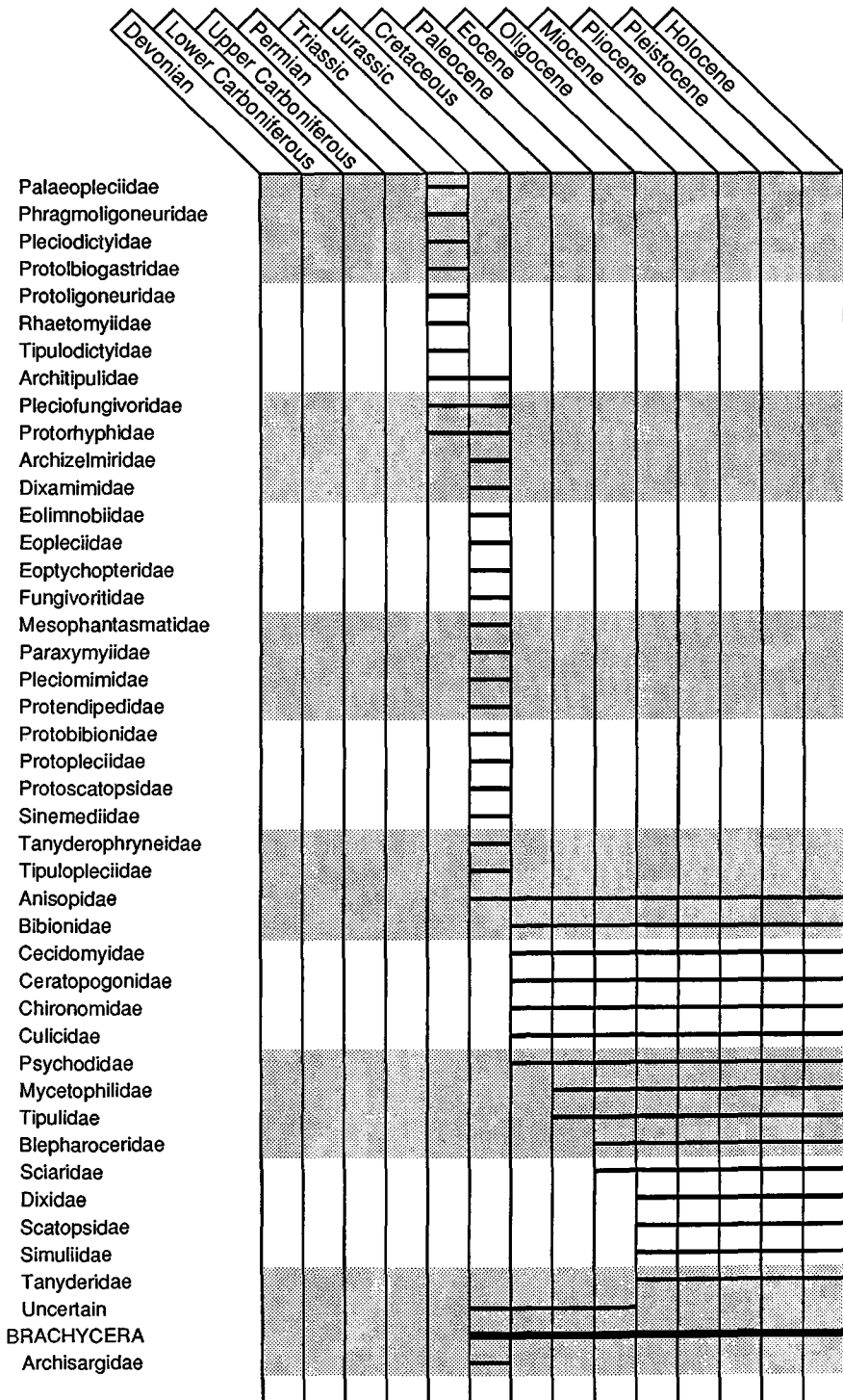


TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Eomyiidae														
Eostratiomyiidae														
Eremochaetidae														
Palaeophoridae														
Palaeostratiomyiidae														
Protempidae														
Protobrachycerontidae														
Protomphralidae														
Acroceridae														
Nemestrinidae														
Rhagionidae														
Calliphoridae														
Dolichopodidae														
Empididae														
Ironomyiidae														
Sciadoceridae														
Stratiomyidae														
Dryomyzidae														
Eophlebomyiidae														
Asilidae														
Platypzeidae														
Syrphidae														
Tabanidae														
Proneottiophilidae														
Acartophthalmidae														
Agromyzidae														
Anthomyzidae														
Asteiidae														
Athericidae														
Aulacigastridae														
Bombyliidae														
Camillidae														
Carnidae														
Chamaemyiidae														
Chloropidae														
Chyromyiidae														
Clusiidae														
Conopidae														
Cryptochaetidae														
Cypselosomatidae														
Diastatidae														
Diopsidae														
Drosophilidae														
Glossinidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Heleomyzidae														
Hippoboscidae														
Lauxaniidae														
Lonchaeidae														
Megamerinidae														
Micropezidae														
Milichiidae														
Muscidae														
Mydidae														
Neurochaetidae														
Odiniidae														
Opomyzidae														
Otitidae														
Pallopteridae														
Periscelididae														
Phoridae														
Piophilidae														
Pipunculidae														
Pseudopomyzidae														
Psilidae														
Richardiidae														
Scatophagidae														
Sciomyzidae														
Sepsidae														
Therevidae														
Xylomyidae														
Xylophagidae														
Tephritidae														
Gasterophilidae														
Uncertain														
HYMENOPTERA														
SYMPHYTA														
Xyelidae														
Gigasiricidae														
Karatavidae														
Parapamphiliidae														
Paroryssidae														
Sepulcidae														
Xyelydidae														
Praesiricidae														
Xyelotomidae														
Pseudosiricidae														
