Hexapoda


**Sypharoptera** Handlirsch, 1911, p. 372 [*S. pneuma;* OD]. Little-known genus, based on incomplete wings. [Originally placed in the new order Sypharopteroidea by Handlirsch (1911); transferred to order Diaphanopteroidea by Rohdendorf (1962a).] Handlirsch, 1919b, 1922. *U. Carb.*, USA (Illinois).


**Triatologus** 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.

**Wulasu** Tan, 1980, p. 159 [*W. maculata; OD]. Little-known genus, based on poorly preserved, small fragment of a wing. [Originally placed in the Diaphanopteroidea.] *Perm.*, China (Inner Mongolia).

**Xenoneura** Scudder, 1868c, p. 206 [*X. antiquorum; OD]. Little-known genus, based on wing fragment. [Type of the family Xenoneuridae Scudder, 1885b. Originally placed in the Palaeodictyoptera.] Scudder, 1880; Handlirsch, 1906b, 1922. *U. Carb.*, Canada (New Brunswick).

Infraclass NEOPTERA

**Martynov, 1923**

[Neoptera Martynov, 1923, p. 89]

Wings articulated to thorax by sclerotized plates (axillaries), not fused or rigidly connected; third axillary Y-shaped and attached to second axillary and posterior notal process, and connected by flexor muscle to thorax; venation basically as in Palaeoptera, but vein MA flat or nearly so or absent; cerci commonly present but vestigial or absent in higher orders. Immature stages very diverse in structure and development. *U. Carb.*—*Holot.

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.*—*Holot.

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.
Family PALAEOPERLIDAE
Sharov, 1961

Costal area of fore wing with 4 or 5 veinlets; 3 or 4 veinlets from vein R to margin; free basal piece of MA slightly oblique; MP+CUA with 3 terminal branches; anal area narrow. Hind wing and body unknown.
ous between MA and MP+CUA, few elsewhere. Perm., USSR (Asian RSFSR).—Fig. 55,2a. *P. exacta; fore wing, ×5.5 (Sharov, 1961e).—Fig. 55,2b. P.(?) prisca Sharov; nymph, ×9 (Sharov, 1961e).

**Family PERLOPSEIDAE**
Martynov, 1940

[nom. correct. Rohdendorf, 1957, p. 81, pro Perlopsidae Martynov, 1940, p. 31]

Fore wing as in Palaeoperlidae but with only 1 veinlet from vein R to margin, 2 branches on MP+CUA. Hind wing unknown. Body slender, legs long, tarsi with 3 segments. Perm.

**Perlopsis** Martynov, 1940, p. 31 (*P. filicornis; OD). Costal area very narrow; wing widest beyond middle. Perm., USSR (Asian RSFSR).—Fig. 55,1. *P. filicornis; a, fore wing, ×3.2 (Rohdendorf, 1962a); b, body, ×4.0 (Martynov, 1940).

**Family SIBERIOPERLIDAE**
Sinitshenkova, 1983

[Siberioperlidae Sinitshenkova, 1983, p. 96]

Antennae long, moniliform, shorter than body. Wings of females of normal size, with branches of RS directed posteriorly and MA and MP unbranched; hind wings with enlarged anal area; anal veins branched. Males micropterous; costal region of the fore wing unusually wide. Legs short, femora wide; cerci shorter than body. Nymphs with body densely covered with short hairs; antennae and cerci relatively short; tracheal gills absent. Apparently related to the existing family Gripopterygidae. Jurr.

**Siberioperla** Sinitshenkova, 1983, p. 96 (*S. lacunosa; OD). Posterior margin of head convex; first antennal segment short. Female with fore wing about three times as long as wide; RS with 4 or 5 branches; CUA with 2 or 3 branches. Jurassic. USSR (Asian RSFSR).

**Family EUSTHENIIDAE** Tillyard, 1921

[Eustheniidae Tillyard, 1921d, p. 35]

Fore wing with few to many veinlets in costal area; vein RS with at least 3 branches; 3 anal veins; crossveins present over most of wing. Hind wing with prominent anal area but without marginal indentation at end of CUP. Nymphs with 5 or 6 pairs of lateral abdominal gills. Perm.—Holocene.

**Eusthenia** Westwood, 1832, p. 348. Holocene.

**Stenoperlum** Tillyard, 1935c, p. 386 [*S. permianum; OD]. Similar to *Stenoperla* (recent) but

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with fewer crossveins and with the broadest part of wing proximal to midwing. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).——FIG. 55, 3. *S. permianum*; fore wing, X2 (Tillyard, 1935c).

**Family TAENIOPTERYGIDAE**

*Klapálek, 1905*

*Taeniopterygidae Klapálek, 1905, p. 30*

Costal area of fore wing with few veinlets; vein R with not more than single veinlet leading to margin; MA commonly with 2 branches; crossveins fewer than in Palaeoperlidae. *Perm.*—*Holoc.

**Mesotaeniopteryx Pictet, 1841, p. 343. Adults. Hagen in Pictet & Hagen, 1856; Illies, 1965. Oligo., Europe (Baltic)—Holoc.**

**Brachyptera Newport, 1848, p. 388. Illies, 1967a. Plio., Europe (Germany) Holoc.**

**Mesonemura Brauer, Redtenbacher, & Ganglbauer, 1889, p. 11 [*M. maaki*; OD]. Crossveins from end of SC to MA forming continuously curved series. *Jur.*, USSR (Asian RSFSR).——Fig. 56, 6. *M. turanica Martynov; fore wing, X5.5 (Martynov, 1937a).**

**Mesotaeniopteryx Martynov, 1937a, p. 81 [*M. elongata*; OD]. RS forked to level of end of SC; MP+CUA with 3 terminal branches, first 2 close together, curved, and directed anteriorly; crossveins numerous between MA and MP+CUA.**

Fig. 56. Taeniopterygidae, Notonemouridae, Platyperlidae, and Perlidae (p. 95-97).
more numerous between MP+CUA and CUP. Jur., USSR (Tadzhik).—Fig. 56, 7. *M. splendidida* Martynov; fore wing, X 2.5 (Martynov, 1937a).

**Palaeonemoura** Sharov, 1961e, p. 233 [*P. clara*; OD]. Fore wing as in *Palaeotaeniopteryx* but with MA more strongly curved and with fewer crossveins between MA and MP+CUA. Perm., USSR (Asian RSFSR).—Fig. 56, 5. *P. clara*; fore wing, X 6.5 (Sharov, 1961e).

**Palaeotaeniopteryx** Sharov, 1961e, p. 230 [*P. elegans*; OD]. MA forked before level of end of SC; several crossveins between MA and MP+CUA. Perm., USSR (Asian RSFSR).—Fig. 56, 1. *P. elegans*; a, fore and b, hind wings, X 8; c, nymph, X 10 (all Sharov, 1961e).


**Family LEUCTRIDAE** Klapalek, 1905

[Leuctridae Klapálek, 1905, p. 32]

Costal area with 1 or 2 veinlets; vein R with l veinlet to margin; RS forked to about half its length, branches parallel to those of MA; MP+CUA and CUP markedly divergent distally. Eoc.—Holo.

**Leuctra** Stephens, 1836, p. 144. Adults. Pictet & Hagen, 1856; Cockerell, 1922b; Illies, 1965; Jarzemowski, 1980. Eoc./Oligo., England; Oligo., Europe (Germany, Baltic), USA (Colorado)—Holo.


**Family NOTONEMOURIDAE** Rickert, 1950

[Notonemouridae Rickert, 1950, p. 201]


**Mesoleuctra** Brauer, Redtenbacher, & Ganglbauer, 1889, p. 9 [*M. gracilis*; OD]. Nymph: posterior margin of head rounded; basal antennal segment about as wide as long; mandibles slightly longer than wide, with many denticles; femora only slightly shorter and broader than tibiae; pronotum about as long as wide; posterior wing pads slightly broader than the fore pair; cerci very thin distally; body without hair covering. Ping, 1928; Illies, 1965; Sinitshenkova, 1982. Jur., USSR (Asian RSFSR); Cret., China (Inner Mongolia).—Fig. 56, 2. *M. gracilis*; restoration, dorsal view, X 2 (Sinitshenkova, 1982).

**Family PERLIDIDAE** Klapálek, 1912

[Perlidae Klapálek, 1912, p. 5]

Venation very diverse; costal space usually with several short veinlets; veinlets from vein R to margin commonly longer and more oblique than those of costal area; RS commonly with several branches; MP+CUA diverging anteriorly in distal region, appearing to coalesce with branches of MA. Oligo.—Holo.


**Family PLATYPERLIDAE** Sinitshenkova, 1982

[Platyperlidae Sinitshenkova, 1982, p. 118]

Nymph: head about as long as wide; antennae long, basal segment large; labrum transverse; mandibles with only a few denticles apically; pronotum transverse; femora and tibiae relatively short and broad; 2 basal segments of tarsi short and broad, their combined lengths less than that of third segment; tarsal claws prominent; fore wing pads relatively long, hind pair much shorter and broader; body covered with hair; external gills apparently absent. Jur.

**Platyperla** Brauer, Redtenbacher, & Ganglbauer, 1889, p. 10 [*P. platypoda*; OD]. Posterior margin of head strongly convex; basal segment of antenna conical; pronotum with prominent posterior angles; posterior margin of terminal abdominal tergite with a short, broad median projection. Ping, 1928; Sinitshenkova, 1982. Jur., USSR (Asian RSFSR).—Fig. 56, 3. *P. platypoda*; restoration of nymph, dorsal view, X 2 (Sinitshenkova, 1982).

**Family PERLIDAE** Latreille, 1802

[Perlidae Latreille, 1802, p. 292]

Costal area with numerous, short veinlets, those between vein R and margin continuing
series; RS usually with 3 or 4 branches; distal part of MP + CUA curving anteriorly. *Cret.—Holos.*


**Sinoperla Ping**, 1928, p. 28 [*S. abdominalis; OD.*]
Little-known wings, with 2 crossveins between R and RS near end of SC; ILLIES, 1965. *Cret., China.*—Fig. 56, 4. *S. abdominalis; fore wing, X5.3 (Ping, 1928).*

**Family UNCERTAIN**

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

**Euxenoperla Riek**, 1973, p. 531 [*E. simplex; OD.*]
Little-known genus, possibly related to the Gripopterygidae. Vein RS of fore wing arched anteriorly at level of end of SC; RS with 3 or 4 branches; M deeply forked, branching before midwing; few crossveins. *Perm., South Africa; Trias., Australia (Queensland).—Fig. 55, 4.* *E. simplex, South Africa; fore wing, X2.8 (Riek, 1973).*

**Euxenoperlella Riek**, 1968a, p. 770 [*E. jacqueti; OD.*]
Similar to *Euxenoperla*, but RS with only 2 branches and M forking more distally. *Perm., South Africa.*

**Gondwanoperladium Pinto & Purper**, 1978, p. 79 [*G. argentinum; OD.*]
Little-known genus, similar to *Euxenoperla*, but fore wings with many more crossveins. *Trias., South America (Argentina).*

**Mesonopera Riek**, 1954c, p. 167 [*M. sinuata; OD.*]
Fore wing fragment, possibly of an eustheniid. *Trias., Australia (New South Wales).*

**Permoleuctropsis Martynov**, 1937b, p. 34 [*P. gracilis; OD.*]
Little-known nymph. *Perm., USSR (European RSFSR).*

**Uralonympha Zalesky**, 1939, p. 64 [*U. varica; OD.*]
Little-known nymph. *Perm., USSR (Asian RSFSR); Jur., Antarctica (Ohio Range).*

**Order PROTORHTOPTERA**

**Handlirsch**, 1906

[Protorthoptera Handlirsch, 1906a, p. 695] [*Hadentomoidea Handlirsch, 1906a, p. 692; Hapalopteraoida Handlirsch, 1906a, p. 694; Protoblattoidea Handlirsch, 1906a, p. 704; Reculoidae Handlirsch, 1906b, p. 127; Protorthopteraria Traylor, 1928b, p. 187; Cenemidoidea Handlirsch, 1937, p. 63; Paraplecoptera Martynov, 1938b, p. 98; Strephocladodea Martynov, 1938b, p. 100; Protocicadida Haupt (in part), 1941, p. 75; Protogomphida Haupt (in part), 1941, p. 73*] (The ordinal name *Protoblattoidea Handlirsch* (1906a) was changed to *Protoblattoidea* by *Smirnov* (1962a) and has generally been accepted.)

Wings typically containing all main veins, including MA and MP, but without complete alternation of convexities and concavities; MA apparently absent in some families (see below). Main veins usually independent; in some families CUA anastomosed with part of M or MP and CUP; in a few families MA tending to coalesce with branches of RS. Fore and hind wings commonly similar in form and venation, anal area of hind wing rarely expanded to form prominent lobe. Fore wing membranous in more primitive groups, but slightly coriaceous or distinctly coriaceous in others; hair covering usually well developed on membranous wings, reduced or absent on coriaceous wings; prominent setae may be present on certain parts of wings; wing area between veins with archedictyon, resembling that of Palaeodictyoptera, or with coarse network of crossveins or more commonly with regular system of nearly straight crossveins; anal area in many families set off from remigium by strongly concave CUP. Hind wing membranous, venation of remigium usually slightly different from that of fore wing; RS arising nearer wing base, and stems of CUA and M coalesced; CUA much less developed; CUP setting off anal area, which includes several anal veins. Fore wings (and more rarely hind wings) may have conspicuous maculations or prominent cuticular thickenings.

Body structure: antennae prominent, usually long (e.g., Liomopteridae), with numerous segments; head (known in very few families) small, almost always hypognathous; prothorax commonly bearing pronotal disc (e.g., Liomopteridae) or slender, without such disc; some families (e.g., Geraridae) with elongate prothorax, which may bear prominent spines; prothorax very rarely (e.g., Lemmatophoridae) with pair of membranous paranotal lobes (Fig. 57, *Lemmatophora*), resembling those of certain Palaeodictyoptera; pterothorax with usual form; legs usually cursorial, but forelegs in some families apparently raptorial; in none, as the order is treated here, were hind legs modified for jumping (saltatorial); five tarsomeres (little known). Abdomen of moderate length; cerci usually prominent, long in some forms (e.g., Liomopteridae), but commonly small (e.g.,...
Protomphiidae) or modified (e.g., males, Chelopteridae).

Nymphal forms little known; antennae and cerci well developed; most nymphs clearly terrestrial (e.g., Liomopterites, Kaltanympha), others apparently modified for aquatic life, with tracheal gills along sides of abdomen (see Fig. 61,1b, Lemmatophora). U. Carb.—Trias.

The extinct order Protorthoptera was named by Handlirsch (1906a, 1906b) for a diverse assemblage of Paleozoic species with presumed orthopteroid affinities. He also named another extinct order, Protoblattoidea, for other species that he considered to be intermediate between the Palaeodictyoptera and the Blattoidea, Manteidea, and Phasmatodea; at the same time he named a
third order, "Protorthoptera vel Protoblattodea," for species that were apparently intermediate between the Protorthoptera and the Protoblattodea. As more Paleozoic insects became known, a gradual diminution of the distinctions between the Protorthoptera and the Protoblattodea became apparent, the number of genera placed in the "Protorthoptera vel Protoblattodea" complex being nearly double that in the Protoblattodea (Handlirsch, 1922). This classification proved unsatisfactory, and Martynov subsequently (1937b, 1938b) proposed that the order Protorthoptera be restricted to species having saltatorial hind legs, like the true Orthoptera, and that the remaining species in that order be placed in another new, extinct order, Paraplecoptera. In the same year Zeuner transferred the saltatorial species cited by Martynov to the order Orthoptera, where they clearly belonged (Zeuner, 1937). The cursorial species were then distributed among the other three orders, the Protorthoptera, Protoblattodea, and Paraplecoptera. This arrangement was followed for many years. However, Sharov (1961a, 1966a) was convinced that one family, Sthenaropodidae, which had slender, cursorial hind legs and which was previously included in the Protorthoptera, represented the actual stock from which the true Orthoptera were derived. Accordingly, he proposed that the order Protorthoptera be limited to that family. He placed the other families in the Protoblattodea and Paraplecoptera. Carpenter (1966), objecting to Sharov's concept of the Sthenaropodidae, proposed that the Protoblattodea and Paraplecoptera be merged with the Protorthoptera to form a single order until more is known of the morphology of the families involved. Sharov (1968) agreed with Carpenter that the Protoblattodea and Paraplecoptera were inseparable and should be combined into one order, the Protoblattodea, but insisted that the order Protorthoptera, with its single family, Sthenaropodidae, should be retained. Since then, there has been little consistency in the use of these ordinal names.

