

[**Palaeodictyopteron* (collective group) *bigginsi* HANDLIRSCH, 1906b, p. 125; OD]. Little-known genus, based on small basal fragment of wing. [Originally placed in the Palaeodictyoptera, *incertae sedis*.] BOLTON, 1921, 1934. *U. Carb.*, England.

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

Titanoptera BRONGNIART, 1893, p. 379 [**T. maculata*; OD]. Little-known genus, based on small fragment of wing; probably a palaeodictyopteron. HANDLIRSCH, 1906b; LAMEERE, 1917b. *U. Carb.*, Europe (France).

Triadologus RIEK, 1976b, p. 793 [**T. biseriatatus*; OD]. Little-known genus, based on small fragment of wing. [Placed in the Protodonata by RIEK (1976b) and in the Odonata by PRITYKINA (1981).] *Trias.*, South Africa.

Wulasua T'AN, 1980, p. 159 [**W. maculata*; OD]. Little-known genus, based on a poorly preserved, small fragment of a wing. [Originally placed in the Diaphanopteroidea.] *Perm.*, China (Inner Mongolia).

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

Infraclass NEOPTERA

Martynov, 1923

[Neoptera MARTYNOV, 1923, p. 89]

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

This infraclass has been the predominant one since the Permian. It includes 25 existing

orders and about 98 percent of the existing species of insects.

Division EXOPTERYGOTA

Sharp, 1899

[Exopterygota SHARP, 1899, p. 247]

Immature stages typically resembling the adults in general form, living in the same kind of environments, and having similar feeding habits; metamorphosis to adults gradual, wings developing within an externally visible cuticular sheath; pupal stage absent. *U. Carb.—Holo.*

Fifteen existing orders are generally recognized in this division, including about 11 percent of the existing species of insects. The orders are usually grouped into two categories, the orthopteroids and the hemipteroids, which have basic structural differences and which appear to represent two distinct lines of exopterygote evolution, although there is some doubt that either one is monophyletic (RICHARDS & DAVIES, 1977; I. M. MACKERRAS, 1970). The orthopteroids have mandibulate mouthparts; the fore wings are commonly tegminous or rarely elytrid; the hind wings commonly have a large fan-shaped anal area; cerci are present and are commonly well developed. These insects are known from the Upper Carboniferous to the present. Four very small, existing orders (Grylloblattodea, Zoraptera, Mallophaga, and Anoplura) belonging here are the only existing orders of insects absent from the geological record. They are discussed briefly below, within the Exopterygota.

The hemipteroids have haustellate mouthparts and feed on liquid food; the fore wings are diverse in structure, membranous or modified to hemelytra or elytra. The hind wings are broad, commonly with an anal fan in the more primitive families, but are small or very small in the more specialized families. Cerci are absent. These orders are known from the Permian to the present.

ORTHOPTEROID EXOPTERYGOTES

Order PERLARIA Latreille, 1802

[*nom. transl.* HANDLIRSCH, 1903, p. 733, *ex* Perlariae LATREILLE, 1802a, p. 292] [=Plecoptera BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 863] [Although the name Plecoptera is often used for this order, it has the distinct disadvantage of being easily confused with the ordinal name Plecoptera, occasionally used for mayflies. Perlaria is the older name.]

Fore wing membranous; costa marginal; vein SC usually extending to about midwing, rarely beyond, terminating on costa but connected distally to R; costal veinlets commonly few, even absent; R with several oblique veinlets leading to wing margin; RS arising at or before midwing, commonly near base, with 3 or 4 branches; M apparently dividing into MA and MP very near wing base; MA forked; MP obliquely or transversely directed toward CUA and anastomosed with it; MP+CUA with at least 2 terminal branches; CUA diverging from CUP near wing base; CUP, 1A, and 2A unbranched. Hind wing typically with expanded and folded anal area, reduced or absent in a few specialized genera; RS arising at or near wing base; M coalesced with base of RS; MA forked; MP diverging toward and anastomosing with CUA; MP+CUA and also CUP unbranched; anal veins varying in number and degree of development; crossveins usually few, highly variable, and in many genera restricted to certain areas of wing. Wings at rest held flat, not slanted, over abdomen. Mouthparts mandibulate, weak in recent species; antennae setaceous, long; body weakly sclerotized; cerci usually well developed, with numerous segments; ovipositor absent or vestigial. Nymphs similar to adults in general form but aquatic; tracheal gills on thorax, coxae, or other parts of body, including sides of abdominal segments (Eustheniidae). *Perm.—Holo.*

Difference of opinion exists about the homologies of some wing veins. The media (M) appears to be represented by a forked vein that has been generally interpreted as

MA (HANDLIRSCH, 1906b, 1907, 1908a; ROHDENDORF, 1962a). SHAROV (1961b) concluded that MP is actually present at the wing base, diverging from MA and coalescing with CUA, as in certain families of Protorthoptera. The free, diverging part of MP is apparently more distinct in the hind wing than in the fore. This interpretation of MA, MP, and CUA is followed here.

The existing Perlaria are usually divided into several suborders, but opinions differ about the number of these and the structural bases for the divisions (cf. ILLIES, 1965, and RASNITSYN, 1980d). However, since almost none of the fossil specimens shows the morphological features used in the subordinal classification, these groups are omitted from the following account.

The recognition of two Permian genera, *Stenoperlidium* and *Palaeotaeniopteryx*, as members of living families (Eustheniidae and Taeniopterygidae, respectively) is necessarily dubious. Only part of the fore wings and none of the hind wings are known for *Stenoperlidium*; the fore wings and part of the hind are known for *Palaeotaeniopteryx* but not the anal area of the hind wing. Nevertheless, the geological record as now known suggests that the stone flies were well established at the ordinal level before the end of the Paleozoic Era and that relatively few modifications, such as the reduction of the anal area of the hind wing and of crossveins, have taken place in the adults subsequently.

Family PALAEOPERLIDAE Sharov, 1961

[Palaeoperlidae SHAROV, 1961e, p. 227]

Costal area of fore wing with 4 or 5 veinlets; 3 or 4 veinlets from vein R to margin; free basal piece of MA slightly oblique; MP+CUA with 3 terminal branches; anal area narrow. Hind wing and body unknown. *Perm.*

Palaeoperla SHAROV, 1961e, p. 227 [**P. exacta*; OD]. RS with 3 or 4 branches; crossveins numer-

ous between MA and MP+CUA, few elsewhere. *Perm.*, USSR (Asian RSFSR).—FIG. 55,2a. **P. exacta*; fore wing, $\times 5.5$ (Sharov, 1961e). —FIG. 55,2b. *P.(?) prisca* SHAROV; nymph, $\times 9$ (Sharov, 1961e).

Family PERLOPSEIDAE

Martynov, 1940

[*nom. correct.* ROHDENDORF, 1957, p. 81, *pro* Perlopsididae MARTYNOV, 1940, p. 31]

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

Perlopsis MARTYNOV, 1940, p. 31 [**P. flicornis*; OD]. Costal area very narrow; wing widest beyond middle. *Perm.*, USSR (Asian RSFSR).—FIG. 55,1. **P. flicornis*; a, fore wing, $\times 3.2$ (Rohdendorf, 1962a); b, body, $\times 4.0$ (Martynov, 1940).

Family SIBERIOPERLIDAE

Sinitshenkova, 1983

[Siberioperlidae SINITSHENKOVA, 1983, p. 96]

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

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

Family EUSTHENIIDAE Tillyard, 1921

[Eustheniidae TILLYARD, 1921d, p. 35]

Fore wing with few to many veinlets in costal area; vein RS with at least 3 branches; 3 anal veins; crossveins present over most of wing. Hind wing with prominent anal area

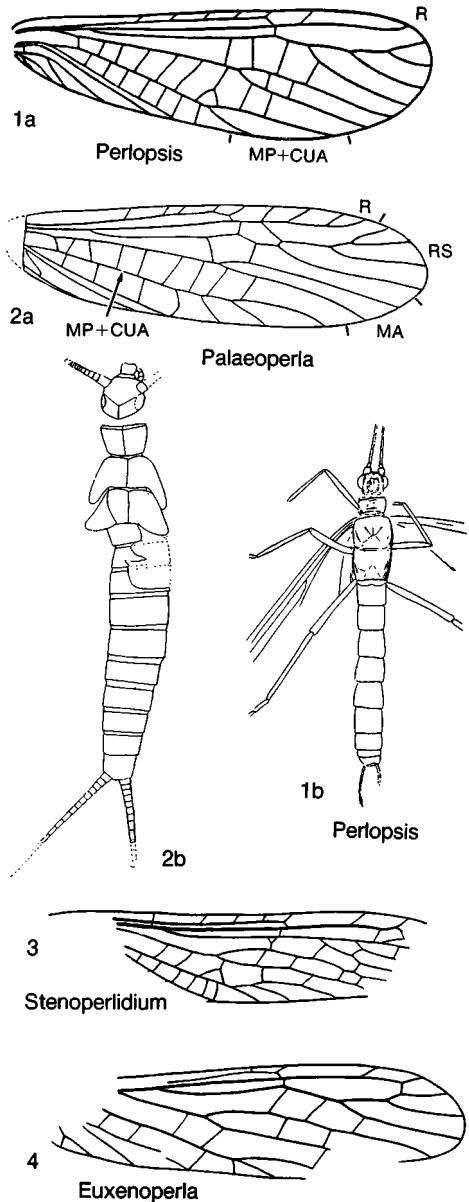


FIG. 55. Palaeoperlidae, Perlopseidae, Eustheniidae, and Uncertain (p. 94–97).

but without marginal indentation at end of CUP. Nymphs with 5 or 6 pairs of lateral abdominal gills. *Perm.*—*Holo.*

Eusthenia WESTWOOD, 1832, p. 348. *Holo.* **Stenoperlidium** TILLYARD, 1935c, p. 386 [**S. permianum*; OD]. Similar to *Stenoperla* (recent) but

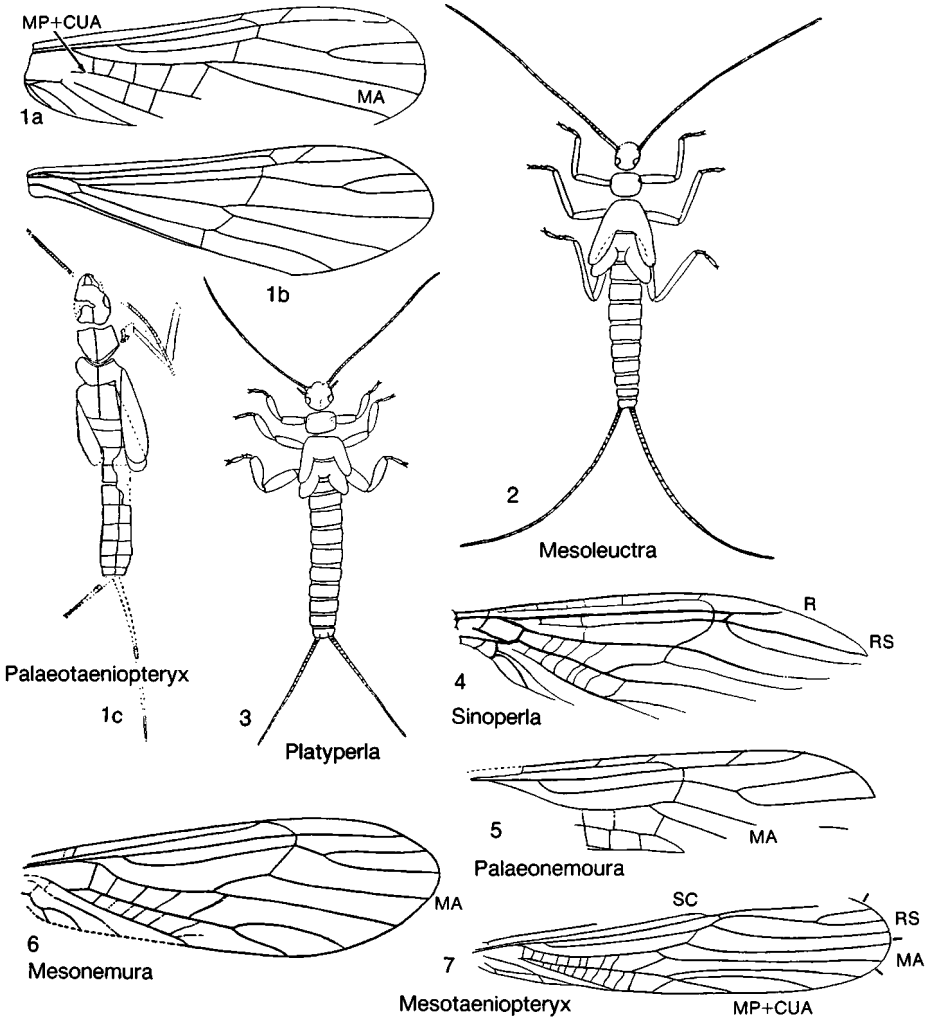


FIG. 56. Taeniopterygidae, Notonemouridae, Platyperlidae, and Perlidae (p. 95-97).

with fewer crossveins and with the broadest part of wing proximal to midwing. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).—FIG. 55,3. **S. permianum*; fore wing, $\times 2$ (Tillyard, 1935c).

Family TAENIOPTERYGIDAE
Klapálek, 1905

[Taeniopterygidae Klapálek, 1905, p. 30]

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

Taeniopteryx PICTET, 1841, p. 343. Adults. HAGEN in PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Brachyptera NEWPORT, 1848, p. 388. ILLIES, 1967a. *Plio.*, Europe (Germany)—*Holo.*

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, $\times 5.5$ (Martynov, 1937a).

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

more numerous between MP+CUA and CUP. *Jur.*, USSR (Tadzhik).—FIG. 56,7. *M. splendida* MARTYNOV; fore wing, $\times 2.5$ (Martynov, 1937a).

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

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

Perlariopsis PING, 1928, p. 31 [**P. peipiaoensis*; OD]. Little-known adult. [Family assignment doubtful.] ILLIES, 1965. *Cret.*, China.

Sinonemoura PING, 1928, p. 24 [**S. grabaui*; OD]. Little-known nymph. [Family position doubtful.] ILLIES, 1965. *Cret.*, China.

Family LEUCTRIDAE Klapálek, 1905

[Leuctridae Klapálek, 1905, p. 32]

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

Leuctra STEPHENS, 1836, p. 144. Adults. PICTET & HAGEN, 1856; COCKERELL, 1922b; ILLIES, 1965; JARZEMBOWSKI, 1980. *Eoc./Oligo.*, England; *Oligo.*, Europe (Germany, Baltic), USA (Colorado)—*Holo.*

Megaleuctra NEAVE, 1934, p. 4. Adult female. RICKER, 1935; ILLIES, 1967b; ZWICK, 1973. *Oligo.*, Europe (Baltic)—*Holo.*

Family NOTONEMOURIDAE

Ricker, 1950

[Notonemouridae RICKER, 1950, p. 201]

Similar to Nemouridae (recent). Adults with vein SC arching toward C. Nymphs small, lacking external gills; cerci multisegmented, almost as long as antennae. ZWICK, 1973. *Jur.*—*Holo.*

Notonemoura TILLYARD, 1923, p. 215. *Holo.*

Mesoleuctra BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 9 [**M. gracilis*; OD]. Nymph: posterior margin of head rounded; basal antennal segment about as wide as long; mandibles slightly longer than wide, with many denticles; femora only slightly shorter and broader than tibiae; pronotum about as long as wide; posterior wing pads slightly broader than the fore pair; cerci

very thin distally; body without hair covering. PING, 1928; ILLIES, 1965; SINITSHENKOVA, 1982. *Jur.*, USSR (Asian RSFSR); *Cret.*, China (Inner Mongolia).—FIG. 56,2. **M. gracilis*; restoration, dorsal view, $\times 2$ (Sinitshenkova, 1982).

Family PERLODIDAE Klapálek, 1912

[Perlodidae Klapálek, 1912, p. 5]

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

Perlodes BANKS, 1903, p. 241. Adult. PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Isoperla BANKS, 1906, p. 175. Adult. PICTET & HAGEN, 1856; ILLIES, 1965. *Oligo.*, Europe (Baltic)—*Holo.*

Family PLATYPERLIDAE

Sinitshenkova, 1982

[Platyperlidae SINITSHENKOVA, 1982, p. 118]

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

Platyperla BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 10 [**P. platypoda*; OD]. Posterior margin of head strongly convex; basal segment of antenna conical; pronotum with prominent posterior angles; posterior margin of terminal abdominal tergite with a short, broad median projection. PING, 1928; SINITSHENKOVA, 1982. *Jur.*, USSR (Asian RSFSR).—FIG. 56,3. **P. platypoda*; restoration of nymph, dorsal view, $\times 2$ (Sinitshenkova, 1982).

Family PERLIDAE Latreille, 1802

[Perlidae LATREILLE, 1802a, p. 292]

Costal area with numerous, short veinlets, those between vein R and margin continuing

series; RS usually with 3 or 4 branches; distal part of MP+CUA curving anteriorly. *Cret.—Holo.*

Perla GEOFFROY, 1762, p. 229. Adult. PICTET & HAGEN, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

Sinoperla PING, 1928, p. 28 [**S. abdominalis*; OD]. Little-known wings, with 2 crossveins between R and RS near end of SC. ILLIES, 1965. *Cret.*, China. —FIG. 56,4. **S. abdominalis*; fore wing, $\times 5.3$ (Ping, 1928).

Family UNCERTAIN

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

Euxenoperla RIEK, 1973, p. 531 [**E. simplex*; OD]. Little-known genus, possibly related to the Gripopterygidae. Vein RS of fore wing arched anteriorly at level of end of SC; RS with 3 or 4 branches; M deeply forked, branching before midwing; few crossveins. *Perm.*, South Africa; *Trias.*, Australia (Queensland). —FIG. 55,4. **E. simplex*, South Africa; fore wing, $\times 2.8$ (Riek, 1973).

Euxenoperlella RIEK, 1976a, p. 770 [**E. jacquesi*; OD]. Similar to *Euxenoperla*, but RS with only 2 branches and M forking more distally. *Perm.*, South Africa.

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

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

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

Uralonympha ZALESSKY, 1939, p. 64 [**U. varica*; OD]. Little-known nymph. CARPENTER, 1969. [Ordinal assignment uncertain.] *Perm.*, USSR (Asian RSFSR); *Jur.*, Antarctica (Ohio Range).