Anaxyelidae														
Cephidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Pamphiliidae														
Siricidae														
Cimbicidae														
Tenthredinidae														
Electrotomidae														
Argidae														
Blasticotomidae														
Diprionidae														
Uncertain														
APOCRITA														
Anomopterellidae														
Bethylonymidae														
Ephiaitidae														
Jurapriidae														
Karataidae														
Mesoserphidae														
Praeaulacidae														
Heloridae														
Megalyridae														
Baissodidae														
Cretevanidae														
Falsiformicidae														
Ichneumonimimidae														
Maimetshidae														
Praeichneumonidae														
Serphitidae														
Stigmaphronidae														
Aulacidae														
Bethylidae														
Braconidae														
Chrysididae														
Cynipidae														
Dryinidae														
Formicidae														
Ichneumonidae														
Megaspilidae														
Mutillidae														
Mymaridae														
Pompilidae														
Scelionidae														
Scolecbythidae														
Sphecidae														
Tetracampidae														
Trichogrammatidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Trigonaliidae														
Anthophoridae														
Apidae														
Eumenidae														
Vespidae														
Pelecinopteridae														
Agantidae														
Andrenidae														
Chalcidae														
Diapriidae														
Encyrtidae														
Eulophidae														
Eurytomidae														
Evaniidae														
Figitidae														
Halictidae														
Ibalidae														
Megachilidae														
Melittidae														
Proctotrupidae														
Pteromalidae														
Stephanidae														
Tiphiidae														
Torymidae														
Uncertain														
UNCERTAIN														
LEPIDOPTERA														
ZEUGLOPTERA														
Micropterygidae														
DITRYSIA														
Copromorphidae														
Geometridae														
Lycaenidae														
Nymphalidae														
Pyrallidae														
Tineidae														
Papilionidae														
Thyrididae														
Prolyonetiidae														
Cossidae														
Ctenuchidae														
Elachistidae														
Hesperiidae														
Libytheidae														

TABLE 2. (Continued.)