In a general review of the orthopteroids, Rasnitsyn (1980c) transferred the Sthenaropodidae to the order Orthoptera, completely dropping the names Protorthoptera, Protoblattodea, and Paraplecoptera, and assigned most of the families previously included in those orders to the small existing order of flightless insects, the Grylloblattodea. The family Geraridae, formerly included in the Paraplecoptera, was placed in a new order, Gerarida. More recently, Burnham (1983), following her study of the types of orthopteroids in the Museum d'Histoire Naturelle in Paris, including those of Sthenaropoda, the type genus of Sthenaropodidae, placed Sthenaropoda in synonymy with Gerarus, the type genus of the Geraridae. It is clear that we need to know much more about the morphology of these extinct families before we can reach an acceptable conclusion about their relationships.

In the present work the order Protorthoptera is retained and includes the families formerly in the Protoblattodea and Paraplecoptera, as well as in the Protorthoptera itself. However, a substantial number of genera, based on fragments of wings, have been placed in the category of order Uncertain. The division of the Protorthoptera into suborders seems virtually meaningless at present. Although a few groups of families can be recognized, most of the families remain isolated, mainly as a result of the lack of detailed knowledge of both fore and hind wings and the body. The lines of evolution within this Paleozoic complex have not yet been satisfactorily untangled. The assumption of most workers that these lines must lead to existing orders (e.g., Blattodea, Orthoptera, Perlaria) appears incorrect; more likely they radiated in diverse directions, only a very few leading to existing ordinal groups.

The homologies of the protorthopterous venation present no special difficulties, except for the media. In palaeoopterous orders the anterior and posterior median veins (MA, MP) are readily recognizable as convex and concave, respectively. That both MA and MP exist in any of the orthopteroids (or in any
Hexapoda

of the Neoptera) is not certain; the loss of the convex vein in the median complex of the Neoptera has convinced some entomologists that the only element remaining is MP. On the other hand, even this vein is not always clearly concave, the coriaceous nature of the tegmen altering the thickness and general nature of the wing surface and membrane. Evidence for the presence of both MA and MP in the primitive Neoptera is indicated by the similarity between the fore wing venation of primitive Palaeodictyoptera (e.g., Dictyoneuridae) and that of the existing Orthoptera of the family Pneumoridae (Ragge, 1955a).

In the following account of the Protorthoptera, the branches of the media are designated MA and MP only if the media divides before or near the middle line of the wing, and then only if there is no specific evidence against this interpretation, such as the presence of a media that is strongly concave entirely. In view of the uncertainties noted above, as well as the lack of knowledge of hind wings and body structures of most Protorthoptera, it is not possible to identify with confidence the most primitive families in the order. However, the Homoeodictyidae, Thoronysididae, and Paoliidae, which have an archedictyon as well as a concave MP in the fore wing, might well occupy that position. The venational specializations that have developed in the order have apparently involved the loss of the archedictyon and its replacement by a reticulation of crossveins and eventually by more regular crossveins; this has apparently taken place independently of the development of the fore wing as a tegmen. In contrast to most other orders of insects, only rarely has MA tended to anastomose with R and RS. On the other hand, in many families, MP and CUA show various degrees of anastomosis (Cacurgidae, Aenigmatodidae, Protokollariidae); in some of these, the stem of CUA is apparently anastomosed with the stem of M (or MP), CUP arising independently from the wing base. Also, in some of these genera, CUA, after diverging from MP, coalesces for a short distance with a branch of CUP. In all probability, these specializations of MP, CUA, and CUP, have been developed independently several times within the order. The fore wings commonly bear maculations (see Fig. 61,3, Liscia) or more elaborate markings (see Figs. 75 and 76, Protodialphipnoida).

The hind wing is known in so few families of Protorthoptera that little can be said about its evolution. A well-developed anal area was present in many families (Lemmatophoridae, Liomopteridae), and this probably indicates a specialized condition of the hind wing. In others (Geraridae), the hind wing apparently had a very small anal area.

The general body structure is known in a very few families of Protorthoptera, and details of structure are known in even fewer (Lemmatophoridae, Chelopteridae, Probniidae, Liomopteridae, and Euceniidae). The prothorax seems to show the greatest diversity of structure. In some families (e.g., Liomopteridae) the prothorax consists of a discrete pronotal plate surrounded by an oval or nearly oval disc, which in some genera may be covered with fine hairs. In the Lemmatophoridae the prothorax bears a pair of distinct paranotal lobes, which are membranous and covered with microtrichia, like those on the wings. In other families the prothorax is more slender, and in the Geraridae it is long and bears numerous long spines. The legs of the Protorthoptera also show various structural trends. In most families the three pairs of legs are similar, the third pair being slightly longer than the others. In a few families the forelegs are apparently adapted for raptorial purposes.

There are several basic features characteristic of the Protorthoptera in addition to the cursorial legs. The wings at rest, as far as is known, were folded flat over the abdomen, not slanted, as in the Orthoptera. The costal vein of the fore wing was usually marginal basally, but if it were submarginal the subcostal area was small and included only a few veinlets at most, in contrast to the Orthoptera, in which the precostal area tended to be long and replete with veinlets.
As treated here, the order Protorthoptera was almost exclusively Permo-Carboniferous, with most of the genera from the Permian. Two genera, not well known, are from the Triassic: *Tomia Martynov* (family Tomiidae) and *Mesorthopteron Tillyard* (family uncertain). Both of these are poorly known and may turn out to belong elsewhere.

**Family HOMOEODICTYIDAE**

Martynov, 1937

[Homoeodictyidae Martynov, 1937b, p. 26]

Fore wing slender, with fine archedictyon; vein SC terminating on costa; MA without definite convexity; MP concave; CUP branched. *Perm.*

**Homoeodictyon Martynov, 1937b, p. 26 [*H. elongatum*; OD].** Fore wing with broad costal area, traversed by several distinct veinlets, and with archedictyon. *Perm.*, USSR (European RSFSR).—Fig. 58.3. *H. elongatum*; fore wing, ×1 (Martynov, 1937b).

**Family THORONYSIDIDAE**

Handlirsch, 1919

[Thoronyсидidae Handlirsch, 1919b, p. 544]

Fore wing slender, crossoveins forming irregular coarse network over entire wing, no anastomosis of main veins. Vein CUA extensively developed, its most distal branch terminating well beyond midwing. Hind wing unknown. *U. Carb.*

**Thoronyysis Handlirsch, 1906b, p. 139 [*Oedischia ingbertensis von Ammon*, 1903, p. 282; OD].** Fore wing with SC terminating on R near wing apex; M forking before midwing and after origin of R.S. Guthörl, 1934. *U. Carb.*, Europe (Germany).—Fig. 58.11. *T. ingbertensis* (von Ammon); fore wing, ×0.9 (Guthörl, 1934).

**Family PAOLIIDAE**

Handlirsch, 1906

[Paoliidae Handlirsch, 1906a, p. 682]

Fore wing oval, slender, with broad costal area; fine network, resembling archedictyon, over entire wing; veinlets also present in costal area and some other parts of wing; vein SC terminating (usually on R) in distal fourth of wing; RS arising proximally of midwing; MA apparently absent; MP (concave) well developed; CU dividing very close to wing base; CUA branched; anal area weakly set off by marginal indentation at end of CUP. Hind wing triangular, with anal-posterior extension but no anal fan; venation basically as in fore wing. *Kukalová, 1958a. U. Carb.*

**Paolia Smith, 1871, p. 44 [*P. vetusta*; OD].** Hind wing with MP dividing before midwing but distally of origin of RS; proximal part of wing only slightly broader than distal half. Laurentiaux, 1950; Kukalová, 1958a. *U. Carb.*, USA (Indiana), Europe (The Netherlands).—Fig. 58.3. *P. vetusta*, Indiana; hind wing, ×8 (Smith, 1871).

**Holasicia Kukalová, 1958a, p. 942 [*H. vetula*; OD].** Fore wing slender; MP forked at midwing; costal margin straight. *U. Carb.*, Europe (Czechoslovakia).—Fig. 58.1. *H. vetula*; fore wing, ×1.4 (Kukalová, 1958a).

**Olinka Kukalová, 1958a, p. 944 [*O. modica*; OD].** Little-known genus; similar to *Holasicia*, but fore wing with convex costal margin and MP forking distally of midwing. *U. Carb.*, Europe (Czechoslovakia).—Fig. 58.9. *O. modica*; fore wing, ×1.5 (Kukalová, 1958a).

**Paoliola Handlirsch, 1919b, p. 533 [*P. gurleyi*; OD].** Hind wing similar to that of *Paolia* but with MP forked more deeply. Melander, 1903. *U. Carb.*, USA (Indiana).—Fig. 58.10. *P. gurleyi*; hind wing, ×1.4 (Melander, 1903).

**Pseudofouquea Handlirsch, 1906b, p. 125 [*Fouquea cambrensis Allen*, 1901, p. 68; OD].** Fore wing similar to *Olinka*, but costal space narrower and MP dividing before midwing. Laurentiaux, 1950. *U. Carb.*, Wales.—Fig. 58.12. *P. cambrensis* (Allen); fore wing, ×1 (Laurentiaux, 1950).

**Sustaia Kukalová, 1958a, p. 946 [*S. impar*; OD].** Little-known fore wing, similar to *Olinka* but much larger; hind wing with branch of MP terminating on apical end of hind margin. *U. Carb.*, Europe (Czechoslovakia).—Fig. 58.7. *S. impar*; a, fore and b, hind wings, ×0.4 (Kukalová, 1958a).

**Zdenekia Kukalová, 1958a, p. 937 [*Z. grandis*; OD].** Fore wing broader than in *Holasicia*; costal margin convex; MP forked at midwing. Hind wing much broader proximally than in distal half; branches of MP terminating along middle part of hind margin. *U. Carb.*, Europe (Czechoslovakia).—Fig. 58.8. *Z. grandis*; a, fore wing, ×1; b, hind wing, ×0.8 (both Kukalová, 1958a).

**Family STYGNIDAE**

Handlirsch, 1906

[Stygidae Handlirsch, 1906b, p. 115]

Related to Paoliidae, but crossoveins distinct, though irregular, and vein MP less developed. *U. Carb.*
Stygne Handlirsch, 1906b, p. 115 [*S. roemerii; OD]. Fore wing with narrow costal area; RS arising very close to base of wing, its first branch at about midwing. Schwarzbach, 1939. U. Carb., Poland (Upper Silesia).—Fig. 58.6. *S. roemerii; fore wing, x2.2 (Handlirsch, 1906b).

Family HAPALOPTERIDAE
Handlirsch, 1906

[Hapalopteridae Handlirsch, 1906b, p. 304]

Fore wing similar to that of Cacurgidae but with fewer branches of main veins; vein...
CUP forking further from wing base; cuticular spots absent from wings. *U. Carb.*

**Hapaloptera** Handlirsch, 1906a, p. 694 [*H. gracilis; OD*]. Fore wing with SC extending nearly to wing apex; costal veinslets unbranched; RS with 4 branches; MP forked to about midwing; CUA with terminal fork only; crossveins numerous, weakly formed. Carpenter, 1965. *U. Carb.*, USA (Pennsylvania).—Fig. 59,1. *H. gracilis*; fore wing, X4 (Carpenter, 1965).

**Family PACHYTYLOPSIDAE** Handlirsch, 1906


Fore wing with vein SC terminating on costal margin well before apex; MA apparently absent; CUA anastomosed with MP for a short interval basally; crossveins weak, apparently forming an irregular network over most of wing. Probably related to Paoliidae. *U. Carb.*

**Pachytylopsis** Borre, 1875a, p. xi [*P. persenai; SD Borre, 1875b, p. ivi*] (=Palorthopteron Handlirsch, 1904a, p. 3 [type, *P. melasi*]). Costal area of moderate width; MP1+2 directed anteriorly shortly after its separation from CUA1 and connected to RS by a short but stout crossvein; R with several terminal branches. Handlirsch, 1906b; Pruvost, 1930, 1933b; Laurentiaux & Laurentiaux-Vieira, 1981. *U. Carb.*, Europe (Belgium).—Fig. 58,2. *P. persenai*; fore wing, X1.4 (Handlirsch, 1904a).

**Anthraconeura** Laurentiaux & Laurentiaux-Vieira, 1980, p. 407 [*A. silvatica; OD*]. Similar to *Protopachytylopsis*, but costal area much narrower, especially basally; R without terminal branches; CUA with 2 long branches. [Type of family Anthraconeuridae Laurentiaux & Laurentiaux-Vieira.] *U. Carb.*, Europe (Belgium).

**Protopachytylopsis** Laurentiaux & Laurentiaux-Vieira, 1981, p. 83 [*P. leckwycki; OD*]. Similar to *Pachytylopsis*, but costal area broader basally; R without terminal branches; CUA with several short marginal branches. *U. Carb.*, Europe (Belgium).

**Symballiphlebia** Handlirsch, 1904a, p. 3 [*S. latipennis; OD*]. Similar to *Pachytylopsis*, but fore wing much broader; MP1+2 in short contact with RS. [Family assignment doubtful.] Pruvost, 1930. *U. Carb.*, Europe (Belgium).—Fig. 58,4. *S. latipennis*; fore wing, X1.2 (Pruvost, 1930).

**Family BLATTINOPSISIDAE** Bolton, 1925

[Blattinopsidae Bolton, 1925, p. 23] [=Oryctoblattinidae Handlirsch, 1906b, p. 135]

Fore wing with vein SC terminating on costal margin well before apex; R usually sigmoidally curved, numerous oblique veinlets between R and costal margin beyond SC; RS with numerous branches; MA apparently absent; MP often with one or more branches anastomosed with R or RS; CUA anastomosed with basal portion of M, diverging away, and then fusing with CUA2; strong indentation at end of CUP; anal veins straight; crossveins numerous, commonly forming meshwork of cells. Hind wing unknown. *U. Carb.*—Perm.

The venation is highly variable within genera and species of this family. In addition, some specimens show a more or less distinct curving line near the middle of the wing and extending from R to the hind margin. This has led some workers to consider the Blattinopsidae to be Homoptera, related to the Fulgoridae. However, a similar line, present on the wings of some species of roaches, is apparently due to a pressure mark on the tegmina, resulting from the flexed position of the wings. It is commonly better developed on one tegmen than on the other and may be missing from one of them. Such an origin of the cross lines could explain why they are present in some blattinopsid fore wings but lacking in others. Kukalová, 1959b; Carpenter, 1966.

Fig. 59. Hapalopteridae, Blattinopsidae, Cymbopsidae, and Hadentomidae (p. 103–106).

1906a, p. 706). Fore wing with SC extending to midwing; crossveins very close together over most of wing; numerous oblique veinlets between CUA and CUP. KUKALOVÁ, 1959b; CARPENTER, 1966; MÜLLER, 1977. U. Carb., Europe (Germany, France), USA (Ohio); Perm., Europe (Germany, Czechoslovakia).—Fig. 59, 10a. B. angustai KUKALOVÁ, Perm., Czechoslovakia; fore wing, X2 (Kukalová, 1959b).—Fig. 59, 10b. *B. reticulata (GERMAR), U. Carb., Germany; fore wing, X2 (Schlectendal, 1913).

Glaphyrokoris RICHARDSON, 1956, p. 38 [*G. mirandus; OD]. Similar to Glaphyrophlebia but with SC and R longer. U. Carb., USA (Illinois).—Fig. 59, 5. *G. mirandus; fore wing as preserved; X2.6 (Richardson, 1956).
Family CYMBOPSIDAE
Kukalová, 1965

Little-known family of uncertain affinities. Fore wing tegminous; vein SC extending very nearly to wing apex; RS arising in distal third of wing, with several branches; M apparently coalesced with stem R to about midwing; crossveins numerous. [Placed in Protorthoptera by Kukalová, but ordinal assignment doubtful.] Perm.