Order PROTORTHOPTERA Handlirsch, 1906

[Protorthoptera HANDLIRSCH, 1906a, p. 695] [=Hadentomoidea HANDLIRSCH, 1906a, p. 692; Hapalopteroidea HANDLIRSCH, 1906a, p. 694; Protoblattoidea HANDLIRSCH, 1906a, p. 704; Reculoidea HANDLIRSCH, 1906b, p. 127; Protoperlaria TULLYARD, 1928b, p. 187; Cnemidolestoidea HANDLIRSCH, 1937, p. 63; Paraplecoptera MARTYNOV, 1938b, p. 98; Strephocladodea MARTYNOV, 1938b, p. 100; Protocicadida HAUPT (in part), 1941, p. 75; Protofulgorida HAUPT (in part), 1941, p. 75] [The ordinal name Protoblattoidea HANDLIRSCH (1906a) was changed to Protoblattoidea by SHAROV (1962a) and has generally been accepted.]

Wings typically containing all main veins, including MA and MP, but without com-

plete alternation of convexities and concavities; MA apparently absent in some families (see below). Main veins usually independent; in some families CUA anastomosed with part of M or MP and CUP; in a few families MA tending to coalesce with branches of RS. Fore and hind wings commonly similar in form and venation, anal area of hind wing rarely expanded to form prominent lobe. Fore wing membranous in more primitive groups, but slightly coriaceous or distinctly coriaceous in others; hair covering usually well developed on membranous wings, reduced or absent on coriaceous wings; prominent setae may be present on certain parts of wings; wing area between veins with archedictyon, resembling that of Palaeodictyoptera, or with coarse network of crossveins or more commonly with regular system of nearly straight crossveins; anal area in many families set off from remigium by strongly concave CUP. Hind wing membranous, venation of remigium usually slightly different from that of fore wing; RS arising nearer wing base, and stems of CUA and M coalesced; CUA much less developed; CUP setting off anal area, which includes several anal veins. Fore wings (and more rarely hind wings) may have conspicuous maculations or prominent cuticular thickenings.

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

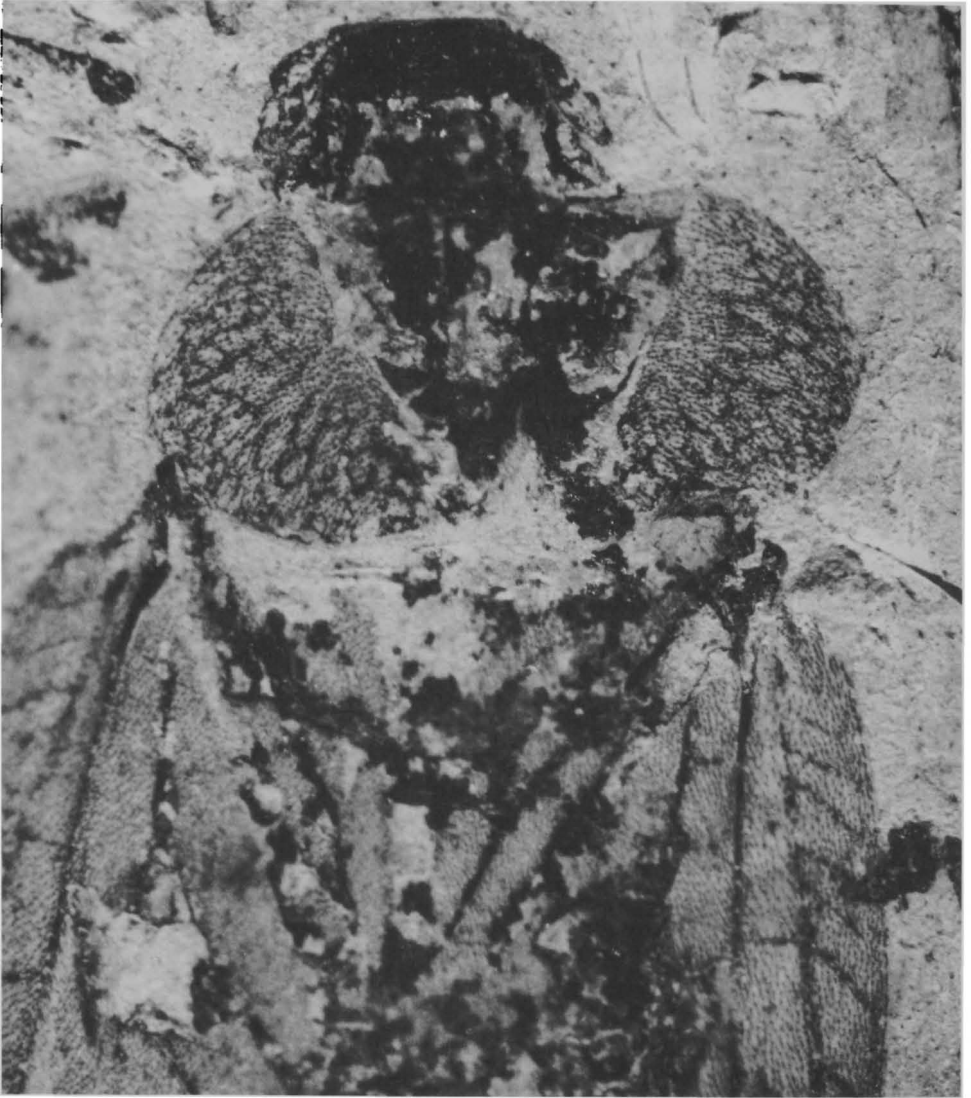


FIG. 57. *Lemmatophora typha* SELLARDS, Lemmatophoridae, Permian of Kansas. Dorsal view of head and anterior portion of thorax, showing the reticulate, pronotal lobes and hair covering. Specimen MCZ 3539, $\times 40$ (Carpenter, new).

Protrembiidae) or modified (e.g., males, Chelopteridae).

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

The extinct order Protorthoptera was named by HANDLIRSCH (1906a, 1906b) for a diverse assemblage of Paleozoic species with presumed orthopteroid affinities. He also named another extinct order, Protoblattodea, for other species that he considered to be intermediate between the Palaeodictyoptera and the Blattodea, Manteodea, and 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 palaeopterous orders the anterior and posterior median veins (MA, MP) are readily recognizable as convex and concave, respectively. That both MA and MP exist in any of the orthopteroids (or in any

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

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

tance with a branch of CUP. In all probability, these specializations of MP, CUA, and CUP, have been developed independently several times within the order. The fore wings commonly bear maculations (see Fig. 61,3, *Lisca*) or more elaborate markings (see Figs. 75 and 76, *Protodiamphipnoa*).

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

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

There are several basic features characteristic of the Protorthoptera in addition to the cursorial legs. The wings at rest, as far as is known, were folded flat over the abdomen, not slanted, as in the Orthoptera. The costal vein of the fore wing was usually marginal basally, but if it were submarginal the subcostal area was small and included only a few veinlets at most, in contrast to the Orthoptera, in which the precostal area tended to be long and replete with veinlets.

As treated here, the order Protorthoptera was almost exclusively Permo-Carboniferous, with most of the genera from the Permian. Two genera, not well known, are from the Triassic: *Tomia* MARTYNOV (family Tomiidae) and *Mesorthopteron* TILLYARD (family uncertain). Both of these are poorly known and may turn out to belong elsewhere.

Family HOMOEODICTYIDAE Martynov, 1937

[Homoeodictyidae MARTYNOV, 1937b, p. 26]

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

Homoeodictyon MARTYNOV, 1937b, p. 26 [**H. elongatum*; OD]. Fore wing with broad costal area, traversed by several distinct veinlets, and with archedictyon. *Perm.*, USSR (European RSFSR).—FIG. 58,5. **H. elongatum*; fore wing, $\times 1$ (Martynov, 1937b).

Family THORONYSIDIDAE Handlirsch, 1919

[Thoronyssididae HANDLIRSCH, 1919b, p. 544]

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

Thoronysis HANDLIRSCH, 1906b, p. 139 [**Oedischbia ingbertensis* VON AMMON, 1903, p. 282; OD]. Fore wing with SC terminating on R near wing apex; M forking before midwing and after origin of RS. GUTHÖRL, 1934. *U. Carb.*, Europe (Germany).—FIG. 58,11. **T. ingbertensis* (VON AMMON); fore wing, $\times 0.9$ (Guthörl, 1934).

Family PAOLIIDAE Handlirsch, 1906

[Paoliidae HANDLIRSCH, 1906a, p. 682]

Fore wing oval, slender, with broad costal area; fine network, resembling archedictyon, over entire wing; veinlets also present in costal area and some other parts of wing; vein SC terminating (usually on R) in distal fourth of wing; RS arising proximally of midwing; MA apparently absent; MP (concave) well developed; CU dividing very close to wing

base; CUA branched; anal area weakly set off by marginal indentation at end of CUP. Hind wing triangular, with anal-posterior extension but no anal fan; venation basically as in fore wing. KUKALOVÁ, 1958a. *U. Carb.*

Paolia SMITH, 1871, p. 44 [**P. vetusta*; OD]. Hind wing with MP dividing before midwing but distally of origin of RS; proximal part of wing only slightly broader than distal half. LAURENTIAUX, 1950; KUKALOVÁ, 1958a. *U. Carb.*, USA (Indiana), Europe (The Netherlands).—FIG. 58,3. **P. vetusta*, Indiana; hind wing, $\times 8$ (Smith, 1871).

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, $\times 1.4$ (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, $\times 1.5$ (Kukalová, 1958a).

Paoliola HANDLIRSCH, 1919b, p. 533 [**P. gurleyi*; OD]. Hind wing similar to that of *Paolia* but with MP forked more deeply. MELANDER, 1903. *U. Carb.*, USA (Indiana).—FIG. 58,10. **P. gurleyi*; hind wing, $\times 1.4$ (Melander, 1903).

Pseudofouquea HANDLIRSCH, 1906b, p. 125 [**Fouquea cambrensis* ALLEN, 1901, p. 68; OD]. Fore wing similar to *Olinka*, but costal space narrower and MP dividing before midwing. LAURENTIAUX, 1950. *U. Carb.*, Wales.—FIG. 58,12. **P. cambrensis* (ALLEN); fore wing, $\times 1$ (Laurentiaux, 1950).

Sustaia KUKALOVÁ, 1958a, p. 946 [**S. impar*; OD]. Little-known fore wing, similar to *Olinka* but much larger; hind wing with branch of MP terminating on apical end of hind margin. *U. Carb.*, Europe (Czechoslovakia).—FIG. 58,7. **S. impar*; *a*, fore and *b*, hind wings, $\times 0.4$ (Kukalová, 1958a).

Zdenekia KUKALOVÁ, 1958a, p. 937 [**Z. grandis*; OD]. Fore wing broader than in *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, $\times 1$; *b*, hind wing, $\times 0.8$ (both Kukalová, 1958a).

Family STYGNIDAE Handlirsch, 1906

[Stygnidae HANDLIRSCH, 1906b, p. 115]

Related to Paoliidae, but crossveins distinct, though irregular, and vein MP less developed. *U. Carb.*

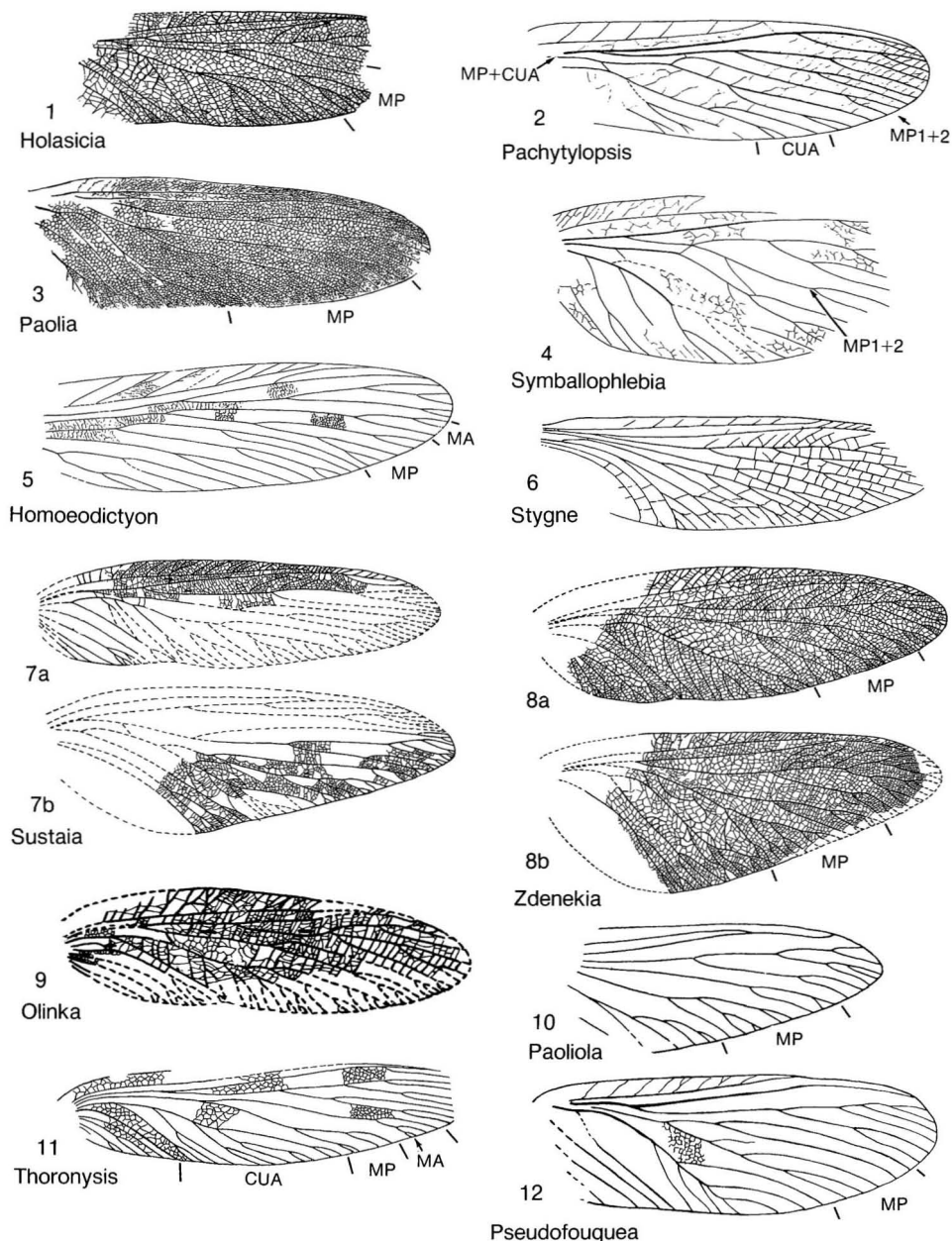


FIG. 58. Homoeodictyidae, Thoronyssididae, Paoliidae, Stygnidae, and Pachytylopsidae (p. 101–103).

Stygne HANDLIRSCH, 1906b, p. 115 [**S. roemeri*; ODJ]. Fore wing with narrow costal area; RS arising very close to base of wing, its first branch at about midwing. SCHWARZBACH, 1939. *U. Carb.*, Poland (Upper Silesia).—FIG. 58,6. **S. roemeri*; fore wing, $\times 2.2$ (Handlirsch, 1906b).

Family HAPALOPTERIDAE Handlirsch, 1906

[Hapalopteridae HANDLIRSCH, 1906b, p. 304]

Fore wing similar to that of *Cacurgidae* but with fewer branches of main veins; vein

CUP forking further from wing base; cuticular spots absent from wings. *U. Carb.*

Haploptera HANDLIRSCH, 1906a, p. 694 [**H. gracilis*; OD]. Fore wing with SC extending nearly to wing apex; costal veinlets unbranched; RS with 4 branches; MP forked to about midwing; CUA with terminal fork only; crossveins numerous, weakly formed. CARPENTER, 1965. *U. Carb.*, USA (Pennsylvania).—FIG. 59,1. **H. gracilis*; fore wing, $\times 4$ (Carpenter, 1965).

Family PACHYTYLOPSIDAE

Handlirsch, 1906

[Pachytylopsidae HANDLIRSCH, 1906b, p. 138] [=Anthraconeuridae LAURENTIAUX & LAURENTIAUX-VIEIRA, 1980, p. 407]

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

Pachytylopsis BORRE, 1875a, p. xl [**P. persenairei*; SD BORRE, 1875b, p. lvi] [=Palorthopteron HANDLIRSCH, 1904a, p. 3 (type, *P. melas*)]. Costal area of moderate width; MP1+2 directed anteriorly shortly after its separation from CUA1 and connected to RS by a short but stout crossvein; R with several terminal branches. HANDLIRSCH, 1906b; PRUVOST, 1930, 1933b; LAURENTIAUX & LAURENTIAUX-VIEIRA, 1981. *U. Carb.*, Europe (Belgium).—FIG. 58,2. **P. persenairei*; fore wing, $\times 1.4$ (Handlirsch, 1904a).

Anthraconeura LAURENTIAUX & LAURENTIAUX-VIEIRA, 1980, p. 407 [**A. silvatica*; OD]. Similar to *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).

Symbalophlebia 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, $\times 1.2$ (Pruvost, 1930).