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
Oecophoridae														
Pieridae														
Psychidae														
Symmocidae														
Tortricidae														
Zygaenidae														
Uncertain														
DACNONYPHA														
Eriocraniidae														
MONOTRYZIA														
Incurvariidae														
UNCERTAIN														
SIPHONAPTERA														
Hystrihopsyllidae														
STREPSIPTERA														
Mengeidae														
Elenchidae														
Myrmecolacidae														
PALAEOPTERA														
DIAPHANOPTERODEA														
Diaphanopteridae														
Parabrodiidae														
Prochropteridae														
Rhaphidiopsidae														
Asthenohymenidae														
Biarmohymenidae														
Elmoidae														
Martynoviidae														
Parelmoidae														
Uncertain														
MEGASECOPTERA														
Anchineuridae														
Aspidothoracidae														
Brodiidae														
Brodiopteridae														
Corydaloididae														
Foririidae														
Ischnoptiliidae														
Mischopteridae														
Sphecopteridae														
Vorkutiidae														
Alectoneuridae														
Ancopteridae														
Arcioneuridae														

TABLE 2. (Continued.)

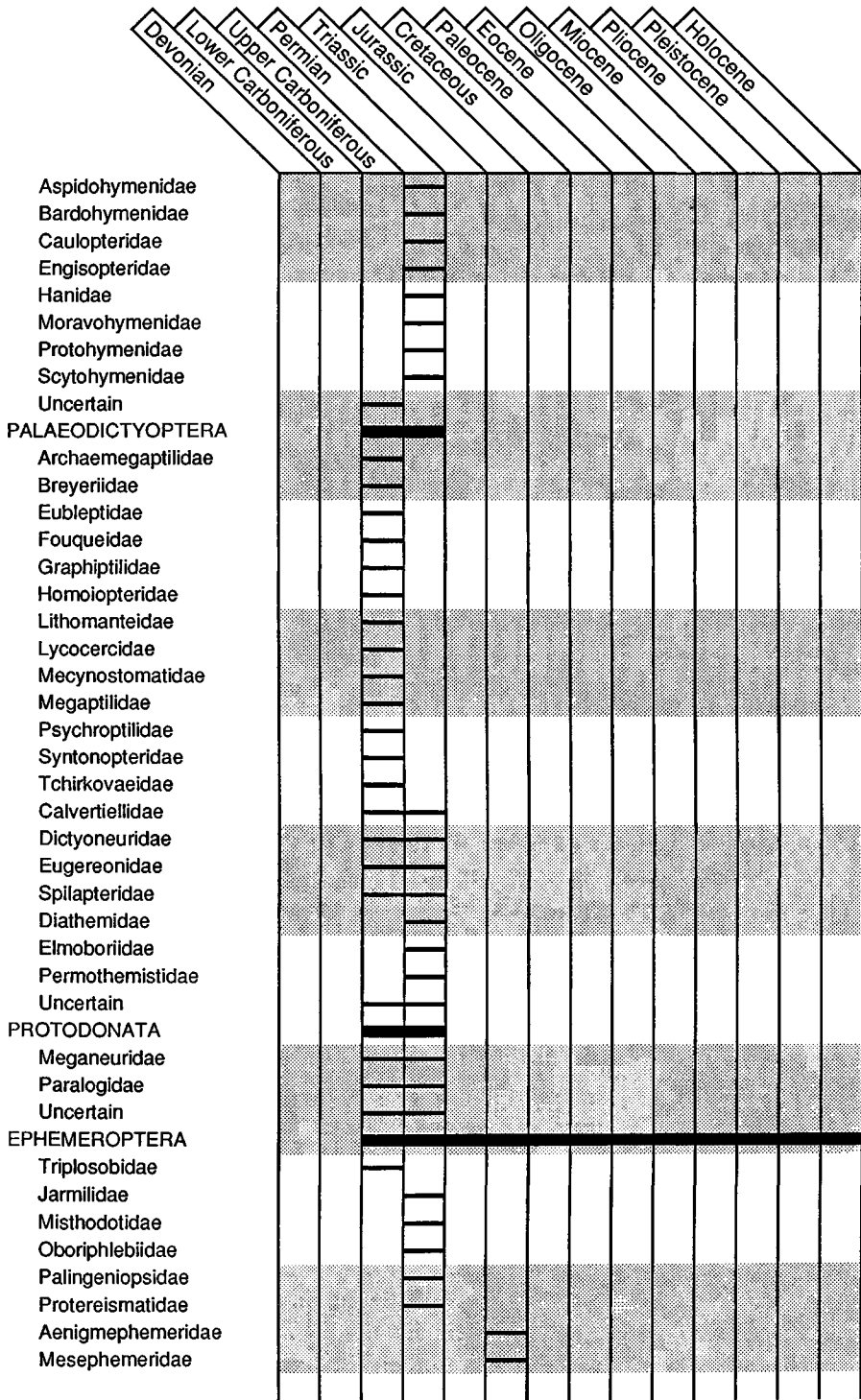


TABLE 2. (Continued.)