Cymbopsis Kukalová, 1965, p. 86 [*C. excelsa; OD]. SC sigmoidally curved; crossveins reticulate only in basal costal area and in area between SC and R + M. Perm., Europe (Czechoslovakia).—Fig. 59.3. *C. excelsa; fore wing, X5.7 (Kukalová, 1965).

Family EUCAENIDAE
Handlirsch, 1906

Fore wing coriaceous, oval; costal space broad, with numerous veinlets; vein R with few distal branches; RS arising near wing base, with many branches; M well developed, with several branches leading to posterior border; CUP curved, well developed. Hind wing little known; costal area narrow; R with few terminal branches; anal area unknown. Head slender, long; antennae long, setaceous; mandibles dentate; maxillary palpi very long; prothorax long, broad posteriorly, narrowed anteriorly, with a constricted area adjoining the head; legs alike, all femora stout; tarsi with 5 segments; abdominal segments with posteriorly directed lateral lobes; cerci very short. Females with a short ovipositor. Carpenter & Richardson, 1976. U. Carb.

Eucaenus Scudder, 1885d, p. 325 [*E. ovalis; OD] [=Teneopteron CARPENTER, 1944, p. 17 (type, T. mirabile)]. Fore wing: veinlets of costal area unbranched; RS with branches directed toward wing apex. Melander, 1903; Handlirsch, 1922; Carpenter & Richardson, 1976. U. Carb., USA (Illinois).—Fig. 60. *E. ovalis; whole insect, X2.8 (Carpenter & Richardson, 1976).

Family HADENTOMIDAE
Handlirsch, 1906

Hadentomum Handlirsch, 1906a, p. 693 [*H. americanum; OD]. M forking at about midwing; RS with at least 3 branches in both wings. Carpenter, 1965. U. Carb., USA (Illinois).—Fig. 59.7. *H. americanum; a, fore and b, hind wings, X2.4 (Carpenter, 1965).

Fabreciella Carpenter, 1934, p. 327 [*F. pennisylvanica; OD]. Fore wing as in Palaeocixius, but costal area broader; M with 6 branches, RS with 4. [Family assignment doubtful.] U. Carb., USA (Pennsylvania).—Fig. 59.2. *F. pennisylvanica; fore wing, X4.2 (Carpenter, 1934).

Fayoliella Meinier, 1908), p. 247 [*F. elongata; OD]. Costal area of fore wing broad, with irregular veinlets; RS and M with 4 branches. [Family assignment doubtful.] U. Carb., Europe (France).—Fig. 59.4. *F. elongata; fore wing, X2.5 (Carpenter, new).

Palaeocixius Handlirsch, 1906b, p. 326 [*P. antiquus; SD Handlirsch, 1922, p. 74] [=Palaeocixius Brongnart, 1885a, p. 67, nom. nud.; Fabreciella Meinier, 1911a, p. 123 (type, F. pygmaea)]. Fore wing with fork of M at about level of origin of RS; RS and MA forking at about same level; RS with 2 branches, M with 5; a few large cells formed in region of M and
in anal area. U. Carb., Europe (France). — Fig. 59.6. *P. antiquus; fore wing, X4 (Carpenter, new).

**Protoblattina** MEUNIER, 1909d, p. 48 [*P. bouvieri; OD]. Fore wing as in *Palaeocixius*, but RS with 3 branches, M with 6. U. Carb., Europe (France). — Fig. 59.8a. *P. bouvieri; fore wing, X2.8 (Carpenter, new). — Fig. 59.8b. P. giardi MEUNIER, 1912d; fore wing, X2 (Carpenter, new).

**Family LEMMATOPHORIDAE** Sellards, 1909

[Lemmatophoridae Sellards, 1909, p. 162] [=Otaidae Sellards, 1909, p. 167; Lecoriidae HANDLIRSCH, 1919b, p. 516]

Fore wing with costal area moderately broad; vein SC terminating on costa at least slightly beyond midwing; R unbranched; MA and MP present, but neither convex nor concave; proximal half of MP obsolescent; CUA very strongly developed, usually with 3 branches; CUP obsolescent, forming a straight vena dividens; 2 analis present. Hind wing shorter than fore wing but with expanded anal area, and with at least slight incision of wing margin at end of CUP; R unbranched; MA unbranched and coalesced to variable extent with RS; CUA well developed, CUP obsolescent; anal fan with four main veins. Venation highly variable among species. Antennae long, multisegmented; head small, hypognathous; eyes small; prothorax bearing pair of membranous paranota, with reticulated venation and covered with microtrichia; mesonotum and metanotum broad and flat; five tarsomeres; abdomen unspecialized but bearing on the first nine segments small lateral processes resembling vestigial gills; cerci about as long as abdomen; female with very short ovipositor. Nymphs apparently aquatic, with lateral gills on first nine abdominal segments. Carpenter, 1935a, 1939. Perm.

**Lemmatophora** Sellards, 1909, p. 162 [*L. typa; SD TILLYARD, 1928b, p. 189]. SC terminating just beyond midwing; RS unbranched; hind wing with deep incision at end of CUP. Perm., USA (Kansas). — Fig. 57. *L. typa; head, prothorax, prothoracic lobes, neotype, X40 (Carpenter, new). — Fig. 61.1a. *L. typa; restoration of adult, X2.4 (Carpenter, 1935a). — Fig. 61.1b. Lemmatophora sp. (probably typa); nymph, X2.4 (Carpenter, 1935a).

**Artinska** Sellards, 1909, p. 165 [*A. clara; SD TILLYARD, 1928e, p. 321] [=Estadia Sellards, 1909, p. 166 (type, E. elongata); Lectrum Sellards, 1909, p. 167 (type, L. anomalum); Orta Sellards, 1909, p. 168 (type, O. ovaia)]. SC extending well beyond midwing; RS with at least one fork. Perm., USA (Kansas). — Fig. 62.1. *A. clara; a, fore wing, X6 (Carpenter, 1935a); b, hind wing, X6 (Tillyard, 1928e).

**Blania** KUKALOVÁ, 1964c, p. 101 [*B. rotunda; OD]. Fore wing as in *Artinska* but broader and more nearly oval; costal area relatively broad. Perm., Europe (Czechoslovakia). — Fig. 62.4. *B. rotunda; fore wing, X7.5 (Kukalová, 1964c).

**Lecorium** Sellards, 1909, p. 167 [*L. elongatum; OD] [=Stemma Sellards, 1909, p. 168 (type, S. elegans); Sellardsia TILLYARD, 1928e, p. 343 (type, S. kansensis); Metalecorium HANDLIRSCH, 1937, p. 96, nom. nud.; Paralecorium HANDLIRSCH, 1937, p. 96 (type, Lecorium parvum)]. Fore wing with costal area narrow, as in *Paraprisca*; CUA coalesced with M basally but diverging just before origin of MA. Carpenter, 1935a, 1939. Perm., USA (Kansas). — Fig. 61.2. *L. elongatum; adult, X6 (Carpenter, 1935a).

**Lisca** Sellards, 1909, p. 163 [*L. minuta; OD].

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Fore wing with costal area much narrower than in *Lemmatophora*; RS unbranched; RS arising much nearer wing base than in *Lemmatophora*. *Perm.*, USA (Kansas)—Fig. 61,3. *L. minuta*; fore wing, ×8 (Tillyard, 1928e).

**Maculopterus** Kukalová, 1964c, p. 107 ["M. maculatum"; OD]. Little-known genus. Fore wing as in *Torrentopterum* but with numerous maculations. [Probably a synonym of *Torrentopterum*.] *Perm.*, Europe (Czechoslovakia).

**Oborella** Kukalová, 1964c, p. 93 ["O. matura"; OD]. Fore wing as in *Artinska*, but costal area much broader; CU usually anastomosed with M before separating into CUA and CUP. Central disc of pronotum oval. *Perm.*, Europe (Czechoslovakia).

**Paraprisca** Handlirsch, 1919b, p. 555, nom. subst. pro *Prisca* Sellards, 1909, p. 167, non K. W. Fritsch, 1900 ["Prisca fragilis" Sellards, 1909, p. 167]. Fore wing more slender than in *Lemmatophora*; R straight; CUA not anastomosed with M; hind wing with only slight incision at
CUP. Antennalae longer and legs much longer than in *Lemmatophora*. Zalessky, 1952. Perm., USA (Kansas), USSR (Asian RSFSR).—Fig. 62, 2. *P. fragilis* (Sellards), Kansas; adult, X6 (Carpenter, 1935a).


Torrentopterum Kukalová, 1964c, p. 105 {*T. pallidum*; OD}. Fore wing as in *Lecorium*, but crossveins apparently more numerous. [Probably a synonym of *Lecorium*.] Perm., Europe (Czechoslovakia).

Villopterum Kukalová, 1964c, p. 108 {*V. villosum*; OD}. Fore wing as in *Lecorium* but more elongate and slightly broader distally; RS apparently unbranched; CUA1 with a deep fork. Perm., Europe (Czechoslovakia).—Fig. 62, 3. *V. villosum*; fore wing, X8 (Kukalová, 1964c).

**Family LIOMOPTERIDAE**

Sellards, 1909

[LIOMOPTERIDAE Sellards, 1909, p. 157] [=Khosaridae Martynov, 1937b, p. 29]

Fore wing membranous, usually with microtrichia well developed on at least part of wing; vein SC terminating on costa beyond midwing; costal area with numerous, slanted veinlets, not forming regular cells; R extending nearly to wing apex; RS with at least two branches; M forked at about level of origin of RS or slightly toward base; MA and MP not anastomosed with other veins; CUA typically diverging anteriorly shortly after its origin and forking into CUA1 and CUA2;
CUP and 1A unbranched. Hind wing with costal area narrow; R extending nearly to apex; RS arising much nearer base than in fore wing; M and CU fused at base; CUA strong and deeply forked; 1A close to CUP; anal area forming lobe containing numerous anal veins. Antennae long, multisegmented; head hypognathous; eyes prominent; prothorax usually with paranotal expansions continuing anteriorly and posteriorly around pronotum itself; reticulation not visible, but paranota commonly membranous and covered with microtrichia; legs slender, hind legs longer than others, not modified for jumping; 5 tarsomeres; cerci long. Carpenter, 1950. Perm.

Liomopterum Sellards, 1909, p. 157 [*L. ornatum; SD Carpenter, 1950, p. 189] (=Horatia Sellards, 1909, p. 158 (type, H. elongatus)). Costal space moderately broad; fork of M proximal to origin of RS; cells (when present) almost exclusively confined to area of CUA and CUP. Perm., USA (Kansas). —Fig. 63, 7. *L. ornatum; adult, X3.5 (Carpenter, 1950).

Abashevia Sharov, 1961d, p. 194 [*A. suchovi; OD]. Similar to Parapermula, but costal area narrower and branches of MA arising pectinately. Perm., USSR (Asian RSFSR). —Fig. 63, 3. *A. suchovi; fore wing, X1.8 (Sharov, 1961d).

Alicula Schlechtendal, 1913, pl. 2 [*A. lebachensis; OD] [=Purmula Handslriech, 1919b, p. 542, obj.]. Little-known genus, with fore wing apparently similar to that of Liomopterum, but crossveins numerous and forming a fine reticulation; CUA with several additional branches. [Handslich (1919b) considered the names Alicula lebachensis to be nomina nuda, but under article 12, section 7, of the ICZN (p. 35, 1985 ed.) both names are available.] Kukalova, 1964c. Perm., Europe (Germany, Czechoslovakia). —Fig. 64,1. A. acra (Kukalova); fore wing as preserved, X3 (after Kukalova, 1964c).

Ceresopterum Kukalova, 1964c, p. 60 [*C. gracile; OD] . Fore wing as in Tapopterum, but RS with only 3 branches. Perm., Europe (Czechoslovakia). —Fig. 64, 4. *C. gracile; fore wing, X6 (Kukalova, 1964c).

Climaconeuretes Sharov, 1961d, p. 195 [*C. asiaticus; OD]. MA branching dichotomously; anterior branch of MA anastomosed for short distance with RS. Perm., USSR (Asian RSFSR). —Fig. 63, 1. *C. asiaticus; a, fore wing; b, hind wing, X2.6 (Sharov, 1961d).

Depressopterum Kukalova, 1964c, p. 48 [*D. senior; OD]. Little-known genus. Fore wing as in Parapermula but more elongate and with less convex anterior margin. Perm., Europe (Czechoslovakia). —Fig. 64, 2. *D. senior; fore wing as preserved, X4 (Kukalova, 1964c).

Donopterum Kukalova, 1964c, p. 54 [*D. carpenteri; OD]. Fore wing as in Turbopteron but broader; costal area narrower; RS and MA with more branches. Perm., Europe (Czechoslovakia). —Fig. 64, 3. *D. carpenteri; fore wing, X2 (Kukalova, 1964c).

Drahania Kukalova, 1964c, p. 51 [*D. avia; OD]. Similar to Depressopterum, but fore wing more slender; CUA with only 2 main branches. Perm., Europe (Czechoslovakia). —Fig. 64, 3. *D. avia; fore wing, X5 (Kukalova, 1964c).

Fumopterum Kukalova, 1964c, p. 59 [*F. lagrum; OD]. Little-known genus, based on distal half of wing. Venation as in Donopterum, but wing much more slender. Perm., Europe (Czechoslovakia).

Ideliopsis Carpenter, 1948b, p. 101 [*I. ovalis; OD]. Costal margin only slightly curved; MP coalesced proximally with CUA1. Crossveins numerous, regular; no reticulation in apical part of wing. [Family assignment doubtful.] Perm., USA (Texas). —Fig. 63, 4. *I. ovalis; fore wing, X1.8 (Carpenter, 1948b).

Kaltanella Sharov, 1961d, p. 206 [*K. lata; OD]. Fore wing broadly oval, with almost no cells; MA with 2 main stems arising before level of origin of RS. Perm., USSR (Asian RSFSR). —Fig. 63, 8. *K. lata; a, fore and b, hind wings, X2.6 (Sharov, 1961d).


Kazanella Martynov, 1930d, p. 1116 [*K. rotundipennis; OD]. Little-known fore wing, with broad costal margin. Perm., USSR (European RSFSR). —Fig. 63, 6. *K. rotundipennis; fore wing, X4 (Sharov, 1962b).

Khosara Martynov, 1937b, p. 30 [*K. permiakovaev; OD]. Apex of fore wing rounded but markedly asymmetrical; no cells; MA with long branches. Perm., USSR (European RSFSR). —Fig. 63, 5. *K. permiakovaev; fore wing, X2.2 (Sharov, 1962c).

Lioma Kukalova, 1964c, p. 56 [*L. moravia; OD]. Fore wing as in Donopterum but more slender and with a longer SC. Perm., Europe (Czechoslovakia).

Liomopterella Sharov, 1961d, p. 202 [*L. vulgaris; OD]. Similar to Abashevia, but M forking well before origin of RS and MA dichotomously branched. Perm., USSR (Asian RSFSR). —Fig. 65, 1. *L. vulgaris; a, fore and b, hind wings, X2.6 (Sharov, 1961d).

Liomopterina Riek, 1973, p. 518 [*L. clara; OD]. Little-known genus, based on proximal fragment
of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).

**Liomopterites Sharov**, 1961d, p. 207 [*L. expletus; OD*]. Fore wing similar to that of *Liomopterum* but with curvature of CUA less pronounced and with fewer crossveins; in hind wing, MA anastomosed with RS. Nymph slender, apparently terrestrial. *Perm.*, USSR (Asian RSFSR). — Fig. 65,2a. *L. expletus*; fore wing, ×4.5 (*Sharov, 1961e*). — Fig. 65,2b. *L. comansa Sharov*; hind wing, ×4.5 (*Sharov, 1961e*). — Fig. 65,2c. *L. (?) gracilis Sharov*; nymph, ×6 (*Sharov, 1961d*).


**Mioloptera Riek**, 1973, p. 515 [*M. stuckenbergi*;
Protorthoptera


MILOPTOPOIDES RIEK, 1976a, p. 761 [*M. andrei; OD]. Little-known genus, based on wing fragment; similar to Mioloptera. Perm., South Africa (Natal).