Family BLATTINOPSIDAE

Bolton, 1925

[Blattinopsidae BOLTON, 1925, p. 23] [=Oryctoblattinidae HANDLIRSCH, 1906b, p. 155]

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

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

Blattinopsis GIEBEL, 1867, p. 417 [**Blattina reticulata* GERMAR, 1851 in GERMAR, 1844–1853, p. 87; OD] [=Oryctoblattina SCUDDER, 1879b, p. 122, obj.; *Protociccus* BRONGNIART, 1885a, p. 67, nom. nud.; *Prisca* K. W. FRITSCH, 1900, p. 45 (type, *P. wittinensis*); *Oryctomylabris* HANDLIRSCH, 1906b, p. 346 (type, *Oryctoblattina oblonga* DEICHMÜLLER, 1882, p. 41); *Pseudofulgora* HANDLIRSCH, 1906b, p. 357 (type, *Fulgora ebersi* DOHRN, 1867, p. 131); *Blattinopsiella* MEUNIER, 1907, p. 523 (type, *B. pygmaea*); *Anadymenella* STRAND, 1929, p. 19, nom. subst. pro *Anadymene* K. W. FRITSCH, 1900, p. 45, non GISTEL, 1848 (type, *A. huyseni*); *Palaeorincanites* HAUPT, 1941, p. 90 (type, *Blattinopsis anthracina* HANDLIRSCH,

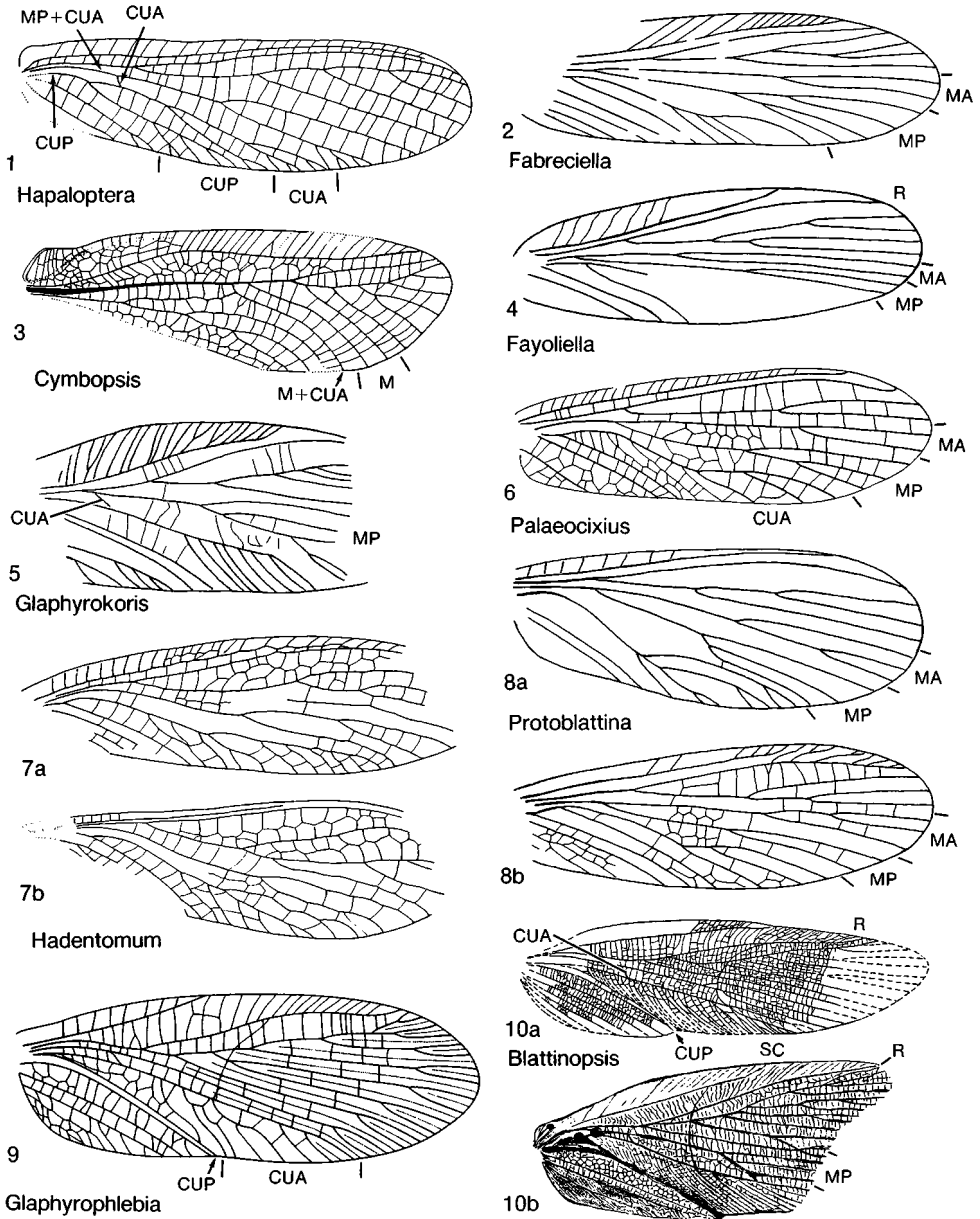


FIG. 59. Haplopteridae, Blattinopsidae, Cymbopsidae, and Hadentomidae (p. 103–106).

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

wing, $\times 2$ (Kukalová, 1959b).—FIG. 59,10b. **B. reticulata* (GERMAR), *U. Carb.*, Germany; fore wing, $\times 2$ (Schlectendal, 1913). Glaphyrokoris RICHARDSON, 1956, p. 38 [**G. mirandus*; OD]. Similar to *Glaphyrophlebia* but with SC and R longer. *U. Carb.*, USA (Illinois).—FIG. 59,5. **G. mirandus*; fore wing as preserved; $\times 2.6$ (Richardson, 1956).

Glaphyrophlebia HANDLIRSCH, 1906a, p. 707 [**G. pusilla*; OD] [= *Pursa* SELLARDS, 1909, p. 153 (type, *P. ovata*); *Sindon* SELLARDS, 1909, p. 154 (type, *S. speciosa*)]. Similar to Blattinopsis but with 2 rows of cells proximally between CUA and CUP. BOLTON, 1934; KUKALOVÁ, 1965; CARPENTER, 1966. *U. Carb.*, USA (Pennsylvania), Wales; *Perm.*, USA (Kansas), Europe (Czechoslovakia).—FIG. 59,9. *G. speciosa*, (SELLARDS), *Perm.*, Kansas; fore wing, $\times 7$ (Carpenter, 1966).

Protoblattiniella MEUNIER, 1912d, p. 1194 [**P. minutissima*; OD]. Little-known genus, based on fragment of nymph. [Family assignment doubtful.] LAURENTIAUX, 1959b. *U. Carb.*, Europe (France).

Family CYMBOPSIDAE Kukalová, 1965

[Cymbopsidae KUKALOVÁ, 1965, p. 86]

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

Cymbopsis KUKALOVÁ, 1965, p. 86 [**C. excelsa*; OD]. SC sigmoidally curved; crossveins reticulate only in basal costal area and in area between SC and R + M. *Perm.*, Europe (Czechoslovakia).—FIG. 59,3. **C. excelsa*; fore wing, $\times 5.7$ (Kukalová, 1965).

Family EUCAENIDAE Handlirsch, 1906

[Eucenidae HANDLIRSCH, 1906a, p. 709] [= *Teneopteridae* RICHARDSON, 1956, p. 46]

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

ments with posteriorly directed lateral lobes; cerci very short. Females with a short ovipositor. CARPENTER & RICHARDSON, 1976. *U. Carb.*

Eucaenus SCUDDER, 1885d, p. 325 [**E. ovalis*; OD] [= *Teneopteron* CARPENTER, 1944, p. 17 (type, *T. mirabile*)]. Fore wing: veinlets of costal area unbranched; RS with branches directed toward wing apex. MELANDER, 1903; HANDLIRSCH, 1922; CARPENTER & RICHARDSON, 1976. *U. Carb.*, USA (Illinois).—FIG. 60. **E. ovalis*; whole insect, $\times 2.8$ (Carpenter & Richardson, 1976).

Family HADENTOMIDAE Handlirsch, 1906

[Hadentomidae HANDLIRSCH, 1906b, p. 303] [= *Fayoliellidae* HANDLIRSCH, 1919b, p. 558; *Palaecixiidae* HANDLIRSCH, 1919b, p. 539]

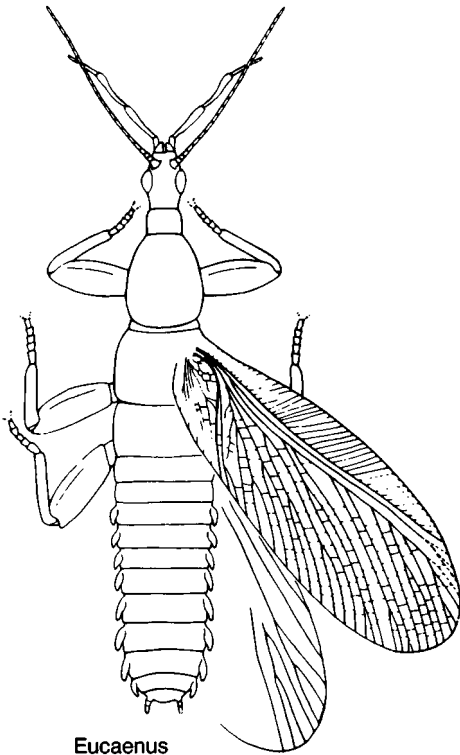
Fore wing with vein SC ending on costal margin well beyond level of midwing; costal area with a series of veinlets, mostly straight; RS arising well before midwing, with 2 to 4 long branches; M forking near or before midwing; CUA with several terminal branches. Hind wing with venation essentially as in fore wing, but costal area much narrower; anal area unknown. [Placed by HANDLIRSCH (1906a) in order Hadentomidea.] CARPENTER, 1965. *U. Carb.*

Hadentomum HANDLIRSCH, 1906a, p. 693 [**H. americanum*; OD]. M forking at about midwing; RS with at least 3 branches in both wings. CARPENTER, 1965. *U. Carb.*, USA (Illinois).—FIG. 59,7. **H. americanum*; a, fore and b, hind wings, $\times 2.4$ (Carpenter, 1965).

Fabreciella CARPENTER, 1934, p. 327 [**F. pennsylvanica*; OD]. Fore wing as in *Palaecixius*, but costal area broader; M with 6 branches, RS with 4. [Family assignment doubtful.] *U. Carb.*, USA (Pennsylvania).—FIG. 59,2. **F. pennsylvanica*; fore wing, $\times 4.2$ (Carpenter, 1934).

Fayoliella MEUNIER, 1908j, p. 247 [**F. elongata*; OD]. Costal area of fore wing broad, with irregular veinlets; RS and M with 4 branches. [Family assignment doubtful.] *U. Carb.*, Europe (France).—FIG. 59,4. **F. elongata*; fore wing, $\times 2.5$ (Carpenter, new).

Palaecixius HANDLIRSCH, 1906b, p. 326 [**P. antiquus*; SD HANDLIRSCH, 1922, p. 74] [= *Palaecixius* BRONGNIART, 1885a, p. 67, *nom. nud.*; *Fabrecia* MEUNIER, 1911a, p. 123 (type, *F. pygmaea*)]. Fore wing with fork of M at about level of origin of RS; RS and MA forking at about same level; RS with 2 branches, M with 5; a few large cells formed in region of M and



Eucanenus

FIG. 60. Eucanidae (p. 105).

in anal area. *U. Carb.*, Europe (France).—FIG. 59,6. **P. antiquus*; fore wing, $\times 4$ (Carpenter, new).

Protoblattina MEUNIER, 1909d, p. 48 [**P. bouvieri*; OD]. Fore wing as in *Palaeocixius*, but RS with 3 branches, M with 6. *U. Carb.*, Europe (France).—FIG. 59,8a. **P. bouvieri*; fore wing, $\times 2.8$ (Carpenter, new).—FIG. 59,8b. *P. giardi* MEUNIER, 1912d; fore wing, $\times 2$ (Carpenter, new).

Family LEMMATOPHORIDAE

Sellards, 1909

[Lemmatophoridae SELLARDS, 1909, p. 162] [=Ortidae SELLARDS, 1909, p. 167; Lecortiidae HANDLIRSCH, 1919b, p. 556]

Fore wing with costal area moderately broad; vein SC terminating on costa at least slightly beyond midwing; R unbranched; MA and MP present, but neither convex nor concave; proximal half of MP obsolete; CUA very strongly developed, usually with 3 branches; CUP obsolete, forming a straight vena divdians; 2 anals present. Hind wing shorter than fore wing but with expanded

anal area, and with at least slight incision of wing margin at end of CUP; R unbranched; MA unbranched and coalesced to variable extent with RS; CUA well developed, CUP obsolete; anal fan with four main veins. Venation highly variable among species. Antennae long, multisegmented; head small, hypognathous; eyes small; prothorax bearing pair of membranous paranota, with reticulated venation and covered with microtrichia; mesonotum and metanotum broad and flat; five tarsomeres; abdomen unspecialized but bearing on the first nine segments small lateral processes resembling vestigial gills; cerci about as long as abdomen; female with very short ovipositor. Nymphs apparently aquatic, with lateral gills on first nine abdominal segments. CARPENTER, 1935a, 1939. *Perm.*

Lemmatophora SELLARDS, 1909, p. 162 [**L. typa*; SD TILLYARD, 1928b, p. 189]. SC terminating just beyond midwing; RS unbranched; hind wing with deep incision at end of CUP. *Perm.*, USA (Kansas).—FIG. 57. **L. typa*; head, prothorax, prothoracic lobes, neotype, $\times 40$ (Carpenter, new).—FIG. 61,1a. **L. typa*; restoration of adult, $\times 2.4$ (Carpenter, 1935a).—FIG. 61,1b. *Lemmatophora* sp. (probably *typa*); nymph, $\times 2.4$ (Carpenter, 1935a).

Artinska SELLARDS, 1909, p. 165 [**A. clara*; SD TILLYARD, 1928e, p. 321] [=*Estadia* SELLARDS, 1909, p. 166 (type, *E. elongata*); *Lectrum* SELLARDS, 1909, p. 167 (type, *L. anomalum*); *Orta* SELLARDS, 1909, p. 168 (type, *O. ovata*)]. SC extending well beyond midwing; RS with at least one fork. *Perm.*, USA (Kansas).—FIG. 62,1. **A. clara*; a, fore wing, $\times 6$ (Carpenter, 1935a); b, hind wing, $\times 6$ (Tillyard, 1928e).

Blania KUKALOVÁ, 1964c, p. 101 [**B. rotunda*; OD]. Fore wing as in *Artinska* but broader and more nearly oval; costal area relatively broad. *Perm.*, Europe (Czechoslovakia).—FIG. 62,4. **B. rotunda*; fore wing, $\times 7.5$ (Kukalová, 1964c).

Lecorium SELLARDS, 1909, p. 167 [**L. elongatum*; OD] [=*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, $\times 6$ (Carpenter, 1935a).

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

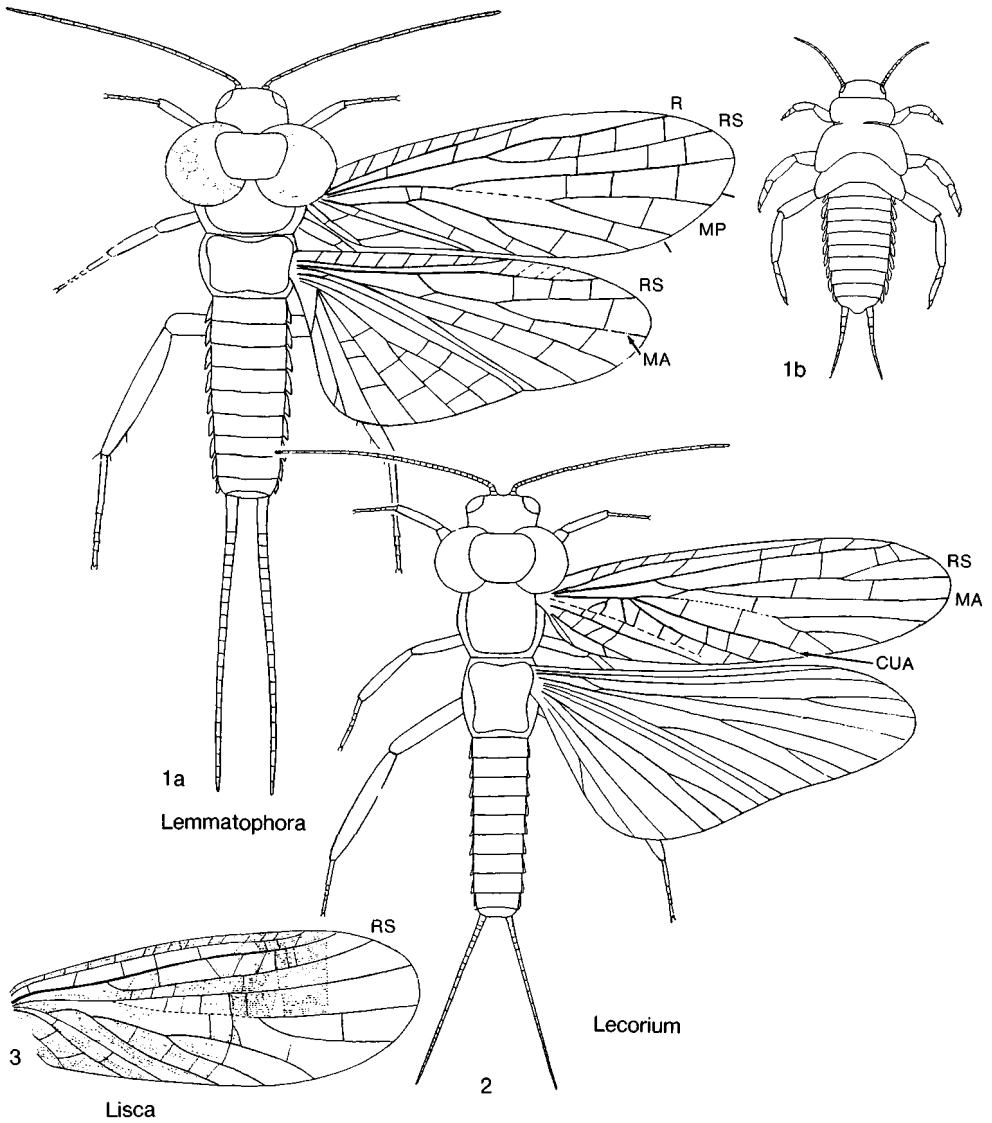


FIG. 61. Lemmatophoridae (p. 106–107).

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

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

Oborella KUKALOVÁ, 1964c, p. 93 [**O. matura*;

OD]. Fore wing as in *Artinska*, but costal area much broader; CU usually anastomosed with M before separating into CUA and CUP. Central disc of pronotum oval. Perm., Europe (Czechoslovakia).