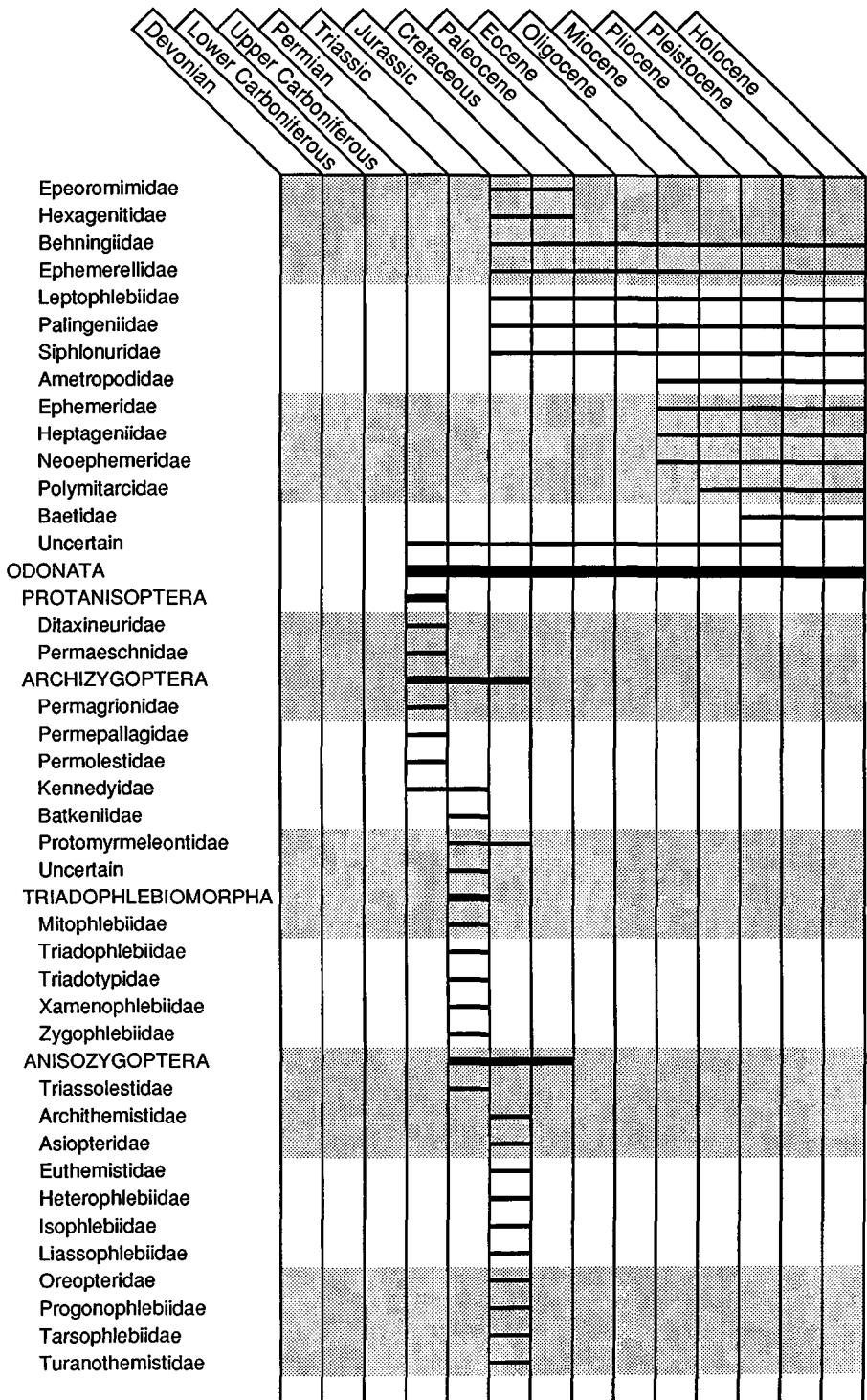