ORNATICOSETA SHAROV, 1961d, p. 197 [*O. magna; OD]. Apex of fore wing acute; costal area with dark pigmentation extending nearly to apex of wing. Perm., USSR (Asian RSFSR).—Fig. 65.3. *O. magna; fore wing, X1 (Sharov, 1961d).

PARALIOMOPTERUM SHAROV, 1961d, p. 218 [*P. paulum; OD]. Similar to Liomopterum, but SC extending much further towards apex. Perm., USSR (Asian RSFSR).—Fig. 65.4. *P. paulum; fore wing, X2.4 (Sharov, 1961d).

SIBIRALELLA SHAROV, 1961d, p. 215 [*S. paucinervis; OD]. Subcostal area nearly as wide as costal area; few crossveins and branches of main veins. Perm., USSR (Asian RSFSR).—Fig. 65.8. *S. paucinervis; fore wing, X3.4 (Sharov, 1961d).

SEMOPTERUM CARPENTER, 1950, p. 197 [*S. venosum; OD]. Fore wing similar to that of Liomopterum but with more numerous crossveins and with several additional anal veins. Perm., USA (Kansas).—Fig. 65.7. *S. venosum; fore wing, X1.8 (Carpenter, 1950).

SIBIRELLA SHAROV, 1961d, p. 215 [*S. paucinervis; OD]. Subcostal area nearly as wide as costal area; few crossveins and branches of main veins. Perm., USSR (Asian RSFSR).—Fig. 65.8. *S. paucinervis; fore wing, X3.4 (Sharov, 1961d).

TAPIOPTERUM CARPENTER, 1950, p. 195 [*T. celsum; OD]. Costal space broader than in Liomopterum; crossveins more numerous, with at least a few cells between most main veins. Perm., USA (Kansas).—Fig. 65.9. *T. celsum; fore wing, X2.5 (Carpenter, 1950).

TURBOPTERUM KUKALOVA, 1964c, p. 52 [*T. finum; OD]. Fore wing as in Drahania, but costal area broader, SC much shorter, and MA with a short fork. Perm., Europe (Czechoslovakia).

TYRANNOPTERUM KUKALOVA, 1964c, p. 70 [*T. minimum; OD]. Similar to Cerasofterum but much smaller; fore wing with branches of RS directed anterioiy, away from M. Perm., Europe (Czecho-

Tyrannopterum KUKALOVA, 1964c, p. 70 [*T. minimum; OD]. Similar to Cerasofterum but much smaller; fore wing with branches of RS directed anterioiy, away from M. Perm., Europe (Czecho-

Family PHENOPTERIDAE

Carpenter, 1950

Related to Liomopteridae. Fore wing membranous, delicate; vein SC terminating on margin well beyond midwing; costal area with numerous, oblique veinlets; RS arising before midwing, with a few branches; M forked at about level of origin of RS, rarely with three branches; CUA with a basal branch (CUA2) and a distal branch dividing near wing margin; crossveins numerous, irregular,
forming irregular reticulation over most of wing. Hind wing with RS, M, and CUA arising from single stem near wing base; CUA branched; anal area well developed. Body structure unknown. Perm.

**Phenopterum** Carpenter, 1950, p. 205, nom. subst. pro Lepium Sellards, 1909, p. 156, non Endre-lein, 1906 [*Lepium elongatum* Sellards, 1909, p. 156; OD]. RS with 3 branches; fork of M slightly basal of origin of RS. Perm., USA (Kansas).—Fig. 66,3. *P. elongatum* (Sellards); a, fore and b, hind wings, X4 (Carpenter, 1950).

**Brunia** Kukalová, 1964c, p. 72 [*B. raketa*; OD]. Similar to Phenopterum, but wings more slender and RS with only 2 branches; costal area very narrow. Perm., Europe (Czechoslovakia).—Fig. 66,2. *B. raketa*; fore wing, X4 (Kukalová, 1964c).

**Chlumia** Kukalová, 1964c, p. 77 [*C. parva*; OD]. Fore wing as in Brunia but much broader. Perm., Europe (Czechoslovakia).
Family HAVLATIIIDAE
Kukalová, 1964

[Havlatiidae Kukalová, 1964c, p. 83]

Similar to Liomopteridae, but fore wing markedly broader distally and crossveins less numerous. *Perm.*

Havlatia KUKALOVA, 1964c, p. 84 [*H. annae; OD]. Costal and subcostal areas very narrow; SC extending nearly to wing apex. *Perm.*, Europe (Czechoslovakia). — Fig. 67, 3. *H. annae*; fore wing. X8 (Kukalová, 1964c).

Venropterum KUKALOVA, 1964c, p. 87 [*V. rapidum; OD]. Little-known genus. Fore wing as in *Zephyropterum*, but subcostal area broader; cross-
Family SKALICIIDAE Kukalová, 1964

Family PROBNIDAE Sellards, 1909

Protorthoptera

Probnis Sellards, 1909, p. 159 [*P. speciosa; SD Tillyard, 1937c, p. 415] [=Espiria Sellards, 1909, p. 160 (type, E. obscuro; Stoichus Sellards, 1909, p. 160 (type, S. elegans); Stinus Sellards, 1909, p. 161 (type, S. breve-cubitalis)]. Fore wing: SC terminating at midwing; R with several veinlets from R to costal margin beyond SC; crossveins straight, widely separated over most of wing; CUA1 extending nearly to wing apex. **Perm.**, **USA** (Kansas).——Fig. 66,5. *P. speciosa;* whole insect, X4 (Carpenter, 1943a).

Family STEGOPTERIDAE

Sharov, 1961

[Stegopteridae Sharov, 1961d, p. 220]

Similar to Liomopteridae, but fore wing more coriaceous and rough. **Perm.**

Stegopterum Sharov, 1961d, p. 221 [*S. hirtum; OD]. Fore wing with few crossveins; no cells. Hind wing with MA free from RS. **Perm.**, **USSR** (Asian RSFSR).——Fig. 66,4. *S. hirtum;* a, fore and b, hind wings, X4.4 (Sharov, 1961d).

Family STEREOPTERIDAE

Carpenter, 1950

[Stereopteridae Carpenter, 1950, p. 201]

Related to Liomopteridae. Fore wing slightly coriaceous, with few patches of conspicuous setae but without covering of microtrichia; vein SC terminating on margin beyond midwing; costal area narrow, with numerous oblique veinlets; RS arising before midwing; CUA anastomosed with stem of M for short distance; crossveins numerous, irregular. Hind wing and body structure little known. **Carpenter, 1966.** **Perm.**

Stereopterum Carpenter, 1950, p. 202 [*S. rotundum; OD]. M forking at level of origin of RS; row of stout setae along basal third of costal margin; smaller setae or branches of M near midwing. **Carpenter, 1966.** **Perm.**, **USA** (Kansas).——Fig. 66,6. *S. rotundum;* fore wing, X4 (Carpenter, 1950).

Family EPIMASTACIDAE

Martynov, 1928

[Epimastacidae Martynov, 1928b, p. 63]

Fore wing narrowed beyond midwing; vein SC remote from wing margin and terminating on costal margin near midwing; RS arising before midwing and with several long branches; CUA anastomosed for a short interval with M basally before forking. **Perm.**

Epimastax Martynov, 1928b, p. 63 [*E. parvaclub; OD]. Fore wing: R with several branches to the costal margin of wing; RS with 5 terminal branches. **Perm.**, **USSR** (European RSFSR), Europe (Czechoslovakia).——Fig. 67,2. *E. celer* Kukalová, 1965; fore wing, X8 (Kukalová, 1965).

Family CAMPTONEURITIDAE

Martynov, 1931

[Camptoneuridae Martynov, 1931a, p. 98, nom. subst. pro Camptoneuridae Martynov, 1928b, p. 53]

Related to Phenopteridae. Fore wing with narrow costal area; vein RS arising before midwing; crossveins forming strong, irregular network; distal branches of RS, MA, and MP straight and parallel, without crossveins. Hind wing unknown. **Perm.**

Camptonereutes Martynov, 1931a, p. 98, nom. subst. pro Camptonereutes Martynov, 1928b, p. 53, non Agassiz, 1846 [*Camptonereutes reticulata* Martynov, 1928b, p. 53; OD]. Fore wing with costal margin slightly concave; 2 rows of irregular cells between MP and CUA. **Perm.**, **USSR** (European RSFSR).——Fig. 66,7. *C. reticulata* (Martynov); fore wing, X3.5 (Martynov, 1928b).

Family ARCHIPROBNIDAE

Sharov, 1961

[nom. correct. Carpenter, herein, pro Archiprobnidae Sharov, 1961d, p. 185]

Fore wing with main veins more widely spaced than in Ideliidae; crossveins irregular but not forming distinct reticulation except in and near anal areas; veins RS and MA arising at same level close to base of wing. Hind wing little known; CUA sharply bent near base, as in some Liomopteridae. **Perm.**

Archiprobnis Sharov, 1961d, p. 186 [*A. repens; OD]. Fore wing broadly oval with rounded apex. **Perm.**, **USSR** (Asian RSFSR).——Fig. 66,1. *A. repens;* a, fore and b, hind wings, X2.5 (Sharov, 1961d).

Family PROTEMBIIDAE

Tillyard, 1937

[Protembiidae Tillyard, 1937b, p. 243] [=Telactinopterygidae Carpenter, 1943a, p. 78]

Related to Phenopteridae. Fore wing slightly coriaceous; distal parts of veins RS, MA, MP bordered by delicate lines on each side; SC terminating on costal margin; costal space very narrow; RS arising at midwing.
branched; M forked before origin of RS; CUA without definite CUA2, having several distal branches; crossveins few, unequally distributed. Hind wing with RS arising near wing base; M forking slightly beyond midwing; CUA forked distally; anal lobe well developed. Antennae long; head small, with large eyes; prothorax with small disc; hind legs
longer than others, all with five tarsomeres; cerci short but distinct. Carpenter, 1950. Perm.

Protorthoptera Tillyard, 1937b, p. 245 [*P. permiana; OD] (=Telactinopteryx Tillyard, 1937, c. p. 422 (type, T. striatipennis)). Fore wing: RS with 3 terminal branches; several veined between R and margin beyond end of SC; a few cells formed between R and RS. Perm., USA (Kansas).—Fig. 68,2. *P. permiana; whole insect, X6.5 (Carpenter, 1950).

Family EUREMISCIDAE Zalessky, 1951

Related to Phenopteridae, but fore wing without network of crossveins. Perm.

Euremica Zalessky, 1951b, p. 82 [*E. splendens; OD]. Slender fore wing, with very narrow costal space. Perm., USSR (Asian RSFSR).—Fig. 68,3. *E. splendens; fore wing, X3.5 (Sharov, 1962c).

Family SYLVAPHLEBIIDAE Martynov, 1940

[Sylvaphlebiidae Martynov, 1940, p. 18] (=Sylviidae Martynov, 1940, p. 26; Sylviodidae Martynov, 1940, p. 23)

Related to Phenopteridae; fore wing coriaceous, without hairs; veins MA and MP long, with few branches; prothorax short and broad, with small or large membranous lobes. Perm.

Sylvaphlebia Martynov, 1940, p. 18 [*S. tuberculata; OD] (=Biarmopteron Zalessky, 1953c, p. 45 (type, B. reticulatus)). Fore wing little known; costal space much broader than in Sylvaphlebia. Perm., USSR (Asian RSFSR).—Fig. 68,6. *S. perloides; fore wing and part of body, X1.6 (Sharov, 1962c).

Family CHELOPTERIDAE Carpenter, 1950

[Chelopteridae Carpenter, 1950, p. 198]

Related to the Liomopteridae. Fore wing membranous or only slightly coriaceous; hairs absent; costal area broad; subcostal area very narrow in proximal region; crossveins numerous, forming coarse reticulation between veins CUA1 and CUA2 and in anal area; crossveins between R and RS very slanted and parallel. Hind wing with RS arising nearer base than in Liomopteridae; CUA unbranched; crossveins forming coarse network in distal and cubital areas of wing. Antennae long, but with fewer segments than in Liomopteridae; head broad; pronotum with flat, membranous marginal area, lacking hairs; tarsi five-segmented; cerci of male modified to form forceps; female with prominent ovipostor. Perm.

Chelopterum Carpenter, 1950, p. 199 [*C. peregrinum; OD]. Fore wing with SC approaching costal margin at about midwing; main fork of M just proximal to origin of RS; MA and MP about equally developed. Perm., USA (Kansas).—Fig. 69,4. *C. peregrinum; complete insect, male, X3.4 (Carpenter, 1950).

Family DEMOPTERIDAE Carpenter, 1950

[Demoptetidae Carpenter, 1950, p. 203]

Related to Liomopteridae. Fore wing with membrane strongly coriaceous; costal margin slightly concave; costal area narrow, about as wide as subcostal; CUA branched only in its distal half. Hind wing unknown. Perm.

Demopterum Carpenter, 1950, p. 203 [*D. gracile; OD]. Fore wing slender; SC with series of stout spines along its proximal part; MP much more extensively developed than MA. Perm., USA (Kansas).—Fig. 69,5. *D. gracile; fore wing, X2.7 (Carpenter, 1950).
Family ATACTOPHLEBIIDAE
Martynov, 1930

[Atactophlebiidae Martynov, 1930c, p. 952]

Fore wing with costal area slightly broader than subcostal; crossveins tending to be irregularly shaped; two rows of irregular cells between veins R and anterior branch of RS. Hind wing little known, with broad costal area and very narrow subcostal. Branching of veins of both wings highly variable. Ovipositor small but distinct. *Perm.*

Atactophlebiia Martynov, 1928b, p. 51 [*A. termitoides; OD]. Fore wing with area of RS narrow; RS with few branches. *Perm.*, USSR (Asian RSFSR).—Fig. 69, 3. *A. termitoides; a, fore and b, hind wings, X1.4 (Martynov, 1930c).

Family MEGAKHOSARIDAE
Sharov, 1961

[Megakhosaridae Sharov, 1961d, p. 178]

Fore wing long, slender; costal area very narrow; both veins MA and MP apparently present; series of strong crossveins between CUP and most posterior branch of CUA, more basal ones being abruptly curved at junction with CUP; crossveins over rest of wing numerous and irregular. Hind wing with MA anastomosed for short distance with RS. *Perm.*

Megakhosara Martynov, 1937b, p. 31 [*M. fasciipennis; OD] (=Syndesmophora Martynov, 1937b, p. 41 (type, S. composita)). Fore wing with RS dichotomously branched; no anastomosis between main veins; both fore and hind wings with irregular crossveins. *Perm.*, USSR (Asian RSFSR).—Fig. 69, 1a. M. dilucida Sharov; fore wing, X1.8 (Sharov, 1961e).—Fig. 69, 1b. *M. fasciipennis; hind wing, X1.5 (Martynov, 1937b).

Megakhosarella Sharov, 1961d, p. 182 [*M. regressa; OD]. Little-known fore wing; MA and RS anastomosed for very short distance. *Perm.*, USSR (Asian RSFSR).—Fig. 69, 2. *M. regressa; fore wing, X3 (Sharov, 1961d).

Family IDELIIDAE
Zalessky, 1929

[Ideiliidae M. D. Zalessky, 1929, p. 21] (=Rachimentomidae G. M. Zalessky, 1939, p. 55]

Fore wing with broad costal area having numerous slanting veinlets, usually forming reticulation; no anastomosis of veins MA and RS; RS usually with more than three branches; stem CU formed as in Liomopteridae but CU more elaborately branched; CUP not so strongly developed as in Liomopteridae; crossveins numerous, usually forming reticulation. Hind wing little known, apparently similar to that of Liomopteridae. Antennae prominent; pronotum with broad, coriaceous expansions; cerci probably well developed, long ovipositor present. *U. Carb.—Perm.*

Stenaropodites Martynov, 1928b, p. 47 [*S. reticulata; OD] (=Idelia Zalessky, 1929, p. 4 (type, I. permiakovi)). Fore wing with fine network of cells, resembling archedictyon; costal margin weakly curved; CUA2 strongly sigmoidal. *Perm.*, USSR (Asian RSFSR).—Fig. 70, 6. *S. permia­kovi (Zalessky); fore wing, X1.2 (Zalessky, 1929).