Paraprisca HANDLIRSCH, 1919b, p. 555, *nom. subst. pro Prisca* SELLARDS, 1909, p. 167, *non* K. W. FRITSCH, 1900 [**Prisca fragilis* SELLARDS, 1909, p. 167]. Fore wing more slender than in *Lemmatophora*; R straight; CUA not anastomosed with M; hind wing with only slight incision at

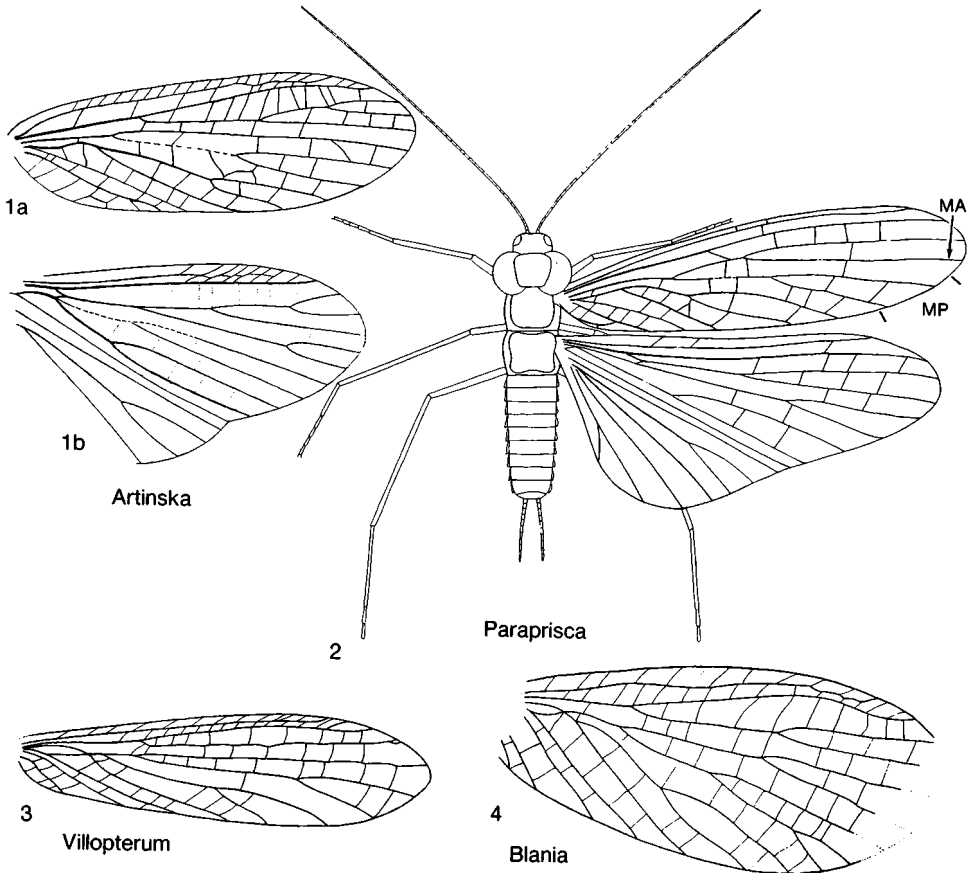


FIG. 62. Lemmatophoridae (p. 106–108).

CUP. Antennae longer and legs much longer than in *Lemmatophora*. ZALESSKY, 1952. *Perm.*, USA (Kansas), USSR (Asian RSFSR).—FIG. 62,2. **P. fragilis* (SELLARDS), Kansas; adult, $\times 6$ (Carpenter, 1935a).

Quecopterum KUKALOVÁ, 1964c, p. 98 [**Q. decusatum*; OD]. Little-known genus. Fore wing as in *Oborella*, but central disc of pronotum irregular in shape. *Perm.*, Europe (Czechoslovakia).

Sharovipterum KUKALOVÁ, 1964c, p. 100 [**S. alatum*; OD]. Little-known genus. Fore wing apparently broadly oval; costal area narrow; RS and MA apparently unbranched. Pronotum subtriangular. *Perm.*, Europe (Czechoslovakia).

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

Villopterum KUKALOVÁ, 1964c, p. 108 [**V. villosum*; OD]. Fore wing as in *Lecorium* but more elongate and slightly broader distally; RS appar-

ently unbranched; CUA1 with a deep fork. *Perm.*, Europe (Czechoslovakia).—FIG. 62,3. **V. villosum*; fore wing, $\times 8$ (Kukalová, 1964c).

Family LIOMOPTERIDAE Sellards, 1909

[Liomopteridae SELLARDS, 1909, p. 157] [=Khosaridae MARTYNOV, 1937b, p. 29]

Fore wing membranous, usually with microtrichia well developed on at least part of wing; vein SC terminating on costa beyond midwing; costal area with numerous, slanted veinlets, not forming regular cells; R extending nearly to wing apex; RS with at least two branches; M forked at about level of origin of RS or slightly toward base; MA and MP not anastomosed with other veins; CUA typically diverging anteriorly shortly after its origin and forking into CUA1 and CUA2;

CUP and 1A unbranched. Hind wing with costal area narrow; R extending nearly to apex; RS arising much nearer base than in fore wing; M and CU fused at base; CUA strong and deeply forked; 1A close to CUP; anal area forming lobe containing numerous anal veins. Antennae long, multisegmented; head hypognathous; eyes prominent; prothorax usually with paranotal expansions continuing anteriorly and posteriorly around pronotum itself; reticulation not visible, but paranotals commonly membranous and covered with microtrichia; legs slender, hind legs longer than others, not modified for jumping; 5 tarsomeres; cerci long. CARPENTER, 1950. *Perm.*

Liomopterum SELLARDS, 1909, p. 157 [**L. ornatum*; SD CARPENTER, 1950, p. 189] [=*Horates* SELLARDS, 1909, p. 158 (type, *H. elongatus*)]. Costal space moderately broad; fork of M proximal to origin of RS; cells (when present) almost exclusively confined to area of CUA and CUP. *Perm.*, USA (Kansas).—FIG. 63,7. **L. ornatum*; adult, $\times 3.5$ (Carpenter, 1950).

Abashevnia SHAROV, 1961d, p. 194 [**A. suchovi*; OD]. Similar to *Parapermula*, but costal area narrower and branches of MA arising pectinately. *Perm.*, USSR (Asian RSFSR).—FIG. 63,3. **A. suchovi*; fore wing, $\times 1.8$ (Sharov, 1961d).

Alicula SCHLECHTENDAL, 1913, pl. 2 [**A. lebachensis*; OD] [= *Permula* HANDLIRSCH, 1919b, p. 542, obj.]. Little-known genus, with fore wing apparently similar to that of *Liomopterum*, but crossveins numerous and forming a fine reticulation; CUA with several additional branches. [HANDLIRSCH (1919b) considered the names *Alicula lebachensis* to be *nomina nuda*, but under article 12, section 7, of the ICZN (p. 35, 1985 ed.) both names are available.] KUKALOVÁ, 1964c. *Perm.*, Europe (Germany, Czechoslovakia).—FIG. 64,1. *A. acra* (KUKALOVÁ); fore wing as preserved, $\times 3$ (after KUKALOVÁ, 1964c).

Cerasopterum KUKALOVÁ, 1964c, p. 60 [**C. gracile*; OD]. Fore wing as in *Tapopterum*, but RS with only 3 branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,4. **C. gracile*; fore wing, $\times 6$ (KUKALOVÁ, 1964c).

Climaconeurites SHAROV, 1961d, p. 195 [**C. asiaticus*; OD]. MA branching dichotomously; anterior branch of MA anastomosed for short distance with RS. *Perm.*, USSR (Asian RSFSR).—FIG. 63,1. **C. asiaticus*; a, fore wing; b, hind wing, $\times 2.6$ (Sharov, 1961d).

Depressopterum KUKALOVÁ, 1964c, p. 48 [**D. senior*; OD]. Little-known genus. Fore wing as in *Parapermula* but more elongate and with less

convex anterior margin. *Perm.*, Europe (Czechoslovakia).—FIG. 64,2. **D. senior*; fore wing as preserved, $\times 4$ (KUKALOVÁ, 1964c).

Donopterum KUKALOVÁ, 1964c, p. 54 [**D. carpenteri*; OD]. Fore wing as in *Turbopterum* but broader; costal area narrower; RS and MA with more branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,5. **D. carpenteri*; fore wing, $\times 2$ (KUKALOVÁ, 1964c).

Drahania KUKALOVÁ, 1964c, p. 51 [**D. avia*; OD]. Similar to *Depressopterum*, but fore wing more slender; CUA with only 2 main branches. *Perm.*, Europe (Czechoslovakia).—FIG. 64,3. **D. avia*; fore wing, $\times 5$ (KUKALOVÁ, 1964c).

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

Ideliopsis CARPENTER, 1948b, p. 101 [**I. ovalis*; OD]. Costal margin only slightly curved; MP coalesced proximally with CUA1. Crossveins numerous, regular; no reticulation in apical part of wing. [Family assignment doubtful.] *Perm.*, USA (Texas).—FIG. 63,4. **I. ovalis*; fore wing, $\times 1.8$ (Carpenter, 1948b).

Kaltanella SHAROV, 1961d, p. 206 [**K. lata*; OD]. Fore wing broadly oval, with almost no cells; MA with 2 main stems arising before level of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 63,8. **K. lata*; a, fore and b, hind wings, $\times 2.6$ (Sharov, 1961d).

Kaltanympha SHAROV, 1961d, p. 220 [**K. thysanuriformis*; OD]. Nymph with long, slender cerci; apparently terrestrial. *Perm.*, USSR (Asian RSFSR).—FIG. 63,2. **K. thysanuriformis*; nymph, $\times 4$ (Sharov, 1961d).

Kazanella MARTYNOV, 1930d, p. 1116 [**K. rotundipennis*; OD]. Little-known fore wing, with broad costal margin. *Perm.*, USSR (European RSFSR).—FIG. 63,6. **K. rotundipennis*; fore wing, $\times 4$ (Sharov, 1962b).

Khosara MARTYNOV, 1937b, p. 30 [**K. permiakovae*; OD]. Apex of fore wing rounded but markedly asymmetrical; no cells; MA with long branches. *Perm.*, USSR (European RSFSR).—FIG. 63,5. **K. permiakovae*; fore wing, $\times 2.2$ (Sharov, 1962c).

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

Liomopterella SHAROV, 1961d, p. 202 [**L. vulgaris*; OD]. Similar to *Abashevnia*, but M forking well before origin of RS and MA dichotomously branched. *Perm.*, USSR (Asian RSFSR).—FIG. 65,1. **L. vulgaris*; a, fore and b, hind wings, $\times 2.6$ (Sharov, 1961d).

Liomopterina RIEK, 1973, p. 518 [**L. clara*; OD]. Little-known genus, based on proximal fragment

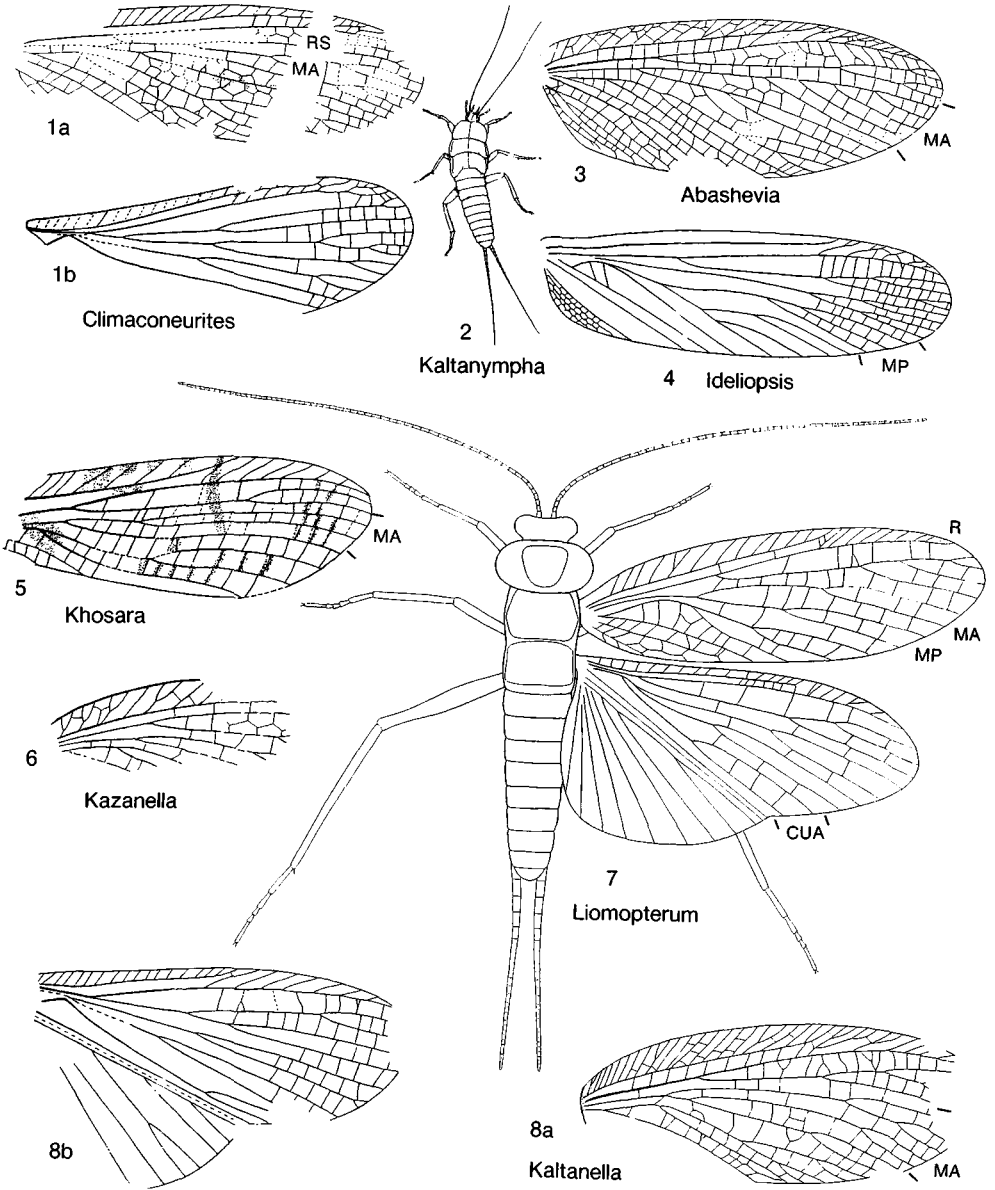


FIG. 63. Liomopteridae (p. 109).

of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).
Liomopterites SHAROV, 1961d, p. 207 [**L. expletus*; OD]. Fore wing similar to that of *Liomopterum* but with curvature of CUA less pronounced and with fewer crossveins; in hind wing, MA anastomosed with RS. Nymph slender, apparently terrestrial. *Perm.*, USSR (Asian RSFSR). — FIG. 65,2a. **L. expletus*; fore

wing, $\times 4.5$ (Sharov, 1961e). — FIG. 65,2b. *L. comans* SHAROV; hind wing, $\times 4.5$ (Sharov, 1961e). — FIG. 65,2c. *L. (?) gracilis* SHAROV; nymph, $\times 6$ (Sharov, 1961d).
Liomoptoides RIEK, 1973, p. 515 [**L. similis*; OD]. Little-known genus, based on small, apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).
Mioloptera RIEK, 1973, p. 515 [**M. stuckenbergi*;

OD]. Little-known genus, apparently similar to *Parapermula*. RIEK, 1976a. *Perm.*, South Africa (Natal).

Miolopterina RIEK, 1976a, p. 762 [**M. tenuipennis*; OD]. Little-known genus, based on small fragment of wing. *Perm.*, South Africa (Natal).

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

Neoliomopterum RIEK, 1976a, p. 762 [**N. picturatum*; OD]. Little-known genus, based on apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa (Natal).

Ornaticosta SHAROV, 1961d, p. 197 [**O. magna*; OD]. Apex of fore wing acute; costal area with dark pigmentation extending nearly to apex of wing. *Perm.*, USSR (Asian RSFSR).—FIG. 65,3. **O. magna*; fore wing, $\times 1$ (Sharov, 1961d).

Paraliomopterum SHAROV, 1961d, p. 218 [**P. paulum*; OD]. Similar to *Liomopterum*, but SC extending much further towards apex. *Perm.*, USSR (Asian RSFSR).—FIG. 65,4. **P. paulum*; fore wing, $\times 2.4$ (Sharov, 1961d).

Parapermula SHAROV, 1961d, p. 191 [**P. sibirica*; OD]. Fore wing oval, with very broad costal space; RS with numerous terminal branches; MA dichotomously branched; at least a few cells between most main veins. *Perm.*, USSR (Asian RSFSR).—FIG. 65,5. **P. sibirica*; a, fore and b, hind wings, $\times 2.5$ (Sharov, 1961d).

Sarbalopterum SHAROV, 1961d, p. 217 [**S. ignorabile*; OD]. Little-known fore wing, with broad costal area and no cells. *Perm.*, USSR (Asian RSFSR).—FIG. 65,6. **S. ignorabile*; fore wing, $\times 6.6$ (Sharov, 1961d).

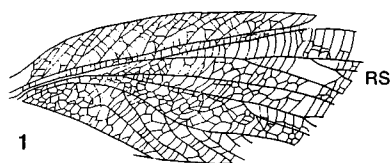
Semopterum CARPENTER, 1950, p. 197 [**S. venosum*; OD]. Fore wing similar to that of *Liomopterum* but with more numerous crossveins and with several additional anal veins. *Perm.*, USA (Kansas).—FIG. 65,7. **S. venosum*; fore wing, $\times 1.8$ (Carpenter, 1950).

Sibirella SHAROV, 1961d, p. 215 [**S. paucinervis*; OD]. Subcostal area nearly as wide as costal area; few crossveins and branches of main veins. *Perm.*, USSR (Asian RSFSR).—FIG. 65,8. **S. paucinervis*; fore wing, $\times 3.4$ (Sharov, 1961d).

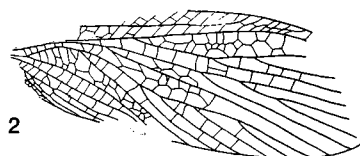
Tapopterum CARPENTER, 1950, p. 195 [**T. celsum*; OD]. Costal space narrower than in *Liomopterum*; crossveins more numerous, with at least a few cells between most main veins. *Perm.*, USA (Kansas).—FIG. 65,9. **T. celsum*; fore wing, $\times 2.5$ (Carpenter, 1950).

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

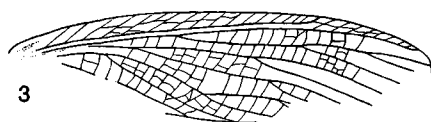
Tyrannopterum KUKALOVÁ, 1964c, p. 70 [**T. minimum*; OD]. Similar to *Cerasopterum* but much smaller; fore wing with branches of RS directed



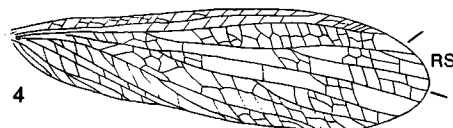
1
Alicula



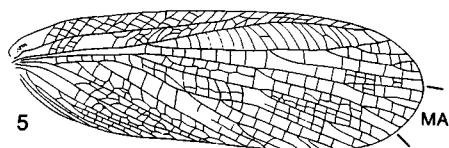
2
Depressopterum



3
Drahania



4
Cerasopterum



5
Donopterum

FIG. 64. Liomopteridae (p. 109).

anteriorly, away from M. *Perm.*, Europe (Czechoslovakia).

