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—*Rhyniella 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

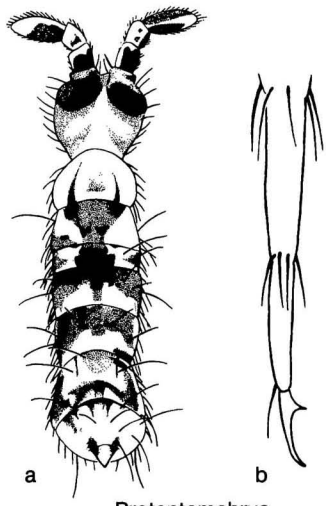


FIG. 1. Protentomobryidae (p. 2).

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.

OLFERS 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, ×100; *b,* distal portion of left arm of furcula, ventral view, ×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* OLFERS, 1907, p. 20 (type, *S. lanuginosus*); *Omo-*

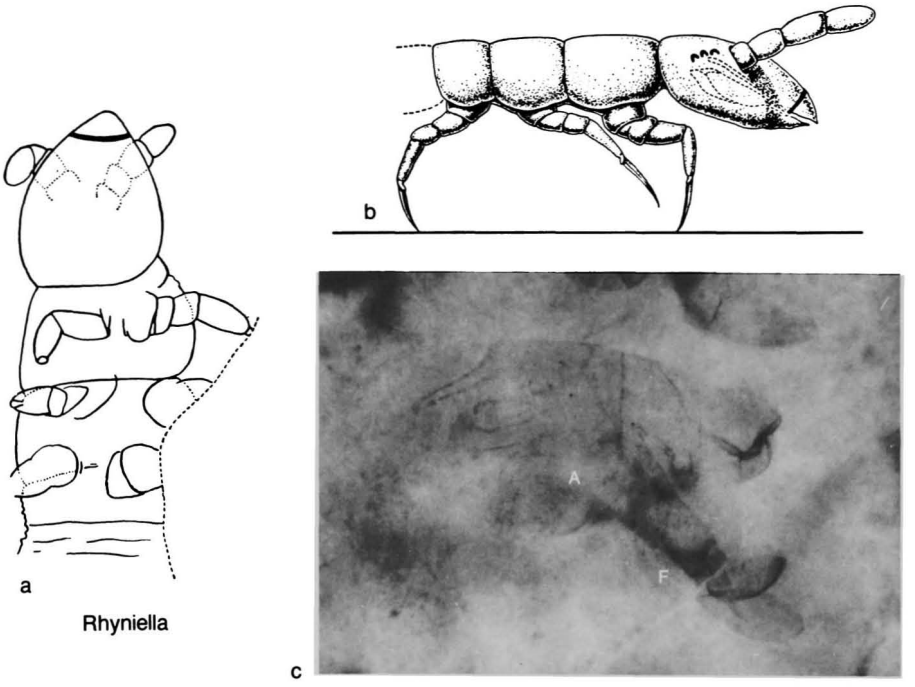


FIG. 2. Uncertain (p. 3).

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, ×55 (Massoud, 1967); *b,* head and thorax, lateral view, reconstruction, ×55 (Delamare Deboutteville & Massoud, 1967); *c,* lateral view of abdomen (A) with furcula (F), ×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. schmidti*; 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

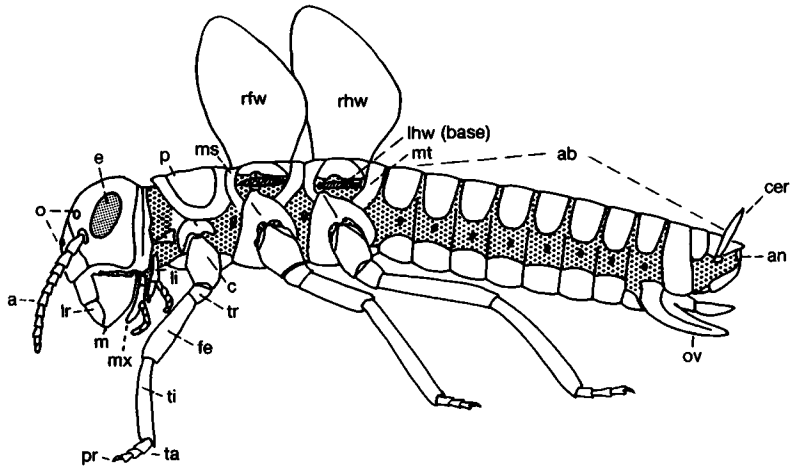


FIG. 3. Lateral view of typical female insect. Head: antenna (a); compound eye (e); labium (li); labrum (lr); mandible (m); maxilla (mx); ocelli (o). Thorax: coxa (c); femur (fe); left hind wing, base (lhw); mesonotum (ms); metanotum (mt); pronotum (p); pretarsus (pr); right fore wing (rfw); right hind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

Industrial Research Organization (CSIRO), Canberra (1970), and *Imms' General Textbook 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 though 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 Commentry, 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*

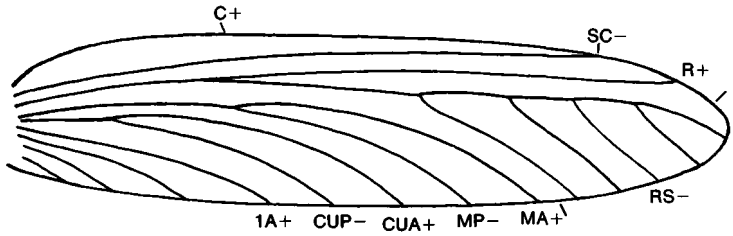


FIG. 4. Fore wing of *Stenodictya* sp., Palaeodictyoptera, Upper Carboniferous of France (Carpenter, new).

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, convex), 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.

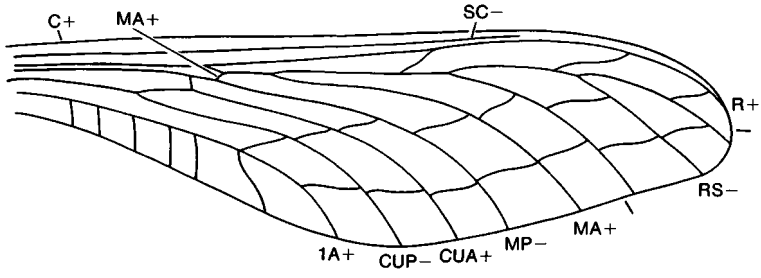


FIG. 5. Fore wing of *Psilothorax* sp., Megasecoptera, Upper Carboniferous of France (Carpenter, 1951).

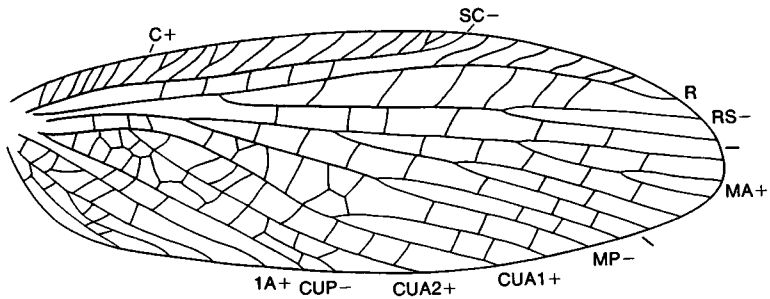


FIG. 6. Fore wing of *Liometopum* sp., Protorthoptera, Permian of Kansas (Carpenter, 1950).

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 descendents 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, paranotal 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

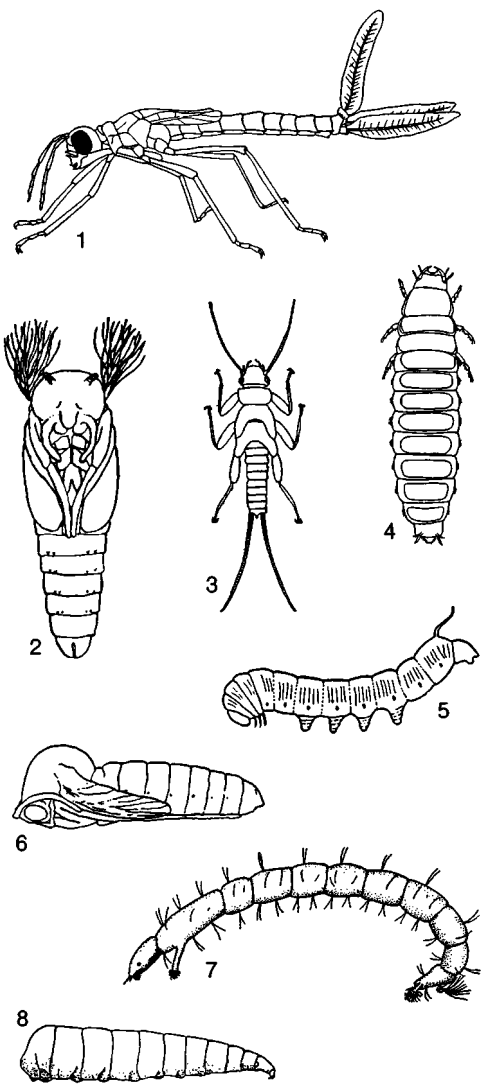


FIG. 7. Immature stages of diverse insects, all Holocene.——*1*. Nymph of *Lestes* sp., Odonata, lateral view (Essig, 1942).——*2*. Pupa of *Simulium* sp., Diptera, ventral view (Brues, Melander, & Carpenter, 1954).——*3*. Nymph of *Perla* sp., Perlaria, dorsal view (Brues, Melander, & Carpenter, 1954).——*4*. 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 *Tanypus* 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 Diaphanopterodea, 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 Diaphanopterodea, 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-

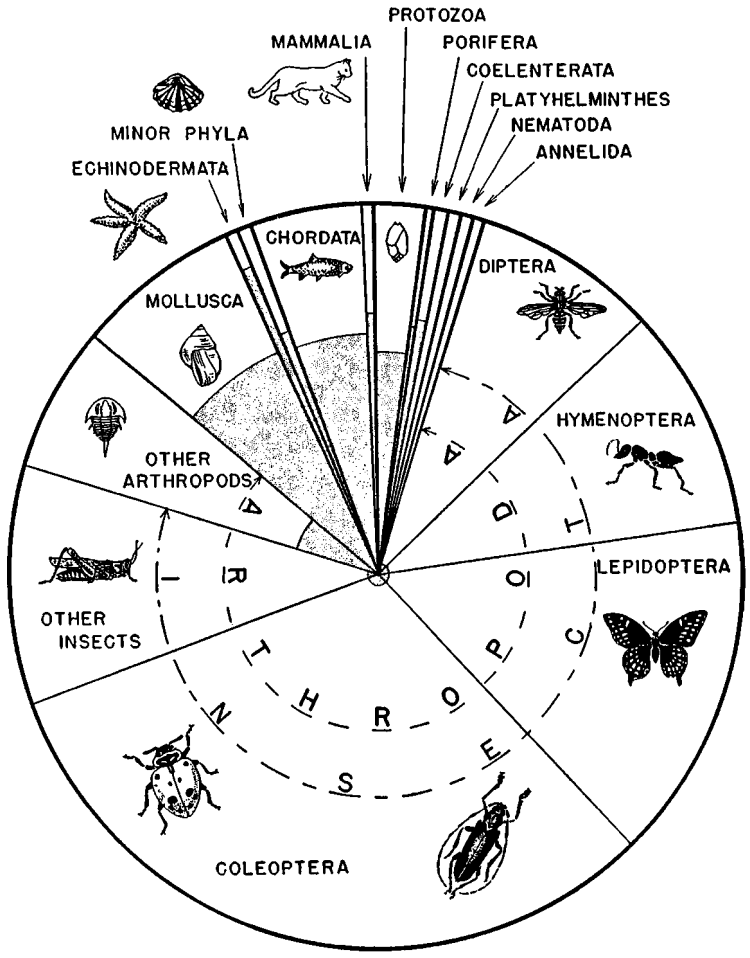


FIG. 8. Relative numbers of living and extinct species of animals. The percentage of extinct species is shown by the relative size of the gray area for each taxon (adapted from Muller & Campbell, 1954).

inated beneath the thoracic cuticle. After a series of molts and ecdyses, the insects pass into the pupal stage, in which the wing pads are evaginated and become external (Fig. 7,*2,6*). This is a quiescent stage, during which there is no feeding, although extensive internal changes occur. With the final ecdysis, the adults emerge and the wings expand as in the exopterygotes. The significance of this metamorphosis is that the immature stages (larvae) are very different in appearance from the adults, occupy very different environments, and feed on different foods (Fig. 7,*4,5,7,8*). Although only nine existing orders belong in this division, termed the Endopterygota, they comprise about 85 percent of all living Neoptera, including such large orders as the Diptera, Hymenoptera, and Coleoptera. No endopterygotes are known from the Upper Carboniferous, but four existing orders are well represented in the Permian. The endopterygotes are generally considered to comprise a monophyletic group.

THE GEOLOGICAL RECORD AND PHYLOGENY OF THE INSECTA

Although the fossil record of the insects includes about six thousand genera, our

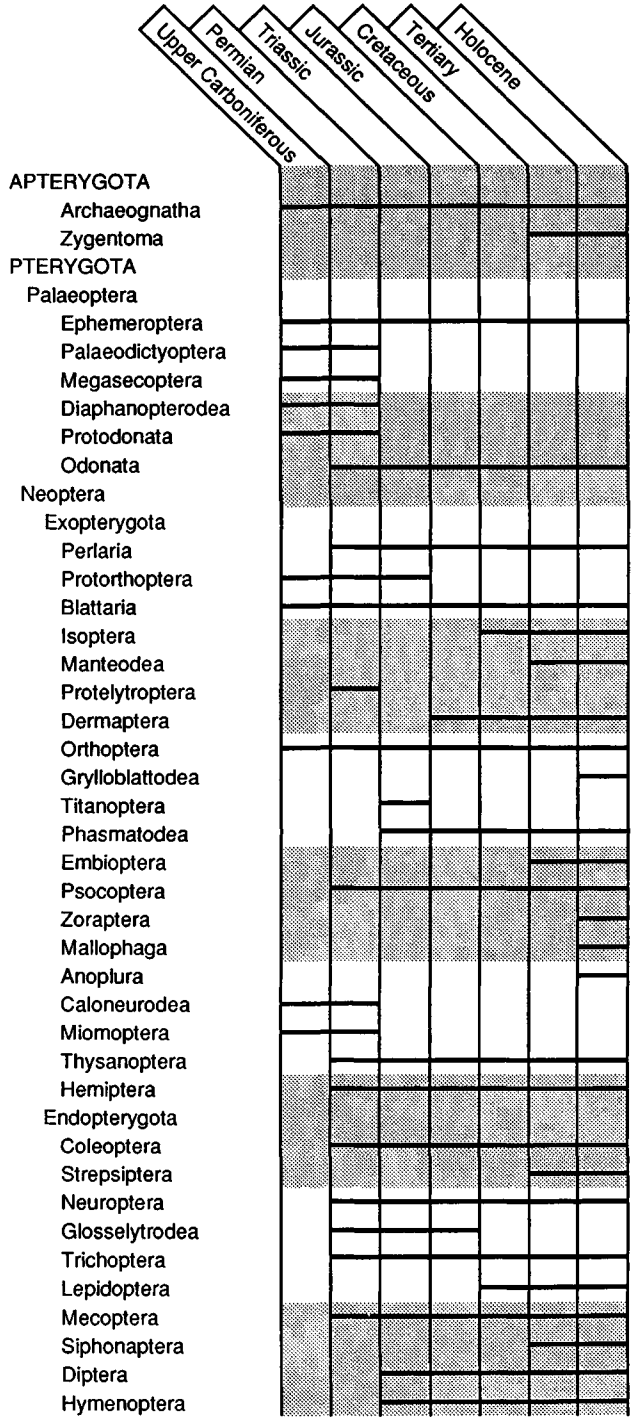


FIG. 9. Geological ranges of orders of insects (Carpenter, new).

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 definitely 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. Mixotermitoidea HANDLIRSCH, 1906a (Neoptera uncertain)
8. Reculoidea HANDLIRSCH, 1906b (Protorthoptera)
9. Hapalopteroidea HANDLIRSCH, 1906a (Protorthoptera)
10. Protephemeroidea 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. **Diaphanopterodea** 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. Pruvostitoptera 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. **Caloneurodea** HANDLIRSCH, 1937
31. Cnemidolestoidea HANDLIRSCH, 1937 (Protorthoptera)
32. Strephocladodea MARTYNOV, 1938b (Protorthoptera)
33. Paraplecoptera MARTYNOV, 1938b (Protorthoptera)
34. **Glosselytrodea** MARTYNOV, 1938c
35. Protocicadida HAUPT, 1941 (Palaeodictyoptera, Protorthoptera)
36. Protofulgorida HAUPT, 1941 (Protorthoptera, Blattaria)
37. Archaehymenoptera HAUPT, 1941 (Palaeodictyoptera)
38. Palaeohymenoptera HAUPT, 1941 (Diaphanopterodea)
39. Perielytrodea 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. Syntonopterodea LAURENTIAUX, 1953 (Palaeodictyoptera)
47. Permoneurodea LAURENTIAUX, 1953 (Palaeoptera uncertain)
48. Paracoleoptera LAURENTIAUX, 1953 (Neoptera uncertain)
49. Eubleptidodea LAURENTIAUX, 1953 (Palaeodictyoptera)
50. Campylopterodea ROHDENDORF, 1962a (Palaeoptera uncertain)
51. **Titanoptera** SHAROV, 1968
52. Dictyoneurida ROHDENDORF, 1977 (Palaeodictyoptera)
53. Permothemistida SINITSHENKOVA, 1980a (Palaeodictyoptera)
54. Hypoperlida RASNITSYN, 1980f (Neoptera uncertain)
55. Blattinopseida RASNITSYN, 1980f (Neoptera uncertain)

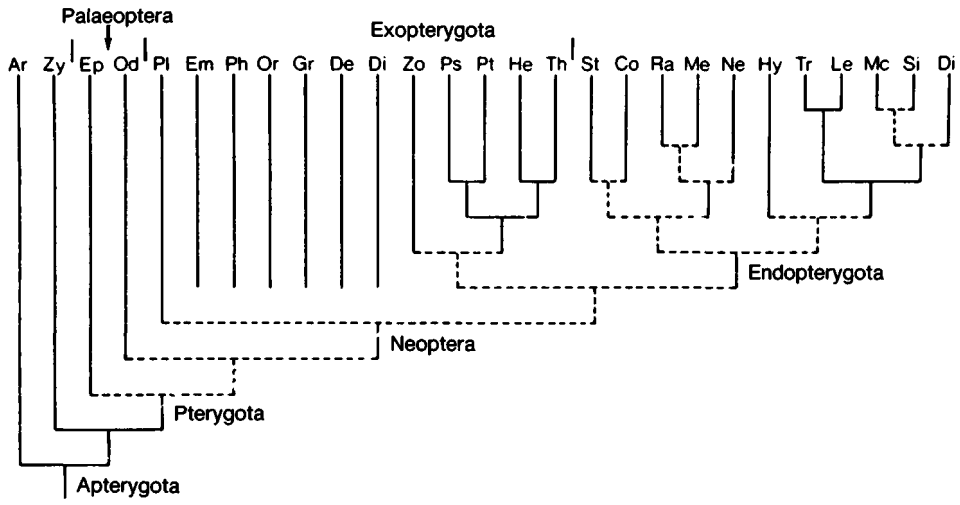


FIG. 10. Phylogeny of existing orders of insects. Higher categories: Apterygota; Pterygota; Palaeoptera; Neoptera; Exopterygota; Endopterygota. Orders: Archaeognatha (Ar); Zygentoma (Zy); Ephemeroptera (Ep); Odonata (Od); Perlaria (Plecoptera) (Pl); Embioptera (Em); Phasmatodea (Ph); Orthoptera (Or); 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.*