Aenigmidelia Sharov, 1961d, p. 175 [*A. incredi­bili; OD]. Fore wing oval, with strongly curved costal margin; SC with basal branch, resembling submarginal costa; main branch of SC coalesced with R basally; crossveins as in Archidelia; M forking at level of origin of RS. *Perm.*, USSR (Asian RSFSR).—Fig. 70, 8. *A. incredi­bili; fore wing, X1 (Sharov, 1961d).

Archidelia Sharov, 1961d, p. 172 [*A. elongata; OD]. Fore wing with strongly convex costal margin; crossveins forming irregular reticulation, much finer than that in Kortshakolia, but no archedictyon; costal veinlets branched; M forking before origin of RS. *Perm.*, USSR (Asian RSFSR).—Fig. 70, 2. *A. elongata; a, fore and b, hind wings, X1 (Sharov, 1961d).

Kortshakolia Sharov, 1961d, p. 171 [*K. ideli­formis; OD]. Little-known genus, based on fragment of fore wing, with costal margin shaped as in Stenaropodites; RS with at least 4 branches; MA directed anteriorly at its origin toward R before curving distally. *U. Carb., USSR (Asian RSFSR).—Fig. 70, 1. *K. ideli­formis; fore wing, X1.6 (Sharov, 1961d).

Metidelia Martynov, 1937b, p. 23 [*M. kargalenis; OD]. Fore wing with costal area narrower than in Stenaropodites; crossveins forming nearly regular network, not so fine as archedictyon. *Perm.*, USSR (Asian RSFSR).—Fig. 70, 3. *M. kargalenis; fore wing, X1.8 (Martynov, 1937b).

Paridelia Sharov, 1961d, p. 175 [*P. pusilla; OD]. Fore wing with costal margin as in Stenaropodites; RS arising near midwing, with 2 branches; MA with 2 branches, MP with 3. *Perm.*, USSR (Asian RSFSR).—Fig. 70, 9. *P. pusilla; fore wing, X1.8 (Sharov, 1961d).

Rachimentomon Zalessky, 1939, p. 56 [*R. reticulatum; OD]. Little-known genus. Costal margin of fore wing nearly straight; fine archedictyon present; venation little known; pronotal disc large; ovipositor well developed, nearly half as long as
Protorthoptera

Family EURYPTILONIDAE
Martynov, 1940

Fore wing oval, with narrow costal area; vein RS arising near midwing; CUA arising from stem of CU at base of wing and coalescing with M for short distance; CUA with several long, parallel branches. Pronotal disc well developed; legs adapted for running, spinous. Perm.

Euryptilon Martynov, 1940, p. 16 [*E. blattoides; OD]. Fore wing with subcostal space much broader than costal; M sigmoidally curved. Perm., USSR (Asian RSFSR).—Fig. 70.7. *S. latipennis; fore wing, ×1.4 (Martynov, 1940).

Family NARKEMIDAE
Handlirsch, 1911

Little-known family. Vein SC of fore wing terminating on R at level of midwing; RS with numerous parallel branches ending on wing apex; M apparently with a single distal fork; CUA apparently extensively branched; anal area unknown. U. Carb.


Family HERBSTIALIDAE
Schmidt, 1953

Related to Cacurgidae (probably synonymous). Fore wing with reticulation of cross-
veins over entire wing surface; cuticular spots as in Cacurgidae. *U. Carb.*

_Herbstiaea_ Schmidt, 1953, p. 153 [*H. herbsti*; OD]. Origin of RS at about same level as first fork of M. [Placed in order Protocicadida.] *U. Carb.*, Europe (Germany).—Fig. 70,4. *H. herbsti*; fore wing, X1.5 (Schmidt, 1953).

_Family CACURGIDAE_ Handlirsch, 1911

*[Cacurgidae Handlirsch, 1911, p. 324]*

Apparantly related to Omalidae. Fore wing oval, apex broadly rounded; vein SC nearly straight, terminating on wing margin beyond midwing; RS arising well before midwing; MA apparently absent; CUA anastomosed with MP basally, diverging before level of origin of RS, then anastomosed with CUP1; crossveins numerous. Hind wing unknown. *U. Carb.*

_Cacurgus_ Handlirsch, 1911, p. 324 [*C. spilopterus*; OD]. Little-known genus. Fore wing broadest at level of midwing; R with several oblique veinlets leading to fore margin of wing; crossveins forming a coarse network over most of wing except costal area; wing membrane with many circular thickenings. *U. Carb.*, USA (Illinois).—Fig. 71,6. *C. spilopterus*; fore wing, X1 (Handlirsch, 1911).

_Heterologus_ Carpenter, 1944, p. 14 [*H. langfordorum*; OD]. Fore wing as in Cacurgus, but costal area narrower and more tapering and no network of crossveins. *U. Carb.*, USA (Illinois).—Fig. 71,8. *H. langfordorum*; fore wing, X3.5 (Carpenter, 1944).

_Protodictyon_ Melander, 1903, p. 196 [*P. palmchripenna*; OD]. Similar to _Heterologus_, but crossveins of fore wing forming a coarse reticulation in several areas of the wing; RS remote from M.
basally. [Placed by Melander in Hemeristina group of Palaeodictyoptera.] U. Carb., USA (Illinois).

Spilomastax Handlirsch, 1911, p. 326 [*S. oligoneurus; OD]. Apparently similar to Cacurgus, but M forked before level of origin of RS. U. Carb., USA (Illinois).

Family OMAILIIDAE Handlirsch, 1906

[Omaliiidae Handlirsch, 1906b, p. 145]

Related to Cacurgidae, but fore wing without circular thickenings and with vein RS less developed than MP; CUA coalesced with MP at base. Hind wing unknown. U. Carb.

Omalia Van Beneden & Coemans, 1867, p. 384 [*O. macroptera; OD] [=Palaeomastax Handlirsch, 1904a, p. 16 (type, P. carbonis)]. Little-known fore wing; costal margin strongly curved and costal area broad; first fork of CUP beyond anastomosis with CUA. U. Carb., Europe (Belgium). — Fig. 71,1. *O. macroptera; fore wing, X1 (Pruvost, 1930).

Anthrakoris Richardson, 1956, p. 36 [*A. aesthenus; OD]. Related to Omalia, but costal margin of fore wing more strongly curved and CUA with only 2 branches. U. Carb., USA (Illinois).
Hexapoda

Fig. 71.3. *A. aestherius;* fore wing, X5 (Carpenter, new).

Coselia BOLTON, 1922, p. 81 [*C. palmiformis; OD].

Family GERARIDAE Scudder, 1885

[Genotype. correct. Handlirsch, 1906a, p. 701; pro Gerarina SCUDDER, 1885b, p. 762] [Sthenaropodidae Handlirsch, 1906b, p. 141; Genoptergidae Richardson, 1956, p. 41].

Fore wing membranous; costal area of uniform width for most of its length, with many crossveins, mostly unbranched; vein SC terminating on C; R without branches; RS commonly anastomosed with M for a short distance or connected to it by a short crossvein; CUA strongly developed, arising from the combined bases of R and M; CUP forked. Hind wing with the costal area more narrow than in the fore wing; RS arising very near the wing base; anal area little known but apparently not enlarged. Head relatively small, with long, filamentous antennae; prothorax long, slender anteriorly but broad posteriorly, bearing prominent spines; legs cursorial, slender, with five tarsal segments. Abdomen very little known. BURNHAM, 1983. U. Carb.

Gerarus SCUDDER, 1885d, p. 344 [*G. vetus; OD]
[=Genopteryx SCUDDER, 1885d, p. 327 (type, G. constricta); Sthenaropoda BRONGNIART, 1885a, p. 59 (type, S. fischeri); Archaeacridites MEUNIER, 1909c, p. 39 (type, A. bruesi); Rossites Richardson, 1956, p. 44 (type, R. inopinus)]. Moderately large species. Fore wing with RS branched 2 or 3 times; M with 4 or 5 branches and either anastomosed for a short interval with RS or connected to it by a strong crossvein. BURNHAM, 1983. U. Carb., USA (Illinois), Europe (France).—Fig. 72,3a. G. bruesi (Meunier); fore wing, X1 (Burnham, 1983).—Fig. 72,3b. G. danielsi; reconstruction, based on many specimens, X0.7 (Burnham, 1983).


Genentomum SCUDDER, 1885d, p. 329 [*G. validum; OD]. Similar to Gerarus, but branches of M straight and parallel in fore wing; first fork of CUP very close to wing base. BURNHAM, 1983. U. Carb., USA (Illinois).

Gerarulus HANDLIRSCH, 1911, p. 316 [*G. radialis; OD]. Little-known genus, based on wing fragments; RS with not more than 4 branches. BURNHAM, 1983. U. Carb., USA (Illinois).

Nacekomia RICHARDSON, 1956, p. 33 [*N. rossae; OD]. Fore wing similar to that of Gerarus but more slender; M not connected to RS by a thickened crossvein. BURNHAM, 1983. U. Carb., USA (Illinois).—Fig. 72,2. *N. rossae;* fore wing, X1.4 (Carpenter, new).

Progenentomum HANDLIRSCH, 1906a, p. 701 [*P. carbonis; OD]. Fore wings as in Gerarus but more pointed; SC shorter; RS with 4 main branches; branches of CUA nearly parallel. BURNHAM, 1983. U. Carb., USA (Illinois).

Family SPANIODERIDAE

Handlirsch, 1906

[Spanioderidae Handlirsch, 1906a, p. 695].

Fore wing coriaceous, with granular surface resembling that of Probnidae; costal margin only slightly curved; costal area narrow, with regular series of oblique, simple crossveins; vein SC terminating on R beyond midwing; RS arising near base; M flat or slightly concave, with several terminal branches; stem of CUA apparently anastomosed with base of M, diverging from M at about level of origin of RS, commonly with a series of long branches; CUP nearly straight; anal area with several veins; crossveins numerous, unbranched. Hind wing little known; remigium as in fore wing, but CUA strongly diverging away from M, its branches shorter than in fore wing; anal area unknown. Head small; prothorax elongate, without spines; legs slender, cursorial; abdomen little known; cerci unknown; ovipositor long. U. Carb.

Propeticus SCUDDER, 1885d, p. 334 [*P. infernus; OD] [=Petroctamus MELANDER, 1903, p. 191 (type, P. indistinctus); Spanioidera HANDLIRSCH, 1906a, p. 696 (type, S. ambulans); Camptophlebia HANDLIRSCH, 1906a, p. 698 (type, Dictyoneura clarinervis MELANDER, 1903); Paracheliphlebia HANDLIRSCH, 1906a, p. 699 (type, Cheliphlebia extensa MELANDER, 1903); Metripia HANDLIRSCH, 1906a, p. 700 (type, M. analis)]. Fore wing with vein R terminating just before wing apex; M with basal fork at about level of origin of RS, anterior branch with at least one fork; CUA with at least 4 to 7 branches. Hind wing narrower than fore wing. BURNHAM, 1986. U. Carb., USA (Illinois).—Fig. 72,1. *P. infernus;* reconstruction, based on type and sev-
eral additional specimens, X 1.3 (Burnham, 1986).

**Dieconeura** SCUDDER, 1885d, p. 336 [*D. arcuata; SD HANDLIRSCH, 1906a, p. 699*]. Little-known genus, with fore wing more slender than in **Propteticus**; M with only one fork, anterior branch briefly anastomosed with branch of RS. [Family assignment doubtful.] U. Carb., USA (Illinois).

**Gerarus** CUA

**Family APITHANIDAE**

Handlirsch, 1911

[Apithanidae HANDLIRSCH, 1911, p. 320]

Related to Spanioideridae. Fore wing with vein R1 extending nearly to apex, a series of oblique veinlets between R1 and the costal margin beyond SC; RS arising in distal third of wing; prothorax shorter than in Spanioideridae. U. Carb.

**Apithanus** HANDLIRSCH, 1911, p. 320 [*A. fociarius; OD*]. Fore wing little known; M apparently forking at about midwing. U. Carb., USA (Illinois).

**Family TILLYARDEMBIIDAE**

Zalessky, 1938

[Tillyardembiidae ZALESSKY, 1938, p. 64] [=Permocapniidae MARTYNOV, 1940, p. 52]

Fore wing little known; vein SC terminating on costa; RS pectinately branched; CUA with at least 4 parallel branches to apical and hind margins. Body slender, with prominent cerci and ovipositor. SHAROV, 1962c. Perm.

**Tillyardembia** ZALESSKY, 1937d, p. 847 [*T. biarmica; OD*] [=Permocapnia MARTYNOV, 1940, p. 52]
Hexapoda

52 (type, P. brevipes). RS with about 6 branches; M with deep fork. Perm., USSR (Asian RSFSR).

---Fig. 71,4. T. brevipes (Martynov); a, complete specimen, X4.5 (Martynov, 1940); b, fore wing, X4 (Sharov, 1962c).

Family EPIDEIGMATIDAE
Handlirsch, 1911

[Epideigmatidae Handlirsch, 1911, p. 356] [=Cymenophlebiidae PruvoSt, 1919, p. 128]

Fore wing coriaceous; costal area of moderate width; vein RS arising in basal third of wing, with several parallel branches; M apparently independent of RS; CUA branching only distally, forming many terminal branches along posterior border; anal area sharply marked by curved suture and very small; irregular reticulation over most of wing. Hind wing unknown. Pronotum elongate, oval. U. Carb.

Epideigma Handlirsch, 1911, p. 357 [*E. elegans; OD]. Fore wing slender, length almost 4 times width; SC terminating on R. U. Carb., USA (Illinois). --- Fig. 71,2. *E. elegans; fore wing, X2 (Handlirsch, 1911).

Cymenophlebia PruvoSt, 1919, p. 128 [*C. carpentieri; OD]. Fore wing as in Epideigma, but costal area wider; SC terminating on costa. U. Carb., Europe (France). --- Fig. 71,5. *C. carpentieri; fore wing, X3 (PruvoSt, 1919).

Family PERMOTERMOPSIDAE
Martynov, 1937

[Permotermopsidae Martynov, 1937b, p. 84]

Fore wing similar to that of Ideliidae, but basal part narrowed and vein CUA more remote distally from wing margin. Hind wing unknown. Perm.

Permotermopsis Martynov, 1937b, p. 84 [*P. roseni; OD]. Costal veinlets simple; crossveins forming delicate, irregular network. Perm., USSR (European RSFSR). --- Fig. 71,7a. *P. roseni; fore wing, X1.0 (Martynov, 1937b). --- Fig. 71,7b. P. pectinata Martynov; fore wing, X1.2 (Martynov, 1937b).

Kolviedelia Zalessky, 1956a, p. 282 [*K. curta; OD]. Little-known fore wing, with costal area broader than in Permotermopsis. [Family assignment doubtful.] Perm., USSR (Asian RSFSR). --- Fig. 71,10. *K. curta; fore wing, X2 (Zalessky, 1956a).

Family ADELONEURIDAE
Carpenter, 1938

[Adeloneuridae Carpenter, 1938, p. 450]

Fore wing with very broad costal area having long, oblique veinlets; vein MA apparently absent; CUA Anastomosed with MP proximally; distinct marginal indentation at end of CUP. U. Carb.

Adeloneura Carpenter, 1938, p. 450 [*A. thomp­soni; OD]. Little-known fore wing, with very narrow subcostal space; CUA and MP separating at about level of origin of RS. U. Carb., USA (Illinois). --- Fig. 71,9. *A. thompsoni; fore wing, X1.6 (Carpenter, 1938).

Family AENIGMATODIDAE
Handlirsch, 1906

[Aenigmatodidae Handlirsch, 1906a, p. 683]

Crossveins forming reticulated network over most of fore wing; vein MA apparently absent; CUA Anastomosed with stem of MP, unbranched. U. Carb.

Aenigmatodes Handlirsch, 1906a, p. 683 [*A. danielsi; OD]. Little-known genus, based on fragment of fore wing; RS and MP with 3 distinct branches. U. Carb., USA (Illinois).