Family PHENOPTERIDAE Carpenter, 1950

[Phenopteridae CARPENTER, 1950, p. 204]

Related to Liomopteridae. Fore wing membranous, delicate; vein SC terminating on margin well beyond midwing; costal area with numerous, oblique veinlets; RS arising before midwing, with a few branches; M forked at about level of origin of RS, rarely with three branches; CUA with a basal branch (CUA2) and a distal branch dividing near wing margin; crossveins numerous, irregular,

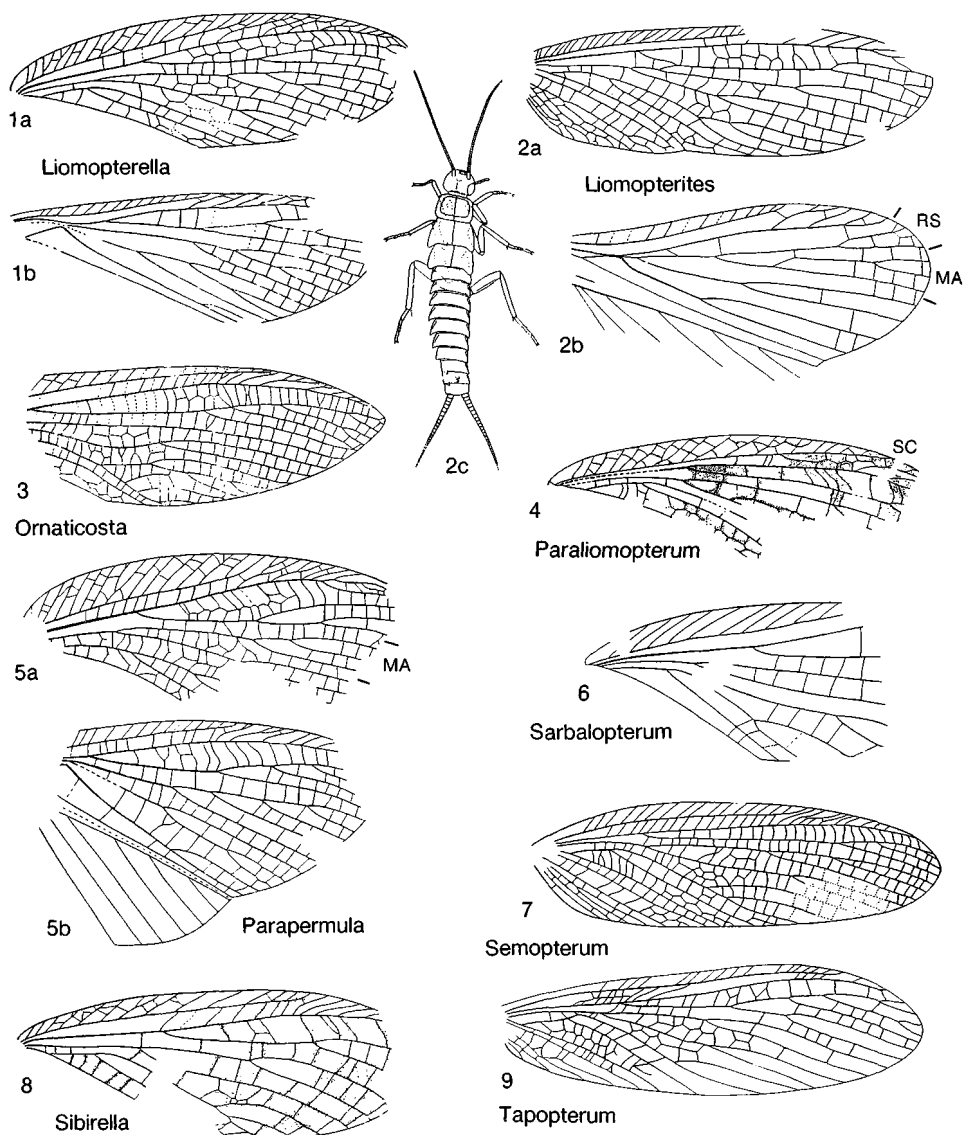


FIG. 65. Liomopteridae (p. 109–111).

forming irregular reticulation over most of wing. Hind wing with RS, M, and CUA arising from single stem near wing base; CUA branched; anal area well developed. Body structure unknown. *Perm.*

Phenopterum CARPENTER, 1950, p. 205, *nom. subst. pro Lepium* SELLARDS, 1909, p. 156, *non* ENDERLEIN, 1906 [*Lepium elongatum* SELLARDS, 1909, p. 156; OD]. RS with 3 branches; fork of M slightly basal of origin of RS. *Perm.*, USA (Kan-

sas).—FIG. 66,3. **P. elongatum* (SELLARDS); *a*, fore and *b*, hind wings, $\times 4$ (Carpenter, 1950). **Brunia** KUKALOVÁ, 1964c, p. 72 [**B. raketa*; OD]. Similar to *Phenopterum*, but wings more slender and RS with only 2 branches; costal area very narrow. *Perm.*, Europe (Czechoslovakia).—FIG. 66,2. **B. raketa*; fore wing, $\times 4$ (Kukalová, 1964c).

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

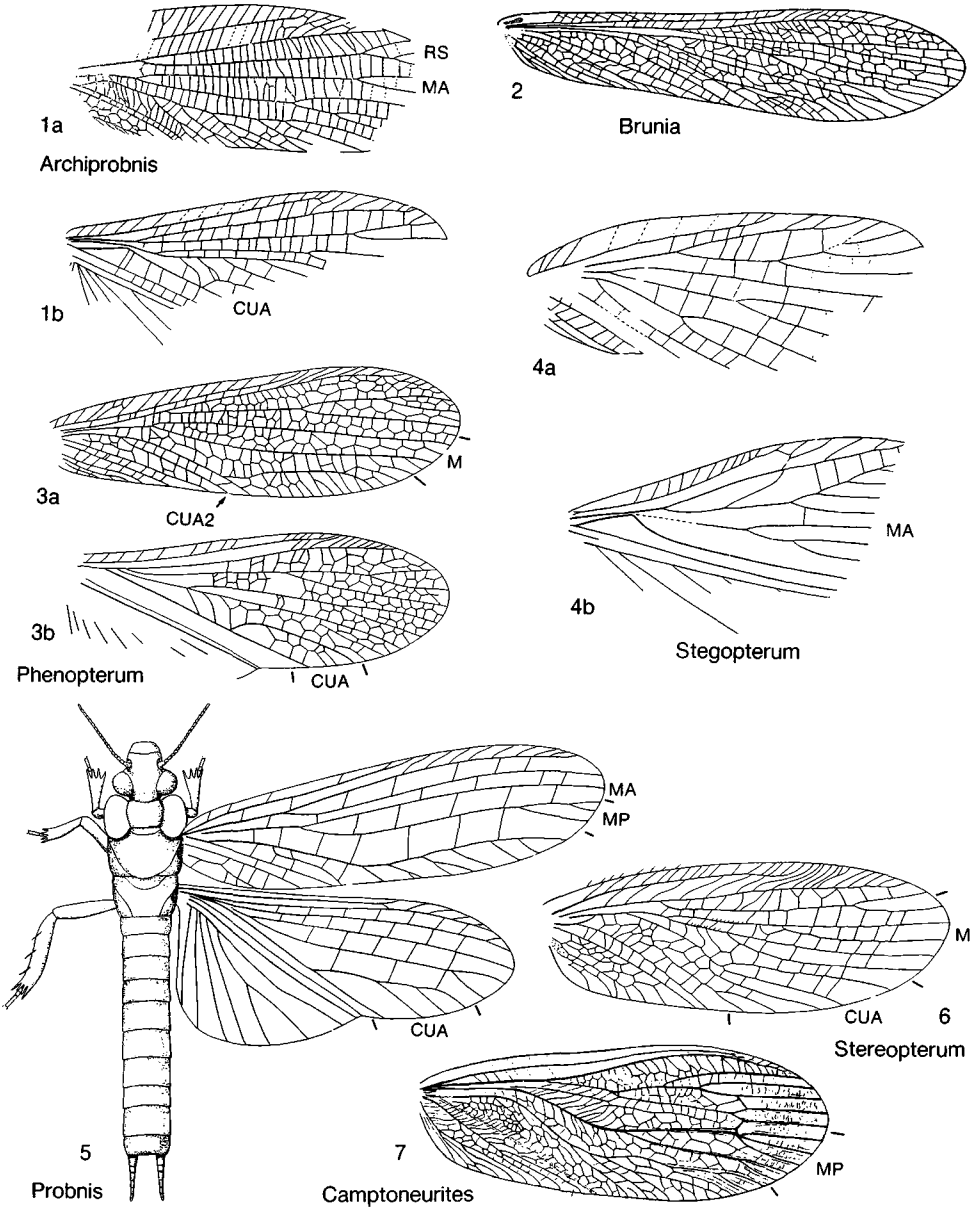


FIG. 66. Phenopteridae, Probnidae, Stegopteridae, Stereopteridae, Camptoneuritidae, and Archiprobnidae (p. 112–115).

Family HAVLATIIDAE
Kukalová, 1964

[Havlatiidae KUKALOVÁ, 1964c, p. 83]

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

Havlatia KUKALOVÁ, 1964c, p. 84 [**H. annae*; OD]. Costal and subcostal areas very narrow; SC extending nearly to wing apex. *Perm.*, Europe (Czechoslovakia). — FIG. 67,3. **H. annae*; fore wing, ×8 (Kukalová, 1964c).

Ventopterum KUKALOVÁ, 1964c, p. 87 [**V. rapidum*; OD]. Little-known genus. Fore wing as in *Zephyropterum*, but subcostal area broader; cross-

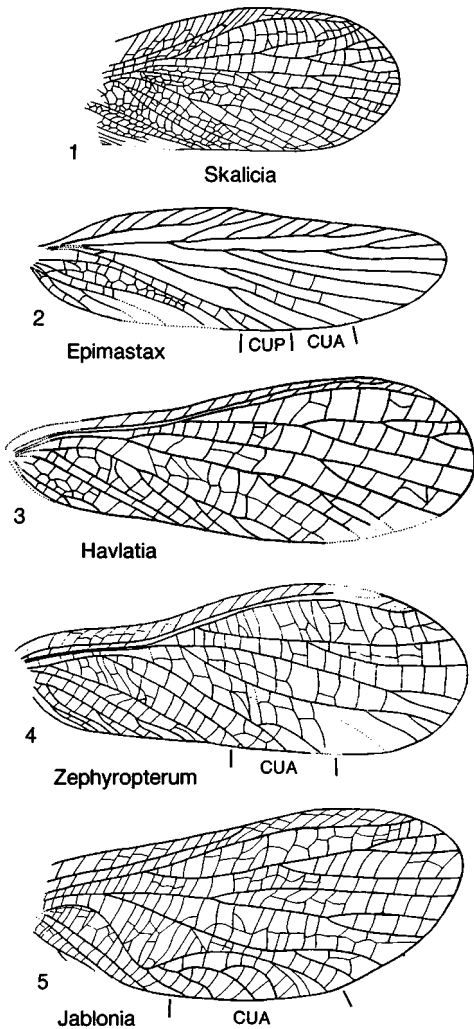


FIG. 67. Havlatiidae, Jabloniidae, Skaliciidae, and Epimastacidae (p. 113–115).

veins more irregular. *Perm.*, Europe (Czechoslovakia).

Zephyropterum KUKALOVÁ, 1964c, p. 85 [**Z. lentum*; OD]. Fore wing as in *Havlatia*, but costal margin more concave before midwing; CUA with 2 long branches. *Perm.*, Europe (Czechoslovakia).—FIG. 67,4. **Z. lentum*; fore wing, $\times 6.5$ (Kukalová, 1964c).

Family JABLONIIDAE Kukalová, 1964

[Jabloniidae KUKALOVÁ, 1964c, p. 81]

Small species, related to the Phenopteridae, but fore wing very broad, with strongly convex hind margin; vein CUA markedly

sigmoidal, its terminal branches almost semi-circular. *Perm.*

Jablonia KUKALOVÁ, 1964c, p. 82 [**J. aestiva*; OD]. Anterior wing margin almost straight; both RS and MA with 3 branches. *Perm.*, Europe (Czechoslovakia).—FIG. 67,5. **J. aestiva*; fore wing, $\times 10$ (Kukalová, 1964c).

Family SKALICIIDAE Kukalová, 1964

[Skaliciidae KUKALOVÁ, 1964c, p. 88]

Fore wing slightly coriaceous, with covering of fine hairs and with prominent setae distally; vein SC terminating well before apex; RS arising near midwing, with several terminal branches; MA and MP terminating near wing apex; CUA2 with long fork; cross-veins reticulate in distal part of wing only. *Perm.*

Skalicia KUKALOVÁ, 1964c, p. 89 [**S. rara*; OD]. Fore wing very broad distally; apex rounded. *Perm.*, Europe (Czechoslovakia).—FIG. 67,1. **S. rara*; fore wing, $\times 3.5$ (Kukalová, 1964c).

Doubravia KUKALOVÁ, 1964c, p. 90 [**D. annosa*; OD]. Little-known genus. Fore wing apparently long and slender. [Family assignment doubtful.] *Perm.*, Europe (Czechoslovakia).

Family PROBNIDAE Sellards, 1909

[*nom. correct.* CARPENTER, herein, *pro* Probnisidae SELLARDS, 1909, p. 159]

Related to Lemmatophoridae. Fore wing coriaceous, granular in texture; costal area narrow; vein R extending nearly to wing apex; RS unbranched; MA and MP separating at about level of origin of RS, their branching very variable; CUA1 producing variable number of arched branches along posterior margin of wing; CUA2 usually unbranched; 1A unbranched. Hind wing membranous but with wrinkles; costal space narrower than in fore wing; RS arising almost at base of wing, unbranched; CUA1 as in fore wing but with longer branches; deep indentation of hind margin at end of CUP; anal fan well developed, with 6 anal veins. Head small, eyes prominent; antennae rather short and robust; prothorax with small lateral lobes, without venation; legs of moderate length; tarsi three-segmented; abdomen robust; cerci short; ovipositor apparently small. CARPENTER, 1943a. *Perm.*

Probnis SELLARDS, 1909, p. 159 [**P. speciosa*; SD TILLYARD, 1937c, p. 415] [= *Espira* SELLARDS, 1909, p. 160 (type, *E. obscura*); *Stoichus* SELLARDS, 1909, p. 160 (type, *S. elegans*); *Stinus* SELLARDS, 1909, p. 161 (type, *S. breve-cubitalis*)]. Fore wing: SC terminating at midwing; R with several veinlets from R to costal margin beyond SC; crossveins straight, widely separated over most of wing; CUA1 extending nearly to wing apex. *Perm.*, USA (Kansas).—FIG. 66,5. **P. speciosa*; whole insect, $\times 4$ (Carpenter, 1943a).

Family STEGOPTERIDAE Sharov, 1961

[Stegopteridae SHAROV, 1961d, p. 220]

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

Stegopterum SHAROV, 1961d, p. 221 [**S. hirtum*; OD]. Fore wing with few crossveins; no cells. Hind wing with MA free from RS. *Perm.*, USSR (Asian RSFSR).—FIG. 66,4. **S. hirtum*; *a*, fore and *b*, hind wings, $\times 4.4$ (Sharov, 1961d).

Family STEREOPTERIDAE Carpenter, 1950

[Stereopteridae CARPENTER, 1950, p. 201]

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

Stereopterum CARPENTER, 1950, p. 202 [**S. rotundum*; OD]. M forking at level of origin of RS; row of stout setae along basal third of costal margin; smaller setae or branches of M near midwing. CARPENTER, 1966. *Perm.*, USA (Kansas).—FIG. 66,6. **S. rotundum*; fore wing, $\times 4$ (Carpenter, 1950).

Family EPIMASTACIDAE Martynov, 1928

[Epimastacidae MARTYNOV, 1928b, p. 63]

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

Epimastax MARTYNOV, 1928b, p. 63 [**E. parvulus*; OD]. Fore wing: R with several branches to the costal margin of wing; RS with 5 terminal branches. *Perm.*, USSR (European RSFSR), Europe (Czechoslovakia).—FIG. 67,2. *E. celer* KUKALOVÁ, 1965; fore wing, $\times 8$ (Kukalová, 1965).

Family CAMPTONEURITIDAE Martynov, 1931

[Camptoneuritidae MARTYNOV, 1931a, p. 98, *nom. subst. pro* Camptoneuridae MARTYNOV, 1928b, p. 53]

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

Camptoneurites MARTYNOV, 1931a, p. 98, *nom. subst. pro* Camptoneura MARTYNOV, 1928b, p. 53, *non* AGASSIZ, 1846 [**Camptoneura reticulata* MARTYNOV, 1928b, p. 35; OD]. Fore wing with costal margin slightly concave; 2 rows of irregular cells between MP and CUA. *Perm.*, USSR (European RSFSR).—FIG. 66,7. **C. reticulata* (MARTYNOV); fore wing, $\times 3.5$ (Martynov, 1928b).

Family ARCHIPROBNIDAE Sharov, 1961

[*nom. correct.* CARPENTER, herein, *pro* Archiprobnisidae SHAROV, 1961d, p. 185]

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

Archiprobnis SHAROV, 1961d, p. 186 [**A. repens*; OD]. Fore wing broadly oval with rounded apex. *Perm.*, USSR (Asian RSFSR).—FIG. 66,1. **A. repens*; *a*, fore and *b*, hind wings, $\times 2.5$ (Sharov, 1961d).

Family PROTEMBIIDAE Tillyard, 1937

[Protembiidae TILLYARD, 1937b, p. 243] [= Telactinopterygidae CARPENTER, 1943a, p. 78]

Related to Phenopteridae. Fore wing slightly coriaceous; distal parts of veins RS, MA, MP bordered by delicate lines on each side; SC terminating on costal margin; costal space very narrow; RS arising at midwing.