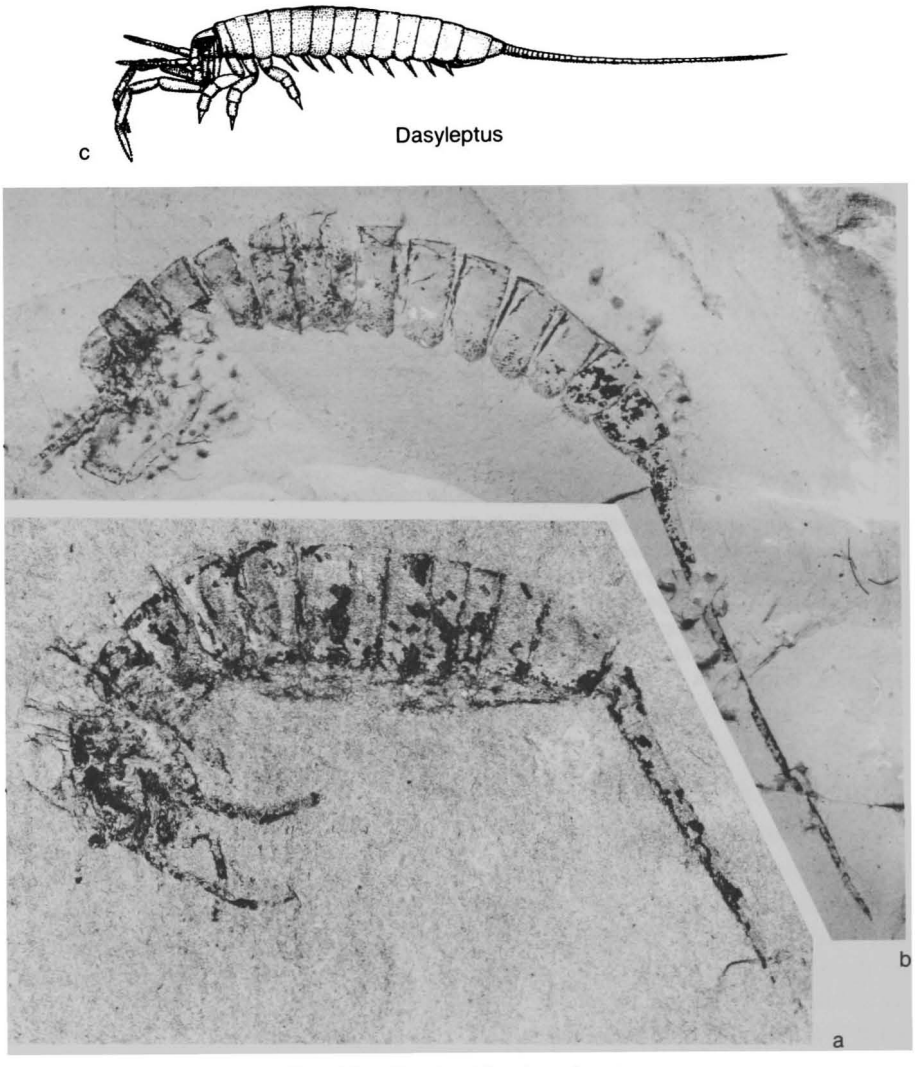


FIG. 11. Dasyleptidae (p. 16–17).

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, ×10 (Carpenter, new).——FIG. 11,*b,c*. *D. brongniarti* SHAROV, Perm.; *b*, lateral view, ×10 (Carpenter, new); *c*, reconstruction, lateral view, ×7 (Sharov, 1957c).

Lepidodasypus 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

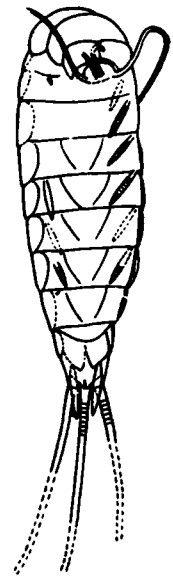
[Machilidae GRASSI, 1888, p. 582] [=Triassomachilidae SHAROV, 1948, p. 517]

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, ×7 (Sharov, 1948).



Triassomachilis

FIG. 12. Machilidae (p. 17).

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, 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* Lepidothricinae SILVESTRI, 1913a, p. 51]

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

Lepidotrix MENGE, 1854, p. 117, footnote [**L. pilifera*; OD] [=*Lepidothrix* 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 *Trichlepidion* (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, ×10 (Silvestri, 1913a).

Family LEPISMATIDAE Latreille, 1802

[Lepismatidae LATREILLE, 1802a, p. 70]

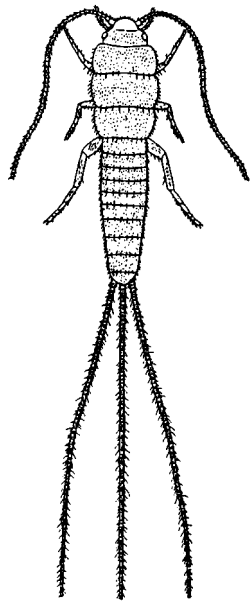
Compound eyes present; body covered with scales; tarsi with 3 or 4 segments. *Oligo.–Holo.*

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; PACLT, 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; mouthparts 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.*



Lepidotrix

FIG. 13. Lepidotrichidae (p. 17).

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 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, Diaphanopterodea, 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 Siphlonuridae, Leptophlebiidae, Palingeniidae, Behningiidae, and possibly the Ephemerellidae. 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 Permoplectoptera 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

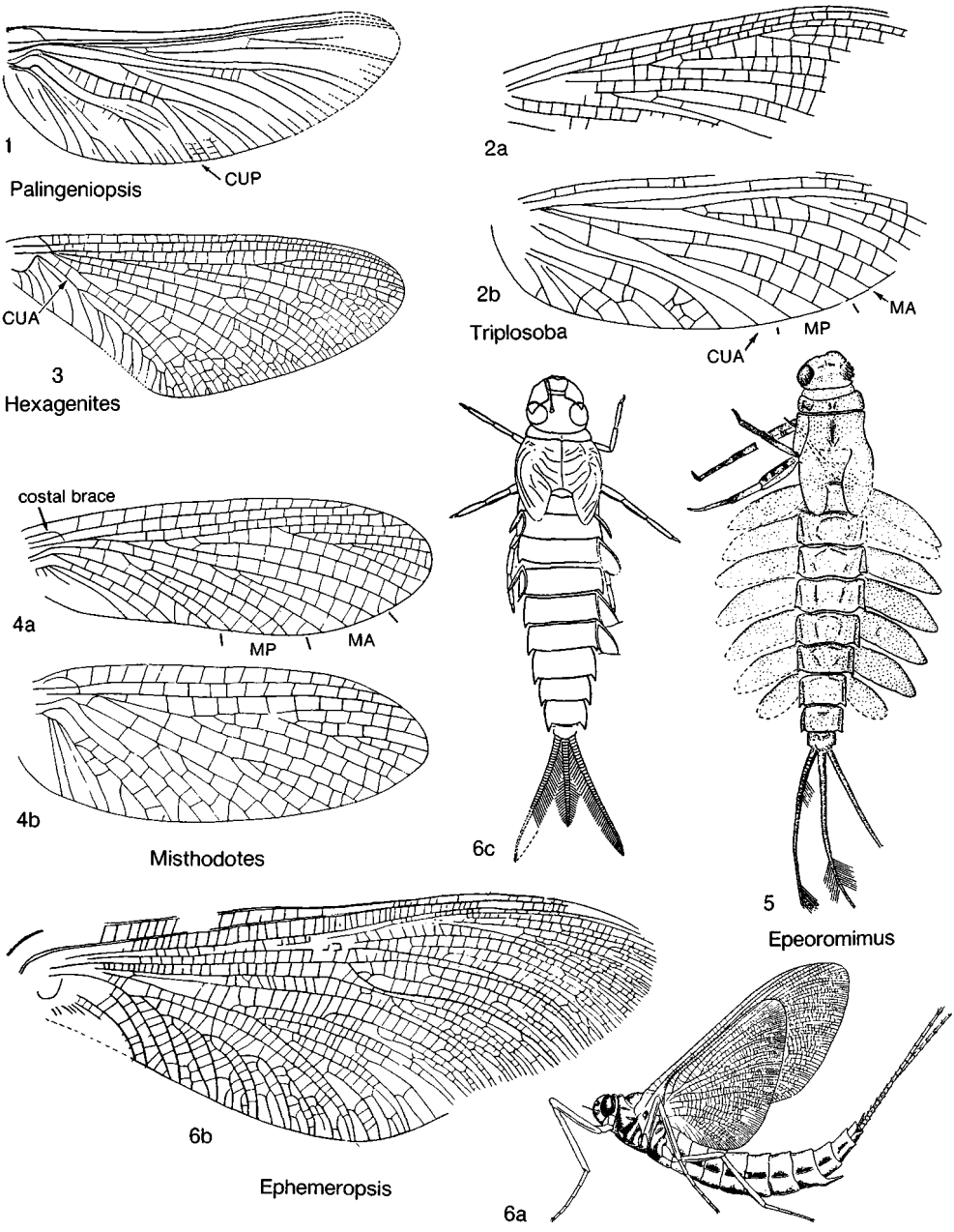


FIG. 14. Triplosobidae, Misthodotidae, Palingeniopsidae, Hexagenitidae, and Epeoromimidae (p. 20–24).

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, ×2.5 (Carpenter, new).

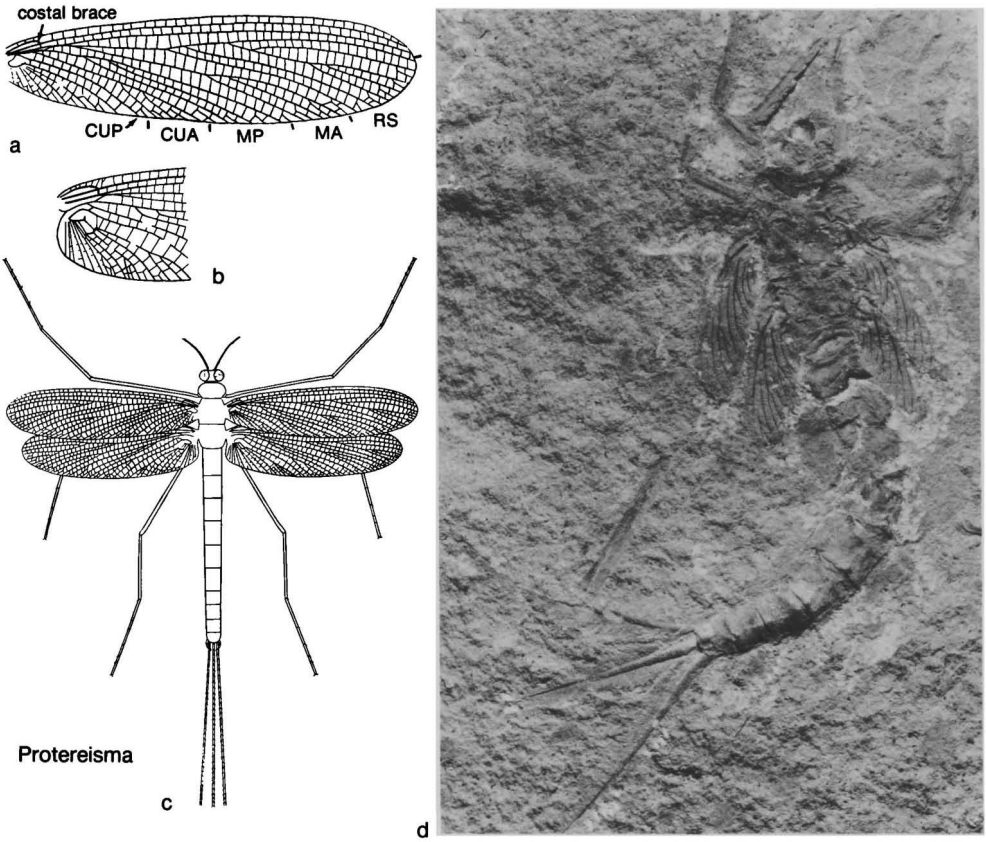


FIG. 15. Protereismatidae (p. 21–22).

Family PROTEREISMATIDAE Lameere, 1917

[*nom. correct.* TILLYARD, 1932b, *ex* Protereismidae 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 mandibles; 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.*

Protereisma 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. curta*); *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 ×3.5; *c,* reconstruction, dorsal view, ×1.5 (all Carpenter, 1933a).——FIG. 15,*d. P. americanum* DEMOULIN, Oklahoma; photograph of nymph, dorsal view, ×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, ×5.5 (Carpenter, 1933a).——FIG. 14,*4b. M. edmundsi* CARPENTER, Oklahoma; hind wing, ×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 OBORIPHLEBIIDAE Hubbard & Kukalová-Peck, 1980

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

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

Oboriphlebia 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, ×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, ×3.5 (Carpenter, 1932a).

Ephemeropsis EICHWALD, 1864, p. 21 [**E. tristalis*; OD] [=*Phacelobranchus* 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, ×0.8 (Tshernova, 1961); *b*, fore wing, ×2.0 (Tshernova & Sinitshenkova, 1974); *c*, nymph, restoration, dorsal view, ×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 (Ukraina), Africa (Algeria).

Family SIPHLONURIDAE Banks, 1900

[Siphlonuridae 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.*

Siphlonurus 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. hennigi*; OD]. Based on female imago; similar to *Chaquihua* (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, ×3.5 (Demoulin, 1968c).

Isonychia EATON, 1871, p. 33. LEWIS, 1977b. *Oligo.*, USA (Montana)–*Holo.*

Oligisca DEMOULIN, 1970c, p. 6 [**Paedephemera schwertschlageri* 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).

Siphlurites 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 ×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.*

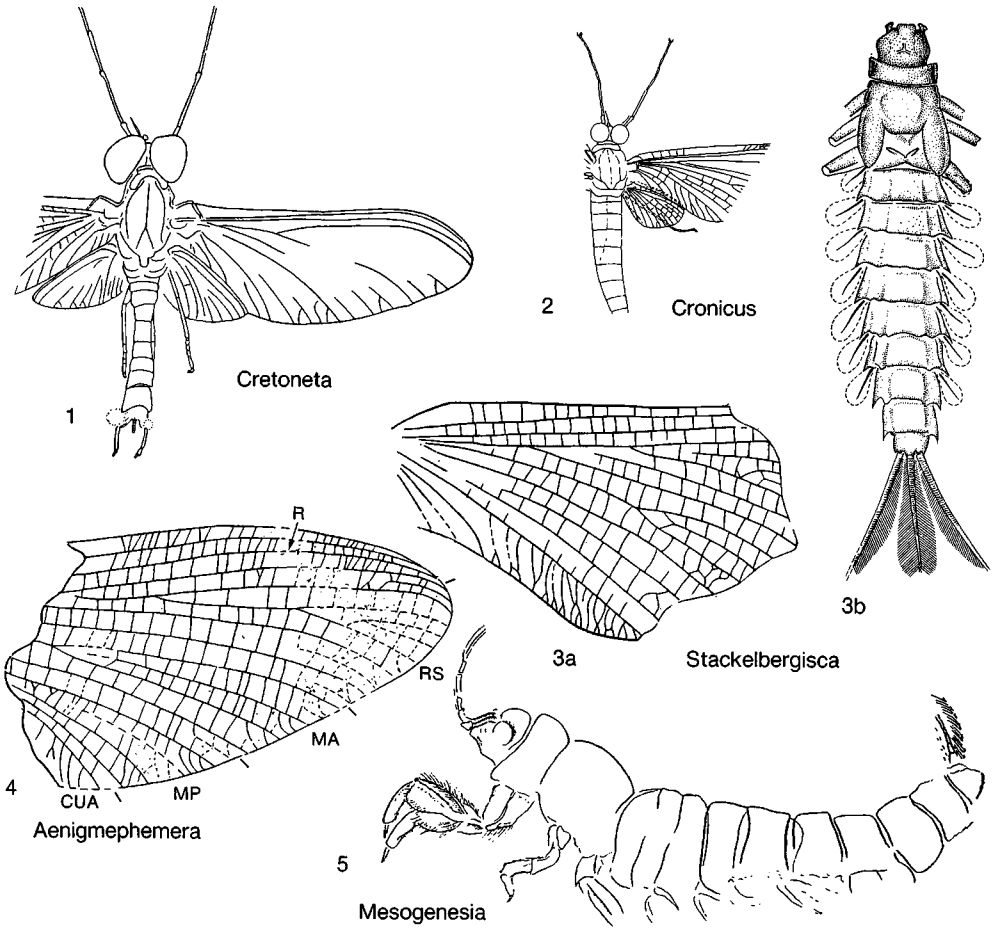


FIG. 16. Siphlonuridae, Aenigmephemeridae, Leptophlebiidae, and Palingeniidae (p. 23–26).

Family EPEOROMIMIDAE Tshernova, 1969

[Epeoromimidae TSHERNOVA, 1969, p. 154]

Known only from nymphs, apparently related to the Heptageniidae. Head and thorax short; 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. SINITSHENKOVA, 1976. *Jur.–Cret.*, USSR (Asian RSFSR).——FIG. 14,5. **E. kuzlauskasi*; dorsal view of nymph, ×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, ×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. hirsuta*; 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, ×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; SINITSHENKOVA, 1976. *Jur.–Cret.*, USSR (Asian RSFSR).

Paraleptophlebia LESTAGE, 1917, p. 340 [=*Oligophlebia* DEMOULIN, 1965, p. 146 (type, *O. calliarcys*)]. 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 (Sinkiang).

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

[Neoephemeridae NEEDHAM in NEEDHAM, TRAVER, & 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.*

Neoephemera 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

[Polymitarcidae 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, ×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 Aphelophlebodidae 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).
Mesoplectopteron 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; Synarmogoidea HANDLIRSCH, 1919b, p. 28; Protocicadida HAUPT (in part), 1941, p. 75; Archaehymenoptera HAUPT, 1941, p. 102; Archodonata MARTYNOV, 1932, p. 12; Anisaxia FORBES, 1943, p. 403; Hemiodonata ZALESSKY, 1946a, p. 63; Breyerida HAUPT, 1949, p. 23; Eopalaeodictyoptera LAURENTIAUX, 1952a, p. 234; Eubleptidodea LAURENTIAUX, 1953, p. 423; Syntonopterodea 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, Archaemegaptilidae, 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 archedictyon, 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 (pteralia). Ultimately, these two orders will probably be merged into one, without even subordinal separation. The Diaphanopterodea 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, ×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, ×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, ×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 & SINITSHENKOVA, 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, ×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 vaillanti* 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, ×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, ×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, ×1 (Guthörl, 1940).