Family STREPHOCladidae
Martynov, 1938

[Strephocladidae Martynov, 1938b, p. 100]

Fore wing coriaceous; precostal area absent; vein SC well developed, extending to mid-wing or beyond, with several branches; RS arising before midwing; R ending well before apex, with several oblique branches to wing margin; RS with several long branches; M forked before origin of RS, anterior branch commonly touching RS or connected to it by a crossvein; CUA longitudinal, with several long branches; branches of RS, M, and CUA parallel and slightly sigmoidal; distinct furrow posterior to CUA; 1A close and parallel to CUP. Crossveins numerous and regularly arranged, an irregular network in costal area and between CUA and CUP and anal veins. Wing membrane with fine microtrichia between veins; prominent setae on most veins. Hind wing and body unknown. [The relationships of this family within the Protor-
Protorthoptera are uncertain; Martynov (1938a) placed it in a new order, Strephocladodea. Carpenter, 1966. U. Carb.–Perm.

Strephocladus Scudder, 1885d, p. 337 [*Pterablabattina subtilis Kliver, 1883, p. 251; OD]. Little-known genus. Costal area with straight, oblique veinlets near level of midwing; branches of CUA and RS dichotomously formed. Kukalová, 1965; Carpenter, 1966. U. Carb., Europe (Germany).—Fig. 73,8. *S. subtilis; fore wing as preserved (holotype), X2 (Carpenter, 1966).

Homocladus Carpenter, 1966, p. 60 [*H. grandis; OD]. Fore wing slender; costal area much as in Spargopteron; branches of RS arising pectinately, those of CUA dichotomously. Perm., USA (Kansas).—Fig. 73,1. *H. grandis; fore wing, X1.3 (Carpenter, 1966).

Paracladus Carpenter, 1966, p. 62 [*P. retardatus; OD]. Fore wing as in Homocladus, but branches of RS, M, and CUA nearly straight. Perm., USA (Kansas).—Fig. 73,4. *P. retardatus; fore wing, X3 (Carpenter, 1966).

Spargopteron Kukalová, 1965, p. 89 [*S. latericius; OD]. Fore wing much broader than in Strephocladus; all veinlets in costal area branched or irregular; branches of RS dichotomous, those of CUA pectinate. Carpenter, 1966. Perm., Europe (Czechoslovakia).—Fig. 73,9. *S. latericius; fore wing, X1.8 (Kukalová, 1965).
Family TOCOCLADIDAE
Carpenter, 1966

Similar to Protokollaridae, but fore wing with anterior branch of vein M anastomosed for short interval with stem of RS; SC ending on R, just beyond midwing; crossveins not reticulate. Body little known (Opisthocladus); head relatively large; pronota of thoracic segments large and nearly circular. Perm.

Tococladus Carpenter, 1966, p. 77 [*T. rallicus; OD]. Area between CUA and CUP very broad, traversed by long crossveins, not reticulate. Perm., USA (Kansas). — Fig. 73.6. *T. rallicus; fore wing, ×2.3 (Carpenter, 1966).

Opisthocladus Carpenter, 1976, p. 342 [*O. arcutatus; OD]. Fore wing as in Tococladus, but costal veinlets looped and RS arising more distally; basal part of costal area thick and strongly sclerotized. Perm., USA (Kansas). — Fig. 73.2. *O. arcutatus; fore wing as preserved, ×4 (Carpenter, 1976).

Family HETEROPTILIDAE
Carpenter, 1976

Insects of moderate size; affinities uncertain within the Protorthoptera. Fore wing oval, anterior margin strongly curved; vein SC unusually remote from wing margin, ending on R near midwing; SC curving posteriorly near midwing; RS with several branches, M with few; CUA nearly straight and ending on hind margin about three-fourths wing length from base; CUP and anal veins close together and straight. Perm.

Heteroptilon Carpenter, 1976, p. 346 [*H. costale; OD]. Fore wing broadest beyond midwing; RS with 8 terminal branches; CUA with a short, distal fork. Perm., USA (Kansas). — Fig. 73.7. *H. costale; fore wing, ×3.7 (Carpenter, 1976).

Family HERDINIDAE
Carpenter & Richardson, 1971

Apparently related to Cacurgidae. Wings very short; venation strongly developed; small tubercles on all main veins and crossveins of fore and hind wings. Fore wing with base of costal area strongly sclerotized; vein SC ending on costal margin well before apex of wing; RS arising at level of midwing, with 3 main branches; M independent of R basally and with two main branches. Crossveins numerous, forming a coarse network over the wing. Hind wing much smaller than fore wing; costal area narrow; venation apparently as in fore wing. Body little known; pronotum large. U. Carb.

Herdina Carpenter & Richardson, 1971, p. 291 [*H. mirificus; OD]. CUA apparently unbranched; CUP forked, one branch directed toward hind margin of wing and very irregular. [It has been suggested by some workers that the specimen on which this genus is based is in fact a nymph, not an adult. However, the wings are well sclerotized, have thick veins, and are covered with tubercles. Two additional specimens, with similarly reduced wings, have more recently been found in the same deposit.] U. Carb., USA (Illinois). — Fig. 73.3. *H. mirificus; a, fore and b, hind wings, ×7 (Carpenter & Richardson, 1971).

Family PSOROPTERIDAE
Carpenter, 1976

Small insects of uncertain affinities. Fore wing membrane coriaceous and rugose, with hair covering; veins M and CU coalesced near base of wing; M with 2 branches, CUA with 3; longitudinal veins thick; crossveins weak. Hind wing and body unknown. Perm.

Psoroptera Carpenter, 1976, p. 345 [*P. cubitalia; OD]. Fore wing with R extending almost to wing apex; RS arising at about level of fork of CUA; 2 rows of cells between M3+4 and CUA. Perm., USA (Kansas). — Fig. 73.5. *P. cubitalia; fore wing, ×9 (Carpenter, 1976).

Family STREPHONEURIDAE
Martynov, 1940

Fot wing with costal area of moderate width; vein SC with branched veinlets and terminating on costa; crossveins numerous, without reticulation; R with series of close veinlets to costal margin distally. Perm.

Strephoneura Martynov, 1940, p. 14 [*S. robusta; OD]. Subcostal area very narrow; MP anastomosed with CUA proximally. Perm., USSR (Asian RSFSR). — Fig. 74.1. *S. robusta; fore wing, ×1 (Sharov, 1962c).
Family ANTHRACOTHREMMIDAE
Handlirsch, 1906

[Anthracothremmidae Handlirsch, 1906a, p. 712]

Little-known insects. Fore wing with branches of vein RS forming series of nearly parallel veins leading to apical area of wing. Hind wing with remigium shaped as in fore wing and venation similar; anal area unknown. *U. Carb.*

**Anthracothremma** Scudder, 1885d, p. 327 [*A. robusta*; OD]. Wings with rounded apex; RS of fore wing with at least 6 straight, main branches, some forked. *U. Carb.*, USA (Illinois).—Fig. 74, 2. *A. robusta*; a, fore and b, hind wings, X2.5 (Carpenter, new).

**Melinophlebia** Handlirsch, 1911, p. 364 [*M. analis*; OD]. Little-known genus, based on fragment of fore wing. RS with only 3 or 4 main branches. *U. Carb.*, USA (Illinois).

**Pericalyphe** Handlirsch, 1911, p. 365 [*P. longa*; OD]. Similar to *Anthracothremma* but larger; RS
with simple branches. [Probably a synonym of Anthracothremma.] U. Carb., USA (Illinois).

Silphion Handlirsch, 1911, p. 365 [*S. latipenne; OD]. Fore wing as in Pericalyphe but broader. U. Carb., USA (Illinois).

Family TOMIIDAE Martynov, 1936
[Tomiidae Martynov, 1936, p. 1254]

Costal area wider than in Atactophlebiidae, with series of evenly spaced veinlets; vein SC terminating slightly beyond mid-wing; R with series of costal veinlets continuing series of veinlets from SC; crossoveins of wing more regular than in Atactophlebiidae. [Ordinal assignment uncertain.] Perm.-Trias.

Tomia Martynov, 1936, p. 1255 [*T. costalis; OD]. Double row of cells between RS and R proximally; other crossoveins simple; MA with 4 branches. Trias., USSR (Asian RSFSR).—Fig. 74.6. *T. costalis; fore wing, X3.5 (Martynov, 1936).

Kargalella Martynov, 1937b, p. 32 [*K. subcostatis; OD]. Little-known genus, based on fragment of fore wing. Costal area broader than in Tomia; single row of cells between all veins. RS anastomosed with MA basally. [Family position doubtful.] Perm., USSR (European RSFSR).

Family ANTHRACOPTILIDAE
Handlirsch, 1922
[Anthracoptilidae Handlirsch, 1922, p. 98]

Related to Ischnoneuridae. Fore wing with vein SC terminating on R well before apex; RS apparently originating about midwing; CUA extensively developed with dichotomous branching; wing membrane granular, as in Probnidae; crossoveins numerous, irregular, and weak. U. Carb.

Anthracoptilus Lameere, 1917b, p. 180 [*Homaloipheria perrieri Meunier, 1909d, p. 46; OD] [=Prostenoneura Handlirsch, 1919b, p. 559, obj.]. All branches of RS directed anteriorly; RS with fewer branches than M. U. Carb., Europe (France).—Fig. 74.5. *A. perrieri (Meunier); fore wing, X1.5 (Carpenter, new).

Family CNEMIDOLESTIDAE
Handlirsch, 1906
[Cnemidolestidae Handlirsch, 1906b, p. 135]

Fore wing similar to that of Ischnoneuridae, but RS arising near midwing and cross-
veins fewer, more widely separated. Hind wing unknown. Prothorax small, about as long as wide; head small, slenderly oval; antennae long and filamentous; forelegs long and apparently raptorial. U. Carb.

**Protodiamphipnoa** BronnIART, 1893, p. 410 [*P. terrinii; OD*] (*=Cnemidolestes* HANDLIRScH, 1906b, p. 135 [type, *Protophasma woodwardi* BronnIART, 1893, p. 427]). Fore wing with M and CUA dividing at level of origin of RS; wings with conspicuous "eye spot." HANDLIRScH, 1937. *U. Carb.* Europe (France).—Fig. 75. *P. terrinii*; fore wings, X1.5 (Carpenter, new).—Fig. 76. *P. gaudryi* (BronnIART); fore wings and part of body, holotype, X1.7 (Carpenter, new).

**Family STENONEURITIDAE**

Lameere, 1917

([Stenoneuritidae Lameere, 1917b, p. 197]

Fore wing similar to that of Stenoneuridae, but RS arising near midwing and MP much less developed, branching only in its distal half near posterior margin. U. Carb.


**Family STENONEURIDAE**

Handlirsch, 1906

([Stenoneuridae Handlirsch, 1906b, p. 132] [=Eoblattidae Handlirsch, 1906b, p. 155]

Fore wing slightly coriaceous; vein SC extending nearly to wing apex, terminating on R; RS arising at wing base, parallel and close to R up to at least midwing; RS with several branches; MA apparently absent; MP dividing at about midwing, the most anterior branch directed anteriorly towards RS; CUA forking well before midwing; each main branch subdividing; CUP marking off the anal area, which contains numerous anal veins, very close together and nearly parallel. Hind wing little known, apparently similar to fore wing except that M is reduced and the anal area is expanded. Prothorax broad, distinctly broader than long; prothoracic legs robust, moderately long. U. Carb.

**Stenoneura** BronnIART, 1893, p. 429 [*S. fayoli; OD*]. Fore wing with numerous crossveins forming very irregular, fine reticulation over most of wing, except anal area. U. Carb., Europe (France).—Fig. 74.9. *S. fayoli; fore wing, X1.2 (Carpenter, new).

**Eoblatta** Handlirsch, 1906b, p. 155 [*Stenoneura robusta* BronnIART, 1893, p. 429; OD]. Fore wing with fewer crossveins than in *Stenoneura*, forming coarse reticulation only in costal area and a few small regions of wing. U. Carb., Europe (France).—Fig. 74.7. *E. robusta* (BronnIART); fore wing, X0.9 (Carpenter, new).

**Family HOMALOPHLEBIIDAE**

Handlirsch, 1906

([Homalophlebiidae Handlirsch, 1906b, p. 136]

Related to Stygnidae, but fore wing with very extensive vein MP; MA apparently absent; CUA forked at margin. Hind wing unknown. U. Carb.

**Homalophlebia** BronnIART, 1893, p. 437 [*H. finoti; SD Handlirsch, 1906b, p. 136]. Fore wing with RS arising about one-third of wing length from base, with several branches; first fork of MP at same level. U. Carb., Europe (France).—Fig. 74.3. *H. finoti; fore wing, X0.8 (Carpenter, new).
Parahomalophlebia Handlirsch, 1906b, p. 137
[*Homalophlebia courinsi Brongniart, 1893, p. 458; OD]. Similar to Homalophlebia, but RS with single fork. U. Carb., Europe (France).

Family ISCHNONEURIDAE
Handlirsch, 1906
[Ischnoneuridae Handlirsch, 1906b, p. 133] [=Stenoneurellidae Handlirsch, 1919b, p. 560]

Related to Stenoneuretidae. Fore wing with vein SC terminating on R well before apex; RS arising close to wing base with several long branches; CUA very extensively developed; crossveins numerous, mostly straight, not forming reticulation. Hind wing unknown. Prothorax and legs long. U. Carb.

Ischnoneura Brongniart, 1893, p. 433, nom. subst. pro Leptoneura Brongniart, 1885a, p. 62, non Wal lengren, 1857 (*Leptoneura oustaleti Brongniart, 1885a, p. 62; SD Handlirsch, 1922, p. 76) [=Ischnoneurilla Handlirsch, 1919b, p. 556 (type, Ischnoneura elongata Brongniart, 1893, p. 433); Ischnoneurona Handlirsch, 1919b, p. 557 (type, Ischnoneura delicatula Brongniart, 1893, p. 433)]. Branches of CUA close together and parallel. U. Carb., Europe (France).—Fig. 74,8. *I. oustaleti (Brongniart); fore wing, X0.6 (Carpenter, new).

Ctenopelthus Lameere, 1917b, p. 180 [*Homalophlebia trouessarti Meunier, 1911a, p. 127; OD]. Similar to Ischnoneura, but branches of CUA more widely separated and divergent. U. Carb., Europe (France).—Fig. 74,12. *C. trouessarti (Meunier); fore wing, X1.4 (Carpenter, new).

Mesopelthus Lameere, 1917b, p. 174 [*M. dollio; OD] [=Pseudoeotischia Handlirsch, 1919b, p. 557 (type, P. berthaudi); Stenoneurella Handlirsch, 1919b, p. 559 (type, S. fayoliana)]. Similar to Ischnoneura, but first branch of RS arising well before midwing; posterior branch of CUA more oblique than in Ischnoneura. U. Carb., Europe (France).—Fig. 74,10. *M. dollio; fore wing, X1.2 (Carpenter, new).

Family PROTOPHASMATIDAE
Brongniart, 1885
[nom. correct. Carpenter, herein, pro Protophasmatidae Brongniart, 1885a, p. 59]

Little-known family, apparently related to Geraridae. Fore wing with small but distinct precostal area; several veinlets arising from costa; crossveins forming network; costal space much broader than subcostal; vein RS arising nearer wing base than in Geraridae, with several branches. U. Carb.

Protophasma Brongniart, 1878, p. 57 [*P. damasi; OD]. Fore and hind wings with several transverse rows of maculations. U. Carb., Europe (France).

Family UNCERTAIN

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

Acridites Germar, 1842, p. 93 [*A. carbonarius; OD]. Little-known genus, based on poorly preserved fore wing with narrow costal area. (Probably related to Geraridae.) U. Carb., Europe (Germany).

Adiphlebia Scudder, 1885d, p. 345 [*A.lacoana; OD]. Based on little-known insect, with short oval wings and robust body. (Type of Adiphlebiidae Handlirsch, 1906a.) U. Carb., USA (Illinois).

Aenigmatella Sharov, 1961c, p. 159 [*A. com-
Fig. 77. Uncertain (p. 130–134).

parabilis; OD]. Costal area broad, with numerous veinlets; RS and M dividing at about same level; CUA very extensively developed. U. Carb., USSR (Asian RSFSR).—FIG. 77,1. *A. comparabilis; fore wing, X1.4 (Sharov, 1961c).

*Aetophlebia* SCUDDER, 1885d, p. 338 [*A. singularis; OD]. Based on fragments of wing. [Type of *Aetophlebiidae* HANDLIRSC, 1906a, p. 708.] U. Carb., USA (Illinois).