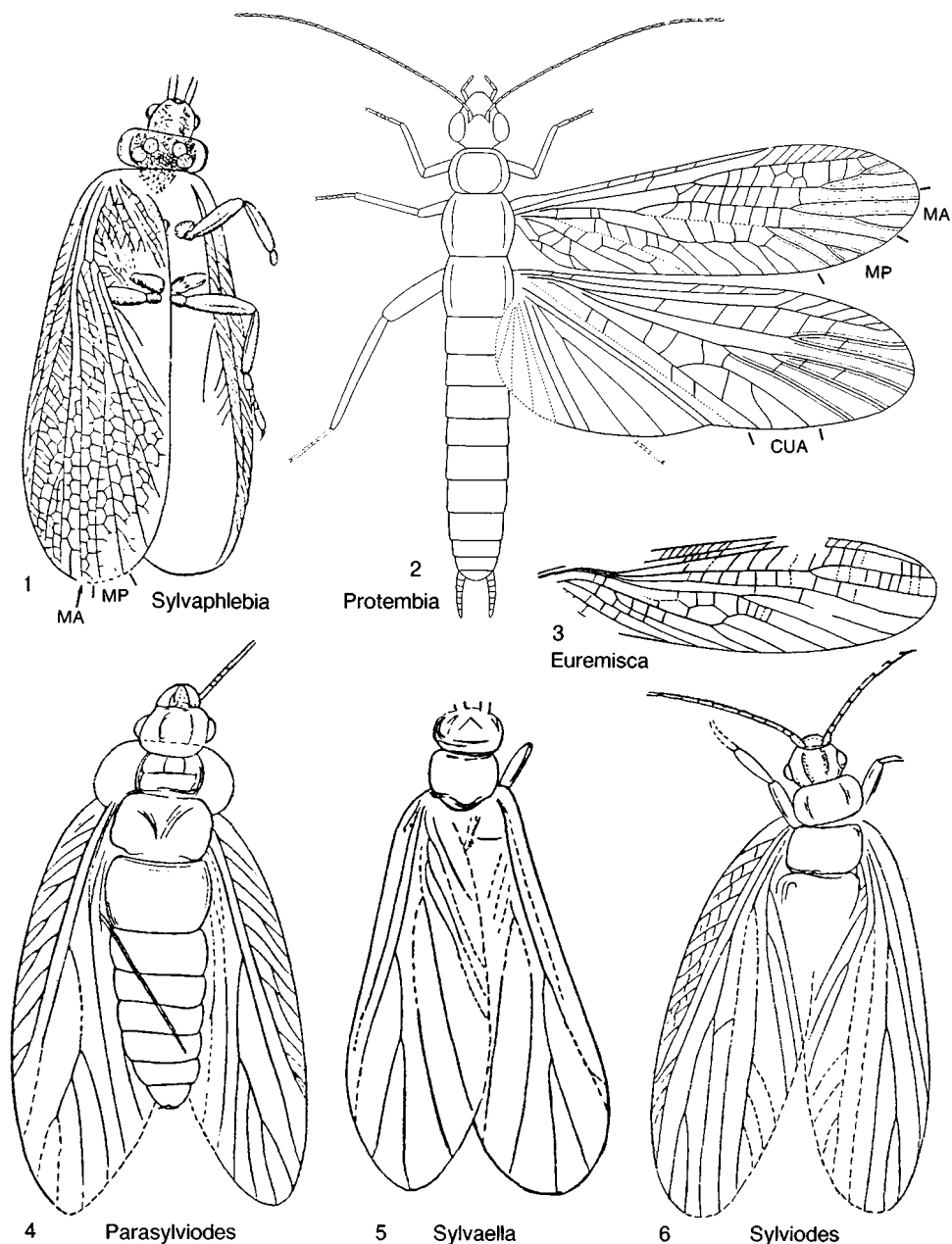


FIG. 68. Protombiidae, Euremisciidae, and Sylvaphlebiidae (p. 117).

branched; M forked before origin of RS; CUA without definite CUA2, having several distal branches; crossveins few, unequally distributed. Hind wing with RS arising near wing

base; M forking slightly beyond midwing; CUA forked distally; anal lobe well developed. Antennae long; head small, with large eyes; prothorax with small disc; hind legs

longer than others, all with five tarsomeres; cerci short but distinct. CARPENTER, 1950. *Perm.*

Protombia TILLYARD, 1937b, p. 245 [**P. permiana*; OD] [= *Telactinopteryx* TILLYARD, 1937c, p. 422 (type, *T. striatipennis*)]. Fore wing: RS with 3 terminal branches; several veinlets between R and margin beyond end of SC; a few cells formed between R and RS. *Perm.*, USA (Kansas).—FIG. 68,2. **P. permiana*; whole insect, $\times 6.5$ (Carpenter, 1950).

Family EUREMISCIDAE Zalessky, 1951

[Euremiscidae ZALESSKY, 1951b, p. 81]

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

Euremisca ZALESSKY, 1951b, p. 82 [**E. splendens*; OD]. Slender fore wing, with very narrow costal space. *Perm.*, USSR (Asian RSFSR).—FIG. 68,3. **E. splendens*; fore wing, $\times 3.5$ (Sharov, 1962c).

Family SYLVAPHLEBIIDAE Martynov, 1940

[Sylvaphlebiidae MARTYNOV, 1940, p. 18] [= *Sylvaelidae* MARTYNOV, 1940, p. 26; *Sylvioididae* MARTYNOV, 1940, p. 23]

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

Sylvaphlebia MARTYNOV, 1940, p. 18 [**S. tuberculata*; OD] [= *Biarmopteron* ZALESSKY, 1953c, p. 42 (type, *B. protoblattoides*)]. Fore wing little known; 2 rows of cells between MA and MP. *Perm.*, USSR (Asian RSFSR).—FIG. 68,1. **S. tuberculata*; fore wing and part of body, $\times 3.2$ (Sharov, 1962c).

Parasyliodes MARTYNOV, 1940, p. 23 [**P. tetracladus*; OD]. Fore wing with very broad costal area; RS arising near midwing; large lobes on prothorax. *Perm.*, USSR (Asian RSFSR).—FIG. 68,4. **P. tetracladus*; fore wings and part of body, $\times 3.4$ (Sharov, 1962c).

Sylvaella MARTYNOV, 1940, p. 55 [**S. paurovenosa*; OD]. Fore wing little known; RS arising at midwing but with fewer branches than in *Parasyliodes*; costal area narrow. *Perm.*, USSR (Asian RSFSR).—FIG. 68,5. **S. paurovenosa*; fore wings and part of body, $\times 6$ (Sharov, 1962c).

Sylviodes MARTYNOV, 1940, p. 23 [**S. perloides*;

OD] [= *Biarmopterites* ZALESSKY, 1953c, p. 45 (type, *B. reticulatus*)]. Fore wing little known; costal space much broader than in *Sylvaphlebia*. *Perm.*, USSR (Asian RSFSR).—FIG. 68,6. **S. perloides*; fore wing and part of body, $\times 1.6$ (Sharov, 1962c).

Family CHELOPTERIDAE Carpenter, 1950

[Chelopteridae CARPENTER, 1950, p. 198]

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

Chelopteron CARPENTER, 1950, p. 199 [**C. peregrinum*; OD]. Fore wing with SC approaching costal margin at about midwing; main fork of M just proximal to origin of RS; MA and MP about equally developed. *Perm.*, USA (Kansas).—FIG. 69,4. **C. peregrinum*; complete insect, male, $\times 3.4$ (Carpenter, 1950).

Family DEMOPTERIDAE Carpenter, 1950

[Demopteridae CARPENTER, 1950, p. 203]

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

Demopteron CARPENTER, 1950, p. 203 [**D. gracile*; OD]. Fore wing slender; SC with series of stout spines along its proximal part; MP much more extensively developed than MA. *Perm.*, USA (Kansas).—FIG. 69,5. **D. gracile*; fore wing, $\times 2.7$ (Carpenter, 1950).

Family ATACTOPHLEBIIDAE

Martynov, 1930

[Atactophlebiidae MARTYNOV, 1930c, p. 952]

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

Atactophlebia MARTYNOV, 1928b, p. 51 [**A. termitoides*; OD]. Fore wing with area of RS narrow; RS with few branches. *Perm.*, USSR (Asian RSFSR).—FIG. 69,3. **A. termitoides*; *a*, fore and *b*, hind wings, $\times 1.4$ (Martynov, 1930c).

Family MEGAKHOSARIDAE

Sharov, 1961

[Megakhosaridae SHAROV, 1961d, p. 178]

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

Megakhosara MARTYNOV, 1937b, p. 31 [**M. fasciipennis*; OD] [= *Syndesmothora* MARTYNOV, 1937b, p. 41 (type, *S. composita*)]. Fore wing with RS dichotomously branched; no anastomosis between main veins; both fore and hind wings with irregular crossveins. *Perm.*, USSR (Asian RSFSR).—FIG. 69,1a. *M. dilucida* SHAROV; fore wing, $\times 1.8$ (Sharov, 1961e).—FIG. 69,1b. **M. fasciipennis*; hind wing, $\times 1.5$ (Martynov, 1937b).

Megakhosarella SHAROV, 1961d, p. 182 [**M. regressa*; OD]. Little-known fore wing; MA and RS anastomosed for very short distance. *Perm.*, USSR (Asian RSFSR).—FIG. 69,2. **M. regressa*; fore wing, $\times 3$ (Sharov, 1961d).

Family IDELIIDAE Zalesky, 1929

[Ideliidae M. D. ZALESSKY, 1929, p. 21] [= *Rachimentomidae* G. M. ZALESSKY, 1939, p. 55]

Fore wing with broad costal area having numerous slanting veinlets, usually forming reticulation; no anastomosis of veins MA and RS; RS usually with more than three branches;

stem CU formed as in Liomopteridae but CUA more elaborately branched; CUP not so strongly developed as in Liomopteridae; crossveins numerous, usually forming reticulation. Hind wing little known, apparently similar to that of Liomopteridae. Antennae prominent; pronotum with broad, coriaceous expansions; cerci probably well developed; long ovipositor present. *U. Carb.*—*Perm.*

Stenaropodites MARTYNOV, 1928b, p. 47 [**S. reticulata*; OD] [= *Idelia* ZALESSKY, 1929, p. 4 (type, *I. permiakovi*)]. Fore wing with fine network of cells, resembling archidictyon; costal margin weakly curved; CUA2 strongly sigmoidal. *Perm.*, USSR (Asian RSFSR).—FIG. 70,6. *S. permiakovi* (ZALESSKY); fore wing, $\times 1.2$ (Zalesky, 1929).

Aenigmidelia SHAROV, 1961d, p. 175 [**A. incredibilis*; OD]. Fore wing oval, with strongly curved costal margin; SC with basal branch, resembling submarginal costa; main branch of SC coalesced with R basally; crossveins as in *Archidelia*; M forking at level of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 70,8. **A. incredibilis*; fore wing, $\times 1$ (Sharov, 1961d).

Archidelia SHAROV, 1961d, p. 172 [**A. elongata*; OD]. Fore wing with strongly convex costal margin; crossveins forming irregular reticulation, much finer than that in *Kortshakolia*, but no archidictyon; costal veinlets branched; M forking before origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 70,2. **A. elongata*; *a*, fore and *b*, hind wings, $\times 1$ (Sharov, 1961d).

Kortshakolia SHAROV, 1961d, p. 171 [**K. ideliformis*; OD]. Little-known genus, based on fragment of fore wing, with costal margin shaped as in *Stenaropodites*; RS with at least 4 branches; MA directed anteriorly at its origin toward R before curving distally. *U. Carb.*, USSR (Asian RSFSR).—FIG. 70,1. **K. ideliformis*; fore wing, $\times 1.6$ (Sharov, 1961d).

Metidelia MARTYNOV, 1937b, p. 23 [**M. kargalensis*; OD]. Fore wing with costal area narrower than in *Stenaropodites*; crossveins forming nearly regular network, not so fine as archidictyon. *Perm.*, USSR (Asian RSFSR).—FIG. 70,3. **M. kargalensis*; fore wing, $\times 1.8$ (Martynov, 1937b).

Paridelia SHAROV, 1961d, p. 175 [**P. pusilla*; OD]. Fore wing with costal margin as in *Stenaropodites*; RS arising near midwing, with 2 branches; MA with 2 branches, MP with 3. SHAROV, 1962c. *Perm.*, USSR (Asian RSFSR).—FIG. 70,9. **P. pusilla*; fore wing, $\times 1.8$ (Sharov, 1961d).

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

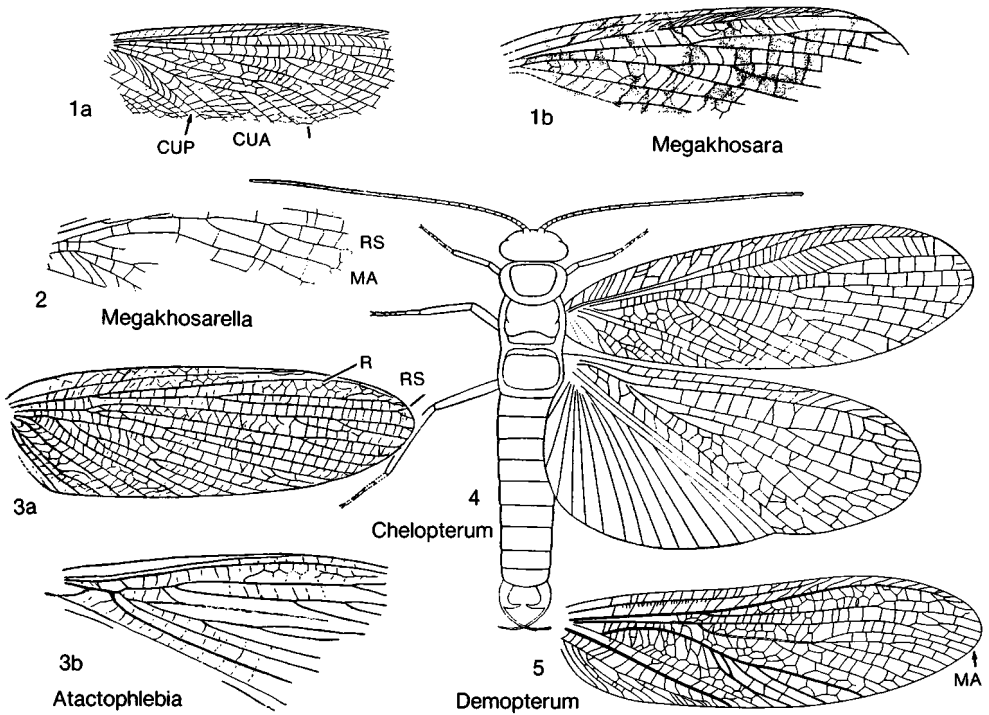


FIG. 69. Chelopteridae, Demopteridae, Atactophlebiidae, and Megakhosaridae (p. 117-118).

abdomen. *Perm.*, USSR (Asian RSFSR).—FIG. 70,5. **R. reticulatum*; whole specimen, $\times 2$ (Zalessky, 1939).
Sylvidelia MARTYNOV, 1940, p. 19 [**S. latipennis*; OD]. Fore wing with archedictyon as in *Stenaropodites* but with more strongly curved costal margin, more branches to RS, and without sigmoidal CUA2. *Perm.*, USSR (Asian RSFSR).—FIG. 70,7. **S. latipennis*; fore wing, $\times 1.4$ (Martynov, 1940).

Family EURYPTILONIDAE
Martynov, 1940

[Euryptilonidae MARTYNOV, 1940, p. 16]

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

Euryptilon MARTYNOV, 1940, p. 16 [**E. blattoides*; OD]. Fore wing with subcostal space much broader than costal; M sigmoidally curved. *Perm.*,

USSR (Asian RSFSR).—FIG. 70,10. **E. blattoides*; fore wing, $\times 5.5$ (Martynov, 1940).

Family NARKEMIDAE
Handlirsch, 1911

[Narkemidae HANDLIRSCH, 1911, p. 321]

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

Narkema HANDLIRSCH, 1911, p. 322 [**N. taeniatum*; OD]. Little-known genus, based on incomplete fore wing. RS with at least 5 terminal branches. Wing with 7 narrow, dark transverse bands. SHAROV, 1961e; PINTO & ORNELLAS, 1978c. *U. Carb.*

Family HERBSTIALIDAE
Schmidt, 1953

[Herbstialidae SCHMIDT, 1953, p. 165]

Related to Cacurgidae (probably synonymous). Fore wing with reticulation of cross-

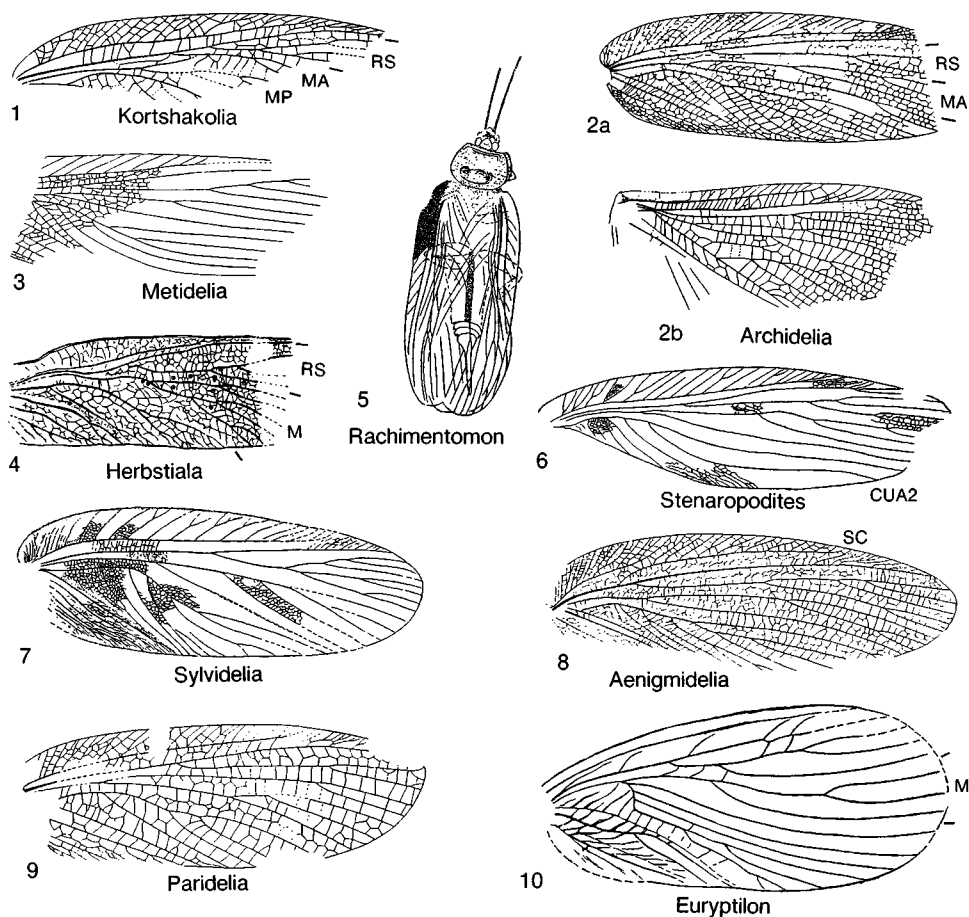


FIG. 70. Ideliidae, Euryptilonidae, and Herbstialidae (p. 118–120).

veins over entire wing surface; cuticular spots as in *Cacurgidae*. *U. Carb.*

Herbstiala SCHMIDT, 1953, p. 153 [**H. herbsti*; OD]. Origin of RS at about same level as first fork of M. [Placed in order Protocicadida.] *U. Carb.*, Europe (Germany).—FIG. 70,4. **H. herbsti*; fore wing, $\times 1.5$ (Schmidt, 1953).