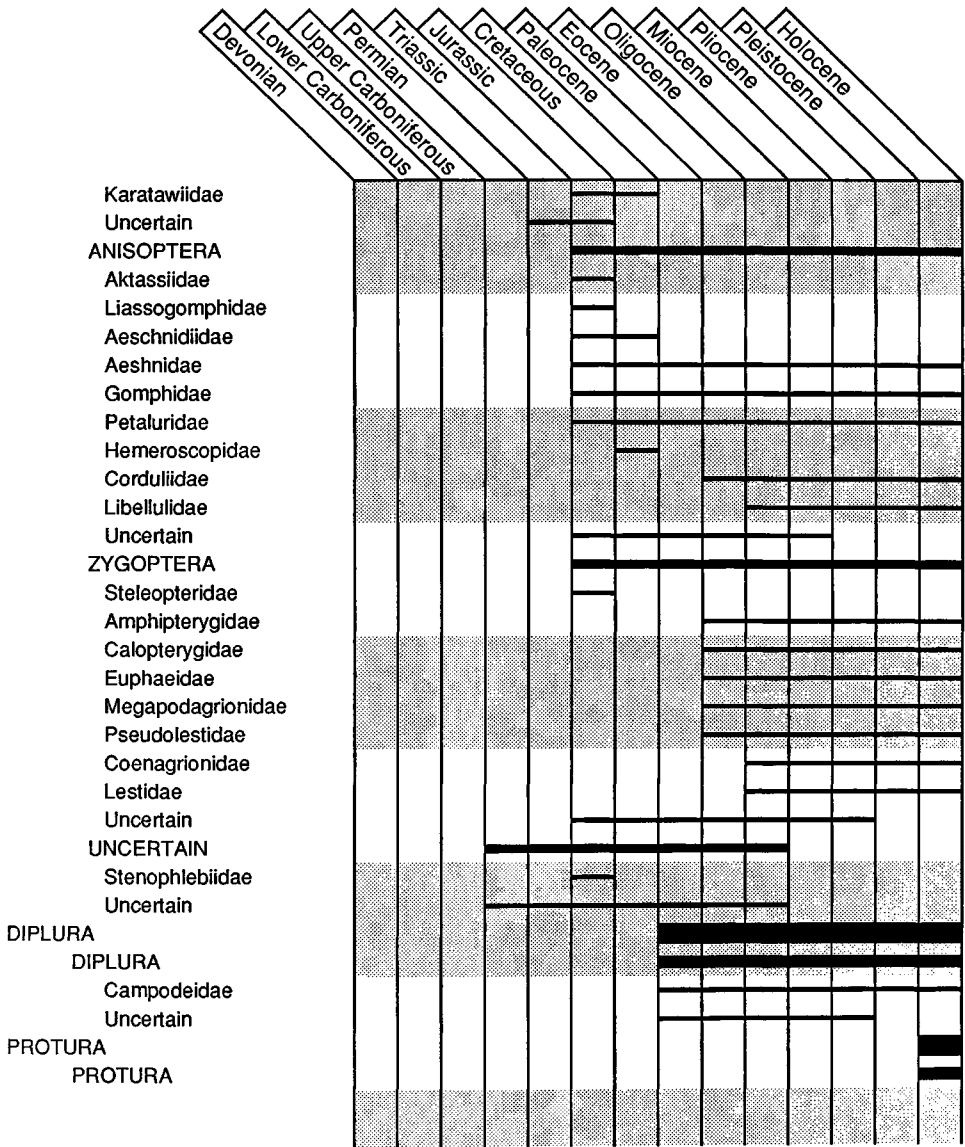


TABLE 2. (Continued.)