*Agogoblattina* HANDLIRSC, 1906a, p. 714 [*Oryctoblattina occidua* SCUDDER, 1885e, p. 37; OD]. Based on fragments of wings and body. U. Carb., USA (Illinois).

*Ampeliptera* PRUVOST, 1927, p. 76 [*A. limburgica; OD]. Little-known genus, based on incomplete fore wing with fine archedictyon; CUA1 apparently anastomosed with M near wing base and diverging away before the level of the origin of RS, as in some Permian Orthoptera. [Placed in Hapalopteridae (order Hapaloptera) by PRUVOST (1927); in Palaeocixiidae (order Protorn
thoptera) by Handlirsch (1937); in family uncertain (order Paraplecoptera) by Martynov (1958b); in new family Amaplippersidae (order Protocicada) by Haupt (1941); and in Paoliidae (order Protophlebiidae) by Kukalova (1958b). U. Carb., Europe (Holland). —— Fig. 77.3. *A. limburgica; fore wing, holotype, X5 (Kukalova, 1958b).

Anegertus Handlirsch, 1911, p. 353 [*A. cubitalis; OD]. Based on wing fragments. U. Carb., USA (Illinois).

Anthracomastax Handlirsch, 1904a, p. 17 [*A. furcifer; OD]. Based on wing fragment. U. Carb., Europe (Belgium).

Archaeologus Handlirsch, 1906a, p. 807 [*A. falcatus; OD]. Based on fore and hind wing fragments. U. Carb., USA (Illinois).

Archimastax Handlirsch, 1906a, p. 806 [*A. americanus; OD]. Based on wing fragment. U. Carb., USA (Arkansas).


Atava Sellards, 1909, p. 157 [*A. ovata; OD]. Based on fragment of hind wing. Perm., USA (Kansas).

Axiologus Handlirsch, 1906a, p. 805 [*A. thoracicus; OD]. Based on fragments of body and wings. U. Carb., USA (Illinois).

Balducriella Meunier, 1925, p. 105 [*B. lattisima; OD]. Based on wing fragment. U. Carb., Europe (Germany).


Cacurgetta Pruvost, 1919, p. 125 [*C. barryi; OD]. Based on wing fragment. U. Carb. Europe (France).

Cheliphlebia Scudder, 1885d, p. 328 [*C. carbnaria; OD]. Little-known genus, based on fragments of fore wings. [Type of Cheliphlebiidae Handlirsch, 1906a, p. 709.] U. Carb., USA (Illinois).

Chrestotes Scudder, 1868b, p. 567 [*C. lapidea; OD]. Based on fragments of wings. U. Carb., USA (Illinois).


Danielsiella Cockerell, 1916c, p. 100 [*D. priscula; OD]. Based on fragments of wings and body. U. Carb., USA (Illinois).

Didymophleps Scudder, 1885d, p. 330 [*Termes contusa Scudder, 1878c, p. 300; OD]. Based on small fragment of wing. U. Carb., USA (Illinois).

Dieconeurites Handlirsch, 1906a, p. 699 [*Dieconeura rigidia Scudder, 1885d, p. 336; OD]. Based on wing fragment. U. Carb., USA (Pennsylvania).

Distasis Handlirsch, 1904a, p. 17 [*D. rhiphora; OD]. Based on distal fragment of hind wing. U. Carb., Europe (Belgium).

Endoismus Handlirsch, 1906a, p. 805 [*E. reticulatus; OD]. Based on wing fragment. U. Carb., USA (Illinois).

Eoblatitana Bolton, 1925, p. 19 [*E. complexa; OD]. Little-known genus, based on fragments of wings and body; fore wing with extensive, sigmooidal CUA having several short, straight branches leading to CUP. U. Carb., Europe (France). —— Fig. 77.2. *E. complexa; fore wing, X1.3 (Bolton, 1925).

Gerapompus Scudder, 1885d, p. 326 [*G. blattinoideus; SD Handlirsch, 1906a, p. 711]. Little-known genus, based on poorly preserved fore wing; R and RS apparently with several long branches distally; M extensively branched. [Type of Gerapompaideae Handlirsch, 1906a, p. 711.] U. Carb., USA (Illinois). —— Fig. 77.9. *G. schucherti Handlirsch; fore wing, X2 (Handlirsch, 1906a).

Gerariantus Handlirsch, 1919b, p. 551 [*G. commen trianus; OD]. Based on wing fragments. U. Carb., Europe (France).

Gerarites Handlirsch, 1919b, p. 551 [*Geratus commentri Bronnliart, 1893, p. 24, fig. 10; OD]. Based on wing fragment. U. Carb., Europe (France).


Gyrophlebia Handlirsch, 1906a, p. 697 [*G. longicollis; OD]. Little-known genus, based on poorly preserved fore wing and body. U. Carb., USA (Illinois).


Haplopterus Martynov, 1928b, p. 84 [*H. majaus; OD]. Based on hind wing fragment. Perm., USSR (European RSFSR).

Hemeristica Dana, 1864, p. 35 [*H. occidentalis; OD] [=Hemeristica Goldenberg, 1877, p. 15, obj.]. Based on wing fragments. U. Carb., USA (Illinois).

Heterologellus Schmidt, 1962, p. 843 [*H. teichmuelleri; OD]. Apparently similar to Omalia, but fore wing with SC terminating on R well before wing apex; MP dividing distally, near

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wing margin; CUA only just touching CUP, not coalesced with it; MP not as extensively branched as CUA. [Placed in Omalidae by Schmidt.] U. Carb., Europe (Germany).—Fig. 77,6. *H. teichmuelleri*; fore wing, X3 (Schmidt, 1962).

**Heterologopsis** Brauckmann & Koch, 1982, p. 18 [*H. rubrensis*; OD]. Little-known genus, apparently related to the Cacurgidae, but SC much shorter and terminating on R. U. Carb., Europe (Germany).


**Kargalodes** Martynov, 1937b, p. 33 [*K. incerta*; OD]. Based on wing fragment. Perm., USSR (European RSFSR).

**Kelleropteron** Brauckmann & Hahn, 1980, p. 308 [*K. kaalbergesiense*; OD]. Little-known genus, based on small fragment of wing. U. Carb., Europe (Germany).

**Khosarophlebia** Martynov, 1940, p. 24 [*K. sylvaensis*; OD]. Based on hind wing fragment. Perm., USSR (Asian RSFSR).

**Klebsiella** Meunier, 1908c, p. 242 [*K. exticta*; OD]. Based on fragments of fore and hind wings. [Type of Klebsiellidae Handlirsch, 1919b, p. 552.] U. Carb., Europe (France).

**Lecopterum** Sellards, 1909, p. 161 [*L. delicosum*; OD]. Based on wing fragment. Perm., USA (Kansas).


**Macrophlebia** Goldenberg, 1869, p. 164 [*M. bollebeni*; OD]. Based on wing fragment. U. Carb., Europe (Germany).

**Megalometer** Handlirsch, 1906a, p. 713 [*M. lata*; OD]. Based on fragments of wings. U. Carb., USA (Illinois).

**Mesorthopteron** Tillyard in Tillyard & Dunstan, 1916, p. 14 [*M. locustoides*; OD]. Little-known genus, based on fragments of fore wing. Fore wing elongate-oval, with fine archedictyon; costal area broad, with numerous, parallel veinlets; SC straight and close to R and RS, with several distal branches; M weakly formed; CUA with numerous long, pectinate branches; anal area small. [Type of family Mesorthopteridae Tillyard, 1922b.] Riek, 1956. *Trias.*, Australia (New South Wales).


**Miamia** Dana, 1864, p. 34 [*M. bronsoni*; OD]. Little-known genus, based on wing fragments. [Possibly belonging to the Spaniopteridae.] U. Carb., USA (Illinois).

**Mitinovia** Sharov, 1961d, p. 223 [*M. dubia*; OD]. Based on hind wing with extensive veinlets from R to costa beyond SC. Perm., USSR (Asian RSFSR).

**Narkemina** Martynov, 1931a, p. 81 [*N. angustata*; OD]. Fore wing elongate-oval; venation with some resemblance to that of the Narkemidae. RS forking near midwing; M dividing near base, MA continuing in a straight line and branching beyond origin of RS; MP diverging posteriorly and coalescing with CUA for a considerable interval before diverging anteriorly, its terminal branches joining some of those of MA; CUA with a few short, terminal branches; CUP unbranched. Hind wing very broad, with an enlarged anal area, but with the venation of the remigium much as in the fore wing. [Pinto & Ornellas (1978c) correctly recognized that the genus Narkemina, formerly placed in the Narkemidae, required a separate family, but they proposed the invalid family name, Narkemocarcurgidae, for the type genus Narkemina.] Sharov, 1961e; Pinto & Ornellas, 1978c; Lewis, 1979; Rasnitsyn, 1980c. U. Carb., USSR (Asian RSFSR), Brazil (Parana Basin), USA (Missouri).

— Fig. 77,7a. *N. angustata*; fore wing, X2.6 (Sharov, 1961e).— Fig. 77,7b. *N. angustiformis* Sharov; fore wing, X2 (Sharov, 1961e).— Fig. 77,7c. *N. rodenendorfi* Pinto & Ornellas; hind wing, X1.2 (Pinto & Ornellas, 1978c).

**Narkeminopsis** Whalley, 1979, p. 87 [*N. eddi*; OD]. Little-known genus. Apparently similar to Narkemina, but fore wing with M diverging posteriorly near wing base, then anastomosing briefly with CUA before diverging anteriorly and joining RS at level of end of SC; few costal veinlets; archedictyon present in costal and CUA areas. U. Carb., England.— Fig. 77,8. *N. eddi*; fore wing, X2.5 (Whalley, 1979).

**Ochotopteron** Cockerell, 1927g, p. 414 [*O. canaliculatum*; OD]. Little-known genus, based on wing fragment. U. Carb., USA (Maryland).

**Orthoneurites** Martynov, 1928b, p. 49 [*O. regularis*; OD]. Based on distal wing fragment. Perm., USSR (European RSFSR).

**Palaeocarria** Cockerell, 1917e, p. 80 [*P. ornata*; OD]. Based on fragment of wing. U. Carb., USA (Illinois).

**Palaeoedischia** Meunier, 1914d, p. 364 [*P. boulei*; OD]. Based on fragment of fore wing. U. Carb., Europe (France).

**Palaeomantopsis** Martynov, 1928b, p. 83 [*P. furcatella*; OD]. Based on distal wing fragment. Perm., USSR (European RSFSR).


**Paranarkemina** Pinto & Ornellas, 1980a, p. 288
**Order BLATTARIA**

Latreille, 1810

[Blattaria Latreille, 1810, p. 246] [=Blattoidea Brunner, 1882, p. 26; Protofoliogidae Haupt (in part), 1941, p. 75]

Exopterygotes with dorsoventrally compressed bodies; head free, commonly hypognathous or opisthognathous, rarely prognathous; antennae filiform, multisegmented; compound eyes of moderate size; mandibles well developed; pronotum large, commonly covering head and extending laterally (Fig. 78); legs cursorial, spinous, with 5 tarsal segments; wings typically well developed, aptery not uncommon; fore wings tegminous, broadly oval, commonly as broad basally as at midwing; hind wings membranous, with an expanded anal fan, at least as large as remigium and containing radiating veins; abdomen with tenth tergite enlarged, forming a conspicuous supra-anal plate; cerci typically multisegmented, commonly of moderate length; external ovipositors absent in existing species but well developed in Paleozoic and many Mesozoic species. Most existing Blattaria nocturnal, omnivorous, commonly occurring in warm, moist environments. *U. Carb.*—*Holo.*

These are primitive orthopteroids, probably most closely related to the Isoptera among existing orders (McKittrick, 1965). The order is now a relatively small one, containing less than 4,000 species (M. J. Mac...
but the geological record indicates that it was one of the largest orders of insects during the late Paleozoic.

The venational pattern of the cockroaches is typically orthopteroid (Fig. 78,1,2,). In the fore wing, however, the costa is completely marginal, there being no precostal area. Veins RS, M, and CUA are well developed, and CUP is strongly concave and curved. Crossveins are numerous but weak in existing species; in most Paleozoic species they are much stronger or commonly form a fine network (archedictyon). The venational pattern of the remigium of the hind wing is like that of the fore wing except that RS, M, and CUA have fewer branches.

The basic venational pattern of the fore wing is unusually constant throughout the order, with very few exceptions. On the other hand, the detailed branching of the veins is extremely variable within all taxonomic levels. Early attempts at family classification, in which wing venation was used (Rehn, 1951), were very controversial, but the one proposed by McKitteck (1964) has been generally accepted. This classification bases the families on the genitalic structures of both sexes, the nature of the proventriculus, egg-laying behavior, and the structure of certain appendages. McKitteck recognized five existing families: Blattidae, Cryptoceridae, Polyphagidae, Blattellidae, and Blaberidae. The existing genera are usually based on the more detailed structure of the genitalia, hind wings, legs, and male tergal glands.

Unfortunately, such details of structure are rarely preserved in fossil roaches, with the exception of those in amber. The vast majority of fossil Blattaria, close to 90 percent, consist of isolated wings or wing fragments. Furthermore, most of the specimens with bodies preserved have the two pairs of wings folded back over the body in the usual resting position, obscuring most of the body structures that are preserved (Fig. 78). Study of extensive series of Paleozoic roaches has shown that their venational variability was at least as great as that of existing species (Schneider, 1977, 1978a, 1978b). The tendency in publications on these fossils has been to place emphasis on slight differences in venation, resulting in many families and genera. At least 25 extinct families and 370 extinct genera have been named from Paleozoic and early Mesozoic deposits, and fully half of these are based on single specimens.

The fossil record shows only a few obvious trends in the evolution of the fore wings of the Blattaria. In the most primitive and largest extinct family of the order, the Archimylacridae, the subcosta arises as a separate vein, isolated from R and giving rise to a series of branches toward the costa (Fig. 79,1,). Also, R arises as a distinct branch of stem R and has several branches. In most specialized species, as in the existing family Blattidae (Fig. 79,2), SC, R, and RS arise from a single stem.

Quite apart from the wings, the geological record has provided some interesting data bearing on the reproduction of the Blattaria.
The females of existing roaches lack a true ovipositor but commonly possess short internal valves that serve only to guide the fertilized eggs (several to many) into the genital atrium, where the ootheca is formed. In some species the oothecae are deposited within a few days, the embryos developing outside the body of the female. In others, the oothecae are first extruded, then retracted, and finally deposited in the brood sac, where the embryos continue their development. When they are mature, the ootheca is extruded again and the nymphs emerge from it (Roth, 1967; M. J. Mackerras, 1970). Several small and obscure fossils, presumed to be oothecae, have been reported from Paleozoic deposits, but these are not very convincing as oothecae, and all are now considered to be fragments of other organisms (Brown, 1957; Vishniakova, 1968). Furthermore, numerous specimens of female Blattaria with long, external ovipositors are known from Upper Carboniferous and Permian deposits of Europe, Asia, and North America (Brongniart, 1889; Sellards, 1904; Zalesky, 1939, 1940, 1953b). In more recent years Dr. V. N. Vishniakova of the Paleontological Institute in Moscow has described similar ovipositors on specimens from Triassic and Jurassic deposits of the USSR (Vishniakova, 1965, 1968, 1973) (Fig. 80, 1–3). From her detailed study of these remarkable fossils, Dr. Vishniakova concluded that these ovipositors were derived from the eighth and ninth abdominal sternites and that they were therefore homologous with the ovipositors of the Orthoptera but not with the short internal valves of the existing Blattaria, which are derived from the seventh sternite (Nel, 1929; Sharov, 1966b). It is noteworthy that in some of the Jurassic species the ovipositor is very short (Fig. 80, 1). The gradual shortening and ultimate loss of the long external ovipositors apparently took place toward the end of the Mesozoic.