Sagenoptera HANDLIRSCH, 1906b, p. 72 [**Termes formosus* GOLDENBERG, 1854, p. 30; OD] [=*Arltia* 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).——

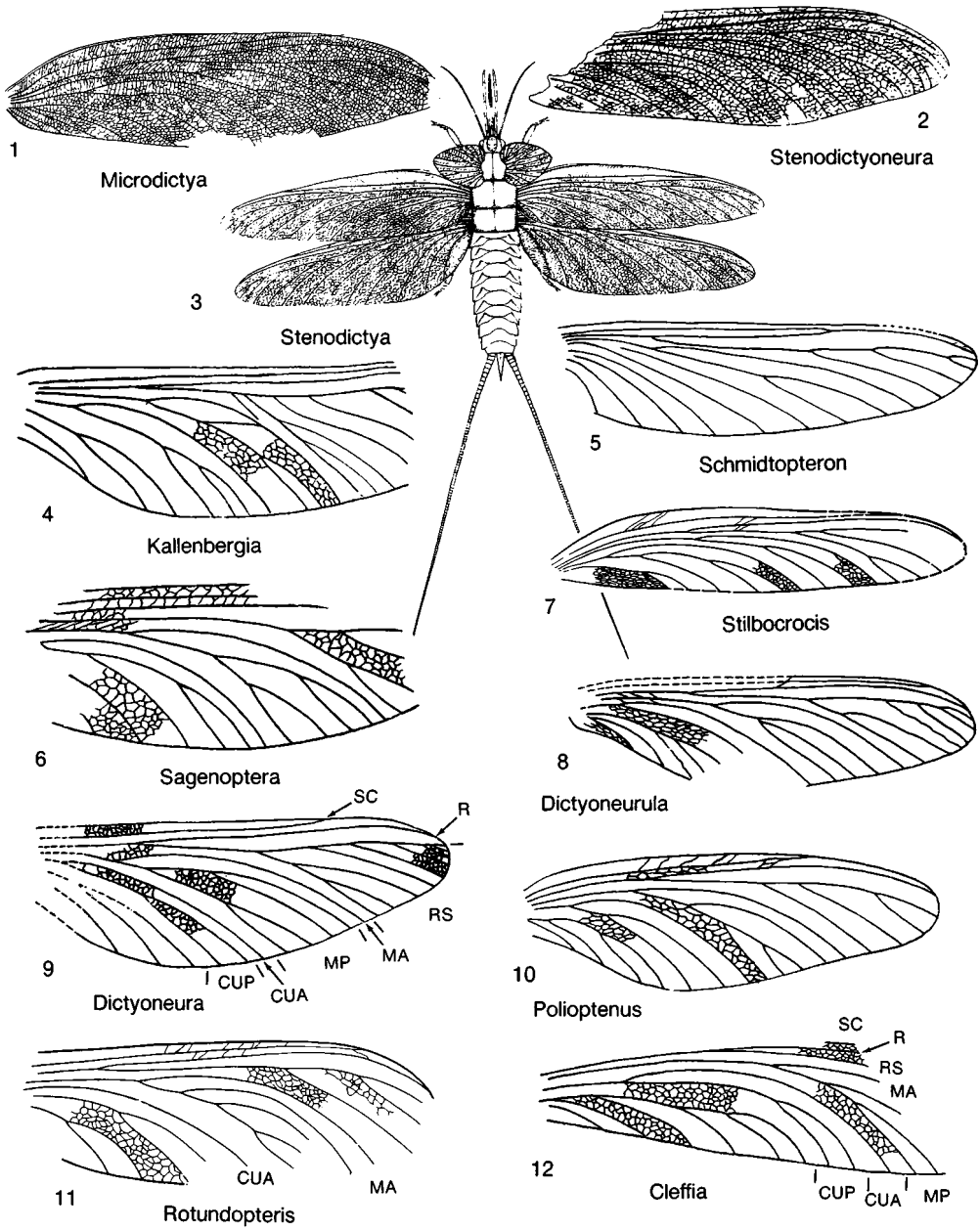


FIG. 17. Dictyoneuridae (p. 28–30).

FIG. 17,6. **S. formosa* (GOLDENBERG); wing, ×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, ×1.8 (Brauckmann & Hahn, 1978).

Siberiodictya SHAROV & SINITSHENKOVA, 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; archedictyon irregular; costal area with thin but dense, regular crossveins. LAURENTIAUX, 1952a; KUKALOVÁ, 1970. *U. Carb.*, Europe (France).——FIG. 17,*3*. *Stenodictya*; reconstruction, ×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, ×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, ×1 (Guthörl, 1940).

Family LITHOMANTEIDAE Handlirsch, 1906

[*nom. correct.* CARPENTER in BRUES, MELANDER, & CARPENTER, 1954, p. 790, *pro* Lithomantidae HANDLIRSCH, 1906a, p. 673] [=Macropteridae 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 bohemica* 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, ×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, ×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, ×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 [**Archaeoptilus 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, ×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.*

Archaemegaptilus 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, ×0.5 (Laurentiaux, 1953); *b*, fore wing base, ×1; *c*, hind wing base, ×1 (both Carpenter, 1964a).

Dictyoptilus BRONGNIART, 1893, p. 390 [**D. renaulti*; OD] [=*Cockerelliella* MEUNIER, 1909a, p. 132, *nom. subst. pro Cockerellia* 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, ×1 (Kukalová, 1969c).——FIG. 20,*2b*. *D. peromapteroides* (MEUNIER); fore and hind wings, ×0.8 (Kukalová, 1969c).

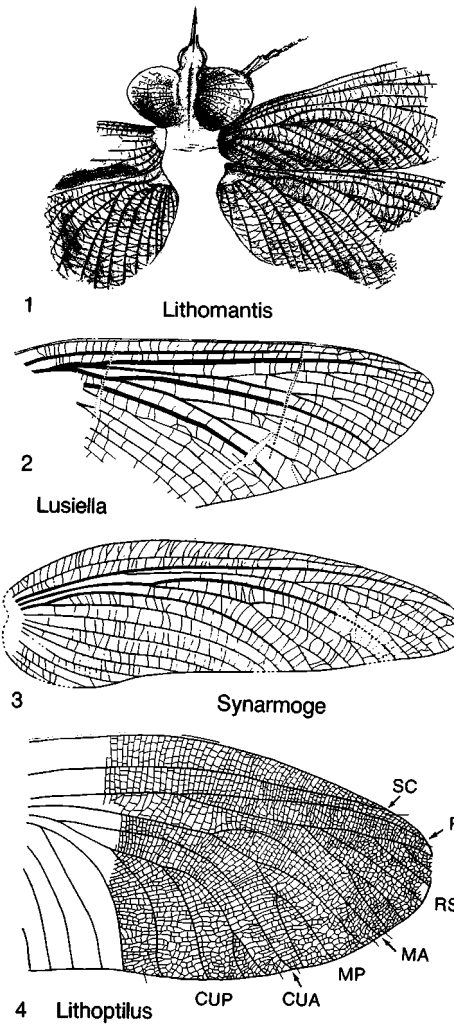


FIG. 18. Lithomanteidae and Megaptilidae (p. 30).

Peromaptera BRONGNIART, 1893, p. 391 [**P. filholi*; 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, ×2 (Carpenter, 1970).

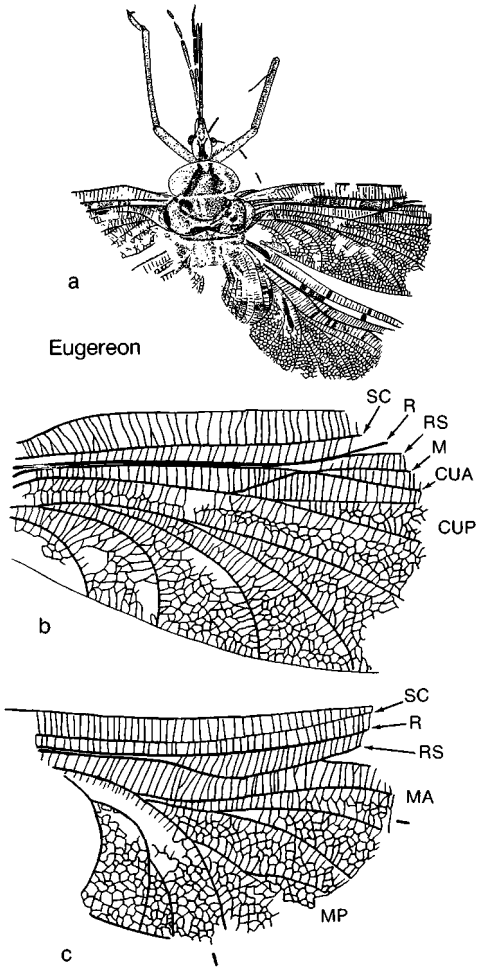


FIG. 19. Eugereonidae (p. 31).

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, ×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, ×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, ×1.2 (Sharov & Sinitshenkova, 1977).

Family LYCOCERCIDAE Handlirsch, 1906

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

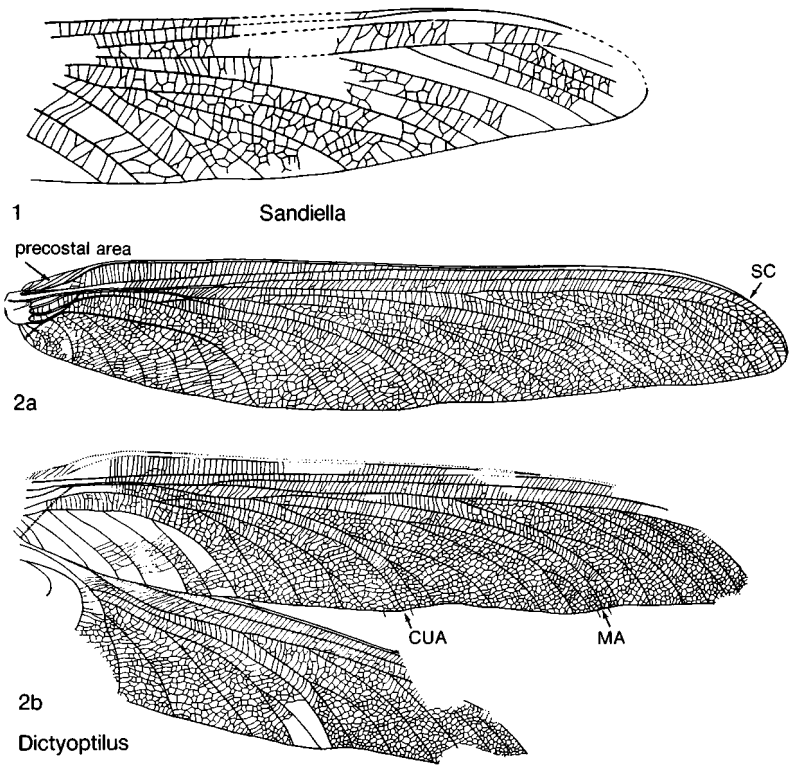


FIG. 20. Eugereonidae (p. 31).

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, ×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).

Lycodemas 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, ×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, ×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

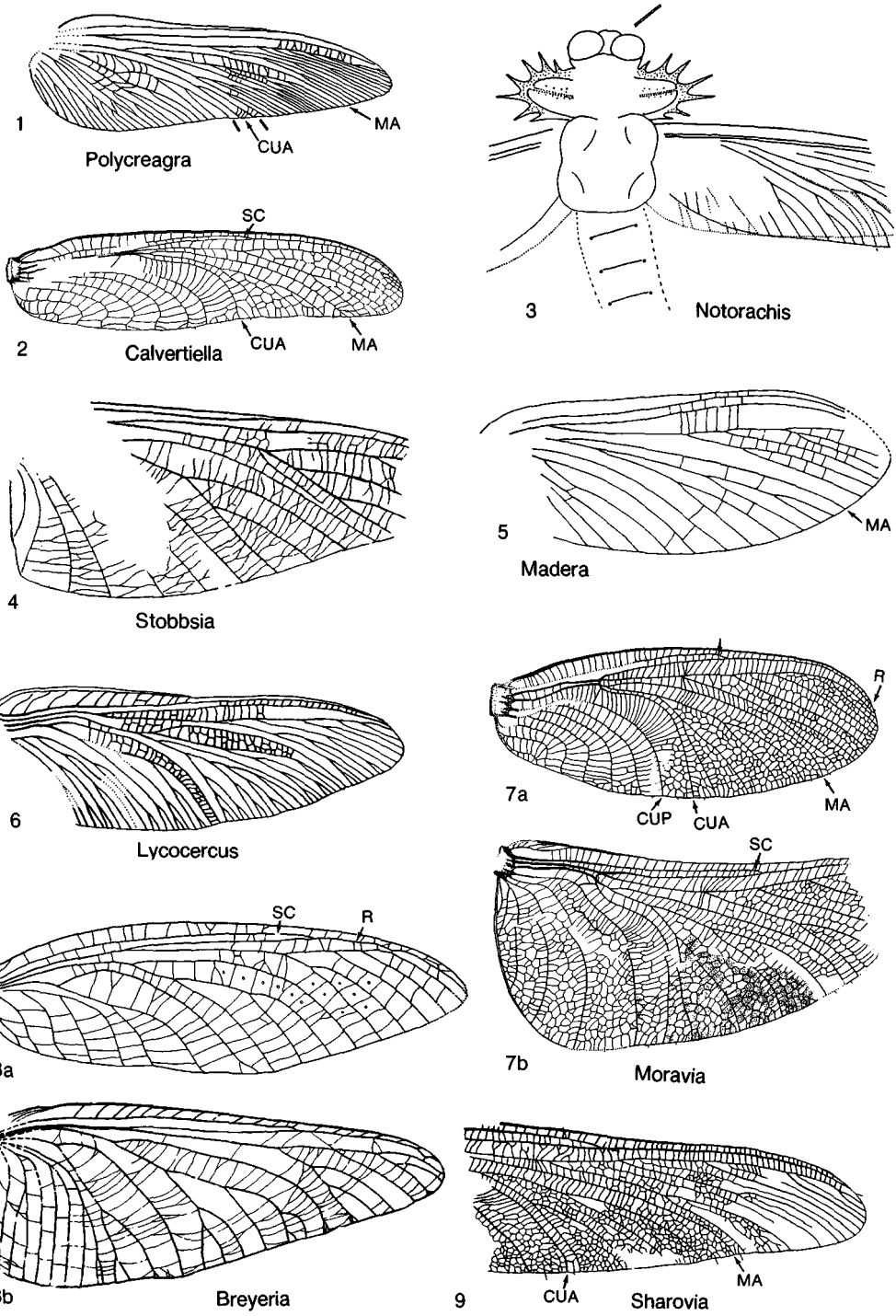


FIG. 21. Calvertiellidae, Lycocercidae, and Breyeriidae (p. 32–35).

Island).——FIG. 21,*1*. **P. elegans*; hind(?) wing, ×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 [**Pachytylopsis 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, ×0.8 (Carpenter, 1967a).——FIG. 21,*8b*. *B. barborae* KUKALOVÁ, Czechoslovakia; hind wing, ×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, ×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.*

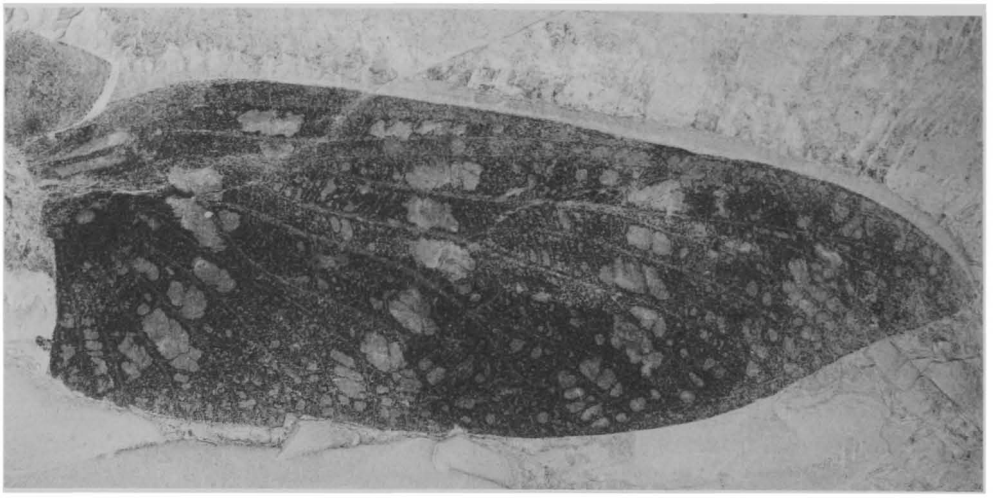
Tchirkovaea M. D. ZALESSKY, 1931, p. 403 [**T. guttata*; OD]. Fore wing with anterior margin strongly convex; SC extending well beyond two-thirds of wing length; MP forked to about half its length; crossveins forming coarse reticulation in several areas. Hind wing with anterior margin almost straight.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



Homoioptera

FIG. 22. Homoiopteridae (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.*

Homoioptera BRONGNIART, 1893, p. 353 [**H. woodwardi*; OD] [=*Homoeophlebia* HANDLIRSCH, 1906b, p. 92 (type, *Homoioptera 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, ×0.7 (Carpenter, new).

Adolarryia 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 *Homoioptera* 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; archedictyon 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, ×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 dohrni* 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. dohrni* (Brongniart); fore wing, head, and foreleg, ×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* Trouessart, 1885 [**Oustaletia lacroixi*; OD] [=*Archaecompsoneura* 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, ×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 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.*

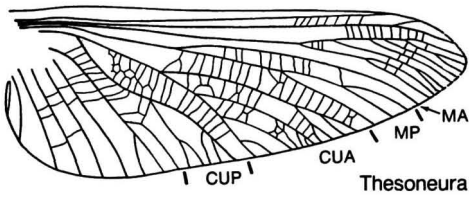


Fig. 23. Homoiopteridae (p. 36).

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, ×2.5 (Carpenter, 1983).