GLOSSARY OF ENTOMOLOGICAL TERMS

The editors of this volume of the *Treatise* have suggested that a glossary of entomological terms might be useful to readers who are not entomologists. I have accordingly included here a glossary of somewhat more than a hundred commonly used terms. If a more extensive glossary is needed, I recommend one of the following:

An Introduction to the Study of Insects, 3rd edition, by Donald J. Borror and Dwight M. DeLong. 812 pages, 655 figures. Holt, Rinehart, & Winston. 1970. [The glossary is on pages 735–752. Many structures mentioned in the glossary are illustrated.]

The Torre-Bueno Glossary of Entomology, revised edition, by George S. Tulloch and Stephen W. Nichols. Managing editor, Randall T. Schuh. 840 pages. Published by the New York Entomological Society and the American Museum of Natural History. 1989.

Some of these terms have multiple definitions that are specific to the order in which they are used. For such terms, I indicate the name of the order in parentheses at the end of the definition.

alate: possessing wings.

alula: the basal membranous portion of the wing.

anal crossing: where the anal veins branch posteriorly from vein CUA to vein A.

anal veins: longitudinal wing veins, posterior to vein CUP.

antennodals: crossveins on the costal margin of wings between C and SC from the base of the wing to the nodus (Odonata).

archedictyon: a primitive network of small wing veins.

arculus: the short, fused bases of RS+MA (Odonata).

areola postica: an open cell between the branches of CUA (Psocoptera).

arolium: a terminal pad between claws.

calipteres: pair of basal lobes on wings, proximal to alula (Diptera).

cerci: paired appendages of the 11th abdominal segment.

claval suture: a suture of the fore wing, between the clavus and the corium (Hemiptera).

clavus: the posterior, triangular area of the fore wing. (Hemiptera).

clypeus: the area of the head between the frons and the labium.

collophore: a ventral tube that projects from the first abdominal segment (Collembola).

corbicula: a concave area on the posterior tibia, used to hold collected pollen (Hymenoptera).

corium: a flexible membrane between segments of appendages and between body segments; or differentiated parts of the fore wing (Hemiptera).

costa: the most anterior of the longitudinal veins of insect wings, typically extending along costal margin.

costal area: the parts of the wing immediately behind the costal margin.

costal brace: a short crossvein extending from the costa at wing base to subcosta.

costal break: an area of the costa that is weak or lacking, the costa appearing to be broken (Diptera).

costal expansion: an area of unusual width in the costal margin, usually in the basal third of the fore wing.

costal fracture: a short transverse line of weakness in a fore wing, often separating the cuneus from the remainder of the corium (Hemiptera).

coxa: the basal segment of the insect leg.

coxal cavity: the area of space of the coxa that articulates to the thorax proper.

ctenidia: comblike structures on the body or appendages of insects.

cubitus: one of the main venational systems of the insect wings, herein treated as composed of CUA (convex) and CUP (concave).

cuneus: an area of the corium, separated from the rest of the corium by a small break in the costa (Hemiptera).

cursorial: legs adapted for running.

discoidal cell: any of three cells (1mcu, 3mcu, 2cua) near the middle of the fore wings (Hymenoptera).

discoidal vein: the part of vein CUA beyond its separation from vein M.

ectognathous mouthparts: exposed mouthparts, characteristic of all members of the class Insecta.

entognathous mouthparts: a facial integument covering all mouthparts, characteristic of the non-insect members of the Hexapoda.

elytron: a leathery fore wing, commonly used as a covering for the hind wing at rest (mostly Coleoptera).

embolium: several differentiated, submarginal parts of the corium in fore wing (Hemiptera).