The systematics of the fossil Blattaria has been in need of a thorough revision for many years, especially considering the additional information acquired during the past twenty years. Recognizing the unsatisfactory state of the classification of the extinct species, in 1977, Dr. Jörg Schneider, of the Department of Geological Sciences, Bergakademie Freiberg, Germany, began a long-range study of type specimens, as well as new material, from the Paleozoic and Mesozoic, with full recognition of the variability of the wing venation. Up to the present time seven papers in this series have been published (Schneider, 1977, 1978a, 1978b, 1980, 1982, 1983, 1984), and others are in preparation. Since Dr. Schneider's studies are continuing, it would be presumptuous and futile for me to attempt to present here a systematic treatment of the extinct genera of the order.
Order ISOPTERA Brullé, 1832

[Wespena Brullé, 1832, p. 66]

Wings membranous, usually very similar, held flat over abdomen at rest, and possessing a transverse humeral or basal suture; veins in anterior part of wings more strongly sclerotized than in remainder; crossveins very weakly developed, commonly forming delicate reticulation covering all or greater part of wing surface; vein C marginal; SC simple or branched, in some species very short or
completely absent as distinct vein; radial system usually consisting of distinct R of variable length, equally distinct RS1+2 arising from R very near base of wing, and more highly developed RS3+4 arising about at origin of RS1+2 and forming a series of branches extending to apical or subapical region of wing (with much variation in degree of development of these radial veins); M weak but often extensively branched, no indication of division into MA and MP; CUA also weak, tending to be extensively branched along posterior margin; CUP usually weak and commonly short; anal fold formed along CUP in some; 1A usually short and reduced. Mouthparts mandibulate; antennae moniliform; cerci distinct in all castes. All species social and polymorphic, their communities composed of reproductive forms and numerous workers and soldiers. Cret.–Holo.

The Isoptera, commonly known as termites, are clearly related to the orthopteroids and show closest affinities with the Blattodea (McKittrick, 1964, 1965). The known range of the existing family Mastotermitidae, universally regarded as the most primitive family, is only from the late Oligocene or early Miocene. The earliest records of the order, however, consist of two genera from the Cretaceous (Emerson, 1967; Jarzembowski, 1981). Both belong to the existing family Hodotermitidae, which, although less specialized than the Termitidae, is distinctly more advanced than the Mastotermitidae with respect to both morphology and social behavior. It seems almost certain, therefore, that some species closely related to the Mastotermitidae will eventually be found in Jurassic or even Triassic deposits.

The brief geological record of the Mastotermitidae is, in fact, of much significance. The family includes only one living species, Mastotermes darwiniensis, restricted to tropical Australia. The Tertiary record of the family, however, contains representatives from all other continents except Africa, suggesting a wide dispersal during the Mesozoic (Emerson, 1965). Also, the presence of specimens of all castes in mid-Tertiary amber from Mexico shows that by that time the family had achieved as complicated a social structure as now exists in M. darwiniensis (Krishna & Emerson, 1983).

That some degree of social behavior was present among the Isoptera as far back as the Cretaceous is also apparent. In all existing termites the main part of the wing is separated from its base by a line of fracture, the humeral or basal suture (Fig. 81, Cretatermes; see also Fig. 82,2a, Mastotermes, and Fig. 83,7a, Proelectrotermes); shortly after the adult’s flight from the parent colony, the
wings break off at the suture, leaving a stub or scale. The dropping of the wings after nuptial flight is obviously related to the founding of a new colony, the wings no longer being useful. The presence of humeral sutures in the Cretaceous specimens is therefore convincing evidence that colony founding had already been developed in the family Hodotermitidae by the Early Cretaceous.

Five of the six families of Isoptera generally recognized (EMERSON & KRISHNA, 1975) have records extending at least into the Tertiary: the Mastotermitidae and Kalotermitidae from the Eocene, the Hodotermitidae from the Cretaceous, the Rhinotermitidae from the Oligocene, and the Termitidae from the Miocene. The family Serritermitidae, which is based on a single genus, has no known geological record.

In the course of their evolution the Isoptera have tended toward a secondarily homonomous condition of the wings. The primitive hind wing of the Mastotermitidae has a small but distinct anal lobe, which does not occur in any other family. In general, also, the tendency has been for reduction of the wing veins, with R and SC losing their identity as the anterior veins become compressed toward the anterior margin. These are relatively minor changes, however, in comparison with the differentiation of castes and the development of social behavior, which reach extraordinary levels of complexity in the Termitidae.

The Isoptera is one of the very few orders of insects of which the extinct forms have received careful study by specialists on recent species. SNYDER’s catalogue of the Isoptera of the world, including the extinct species (1949); EMERSON’s review of the Termopsisinae (1933), his account of the geographic origins of termite genera (1955), and his reviews of the Mastotermitidae (1965), Kalotermitidae (1969), and Rhinotermitidae (1971); and KRISHNA’s earlier revisional study of the Kalotermitidae (1961) and his joint paper with EMERSON on Mastotermitidae (1983) cover almost completely the record of the fossil Isoptera.

## Family MASTOTERMITIDAE
Desneux, 1904

(Hodotermitidae Desneux, 1904a, p. 284)

Hind wing with distinct anal lobe; tarsi clearly with 5 segments; left mandible with 2 marginal teeth. EMERSON, 1965. Eoc.—Holo.


### Blattotermitidae Riek, 1952b, p. 17 [*B. neoxenus*; OD]. Similar to Mastotermitidae but with less consolidation of R.S. COLLINS, 1925; EMERSON, 1965. Eoc., Australia (Queensland); Eoc., USA (Tennessee). — Fig. 82,3a. *B. neoxenus*, Eoc., Australia; fore wing, X2.4 (Riek, 1952a). — Fig. 82,3b. *B. wheeleri* (COLLINS), Eoc., Tennessee; wing, X2.0 (Collins, 1925).

### Miotermitidae von Rosen, 1913, p. 325 [*M. procerus* Heer; OD]. Wing venation as in Mastotermitidae but with more extensively developed M. {Family assignment doubtful.} Mio., Europe (Germany, Yugoslavia). — Fig. 82,1. *M. procerus* (Heer); hind wing, X1.8 (Pongrácz, 1926).

### Spargotermitidae EMERSON, 1965, p. 19 [*S. costalimai* OD]. Hind wings: RS diffuse, with several main branches forking to form additional branches reaching to wing tip. Mio./Plio., Brazil. — Fig. 82,4. *S. costalimai*; hind wing with anal area folded under rest of wing, X3.4 (Emerson, 1965).

## Family KALOTERMITIDAE
Froggatt, 1896

(Kalotermitidae Froggatt, 1896, p. 516)

Wing membrane reticulate; vein R short and almost always unbranched; pronotum as wide as head or nearly so; 4 tarsal segments.


### Electrotermitidae von Rosen, 1913, p. 331 [*Termes*}
Hexapoda


Proelecrottermes von Rosen, 1913, p. 331 [*Kalotermes berendtii Pictet in Pictet & Hagen, 1856, p. 49; OD]. Similar to Kalotermes, but middle tibiae with a single inner-lateral spine and 2 outer-lateral spines; fore wing with a very short SC; branches of RS directed anteriorly and terminating on anterior margin; M slightly nearer to RS than to CU at midwing. Scudder, 1883a; Krishna, 1961; Emerson, 1969. Oligo., Europe (Baltic).—Fig. 83,7. *P. berendtii (Pictet); a, fore wing as preserved, X5.5; b, right middle leg, X6.0 (both Krishna, 1961).

Prokatalotermes Emerson, 1933, p. 189 [*Paratermes hageni Scudder, 1883a, p. 139; OD]. Similar to Proelecrottermes but with 24 to 26 antennal segments. Emerson, 1969; Lewis, 1977a. Oligo., USA (Colorado, Montana).

Family HODOTERMITIDAE

Desneux, 1904

[Hodotermididae Desneux, 1904b, p. 14]

Wings with vein CU well developed; short anal vein present in hind wing; ocelli absent; left mandible with 3 marginal teeth; pronotum usually much narrower than head; tarsi with 4 segments. Cret.—Holo.

Hodotermes Hagen, 1853, p. 480. Holo.


Cretatermes Emerson, 1967, p. 284 [*C. car penteri; OD]. Fore wing small, humeral suture evenly curved; RS area gradually widened from base to apical quarter of wing; M about midway between RS and CU; CU short, not reaching beyond basal half of posterior margin of wing. Cret., Canada (Labrador).—Fig. 81. *C. car penteri; holotype, X16.5 (Carpenter, new).—Fig. 83,5. *C. car penteri; venation of fore wing, X8.0 (Emerson, 1967).

Parotermes Scudder, 1883a, p. 135 [*P. insignis; OD]. Second marginal tooth of left mandible slightly shorter than first marginal tooth; posterior edge of second marginal tooth and anterior edge of third marginal tooth not symmetrical. Oligo., USA (Colorado).—Fig. 83,4. *P. insignis; outline of left mandible, X26 (Emerson, 1933).

Termopsis Heer, 1849, p. 23 [*T. bremii; SD Hagen, 1858c, p. 74] [=Xestotermopsis von Rosen, 1913, p. 330, obj.]. Similar to Zosterotermopsis but having 5 hind tarsal segments visible above and below; humeral suture in fore wing only slightly curved. Emerson, 1933. Oligo,
Europe (Baltic).—Fig. 83,3. *T. bremii; hind tarsus, X7 (Emerson, 1933).

Ulmeriella MEUNIER, 1920a, p. 728 [*U. bauckhorni; OD] [=Diatermes MARTYNOV, 1929, p. 178 (type, D. cockerelli)]. Vein RS with several branches directed posteriorly and terminating on hind margin. MARTYNOV, 1929; ZEUNER, 1938; STATZ, 1939–1940; SNYDER, 1949; WEIDNER, 1967, 1968b, 1971; EMERSON, 1968. Oligo., Europe (Germany), USSR (Kazakh); Mio., Europe (Germany), USA (Washington); Plio., Europe (Germany).—Fig. 83,1. *U. bauckhorni; a, base of fore wing, X8; b, distal half of fore wing, X6 (both Emerson, 1968).

Valditermes JARZEMBOWSKI, 1981, p. 92 [*V. brenanae; OD]. Similar to Cretotermes but larger; fore wing more elongate; branching of RS and CU more complex. Cret., England.—Fig. 83,2. *V. brenanae; fore wing, X5.5 (Jarzembowski, 1981).

Zootermopsis EMERSON, 1933, p. 182. [Generic assignment doubtful.] SCUDDER, 1890. Oligo., USA (Colorado)—Holo.

**Family RHINOTERMITIDAE**

Froggatt, 1896

[Rhinotermitidae Froggatt, 1896, p. 518]

Wings commonly reticulate; vein R much reduced; RS unbranched; M usually approaching very close to CU or coalesced with it; frontal gland always present; left mandible with 3 marginal teeth; ocelli present; tarsi with 4 segments, cerci with 2. Oligo.—Holo.
Rhinotermes Hagen, 1858, p. 233. Holo.


Parastylotermes Snyder & Emerson in Snyder, 1949, p. 378 [*Stylotermes washingtonensis Snyder, 1931, p. 317; OD]. Similar to Reticulitermes, but wing membrane and veins almost without hairs; eyes relatively larger than in Reticulitermes; ocelli distinct; stump of fore wing (basal scale) proportionately large. Snyder, 1950, 1955; Pierce, 1958. Oligo., Europe (Baltic); Mio., USA (Washington, California).

Reticulitermes Holmgren, 1913, p. 60. Armbruster, 1941; Weidner, 1955, 1971; Pierce, 1958; Emerson, 1971. Oligo., Europe (Baltic, Germany), USA (Colorado); Mio., USA (California); Europe (Germany); Plio., Europe (Germany)—Holo.


Family TERMITIDAE
Westwood, 1840

[Weteridae Westwood, 1840, p. 11]

Wings not conspicuously reticulate; vein R greatly reduced or absent; left mandible usually with 2 marginal teeth; frontal gland well developed; basal scale of fore wing always proportionately small. Mio.—Holo.


Family UNCERTAIN

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

Architermes Haupt, 1956, p. 28 [*A. simplex; OD]. Little-known wing. Eoc., Europe (Germany).


Order MANTEODEA
Burmeister, 1838

[Manteoidea Burmeister, 1838 in Burmeister, 1838–1839, p. 517, as Manteoidea]

Fore wings usually regminous, strongly so in most, more rarely membranous; costa marginal, no precostal space; vein SC distinct, long, extending well beyond midwing; R strongly developed, terminating nearly at wing apex; RS arising distally, consisting of 1 or several distal branches, or commonly absent as distinct vein; M well developed, typically dividing near base into 2 main branches, which may represent MA and MP (Sharov, 1962a); CUA apparently anastomosed with stem of posterior branch of M; CUP separating from CUA at wing base, nearly straight, unbranched; anal veins at least slightly sigmoidal; posterior part of anal area commonly expanded to form small, prominent lobe containing distal parts of several anal veins. Hind wings with slender remigium, anal area greatly expanded; RS unbranched, arising near wing base; M fused basally with stem of R; MP apparently diverging from R and anastomosing with CUA; MA continuing nearly straight, unbranched; CUA extensively developed, with several branches; CUP and 1A unbranched, nearly straight; several radiating anal veins. Antennae of moderate length, multisegmented; mouthparts mandibulate; forelegs raptorial, others cursorial; tarsi typically with 5 segments; pronotum not usually extending over head; propororax commonly (but not invariably) elongate, forelegs attached near anterior end; ovipositor not usually developed externally but rarely protruding slightly; cerci usually conspicuous, multisegmented. Oligo.—Holo.

The Manteoidea, although clearly related to the Orthoptera, are less specialized in some respects (e.g., five-segmented tarsi, segmented cerci). In all probability they are even more closely related to the Blattaria (Mikitrick, 1964, 1965) but appear to have been derived independently from a protorthopterous stock and to have evolved.
entirely as predators; the raptorial forelegs, present in all known species, show several types of modification. Although the oldest known Manteodea are from the Baltic amber (Oligocene), the group probably existed in the Mesozoic and even in the Permian. Some of the Late Carboniferous Protorthoptera are known to have possessed raptorial forelegs, but they do not appear to be related closely to the Manteodea.

The venation of the Manteodea is clearly orthopteroid but is characterized by such distinct features as the differences in RS in the fore and hind wings and the apparent anastomosis of MP and CUA in both wings. Convexities and concavities, as in the Orthoptera, are not distinct for all veins. Veins SC and CUP are markedly concave and R and CUA similarly convex; RS and M show no definite topography. That both MA and MP are present in the hind wing is suggested by the basal separation of veins that appear to be main branches of M, although other interpretations of these branches are possible. The evidence for the presence of MP in the fore wing is virtually nonexistent in the Manteodea and rests upon the similarity of that part of the fore wing to the corresponding part of the hind wing.

Family CHAETESSIIDAE
Handlirsch, 1920

Fore wing having vein R with several distinct, anteriorly pectinate branches distally; fore tarsus attached to distal end of tibia; tibia lacking terminal projecting hook. Oligo.—Holo.


Lithophotina Cockerell, 1908s, p. 343 [*L. flacca; OD]. Similar to Chaeteessa (recent) but with more pectinate branches on R in fore wing. Sharov, 1962a. Oligo., USA (Colorado).—Fig. 84. *L. flacca; a, fore wing and b, remigium of hind wing, ×2.5 (Cockerell, 1908s).

Family MANTEIDAE Saussure, 1859

["Mantidae SAUSAUER, 1859, p. 59")

Fore wing having R with 2 or fewer anteriorly pectinate branches distally; fore tibia extending beyond point of tarsal attachment, forming curved, projecting hook. Oligo.—Holo.


Eobruneria Cockerell, 1913b, p. 343 [*E. tesselata; OD]. Little-known genus, based on fragment of fore wing with broad costal area. [Possibly related to Stagmomantis (recent).] Oligo., USA (Colorado).

Order PROTELYTROPTERA
Tillyard, 1931

[Proelyrroptera TILLYARD, 1931, p. 234] [=Protocoleoptera TILLYARD, 1924b, p. 434]

Small to medium-sized insects, related to the orthopteroids. Head small, eyes conspicuous; antennae prominent, moderately long, stout, multisegmented; pronotum broad, flattened, commonly with microtrichia laterally; legs robust, spiny, with 5 tarsal segments. Fore wings typically forming convex elytra (only rarely flat) with distinct venation in primitive forms and weak venation in specialized species; costal area expanded at base of wing, forming prominent, flattened lobe (costal expansion); veins SC, R, RS, M, CUA, CUP, and 3 anal veins present in more generalized forms; in more specialized species only basal parts of SC, RS, and CUP discernible; most species with submarginal thickening (sutural margin) parallel to pos-