Family CACURGIDAE Handlirsch, 1911

[Cacurgidae HANDLIRSCH, 1911, p. 324]

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

crossveins numerous. Hind wing unknown. *U. Carb.*

Cacurgus HANDLIRSCH, 1911, p. 324 [**C. spilopterus*; OD]. Little-known genus. Fore wing broadest at level of midwing; R with several oblique veinlets leading to fore margin of wing; crossveins forming a coarse network over most of wing except costal area; wing membrane with many circular thickenings. *U. Carb.*, USA (Illinois).—FIG. 71,6. **C. spilopterus*; fore wing, $\times 1$ (Handlirsch, 1911).

Heterologus CARPENTER, 1944, p. 14 [**H. langfordorum*; OD]. Fore wing as in *Cacurgus*, but costal area narrower and more tapering and no network of crossveins. *U. Carb.*, USA (Illinois).—FIG. 71,8. **H. langfordorum*; fore wing, $\times 3.5$ (Carpenter, 1944).

Protodictyon MELANDER, 1903, p. 196 [**P. pulchripenne*; OD]. Similar to *Heterologus*, but crossveins of fore wing forming a coarse reticulation in several areas of the wing; RS remote from M.

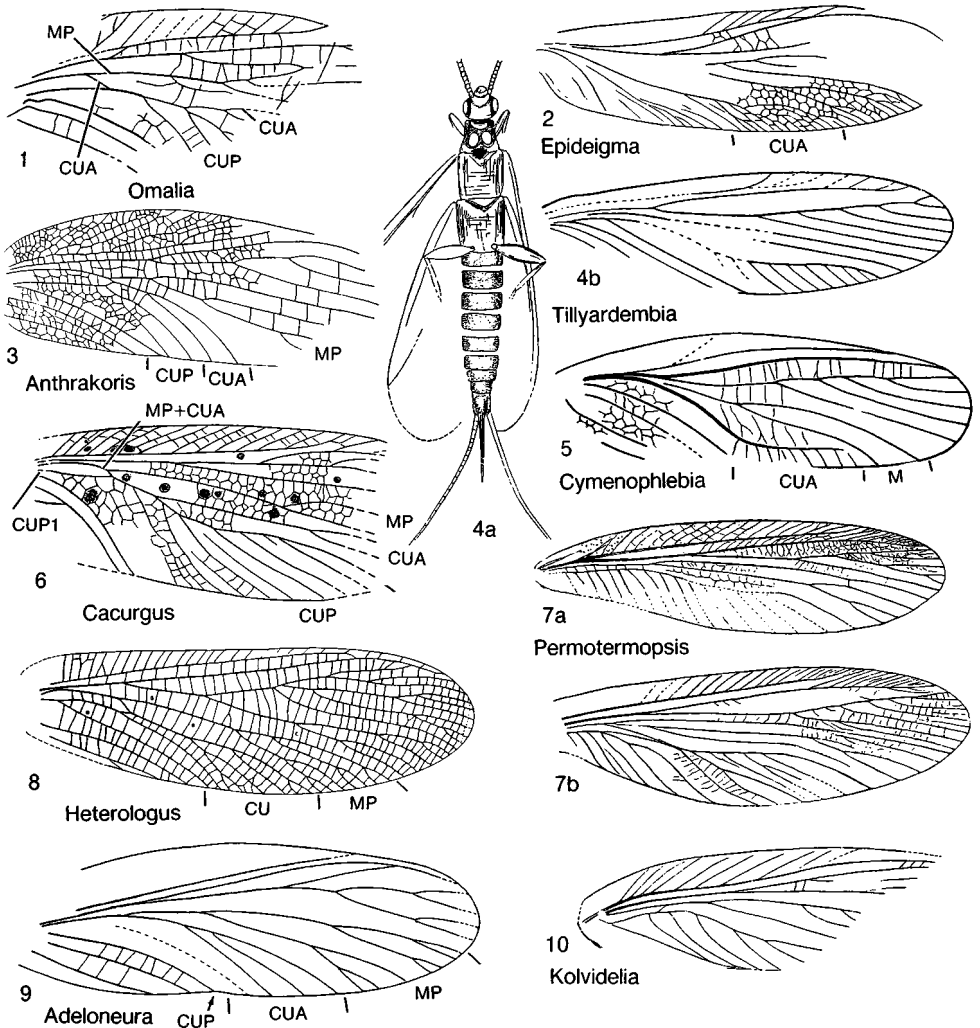


FIG. 71. Cacurgidae, Omaliidae, Tillyardembiidae, Epideigmatidae, Permotermopsidae, and Adelonuridae (p. 120-124).

basally. [Placed by MELANDER in Hemeristina group of Palaeodictyoptera.] *U. Carb.*, USA (Illinois).

Spilomastax 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 OMALIIDAE Handlirsch, 1906

[Omaliidae 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, $\times 1$ (Pruvost, 1930).

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

FIG. 71,3. **A. aetherius*; fore wing, $\times 5$ (Carpenter, new).

Coselia BOLTON, 1922, p. 81 [**C. palmiformis*; OD]. Little-known genus, based on small fragment of wing. [Type of family Coseliidae BOLTON.] PRUVOST, 1930. *U. Carb.*, England.

Family GERARIDAE Scudder, 1885

[*nom. correct.* HANDLIRSCH, 1906a, p. 701, *pro* Gerarina SCUDDER, 1885b, p. 762] [=Schenaropodidae HANDLIRSCH, 1906b, p. 141; Genopterygidae RICHARDSON, 1956, p. 41]

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

Gerarus SCUDDER, 1885d, p. 344 [**G. vetus*; OD] [=Genopteryx SCUDDER, 1885d, p. 327 (type, *G. constricta*); *Sthenaropoda* BRONGNIART, 1885a, p. 59 (type, *S. fischeri*); *Archaeacridites* MEUNIER, 1909c, p. 39 (type, *A. bruesi*); *Rossites* RICHARDSON, 1956, p. 44 (type, *R. inopinus*)]. Moderately large species. Fore wing with RS branched 2 or 3 times; M with 4 or 5 branches and either anastomosed for a short interval with RS or connected to it by a strong crossvein. BURNHAM, 1983. *U. Carb.*, USA (Illinois), Europe (France).—FIG. 72,3a. *G. bruesi* (MEUNIER); fore wing, $\times 1$ (Burnham, 1983).—FIG. 72,3b. *G. danielisi*; reconstruction, based on many specimens, $\times 0.7$ (Burnham, 1983).

Anepitedius HANDLIRSCH, 1911, p. 318 [**A. giraffa*; OD]. Little-known genus, based on wing and body fragments. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

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

Gerarulus HANDLIRSCH, 1911, p. 316 [**G. radialis*; OD]. Little-known genus, based on wing frag-

ments; RS with not more than 4 branches. BURNHAM, 1983. *U. Carb.*, USA (Illinois).

Nacekoma RICHARDSON, 1956, p. 33 [**N. rossae*; OD]. Fore wing similar to that of *Gerarus* but more slender; M not connected to RS by a thickened crossvein. BURNHAM, 1983. *U. Carb.*, USA (Illinois).—FIG. 72,2. **N. rossae*; fore wing, $\times 1.4$ (Carpenter, new).

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

Family SPANIODERIDAE Handlirsch, 1906

[Spanioderidae HANDLIRSCH, 1906a, p. 695]

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

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

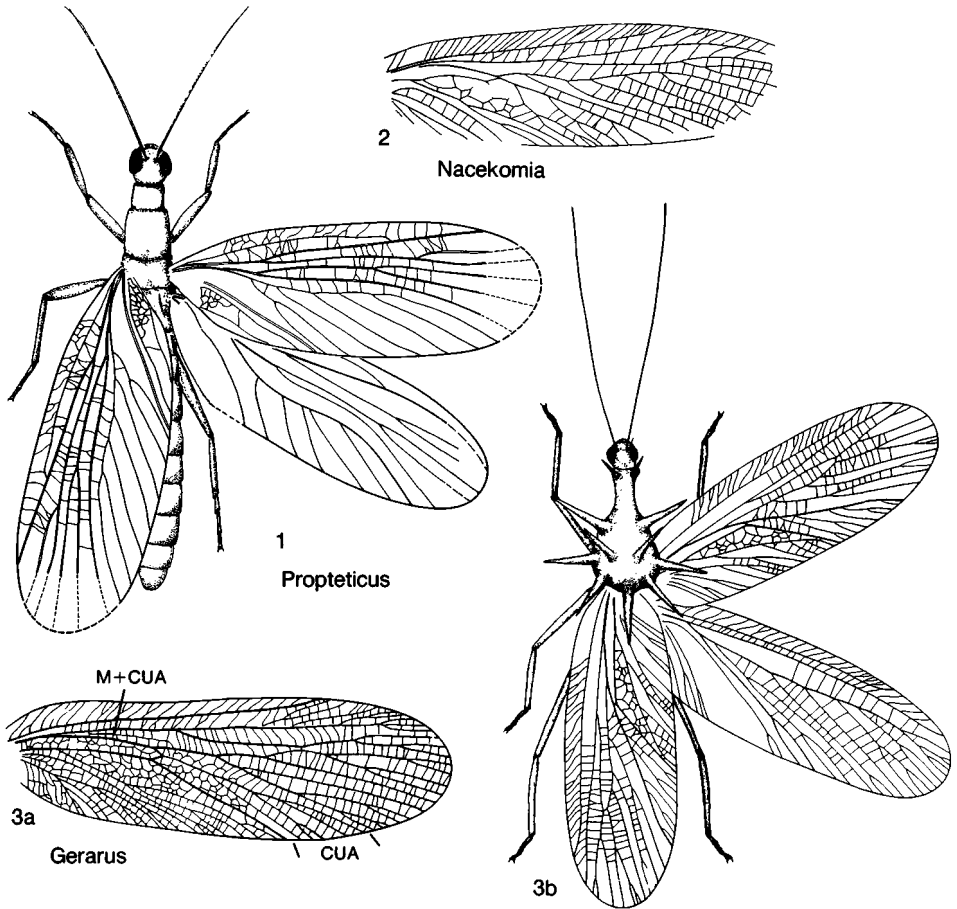


FIG. 72. Geraridae and Spanioderidae (p. 000).

eral additional specimens, $\times 1.3$ (Burnham, 1986).

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

Family APITHANIDAE

Handlirsch, 1911

[Apithanidae HANDLIRSCH, 1911, p. 320]

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

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

Family TILLYARDEMBIIDAE

Zalessky, 1938

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

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

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

52 (type, *P. brevipes*). RS with about 6 branches; M with deep fork. *Perm.*, USSR (Asian RSFSR). —FIG. 71,4. *T. brevipes* (MARTYNOV); *a*, complete specimen, $\times 4.5$ (Martynov, 1940); *b*, fore wing, $\times 4$ (Sharov, 1962c).

Family EPIDEIGMATIDAE Handlirsch, 1911

[Epeideigmatidae HANDLIRSCH, 1911, p. 356 [=Cymenophlebiidae PRUVOST, 1919, p. 128]

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

Epeidigma HANDLIRSCH, 1911, p. 357 [**E. elegans*; OD]. Fore wing slender, length almost 4 times width; SC terminating on R. *U. Carb.*, USA (Illinois). —FIG. 71,2. **E. elegans*; fore wing, $\times 2$ (Handlirsch, 1911).

Cymenophlebia PRUVOST, 1919, p. 128 [**C. carpentieri*; OD]. Fore wing as in *Epeidigma*, but costal area wider; SC terminating on costa. *U. Carb.*, Europe (France). —FIG. 71,5. **C. carpentieri*; fore wing, $\times 3$ (Pruvost, 1919).

Family PERMOTERMOPSIDAE Martynov, 1937

[Permotermopsidae MARTYNOV, 1937b, p. 84]

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

Permotermopsis MARTYNOV, 1937b, p. 84 [**P. roseni*; OD]. Costal veinlets simple; crossveins forming delicate, irregular network. *Perm.*, USSR (European RSFSR). —FIG. 71,7a. **P. roseni*; fore wing, $\times 1.0$ (Martynov, 1937b). —FIG. 71,7b. *P. pectinata* MARTYNOV; fore wing, $\times 1.2$ (Martynov, 1937b).

Kolvidelia ZALESSKY, 1956a, p. 282 [**K. curta*; OD]. Little-known fore wing, with costal area broader than in *Permotermopsis*. [Family assignment doubtful.] *Perm.*, USSR (Asian RSFSR). —FIG. 71,10. **K. curta*; fore wing, $\times 2$ (Zalesky, 1956a).

Family ADELONEURIDAE Carpenter, 1938

[Adeloneuridae CARPENTER, 1938, p. 450]

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

Adeloneura CARPENTER, 1938, p. 450 [**A. thompsoni*; OD]. Little-known fore wing, with very narrow subcostal space; CUA and MP separating at about level of origin of RS. *U. Carb.*, USA (Illinois). —FIG. 71,9. **A. thompsoni*; fore wing, $\times 1.6$ (Carpenter, 1938).

Family AENIGMATODIDAE Handlirsch, 1906

[Aenigmatodidae HANDLIRSCH, 1906a, p. 683]

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

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

Family STREPHOCLADIDAE Martynov, 1938

[Strephocladidae MARTYNOV, 1938b, p. 100]

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

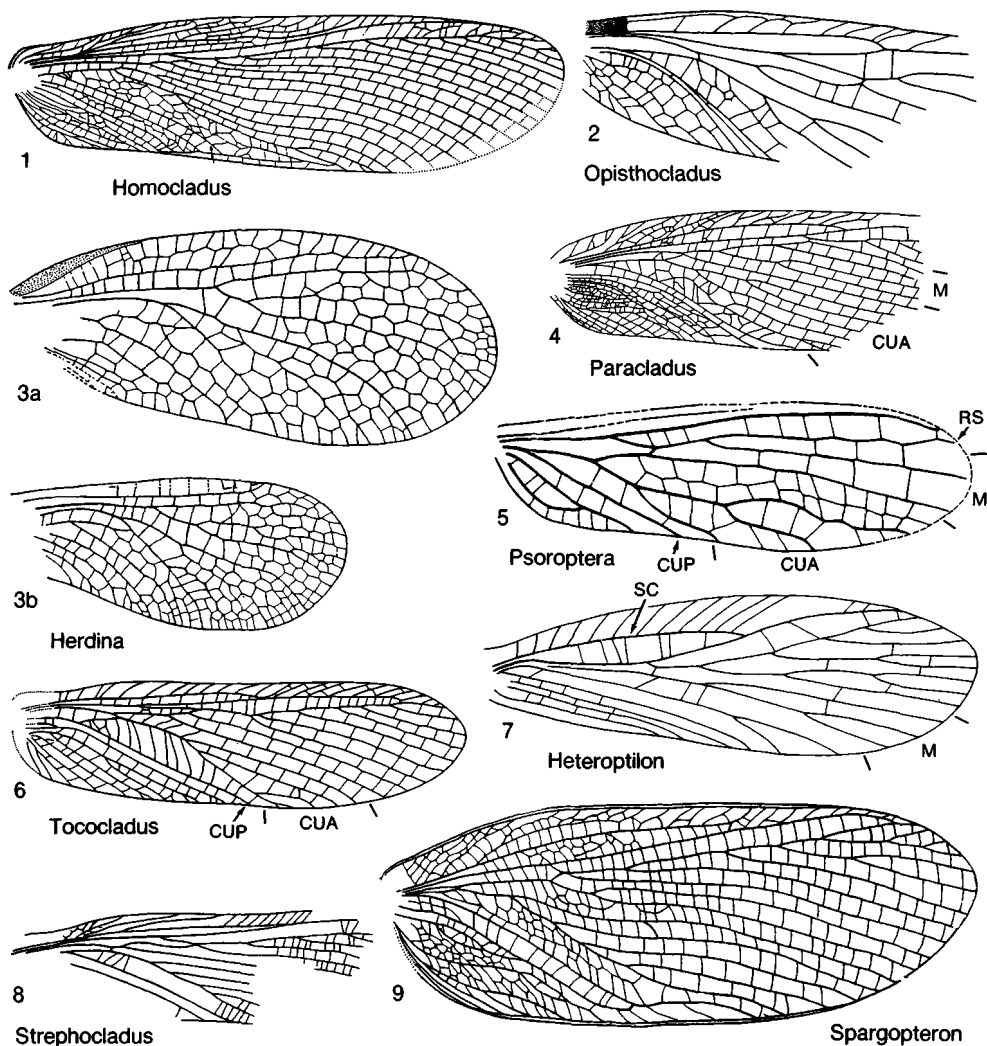


FIG. 73. Strephocladidae, Tococladidae, Heteroptilidae, Herdinidae, and Psoropteridae (p. 125–126).

thoptera are uncertain; MARTYNOV (1938a) placed it in a new order, Strephocladodea.] CARPENTER, 1966. *U. Carb.*—*Perm.*

Strephocladus SCUDDER, 1885d, p. 337 [*Petrablattina subtilis* KLIVER, 1883, p. 251; OD]. Little-known genus. Costal area with straight, oblique veinlets near level of midwing; branches of CUA and RS dichotomously formed. KUKALOVÁ, 1965; CARPENTER, 1966. *U. Carb.*, Europe (Germany).—FIG. 73,8. **S. subtilis*; fore wing as preserved (holotype), $\times 2$ (Carpenter, 1966).

Homocladus CARPENTER, 1966, p. 60 [**H. grandis*; OD]. Fore wing slender; costal area much as in

Spargopteron; branches of RS arising pectinately, those of CUA dichotomously. *Perm.*, USA (Kansas).—FIG. 73,1. **H. grandis*; fore wing, $\times 1.3$ (Carpenter, 1966).