- endopterygotes:** insects having complete metamorphosis.
- exarate pupa:** a pupa with free appendages, not united with the body.
- exopterygotes:** insects with incomplete metamorphosis, the immature stages resembling the adults.
- femoralary organs:** sound-producing structures, the hind legs being rubbed against the tegmina.
- flagellum:** the distal part of the antenna, beyond the pedicel.
- forceps:** pincers at the end of the abdomen.
- frons:** an unpaired sclerite of the insect head between the epicranial sutures and bearing the median ocellus.
- furcula:** a forked process on the fourth abdominal segment, used for jumping (Collembola).
- galea:** the outer lobe of the maxilla, usually segmented.
- gaster:** the rounded and posterior part of the abdomen, excluding the propodeum.
- genal area:** the area of the head on each side, below the eye.
- gonopophyses:** appendages surrounding the gonopore (external opening of the reproductive duct).
- gonostyles:** a pair of slender processes arising ventrally from the end of the abdomen, functioning as claspers in males.
- gressorial:** having legs adapted for walking.
- halteres:** modified and reduced hind wings, functioning as sense organs (Diptera).
- haustellate:** mouthparts adapted for sucking.
- hemelytra:** the anterior wing with the basal part thickened and the distal part membranous.
- humeral suture:** a thoracic suture extending from near the base of the fore wing to the middle coxa.
- hypandrium:** the ninth abdominal segment of males.
- hypognathous:** head vertical, the mouth being ventral.
- intercalary veins:** supplementary veins inserted between the usual wing veins.
- labella:** a pair of lobes near end of the proboscis.
- labial palpi:** the segmented appendages of the labium.
- labrum:** the upper lip of the insect mouth, just below the clypeus.
- laciniae:** inner lobes of the maxillae.
- mandibles:** the anterior jaws of insects.
- maxillae:** the second pair of jaws of insects.
- maxillary palpi:** the secondary appendages of the maxillae.
- media (M):** one of the major venational systems of insect wings, herein treated as composed of MA (convex) and MP (concave).
- mesoscutellum:** the scutellum of the mesothorax.
- mesothorax:** the second thoracic segment.
- metathorax:** the third thoracic segment.
- microtrichia:** cuticular hairs on a hairy membrane.
- moniliform:** segments that are beaded, like a necklace, as in antennae.
- neopterous:** pertaining to insects of the infraclass Neoptera, i.e., those that possess wings that can be folded back along the body at rest.
- nodal line:** a transverse line separating basal half of fore wing from distal half (Hemiptera).
- nodus:** a stout crossvein near middle of costal margin of wing, joining costa, subcosta, and radius.
- nygamata:** spots on insect wings presumed to be associated with sense cells.
- oblongum:** a closed cell in a hind wing, formed by crossveins connecting M and CUA (Coleoptera).
- ocelli:** the simple eyes of insects, usually occurring singly.
- ommatidia:** the usual elements of the compound eyes.
- ootheca:** a cluster of insect eggs, enclosed in secretions.
- opisthognathus:** the mouthparts of insects arranged in a posterior position.
- ovipositor:** the organ in female insects used for depositing eggs.
- palaeopterous:** pertaining to insects of the infra-class Palaeoptera, i.e., those which are unable to fold their wings back over the body at rest.
- pedicel:** the second segment of the antenna.
- petiole:** a stalk or stem, usually connecting the abdomen to the thorax (Hymenoptera).
- posterior cubitus:** see cubitus.
- posterior media:** see media.
- posterior notal process:** a posterior lobe of a wing-bearing plate of the meso- and metathorax.
- postnodals:** a series of crossveins along the front margin of wings distal to the nodus.
- precostal area:** area between the costa and the front margin of wing.
- pretarsus:** the terminal segment of the insect leg, usually consisting of a pair of claws.
- prognathous:** the head of an insect in horizontal position, the jaws projecting anteriorly.
- propleura:** the sides of the prothorax of pterygote insects.
- propodeum:** the apparent posterior part of the thorax although it is usually the first abdominal segment fused with the thorax (Hymenoptera).
- prosternum:** the sternum of the prothorax.
- prothorax:** the first segment of the thorax.
- proventriculus:** the posterior portion of the foregut of insects.
- pteralia:** small plates or sclerites at wing bases.
- pterostigma:** a pigmented spot on the anterior margin of fore and hind wings near the apex.
- pterothorax:** the wing-bearing parts of the thorax, the meso- and metathorax, which are fused in some insects.
- puparium:** a stiff case derived from the skin of the last nymphal instar in which the pupal stage is formed.