Family SPILAPTERIDAE Handlirsch, 1906

[Spilapteridae Handlirsch, 1906b, p. 101] [=Lamproptiliidae Handlirsch, 1906b, p. 109; Dunbariidae 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.*

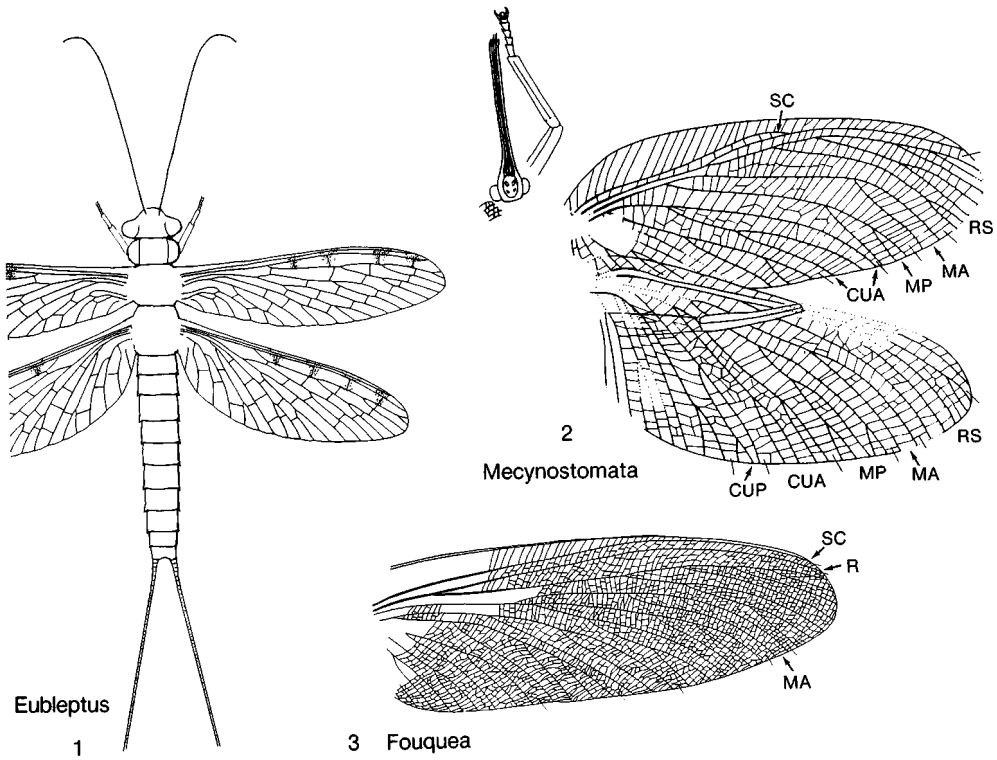


FIG. 24. Mecynostomatidae, Fouqueidae, and Eubleptidae (p. 37).

Spilaptera BRONGNIART, 1885a, p. 63 [**S. packardi*; 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 (Ukraina), USA (Illinois).——FIG. 25,*4*. **S. packardi*; fore wing, ×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, ×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, ×3.6; *b*, hind wing, ×3.7; *c*, dorsal view, ×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, ×1.3 (Kukalová, 1969b). ——FIG. 27,*b. H. dabasinskasi* CARPENTER, Illinois; fore and hind wings, ×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, ×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, ×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 & SINITSHENKOVA, 1977. *U. Carb.,* USSR (Asian RSFSR).——FIG. 25,*1. **N. altaica*; fore wing, ×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 & SINITSHENKOVA, 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, ×1.5 (Sharov & Sinitshenkova, 1977).

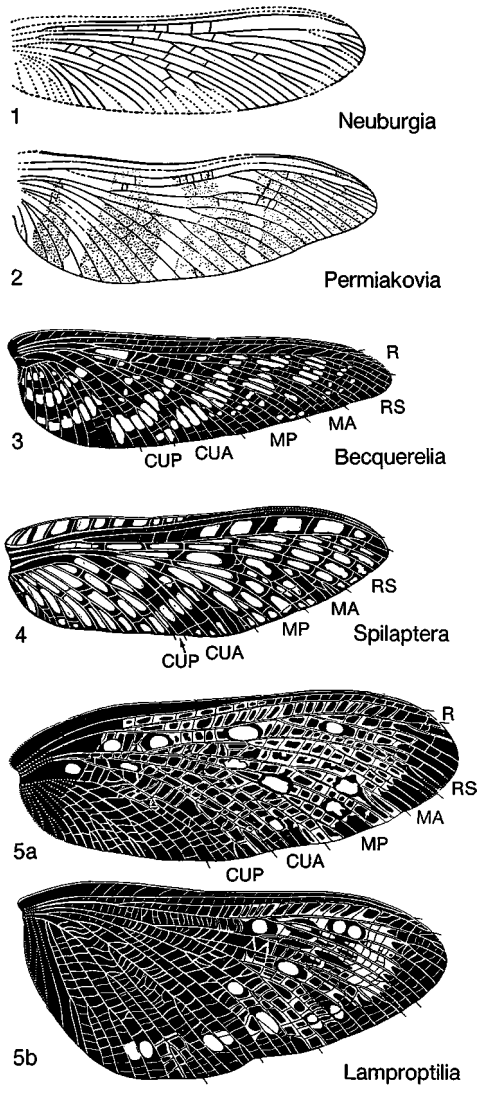


FIG. 25. Spilapteridae (p. 38–39).

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

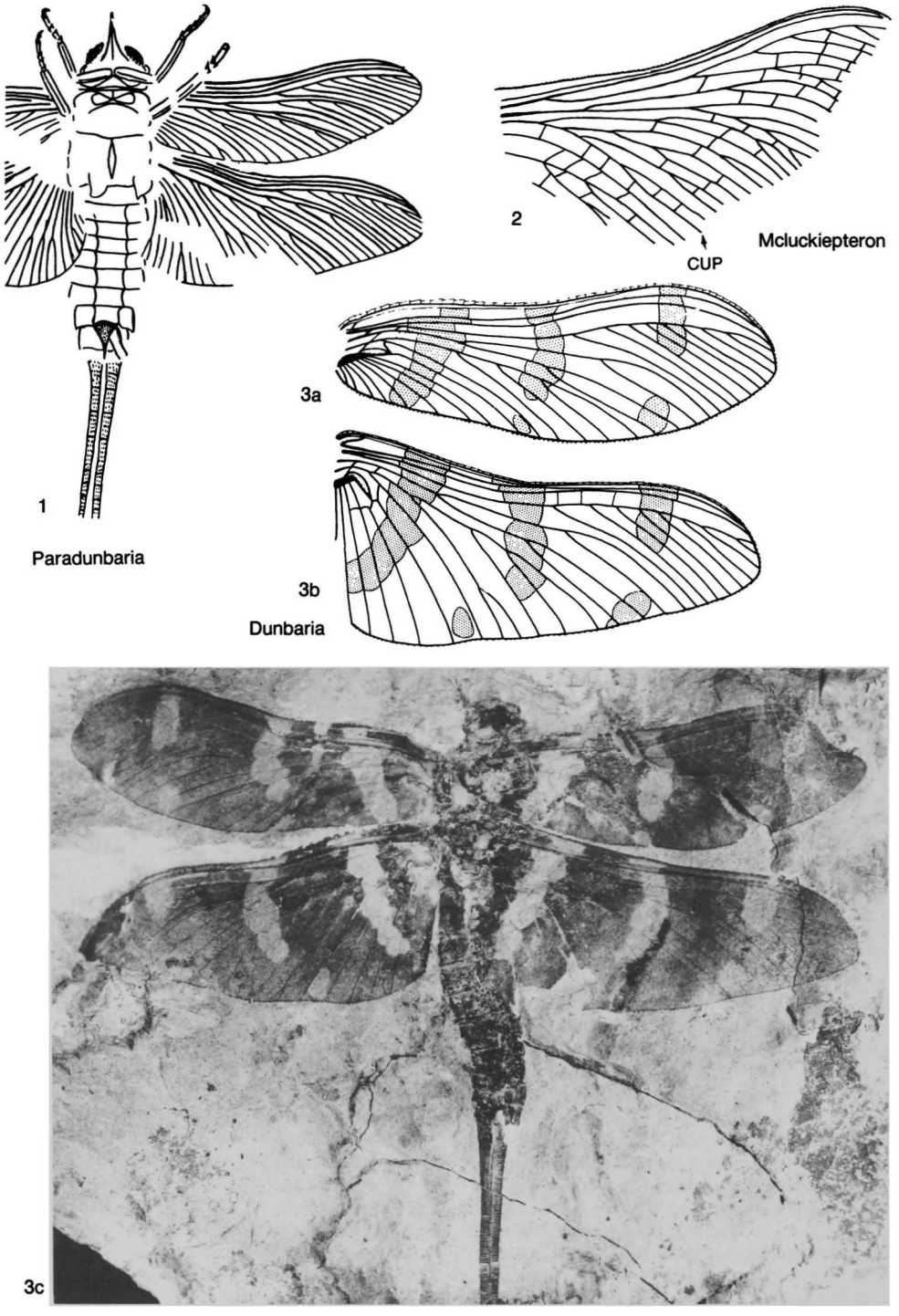


FIG. 26. Spilapteridae (p. 38–39).

elia grehanti BRONGNIART, 1893, p. 359; OD]. Wings without cuticular thickenings between 1A and CUP, with fewer branches than in *Epitethe* and *Palaeoptilus*. 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 multibranched. *Perm.*, USSR (European RSFSR).

Family ELMOBORIIDAE Carpenter, 1976

[Elmoboriidae 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.*

Elmoboria 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).

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

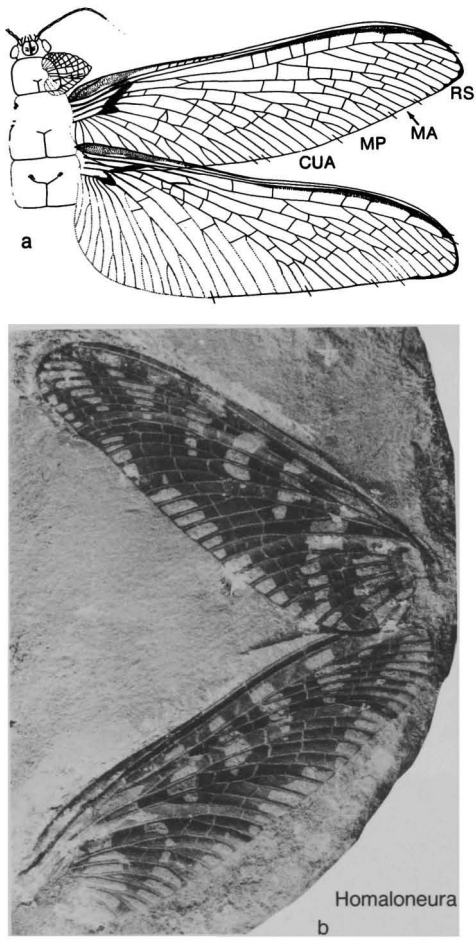


FIG. 27. Spilapteridae (p. 39).

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 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

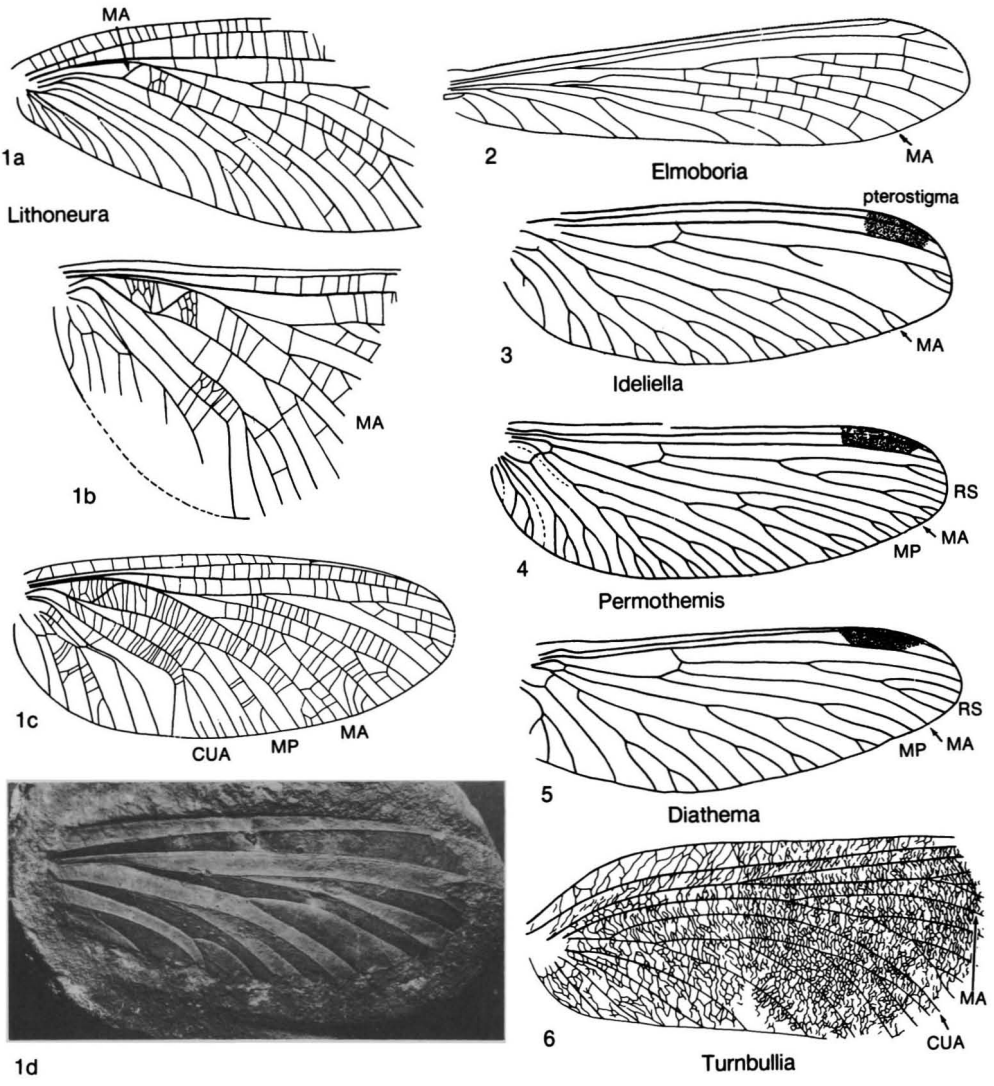


FIG. 28. Elmoboriidae, Syntonopteridae, Permothemistidae, Diathemidae, and Uncertain (p. 41–45).

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. schucherti*; 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, ×1.6 (Carpenter, 1938).——FIG. 28,*1c*. *L. mirifica* CARPENTER; hind wing, ×0.7 (Carpenter, 1944).——FIG. 28,*1d*. *L. carpenteri* RICHARDSON; fore wing, ×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, ×3 (Sinitshenkova, 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, ×4.5 (Sinitshenkova, 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 Sinitshenkova, 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, ×4 (Sinitshenkova, 1980b).

Diathemidia Sinitshenkova, 1980b, p. 105 [**D. monstruosa*; OD]. Fore wing similar to *Diathema,* 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. burrettae*; 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. sahneri*; 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).

Amousus 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).

Compsoneura 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, Archaehymenoptera, 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).

Palaiotaptus 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. dohrnianum*; 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 [**Palingenia 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 archedictyon. 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, ×0.9 (Carpenter, new).

Order MEGASECOPTERA Brongniart, 1885

[*nom. correct.* Handlirsch, 1906a, p. 691, *pro* Megasecopterida Brongniart, 1885a, p. 63] [=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; archedictyon 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 Diaphanopterodea. 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 Diaphanopterodea (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 *Lameereites* (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; SINITSHENKOVA, 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, ×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, ×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

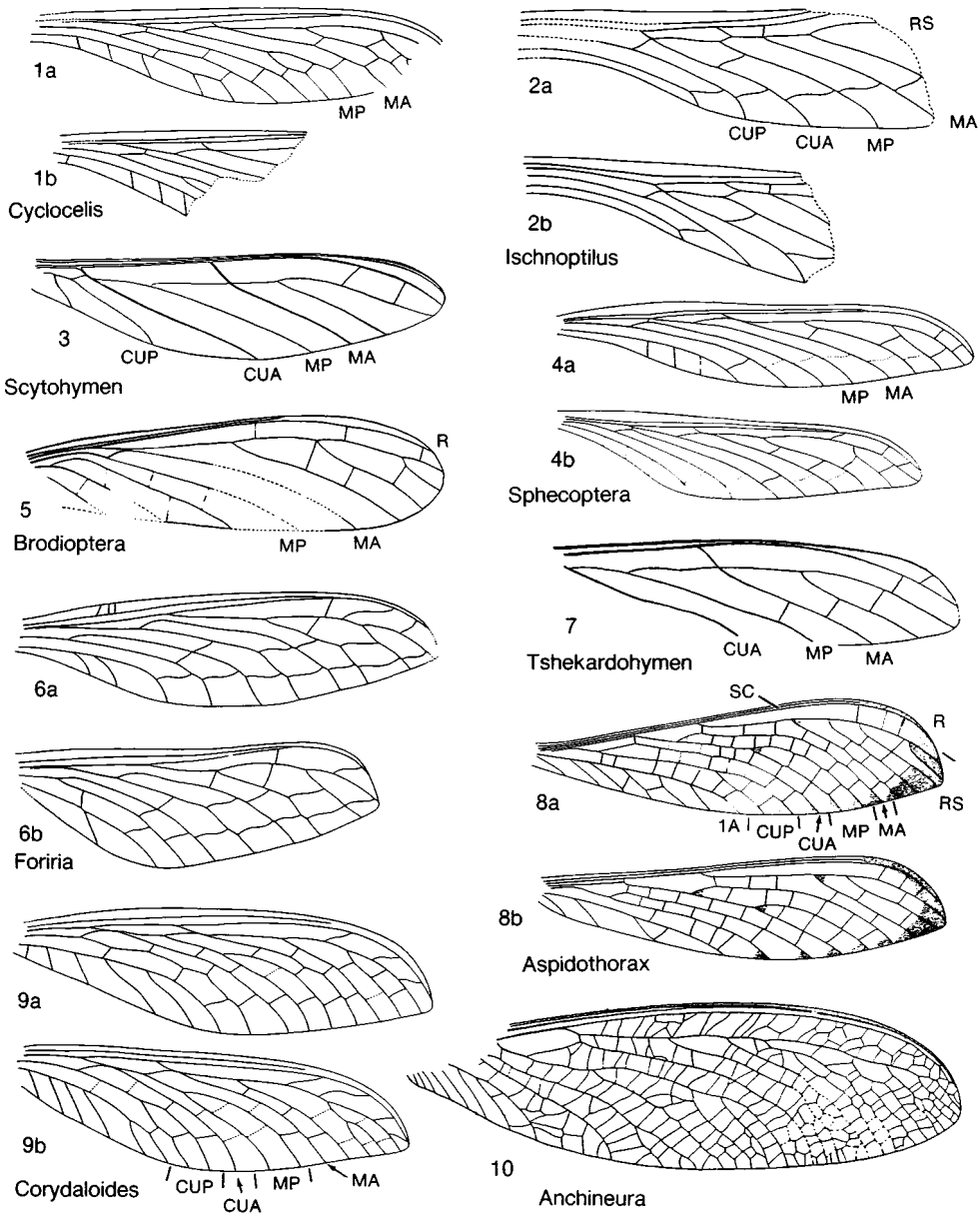


FIG. 29. Aspidothoracidae, Anchineuridae, Corydaloididae, Brodiopteridae, Foririidae, Sphecopteridae, Ischnoptilidae, and Scytohymenidae (p. 46–51).