- quadrilateral cell:** an unusual form of a discoidal cell, undivided in both fore and hind wings (Odonata).
- radius:** one of the major venational systems of insect wings, herein treated as composed of radius (convex) and radial sector (concave).
- radial sector:** see radius.
- rostrum:** the extended portion of the head, bearing the mouthparts.
- saltatorial:** insects with legs modified for jumping, usually refers to the hind pair.
- scape:** the basal segment of the antenna.
- sclerite:** a hard, bodywall plate, bounded by membranes or sutures.
- scopa:** a thick hair covering on the hind tibiae of adults, primarily used for carrying pollen.
- scutellum:** a sclerite of a thoracic notum.
- sensilla:** sense organs, formed of the cuticular sense cells.
- stridulatory organs:** structures used to produce sounds, usually by scraping or rasping.
- subcosta:** a major longitudinal vein (concave) in the wing, next to the costa.
- subquadrilateral cell:** a conspicuous cell in the cubital area of a wing, just before the quadrilateral cell (or q cell) (Odonata).
- suctorial:** mouthparts adapted for sucking.
- sutural margin:** a conspicuous submarginal ridge nearly parallel with the hind margin of an elytron, formed by distal portions of the main veins.
- tarsus:** the segment of an insect leg beyond the tibia.
- tegmen:** a leathery fore wing.
- tibia:** the fourth segment of the insect leg.
- trochanter:** the second segment of an insect leg, between the coxa and the femur.
- tubular probosis:** extended beak-like mouthparts.
- urugomphi:** paired cercus-like processes on last segment of some larvae (Coleoptera).
- vena dividens:** weakly formed CUP in fore wing, usually visible as a conspicuous depression in the wing.

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A reprinted collection (Meunier, 1908i) of these individual papers shows that several pages of the articles, including a number of text-figures, were unintentionally omitted from *Le Naturaliste* (v. 30, 1908); they were first published in the reprinted collection.

- . 1908a. Sur un Odonatoptère du Rhétien de Fort Mouchard (France). *Annales de la Societe scientifique de Bruxelles* 32:91–92, pl. 2.
- . 1908b. Sur quelques Sténodictyoptères du terrain houiller de Commentry. *Annales de la Societe scientifique de Bruxelles (premiere partie)* 32:154–155.
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- . 1908d. Sur quelques Diptères. Xylophagidae, Therevidae, Arthropidae, Stratiomyidae, Tanypezinae et Ortalinae. De l'ambre de la Baltique, de la collection du Prof. Dr. R. Klebs. *Annales de la Societe scientifique de Bruxelles (premiere partie)* 32:258–266, 1 unnumbered pl.
Plate is bound, without explanation, before the article.
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Intended as a reprinted collection of the monographic papers listed under Meunier (1907–1908), this also contains 12 pages of text (including descriptions of 8 new species) and 13 figures (numbers 120–132) unintentionally omitted from the original printing in *Le Naturaliste*.
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- . 1909d. Insectes du Stéphanien de Commentry (sixième note). *Bulletin du Museum national d'histoire naturelle, Paris* 15:40–49, text-fig. 1–7.
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- . 1910b. Les Stratiomyidae de l'ambre de la Baltique (Dipt.). *Bulletin de la Societe entomologique de France* 1910:199–201, text-fig. 1–2.
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