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

Aspidohymen MARTYNOV, 1930a, p. 80 [**A. extensus*; OD]. MA and MP unbranched. CARPENTER, 1930d; MARTYNOV, 1937b; ZALESSKY, 1937c. *Perm.*, USSR (European RSFSR).——FIG. 30,*2*. **A. extensus*; distal half of wing, ×2 (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. scudderi*; SD HANDLIRSCH, 1922, p. 201] [=*Corydaliodes* 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. scudderi*; *a*, fore and *b*, hind wings, ×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, ×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, ×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, ×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, ×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, ×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* BROGNIART, 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, ×0.4, *b*, fore wing, ×0.7, *c*, hind wing, ×0.7 (Carpenter, 1951).——FIG. 30,*3d,e*. *M. douglassi* CARPENTER & RICHARDSON, Illinois; nymph, *d*, ×1.5, *e*, ×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).

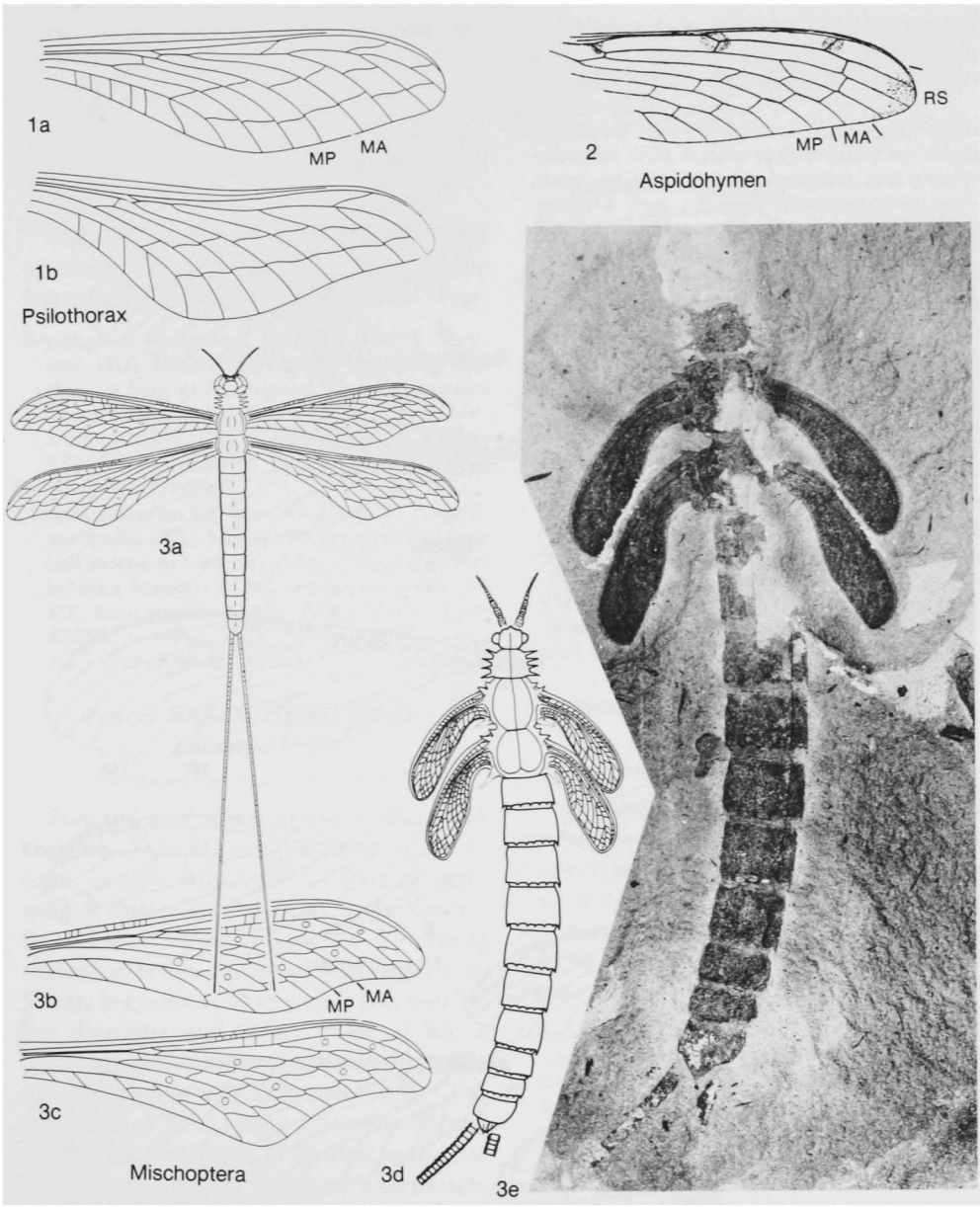


FIG. 30. Aspidohymenidae and Mischopteridae (p. 47–49).

——FIG. 30,*1*. **P. longicauda* (BRONGNIART); *a*, fore and *b*, hind wings, ×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

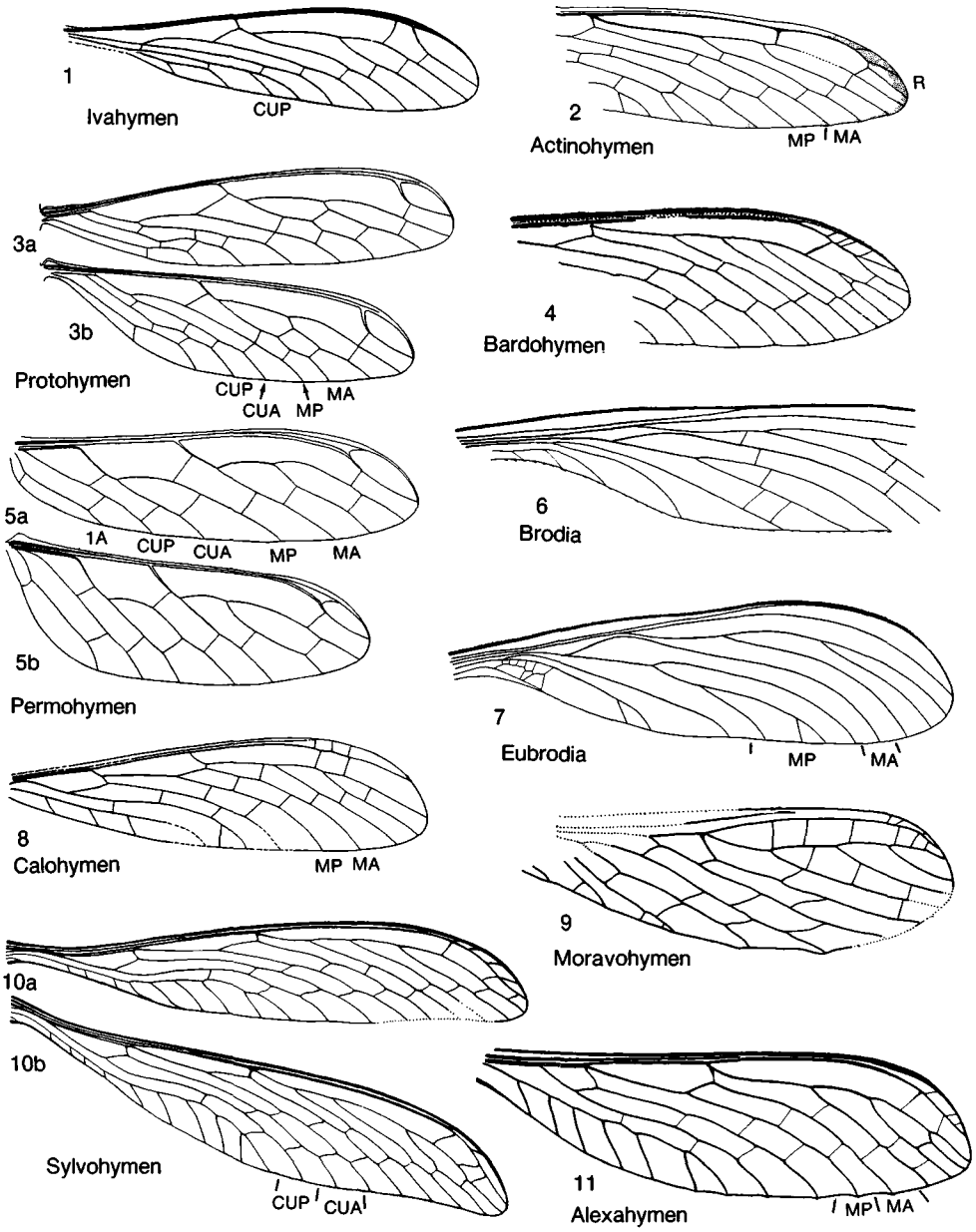


FIG. 31. Protohymenidae, Bardohymenidae, Moravohymenidae, and Brodiidae (p. 49–52).

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, ×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, ×3 (Martynov, 1932).

Permohymen TILLYARD, 1924a, p. 115 [**P. schuchberti*; 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. schucherti; a,* fore and *b,* hind wings, ×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, ×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, ×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, ×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, ×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, ×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, ×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, ×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, ×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, ×1.2 (Carpenter, 1967a).

Eubrodia CARPENTER, 1967a, p. 73 [**E. dabasinskasi*; 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. dabasinskasi*; wing, ×1.2 (Carpenter & Richardson, 1971).

Family ANCOPTERIDAE Kukalová-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, ×1.8 (Kukalová-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. tshernovi*; 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 Kukalová-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, ×5 (Kukalová-Peck, 1975).

Family HANIDAE Kukalová-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. 32,7*a*. **H. filia*; distal part of fore wing, ×1.4 (Kukalová-Peck, 1975).——FIG. 32,7*b*. *H. lineata* KUKALOVÁ-PECK; basal part of wing, ×1.4 (Kukalová-Peck, 1975).

Family ARCIONEURIDAE Kukalová-Peck, 1975

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

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

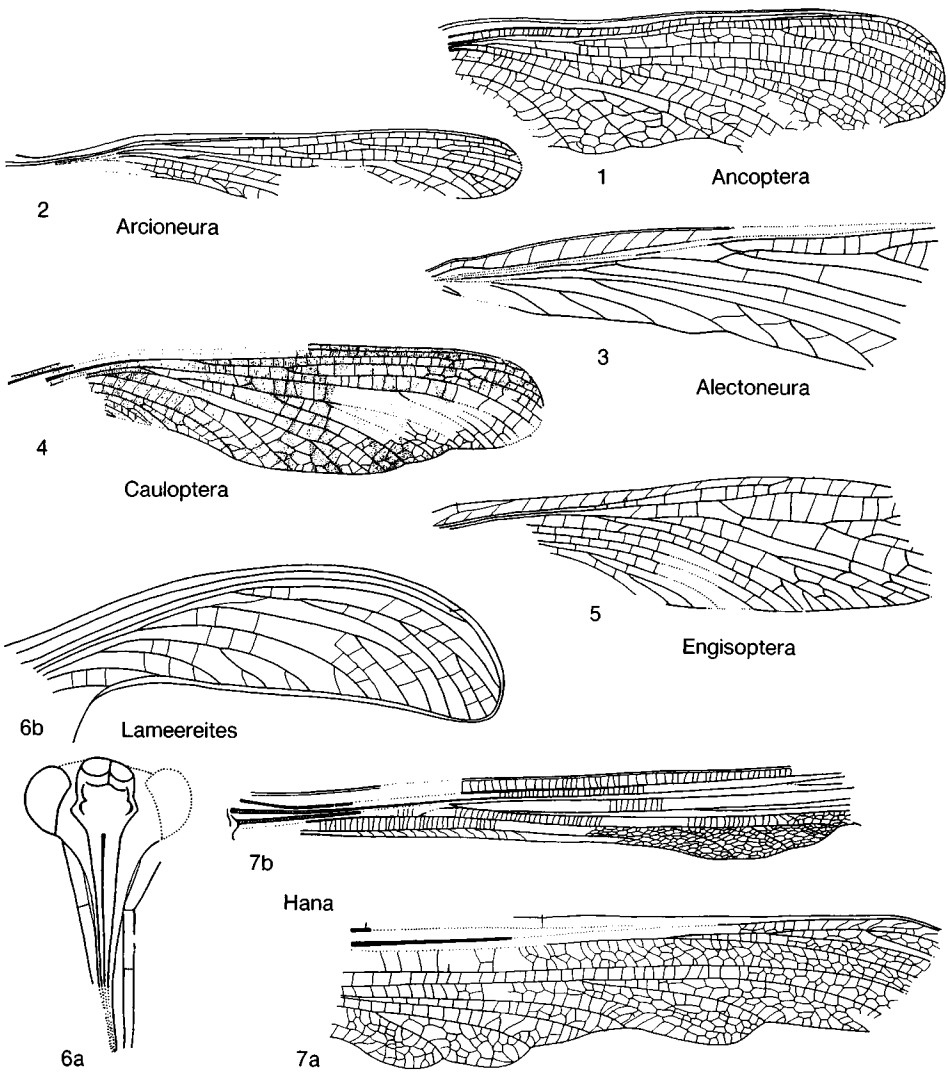


FIG. 32. Ancopteridae, Alectoneuridae, Hanidae, Arcioneuridae, Caulopteridae, Engisopteridae, and Uncertain (p. 52–54).

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, ×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, ×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, ×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, ×6; *b*, wing pad, ×3.8 (Carpenter & Richardson, 1968).

Order DIAPHANOPTERODEA 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; archedictyon 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 Diaphanopterodea in which both wings and body are known (i.e., Diaphanopteridae, Prochoropteridae, 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 Diaphanopterodea 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 Diaphanopterodea and Megasecoptera, as shown in the Protohymenidae of the Megasecoptera and the Asthenohymenidae of the Diaphanopterodea. 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 diaphanopterodean 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); *Pseudanthracothremma* Handlirsch, 1906b, p. 324 (type, *Anthracothremma 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, ×1.5 (Carpenter, 1963d).——Fig. 33,*5c*. **D. munieri*; fore wing, ×1.5 (Carpenter, 1963d).——Fig. 34. *D. superba*; dorsal view, ×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, ×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, ×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, ×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, ×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, ×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, ×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

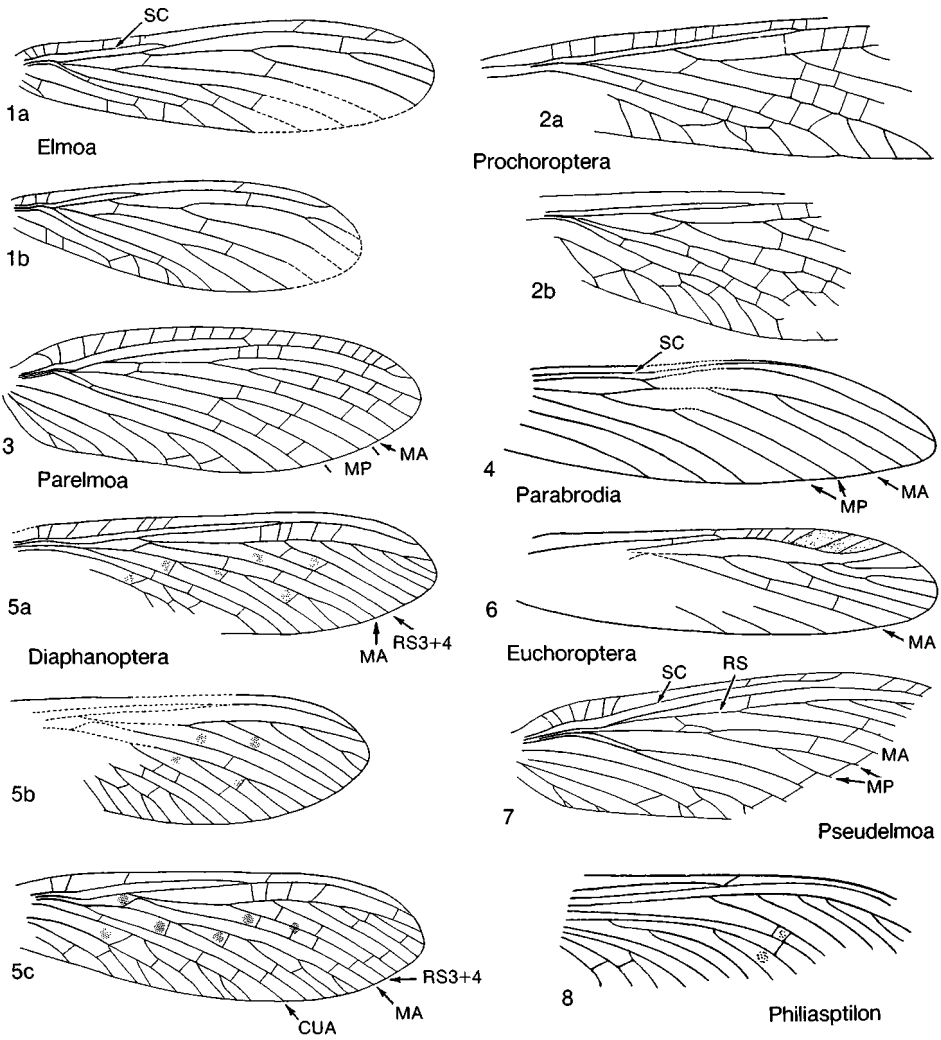


FIG. 33. Diaphanopteridae, Prochoropteridae, Elmoidae, Parelmoidae, and Parabrodiidae (p. 55–58).

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, ×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, ×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, ×4.3 (Carpenter, 1947).

Family BIARMOHYMENIDAE Zalessky, 1937

[Biarmohymenidae ZALESSKY, 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, ×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] [=*Karoohymen* 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, ×12.0 (Carpenter, 1947). ——FIG. 36. **A. dunbari*, Kansas; dorsal view of complete insect, ×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

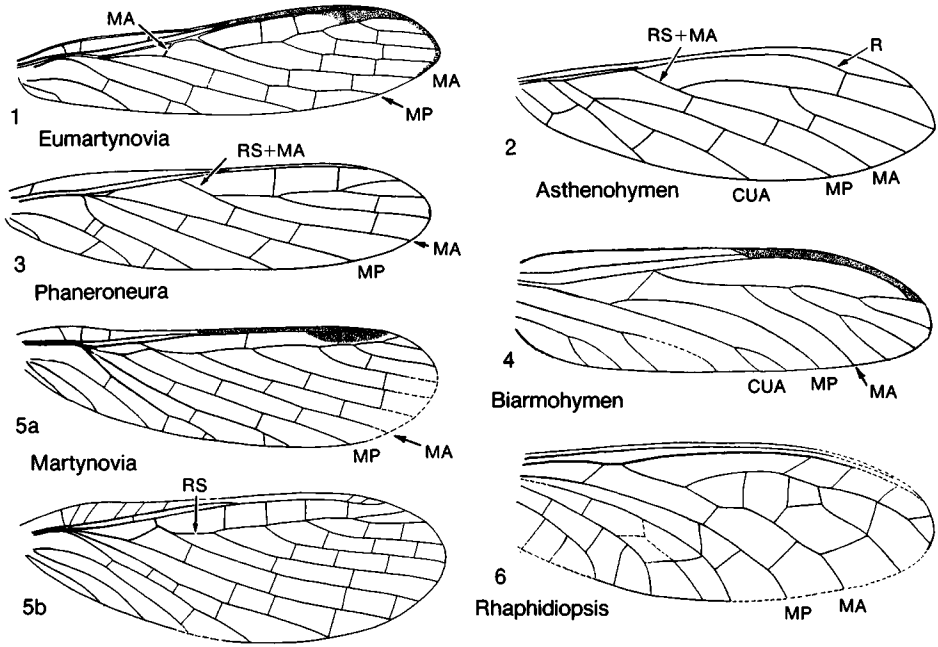


FIG. 35. Martynoviidae, Biarmohymenidae, Asthenohymenidae, and Rhaphidiopsidae (p. 56–58).

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, ×1.6 (Carpenter, 1933a).

Family PARABRODIIDAE 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, ×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, ×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, ×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, ×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, ×3.75 (Kukalová-Peck, 1974a).

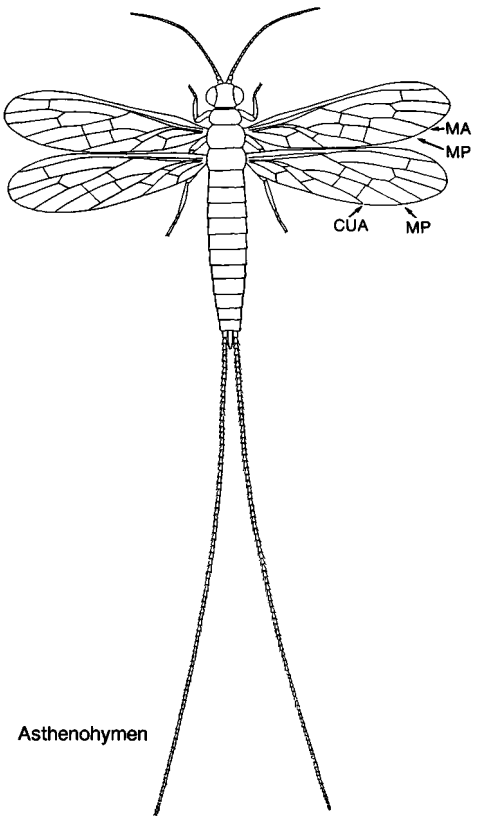


FIG. 36. Asthenohymenidae (p. 57).

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 crossvein; RS with 5 terminal branches. *Perm.*, Europe (Czechoslovakia).——FIG. 37,*5*. **P. maculifera*; hind wing, ×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, ×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 usually 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 suborder 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.

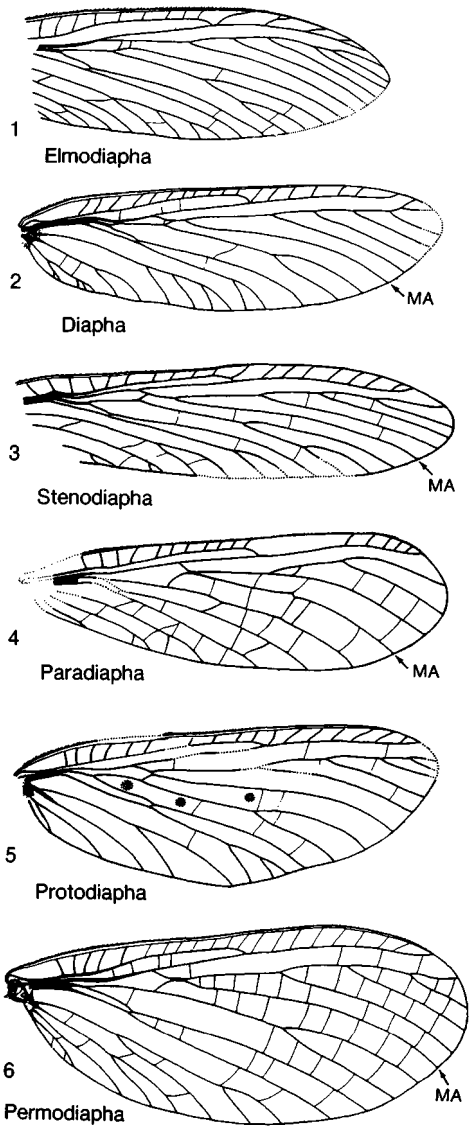


FIG. 37. Uncertain (p. 58–59).

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, charactistic of other palaeopterous insects, has been retained. In some protodonates 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, ×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. kuhni*; OD]. Little-known genus, based on wing fragment, similar to *Tupus*. *U. Carb.*, Europe (Germany).

Meganeuropsis 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, ×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-

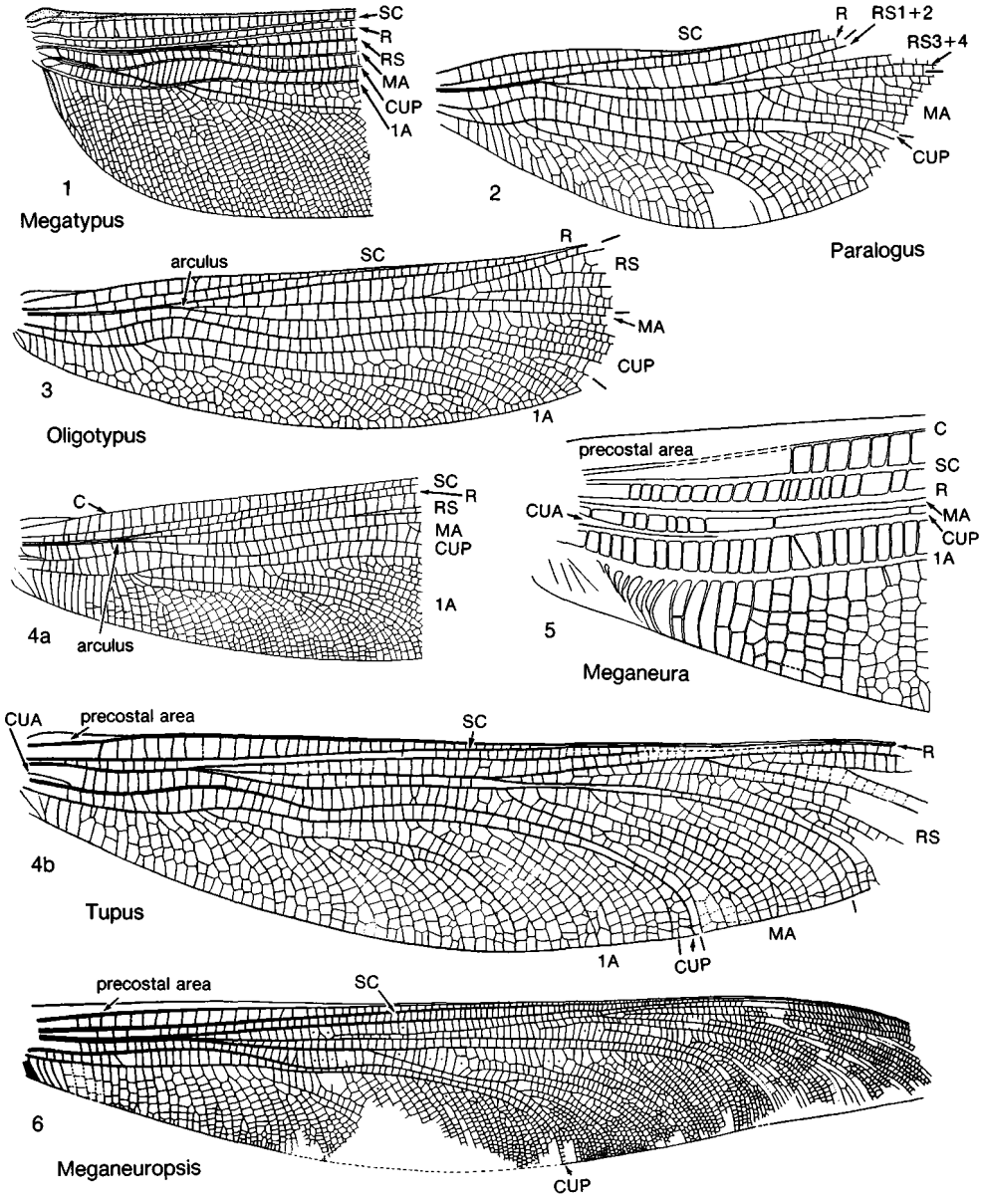


FIG. 38. Meganeuridae and Paralogidae (p. 60–62).

PENTER, 1931a, 1939, 1940b. *Perm.*, USA (Kansas).——FIG. 38,*1*. **M. schucherti*; base of hind wing, ×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*); *Arctotypus* 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, ×0.6 (Carpenter, 1947).——FIG. 38,*4b. *T. permianus* (SELLARDS), Perm., Kansas; fore wing, ×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. aeschnoides*; OD]. Wing nearly oval, with a strongly curved posterior margin. ROHDENDORF, 1940b; CARPENTER, 1960b. *U. Carb.,* USA (Rhode Island). ——FIG. 38,*2. *P. aeschnoides*; fore wing, ×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, ×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).

Truemania 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] [=Permodonata 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

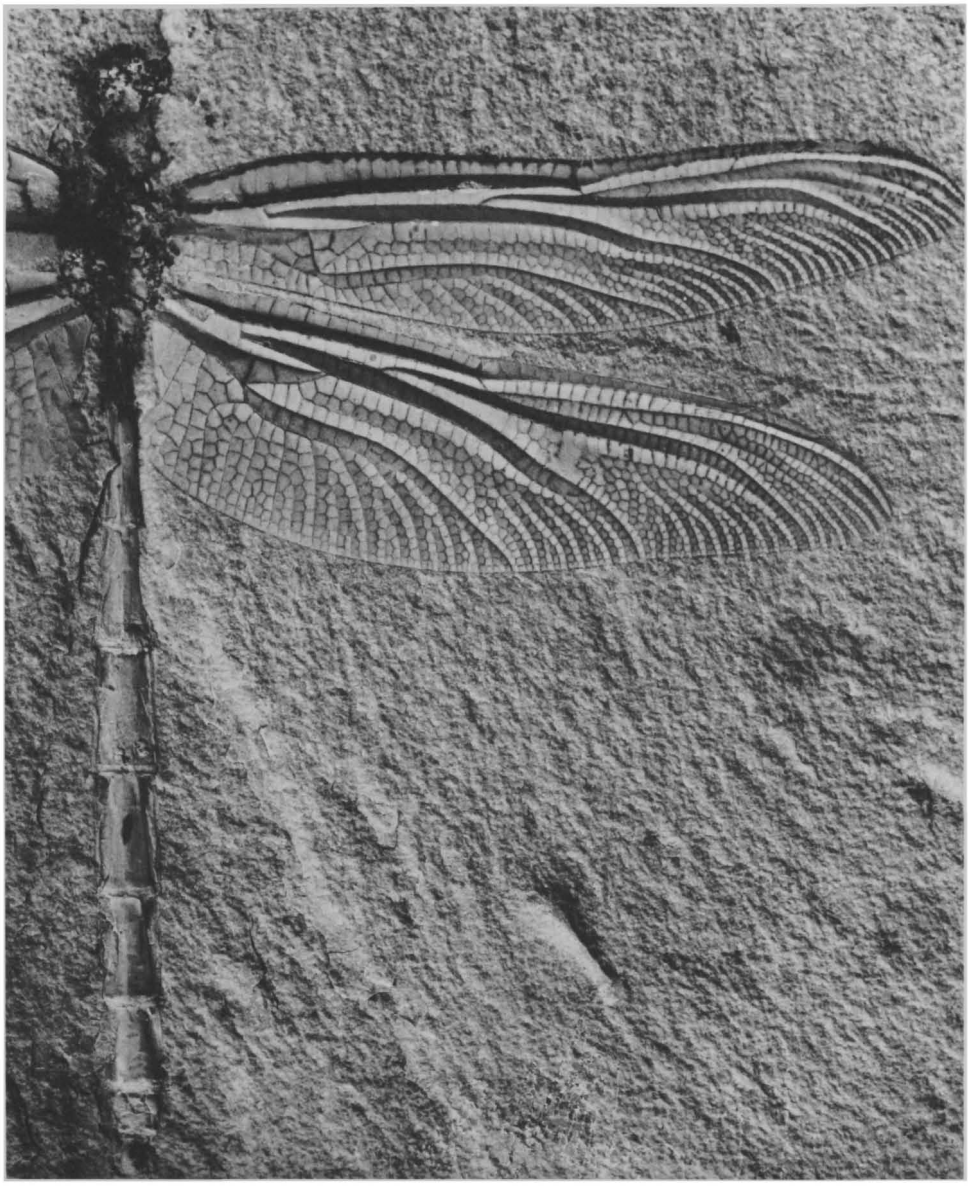


FIG. 39. Odonata; ***Protolindenia wittei*** (GIEBEL), Anisoptera, Gomphidae; ×2 (Carpenter, new). This specimen shows the typical odonate body form and the convexity and concavity of the main wing veins as well as intercalary veins and triads.

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*), Archizygoptera (see Fig. 43,*1,5, Kennedya, Permolestes*), and Anisozygoptera (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 Archizygoptera (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 Anisozygoptera, 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 Anisozygoptera 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.

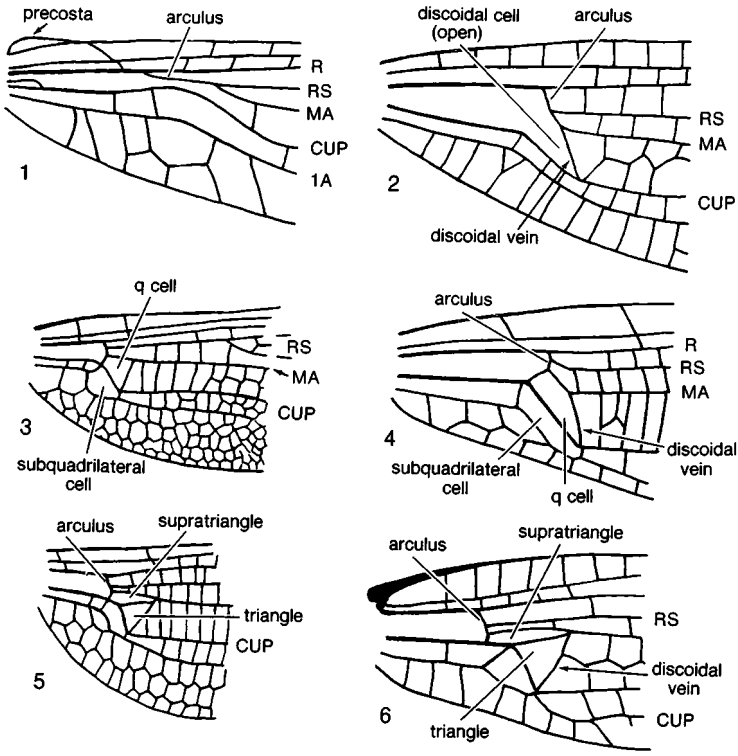


FIG. 40. Odonata; homology of wing structures in the region of the arculus in three suborders. Discoidal cell generally termed the q cell when closed.——*1.* Fore wing of *Ditaxineura anomalostigma,* Protanisoptera (Carpenter, new).——*2.* Fore wing of *Tarsophlebia eximia,* Anisozygoptera (Carpenter, new).——*3.* Fore wing of *Turanothemis nodalis,* Anisozygoptera (after Pritykina, 1968).——*4,5. Heterophlebia buckmani,* Anisozygoptera; *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 Anisozygoptera as well as in all wings of the Zygoptera. In the hind wings of some families of the Anisozygoptera 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, Archizygoptera, Triadophlebiomorpha, Anisozygoptera, Anisoptera, and Zygoptera. 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-

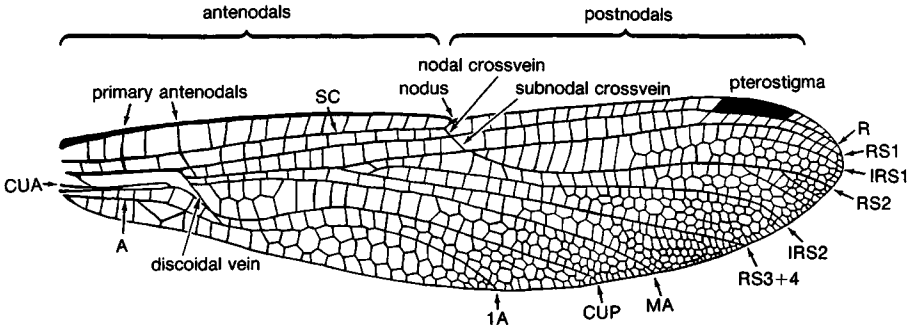


FIG. 41. Odonata; fore wing of *Tarsophlebiopsis mayi,* Anisozygoptera (after Fraser, 1955b).

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 antenodals; 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 antenodals; 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, ×2.5 (Carpenter, 1931a); *b,* hind wing, ×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 antenodals; 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, ×1.2 (Martynov, 1931b).——FIG. 42,*2b. P. camense* (G. M. ZALESSKY); wing as preserved, ×1 (G. M. Zalessky, 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, ×1.8 (Zalessky, 1955a).

Ditaxineurella MARTYNOV, 1940, p. 11 [**D. stigmalis*; OD] [=*Hemizygopteron* 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. stigmalis*; wing as preserved, ×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, ×1.4 (Tillyard, 1935b).

Suborder ARCHIZYGOPTERA Handlirsch, 1906

[Archizygoptera HANDLIRSCH, 1906b, p. 471] [=Protozygoptera 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.*

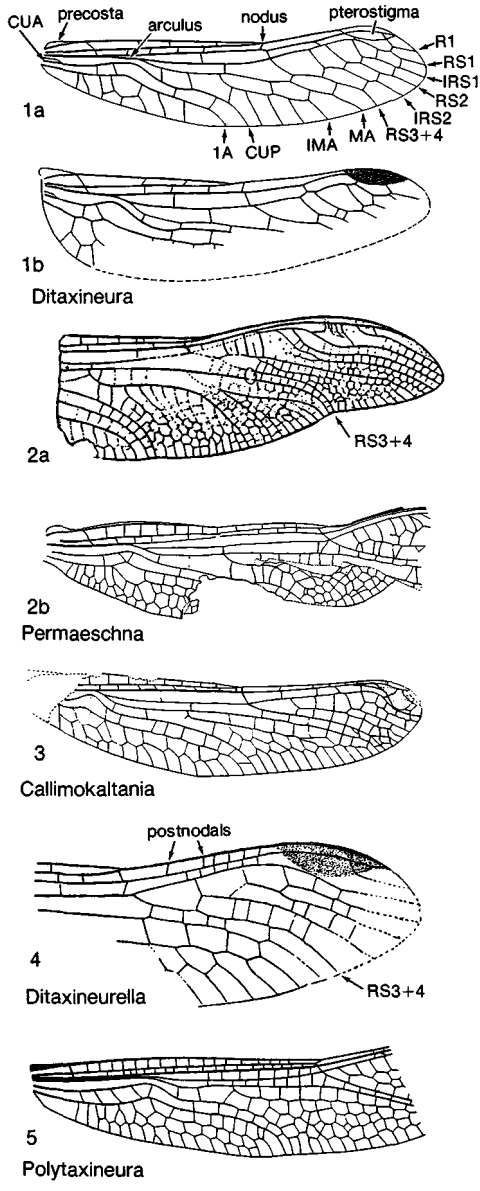


FIG. 42. Ditaxineuridae and Permaeschnidae (p. 66–67).

Kennedya 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, ×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 *Kennedya*. CARPENTER, 1947. *Perm.*, USA (Oklahoma).——FIG. 43,6. *P. nobilis* CARPENTER; wing, ×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, ×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, ×1.7 (Martynov, 1937b).

Scytolestes MARTYNOV, 1937b, p. 18 [**S. stigmalis*; OD]. Similar to *Permolestes*, but wings with arculus 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, ×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, ×2 (Zalessky, 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 relationships 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, ×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* Protomyrmeleonidae 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, ×2.5 (Handlirsch, 1906b).——FIG. 43,12b. *P. handlirschi* MARTYNOV, USSR; wing, ×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

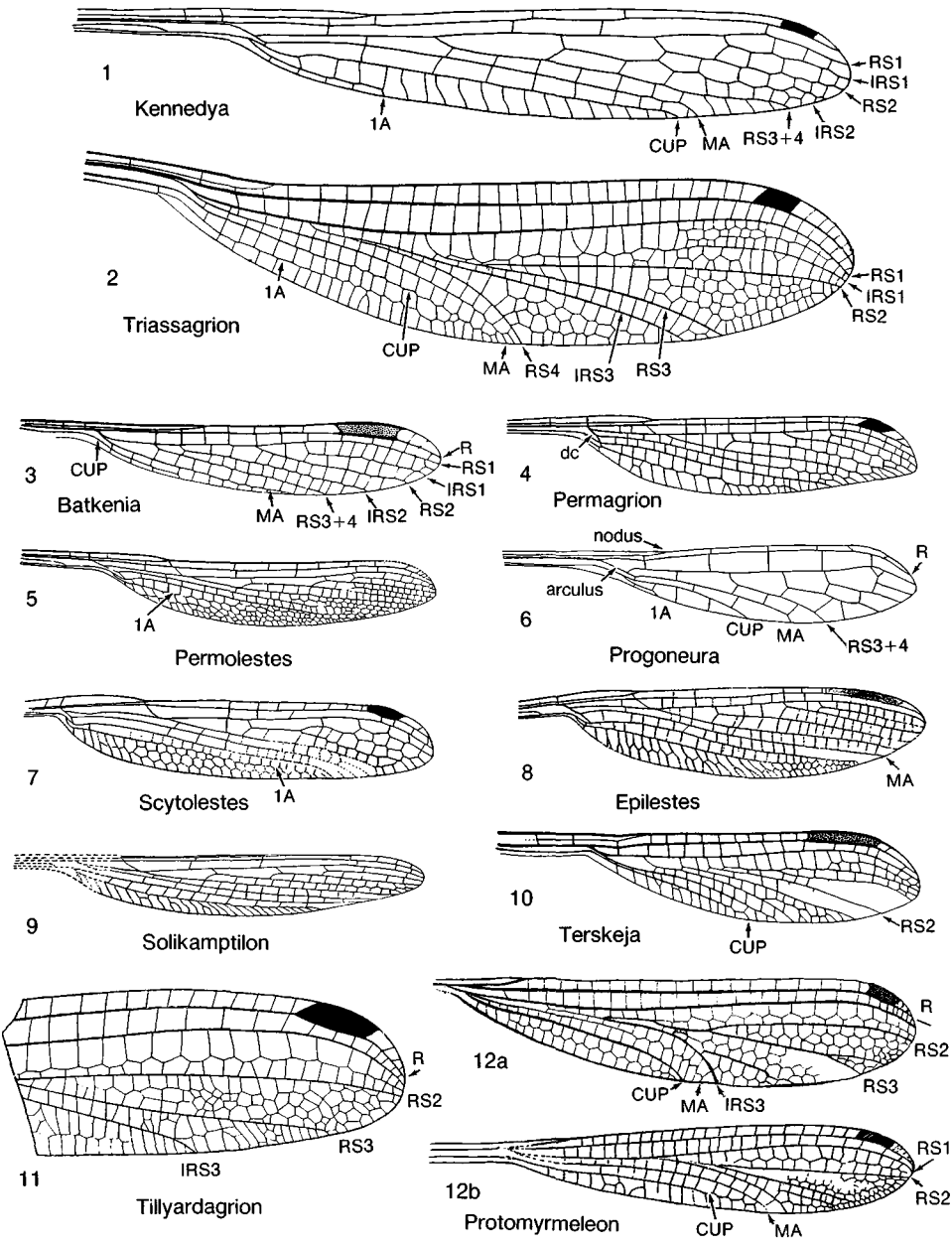


FIG. 43. Kennedyidae, Permolestidae, Permagrionidae, Protomyrmeleontidae, Batkeniidae, and Uncertain (p. 67–70).

IRS1 distally; RS2 and RS3 only slightly divergent; IRS3 and RS3 slightly divergent. *Jur.*, England. —— FIG. 43,*11*. **T. anglicanus* (TILLYARD); wing, ×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, ×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.*

Batkenia 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, ×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, ×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, ×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, ×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, ×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, ×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.*

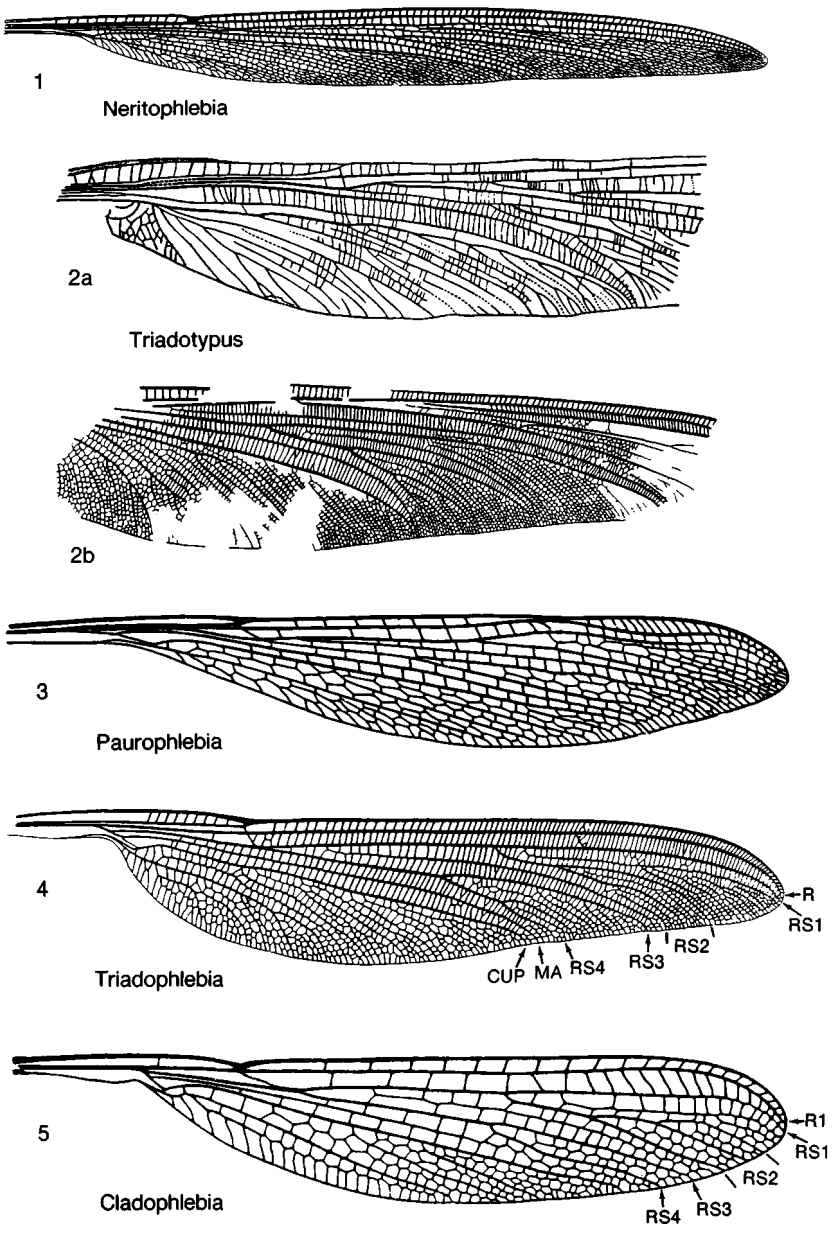


FIG. 44. Triadophlebiidae and Triadotypidae (p. 70–71).

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, ×0.75 (Grauvogel & Laurentiaux, 1952).——FIG. 44,*2b*. *T. sogdianus* PRITYKINA, USSR; hind wing, ×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.*

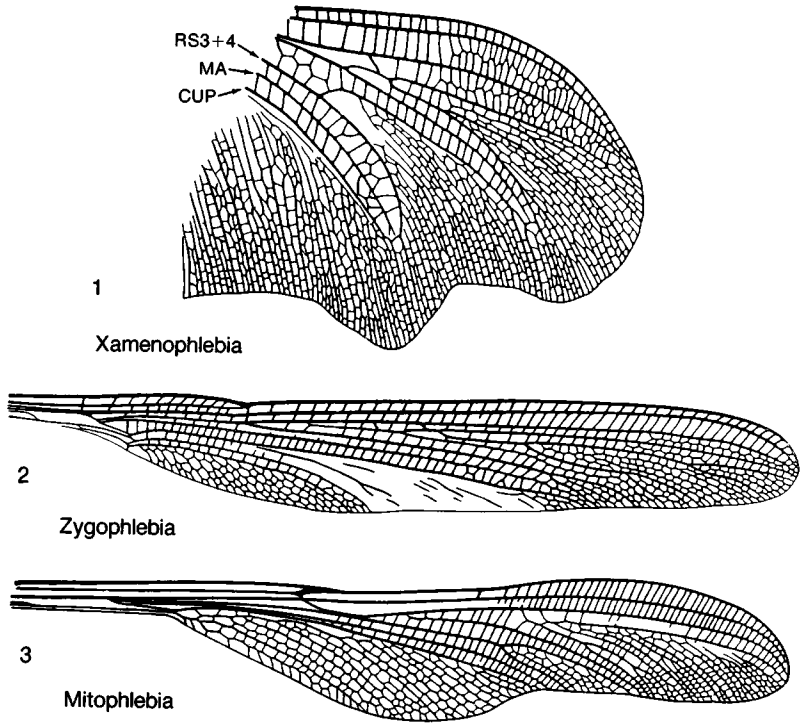


FIG. 45. Mitophlebiidae, Zygophlebiidae, and Xamenophlebiidae (p. 72).

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, ×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, ×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, ×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 subnodal 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, ×1.8 (Hagen, 1866a); *b,* base of fore wing, ×5.3 (Carpenter, 1932a). ——FIG. 46,*1c*. *T. neckini* MARTYNOV, USSR; fore wing base, ×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, ×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, ×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, ×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, ×1 (Deichmüller, 1886).

Family LIASSOPHLEBIIDAE Tillyard, 1925

[Liassophlebiidae TILLYARD, 1925a, p. 11]

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, ×0.7; *b,* hind wing, ×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).

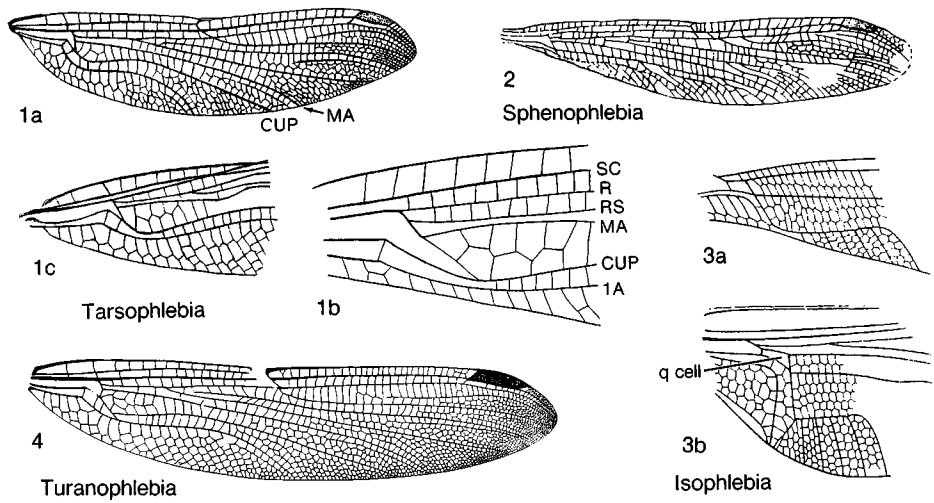


FIG. 46. Tarsophlebiidae and Isophlebiidae (p. 73).

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, ×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, ×1.5 (Tillyard, 1925a).

Pternopteron PRITYKINA, 1970, p. 112 [**P. mirabile*; OD]. Wings long and narrow; 2 strong antenodals, 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 antenodals, 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, ×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 antenodals 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. ZESSIN, 1982. *Jur.,* England, Europe (Germany).——FIG. 47,*3*. **H. buckmani* (BRODIE), England; *a,* fore wing, ×1.6; *b,* base of hind wing, ×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, ×1.4 (Handlirsch, 1939).

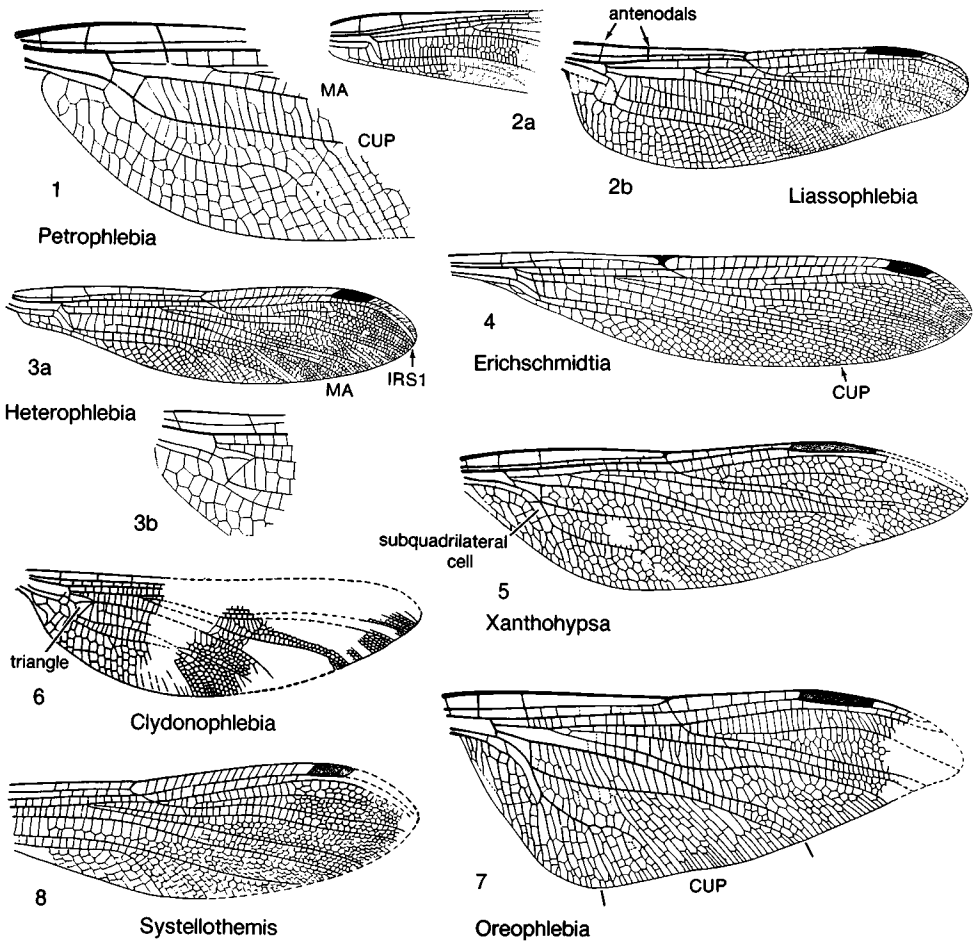


FIG. 47. Liassophlebiidae and Heterophlebiidae (p. 73–75).

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, ×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, ×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 antenodals; at most only a few weak secondary antenodals; 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, ×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, ×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 Architheristidae.] *Jur.*, USSR (Kirghiz).——FIG. 48,7. **S. nana*; wing, ×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] [=Campterophlebiidae 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] [=*Diastatommites* 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, ×1.8 (Handlirsch, 1906b). ——FIG. 48,*4b*. *A. liassina* (STRICKLAND), England; hind wing, ×0.8 (Tillyard, 1925a).

Campterophlebia 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, ×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. jurassica*; 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, ×3.3 (Pritykina, 1968).

Nacholonda PRITYKINA, 1977, p. 83 [**N. crassicosta*; 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. crassicosta*; hind wing as preserved, ×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, ×4 (Pritykina, 1968).——FIG. 49,*2b*. *O. simile* PRITYKINA; hind wing, ×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*;

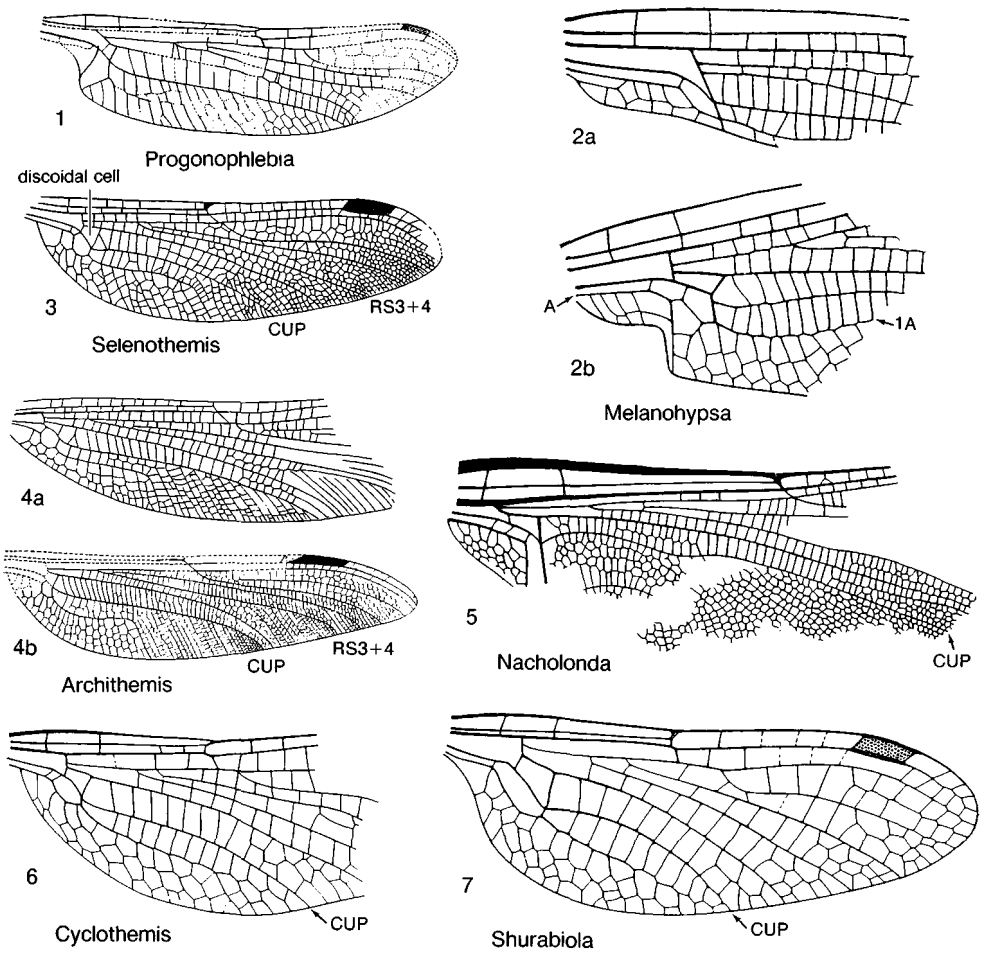


FIG. 48. Progonophlebiidae, Archithemistidae, and Karatawiidae (p. 75–76).

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, ×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, ×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, ×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, ×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. epiophlebioides*; 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, ×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 helle* 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.*

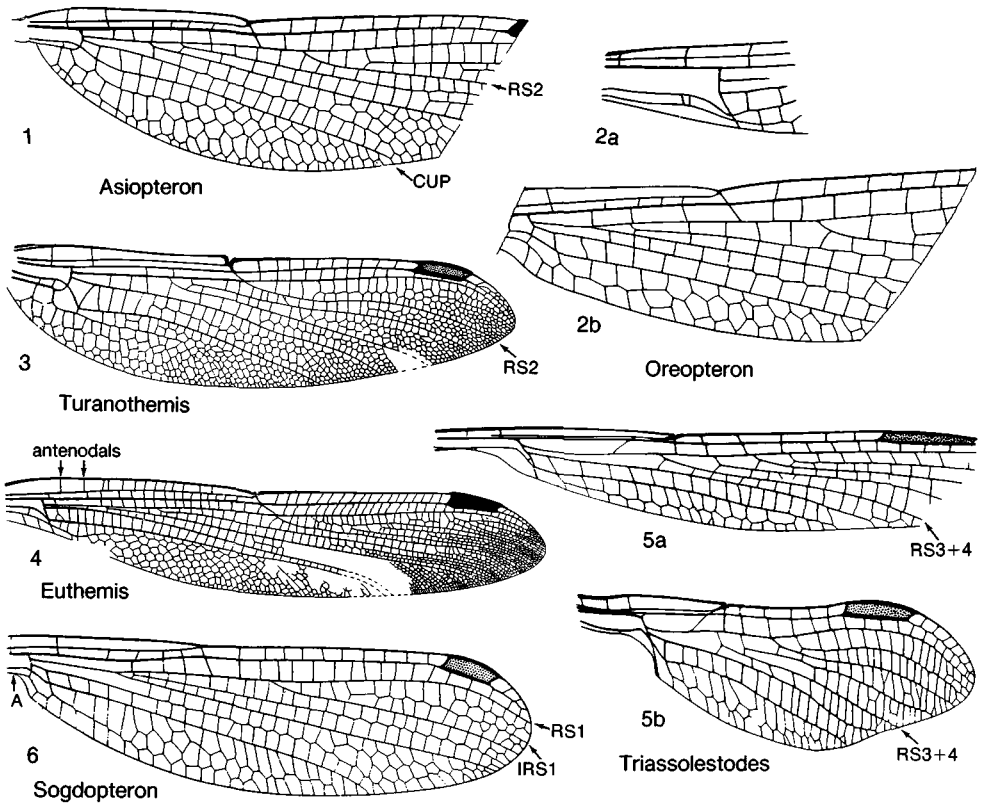


FIG. 49. Oreopteridae, Asiopteridae, Euthemistidae, Turanothemistidae, and Triassolestidae (p. 76–78).

hageni; OD]. Little-known genus, based on wing fragment. *Jur.,* Europe (Germany).

Parelthothemis HANDLIRSCH, 1906b, p. 470 [**P. dobbertinensis*; 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 fragment 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

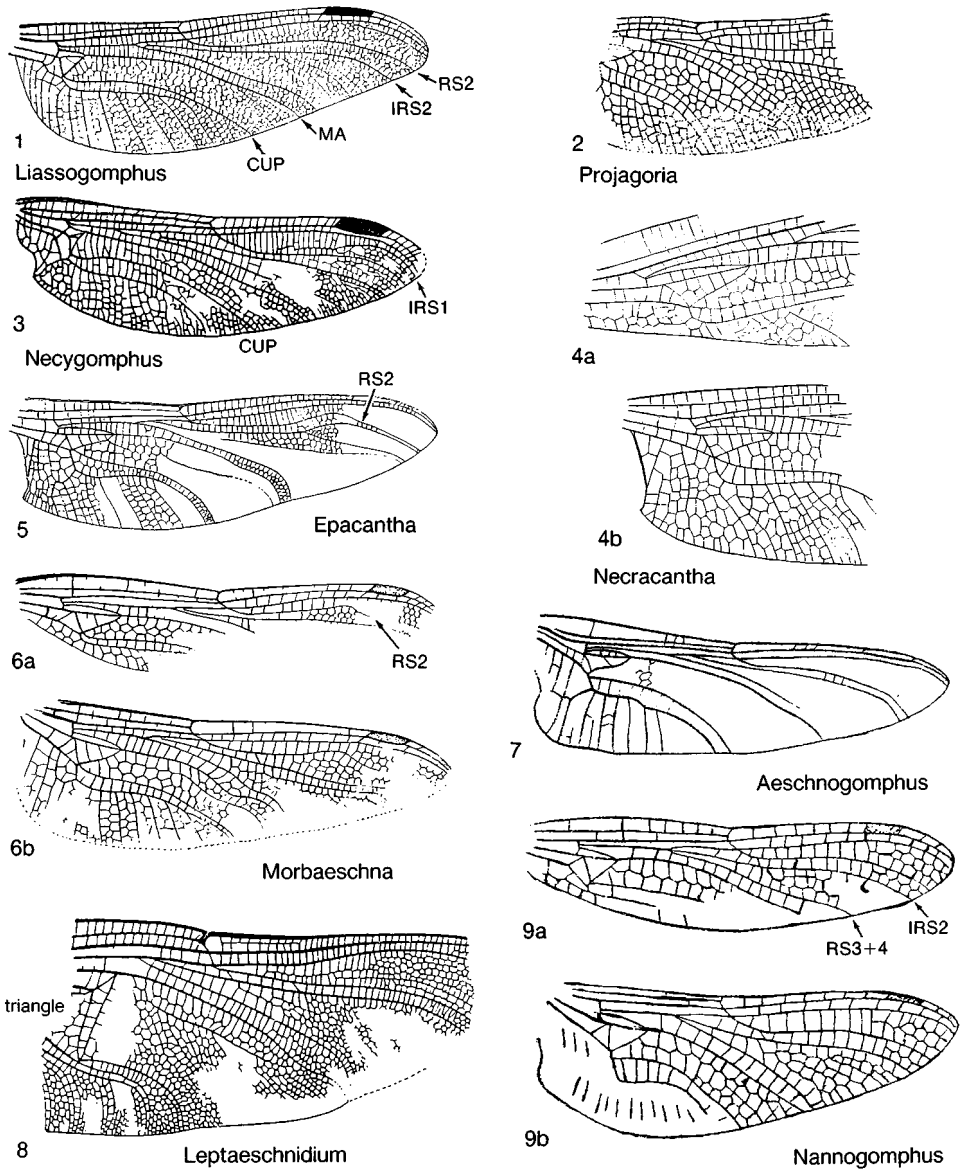


FIG. 50. Liassogomphidae, Gomphidae, and Aeshnidae (p. 81–82).

triangle (posterior), which is commonly divided by additional veins that may even form a reticulation; a third triangle, the subtriangle, 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, ×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: intercalcary vein IRS1 long, arising halfway between nodus and pterostigma. *Jur.,* Europe (Germany).—— Fig. 50,*3*. *N. libera* (Bode); hind wing, ×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 pterostigma; 4 rows of cells to about level 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 (Germany).—— Fig. 50,*7*. **A. charpentieri* (Hagen); hind wing, ×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, ×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, ×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 supratriangles 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, ×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, ×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 [**Aeshna 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, ×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, ×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; Pongrácz, 1928. *Oligo.*, USA (Colorado); *Mio.*, Europe (Denmark, Yugoslavia)–*Holo.*

Projagoria Martynov, 1929, p. 186 [**P. conjuncta*; 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, ×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, ×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, ×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; supratriangle 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, ×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 *Libellulium,* 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 *Libellulium,* 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.

Libellulium 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, ×0.8 (Needham, 1907).

Mesuropetala HANDLIRSCH, 1906b, p. 588 [**Gomphus koehleri* 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 elongate 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.*

Croatcordulia 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, ×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 MUTTKOWSKI (RIS, 1910) to be a corduliid.] COCKERELL, 1921e. *Eoc.,* USA (Colorado, Wyoming).——FIG. 51,*2. *S. carletoni*; fore wing, ×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).

Oligocaemia 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, ×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).

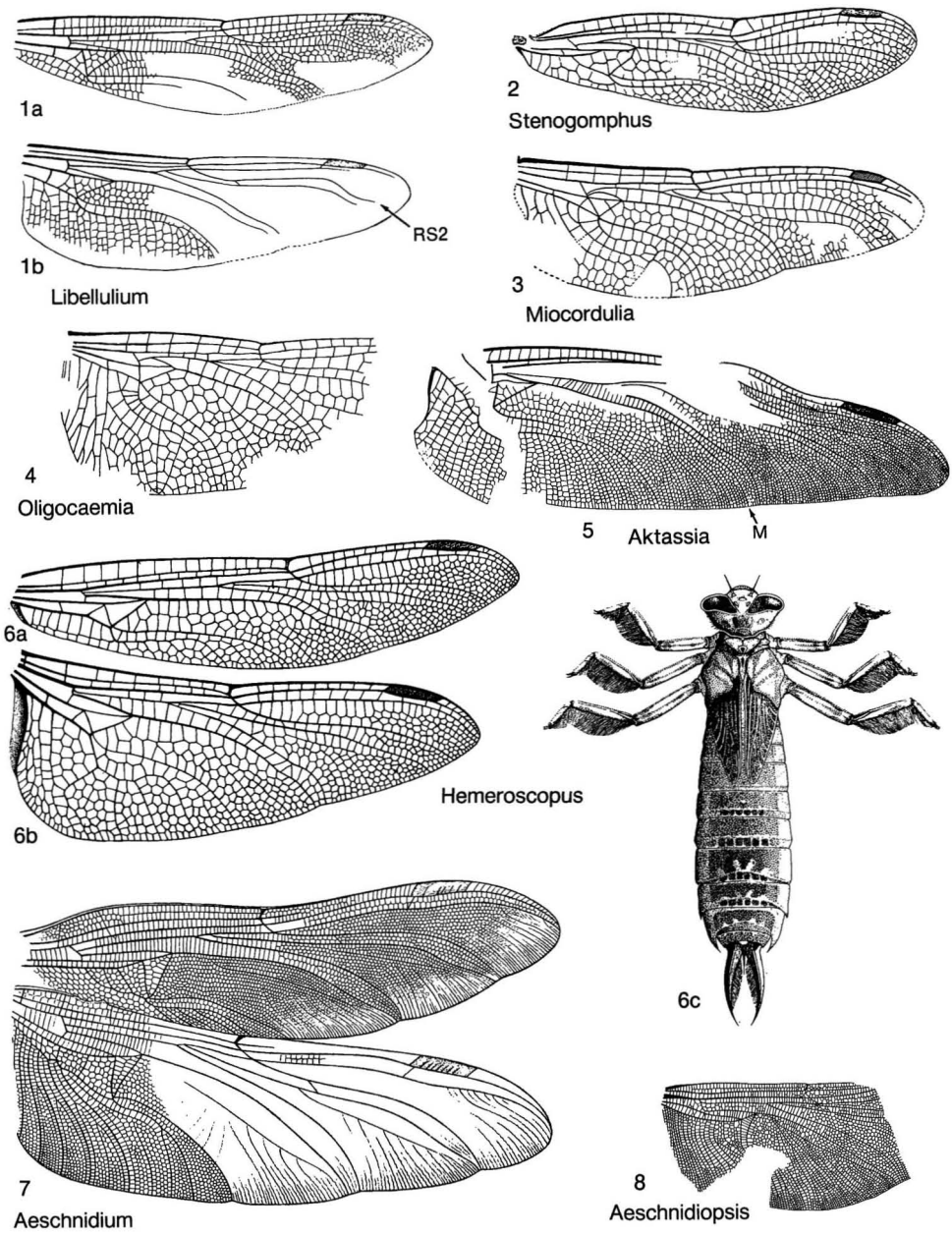


FIG. 51. Aeschnidiidae, Aktassiidae, Petaluridae, Corduliidae, Libellulidae, and Hemeroscopidae (p. (p. 82–85).

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. baissicus*; 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. baissicus; a*, fore wing, *b*, hind wing, *c*, adult nymph, all ×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 PONGRÁCZ, 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. grasselianus*; 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 supratriangle; 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. kirkbyae*)]. 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, ×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

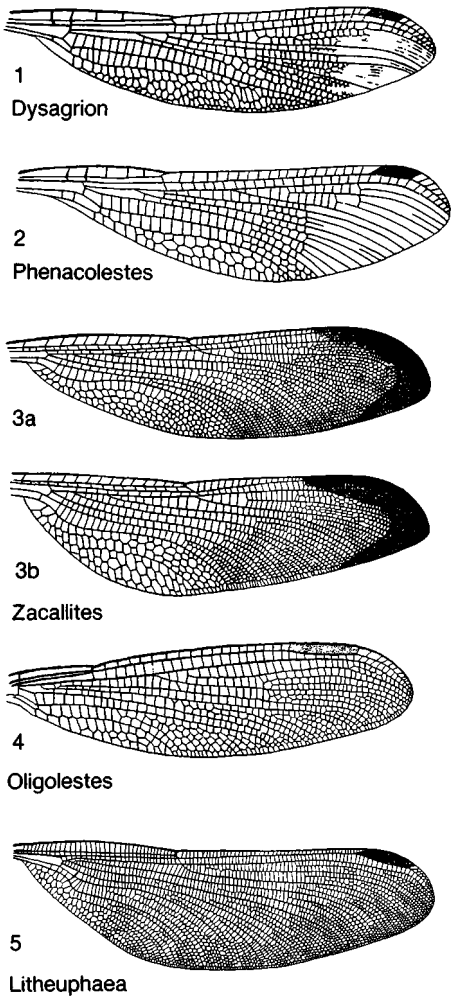


FIG. 52. Lestidae, Pseudolestidae, and Euphaeidae (p. 85–88).

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. scudderi*; 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. hyalinum*; 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 *Thaumatoneura* (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, ×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, ×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. hendersoni*; OD]. Little-known genus, based on wing

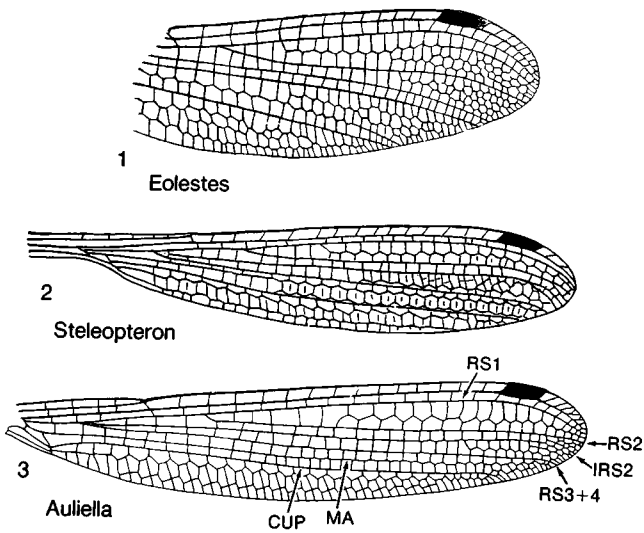


FIG. 53. Steleopteridae and Uncertain (p. 87–88).

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 antenodals. [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 antenodals 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 pterostigma. *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, ×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, ×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; antenodals 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 antenodals. *Eoc.*, USA (Texas).

Family EUPHAEIDAE Selys-Longchamps, 1853

[Euphaeidae SELYS-LONGCHAMPS, 1853, p. 47] [=Zacallitidae COCKERELL, 1928c, p. 297]

Wings subpetiolate or not petiolate; antenodals 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, ×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, ×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 [**Platycnemis 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, ×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. ronzonense*; 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, ×0.7 (Hagen, 1866a); *c,* fore wing, region of discoidal cell, ×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-*

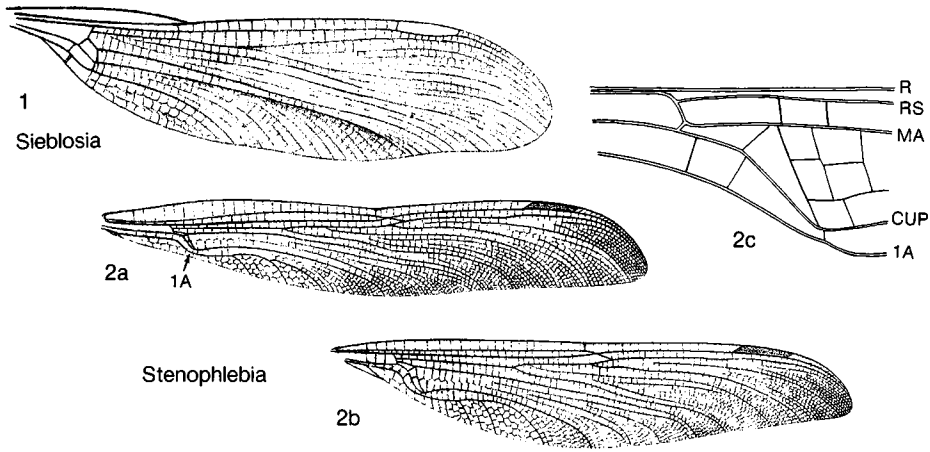


FIG. 54. Stenophlebiidae and Uncertain (p. 88–89).

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 [**Megatypus 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).

Orthaeschnites 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, ×1.8 (Hagen, 1858a).

Syrrhoe BODE, 1953, p. 69 [**S. commissa*; 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 Archaeoptilidae 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.

Bardapteron 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, Permodictyoptera, but transferred by Rohdendorf (1962a) to the Palaeodictyoptera.] *Perm.,* USSR (European RSFSR).

Breyeriodes Handlirsch, 1906b, p. 118 [**B. kliveri*; 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, Campylopterodea, 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 Caloneurodea 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. larischi*; 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 Diaphanopterodea 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, 1976e, p. 150, *non*

DEMOULIN, 1968 [**Xenophlebia optata* RIEK, 1976e, p. 150; OD]. Little-known genus, based on incomplete wing. [Type of the family Litophlebiidae 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) *higginsi* 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 Diaphanopterodea 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. biseriatus*; 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 Diaphanopterodea.] *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 elytroid; 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.