Paracladus CARPENTER, 1966, p. 62 [**P. retardatus*; OD]. Fore wing as in *Homocladus*, but branches of RS, M, and CUA nearly straight. *Perm.*, USA (Kansas).—FIG. 73,4. **P. retardatus*; fore wing, $\times 3$ (Carpenter, 1966).

Spargopteron KUKALOVÁ, 1965, p. 89 [**S. latericius*; OD]. Fore wing much broader than in *Strephocladus*; all veinlets in costal area branched or irregular; branches of RS dichotomous, those of CUA pectinate. CARPENTER, 1966. *Perm.*, Europe (Czechoslovakia).—FIG. 73,9. **S. latericius*; fore wing, $\times 1.8$ (Kukalová, 1965).

Family TOCOCLADIDAE

Carpenter, 1966

[Tococladidae CARPENTER, 1966, p. 77]

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

Tococladus CARPENTER, 1966, p. 77 [**T. rallus*; OD]. Area between CUA and CUP very broad, traversed by long crossveins, not reticulate. *Perm.*, USA (Kansas).—FIG. 73,6. **T. rallus*; fore wing, $\times 2.3$ (Carpenter, 1966).

Opisthocladus CARPENTER, 1976, p. 342 [**O. arcuatus*; OD]. Fore wing as in *Tococladus*, but costal veinlets looped and RS arising more distally; basal part of costal area thick and strongly sclerotized. *Perm.*, USA (Kansas).—FIG. 73,2. **O. arcuatus*; fore wing as preserved, $\times 4$ (Carpenter, 1976).

Family HETEROPTILIDAE

Carpenter, 1976

[Heteroptilidae CARPENTER, 1976, p. 346]

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

Heteroptilon CARPENTER, 1976, p. 346 [**H. costale*; OD]. Fore wing broadest beyond midwing; RS with 8 terminal branches; CUA with a short, distal fork. *Perm.*, USA (Kansas).—FIG. 73,7. **H. costale*; fore wing, $\times 3.7$ (Carpenter, 1976).

Family HERDINIDAE

Carpenter & Richardson, 1971

[Herdinidae CARPENTER & RICHARDSON, 1971, p. 287]

Apparently related to Cacurgidae. Wings very short; venation strongly developed; small tubercles on all main veins and crossveins of fore and hind wings. Fore wing with base of costal area strongly sclerotized; vein SC ending on costal margin well before apex of wing;

RS arising at level of midwing, with 3 main branches; M independent of R basally and with two main branches. Crossveins numerous, forming a coarse network over the wing. Hind wing much smaller than fore wing; costal area narrow; venation apparently as in fore wing. Body little known; pronotum large. *U. Carb.*

Herdina CARPENTER & RICHARDSON, 1971, p. 291 [**H. mirificus*; OD]. CUA apparently unbranched; CUP forked, one branch directed toward hind margin of wing and very irregular. [It has been suggested by some workers that the specimen on which this genus is based is in fact a nymph, not an adult. However, the wings are well sclerotized, have thick veins, and are covered with tubercles. Two additional specimens, with similarly reduced wings, have more recently been found in the same deposit.] *U. Carb.*, USA (Illinois).—FIG. 73,3. **H. mirificus*; *a*, fore and *b*, hind wings, $\times 7$ (Carpenter & Richardson, 1971).

Family PSOROPTERIDAE

Carpenter, 1976

[Psoropteridae CARPENTER, 1976, p. 345]

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

Psoroptera CARPENTER, 1976, p. 345 [**P. cubitalia*; OD]. Fore wing with R extending almost to wing apex; RS arising at about level of fork of CUA; 2 rows of cells between M3+4 and CUA. *Perm.*, USA (Kansas).—FIG. 73,5. **P. cubitalia*; fore wing, $\times 9$ (Carpenter, 1976).

Family STREPHONEURIDAE

Martynov, 1940

[Strephoneuridae MARTYNOV, 1940, p. 14]

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

Strephoneura MARTYNOV, 1940, p. 14 [**S. robusta*; OD]. Subcostal area very narrow; MP anastomosed with CUA proximally. *Perm.*, USSR (Asian RSFSR).—FIG. 74,1. **S. robusta*; fore wing, $\times 1$ (Sharov, 1962c).

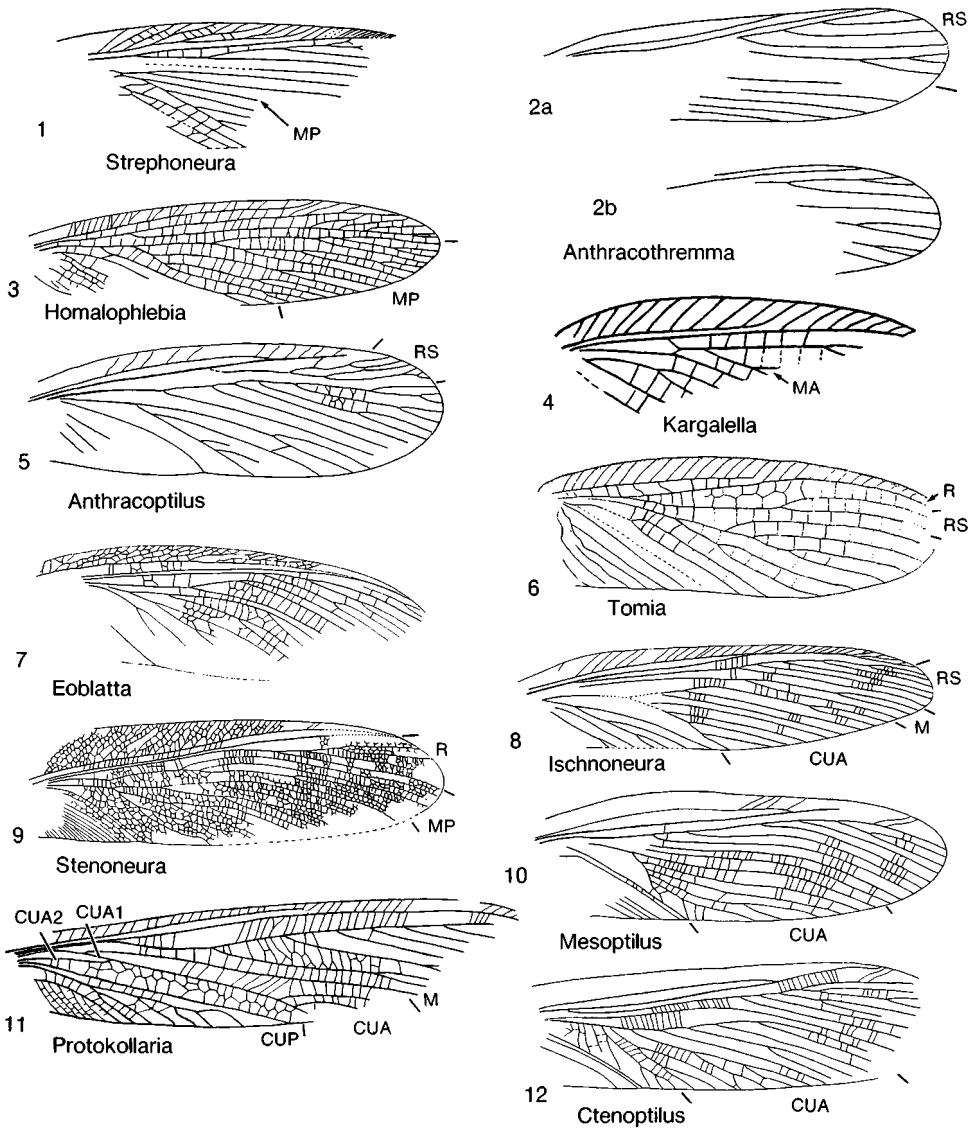


FIG. 74. Strephoneuridae, Anthracothremmidae, Tomiidae, Anthracoptilidae, Stenoneuridae, Homalophlebiidae, Ischnoneuridae, and Protokollariidae (p. 126–130).

Family ANTHRACOTHREMMIDAE
Handlirsch, 1906

[Anthracothremmidae HANDLIRSCH, 1906a, p. 712]

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

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

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

Pericalyphe HANDLIRSCH, 1911, p. 363 [**P. longa*; OD]. Similar to *Anthracothremma* but larger; RS

with simple branches. [Probably a synonym of *Anthracothebma*.] *U. Carb.*, USA (Illinois).

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

Family TOMIIDAE Martynov, 1936

[Tomiidae MARTYNOV, 1936, p. 1254]

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

Tomia MARTYNOV, 1936, p. 1255 [**T. costalis*; OD]. Double row of cells between RS and R proximally; other crossveins simple; MA with 4 branches. *Trias.*, USSR (Asian RSFSR).—FIG. 74,6. **T. costalis*; fore wing, $\times 3.5$ (Martynov, 1936).

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

—FIG. 74,4. **K. subcostilis*; fore wing, $\times 3.5$ (Martynov, 1937b).

Family ANTHRACOPTILIDAE Handlirsch, 1922

[Anthracoptilidae HANDLIRSCH, 1922, p. 98]

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

Anthracoptilus LAMEERE, 1917b, p. 180 [**Homalophlebia perrieri* MEUNIER, 1909d, p. 46; OD] [= *Prostenoneura* HANDLIRSCH, 1919b, p. 559, obj.]. All branches of RS directed anteriorly; RS with fewer branches than *M. U. Carb.*, Europe (France).—FIG. 74,5. **A. perrieri* (MEUNIER); fore wing, $\times 1.5$ (Carpenter, new).

Family CNEMIDOLESTIDAE Handlirsch, 1906

[Cnemidolestidae HANDLIRSCH, 1906b, p. 135]

Fore wing similar to that of *Ischnoneuridae*, but RS arising near midwing and cross-

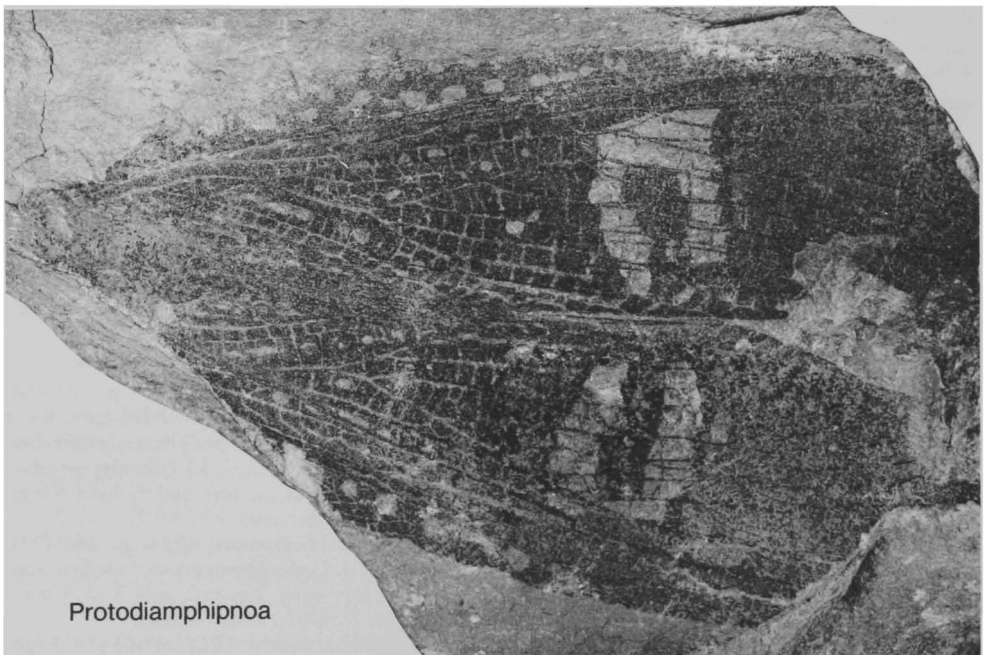


FIG. 75. *Cnemidolestidae* (p. 129).

veins fewer, more widely separated. Hind wing unknown. Prothorax small, about as long as wide; head small, slenderly oval; antennae long and filamentous; forelegs long and apparently raptorial. *U. Carb.*

Protodiamphipnoa BRONGNIART, 1893, p. 410 [**P. tertrini*; OD] [= *Cnemidolestes* HANDLIRSCH, 1906b, p. 135 (type, *Protophasma woodwardi* BRONGNIART, 1893, p. 427)]. Fore wing with M and CUA dividing at level of origin of RS; wings with conspicuous "eye spot." HANDLIRSCH, 1937. *U. Carb.*, Europe (France).—FIG. 75. **P. tertrini*; fore wings, $\times 1.5$ (Carpenter, new).—FIG. 76. *P. gaudryi* (BRONGNIART); fore wings and part of body, holotype, $\times 1.7$ (Carpenter, new).

Family STENONEURITIDAE

Lameere, 1917

[Stenoneuritidae LAMEERE, 1917b, p. 197]

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

Stenoneurites HANDLIRSCH, 1906b, p. 153 [**Stenoneura maximi* BRONGNIART, 1893, p. 430; OD]. MP forking before the origin of RS. *U. Carb.*, Europe (France).

Family STENONEURIDAE

Handlirsch, 1906

[Stenoneuridae HANDLIRSCH, 1906b, p. 152] [= Eoblattidae HANDLIRSCH, 1906b, p. 155]

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

Stenoneura BRONGNIART, 1893, p. 429 [**S. fayoli*; OD]. Fore wing with numerous crossveins forming very irregular, fine reticulation over most of wing, except anal area. *U. Carb.*, Europe (France).



Protodiamphipnoa

FIG. 76. Cnemidolestidae (p. 129).

—FIG. 74,9. **S. fayoli*; fore wing, $\times 1.2$ (Carpenter, new).

Eoblatta HANDLIRSCH, 1906b, p. 155 [**Stenoneura robusta* BRONGNIART, 1893, p. 429; OD]. Fore wing with fewer crossveins than in *Stenoneura*, forming coarse reticulation only in costal area and a few small regions of wing. *U. Carb.*, Europe (France).—FIG. 74,7. **E. robusta* (BRONGNIART); fore wing, $\times 0.9$ (Carpenter, new).

Family HOMALOPHLEBIIDAE

Handlirsch, 1906

[Homalophlebiidae HANDLIRSCH, 1906b, p. 136]

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

Homalophlebia BRONGNIART, 1893, p. 437 [**H. finoti*; SD HANDLIRSCH, 1906b, p. 136]. Fore wing with RS arising about one-third of wing length from base, with several branches; first fork of MP at same level. *U. Carb.*, Europe (France).—FIG. 74,3. **H. finoti*; fore wing, $\times 0.8$ (Carpenter, new).

Parahomalophlebia HANDLIRSCH, 1906b, p. 137 [**Homalophlebia courtini* BRONGNIART, 1893, p. 438; OD]. Similar to *Homalophlebia*, but RS with single fork. *U. Carb.*, Europe (France).

Family ISCHNONEURIDAE

Handlirsch, 1906

[Ischnoneuridae HANDLIRSCH, 1906b, p. 133] [=Stenoneurellidae HANDLIRSCH, 1919b, p. 560]

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

Ischnoneura BRONGNIART, 1893, p. 433, *nom. subst. pro Leptoneura* BRONGNIART, 1885a, p. 62, *non* WALLENGREN, 1857 [**Leptoneura oustaleti* BRONGNIART, 1885a, p. 62; SD HANDLIRSCH, 1922, p. 76] [=*Ischnoneurilla* HANDLIRSCH, 1919b, p. 556 (type, *Ischnoneura elongata* BRONGNIART, 1893, p. 433); *Ischnoneurona* HANDLIRSCH, 1919b, p. 557 (type, *Ischnoneura delicatula* BRONGNIART, 1893, p. 433)]. Branches of CUA close together and parallel. *U. Carb.*, Europe (France).—FIG. 74,8. **I. oustaleti* (BRONGNIART); fore wing, $\times 0.6$ (Carpenter, new).

Ctenoptilus LAMEERE, 1917b, p. 180 [**Homalophlebia trouessarti* MEUNIER, 1911a, p. 127; OD]. Similar to *Ischnoneura*, but branches of CUA more widely separated and divergent. *U. Carb.*, Europe (France).—FIG. 74,12. **C. trouessarti* (MEUNIER); fore wing, $\times 1.4$ (Carpenter, new).

Mesoptilus LAMEERE, 1917b, p. 174 [**M. dolloi*; OD] [=*Pseudoedischia* HANDLIRSCH, 1919b, p. 557 (type, *P. berthaudi*); *Stenoneurella* HANDLIRSCH, 1919b, p. 559 (type, *S. fayoliana*)]. Similar to *Ischnoneura*, but first branch of RS arising well before midwing; posterior branch of CUA more oblique than in *Ischnoneura*. *U. Carb.*, Europe (France).—FIG. 74,10. **M. dolloi*; fore wing, $\times 1.2$ (Carpenter, new).

Family PROTOKOLLARIIDAE

Handlirsch, 1906

[Protokollariidae HANDLIRSCH, 1906b, p. 137] [=Sthenaroceridae HANDLIRSCH, 1906b, p. 149; Laspeyresiellidae SCHLECHTENDAL, 1913, p. 96]

Fore wing very long, slender; vein SC terminating not far beyond midwing; RS arising near wing base, with several long branches. M and CUA1 anastomosed at wing base, separating before level of origin of RS; M apparently unbranched; CUA2 arising inde-

pendently of CUA1 but anastomosed with it shortly after separation of CUA1 from M; crossveins numerous. Hind wing unknown. Head small; antennae thick at base; prothorax narrow; front legs long. *U. Carb.*

Protokollaria BRONGNIART, 1893, p. 409 [**P. ingens*; OD]. CUA with 2 branches arising distally and curved; crossveins between CUA and CUP forming a coarse reticulation. *U. Carb.*, Europe (France).—FIG. 74,11. **P. ingens*; fore wing, $\times 1.5$ (Carpenter, new).

Laspeyresiella SCHLECHTENDAL, 1913, p. 96, *nom. subst. pro Laspeyresia* HANDLIRSCH, 1906b, p. 140, *non* HÜBNER, 1825 [**Laspeyresia wettinensis* HANDLIRSCH, 1906b, p. 140; OD] [=*Laspeyresiella* KRAUSSE, 1922, p. 132, obj. synonym & homonym]. Little-known genus, with wings and body shaped as in *Protokollaria*. *U. Carb.*, Europe (Germany).

Sthenarocera BRONGNIART, 1885a, p. 59 [**S. pachytyloides*; OD]. Similar to *Protokollaria*, but fore wing more slender; crossveins not forming a reticulation. *U. Carb.*, Europe (France).

Family PROTOPHASMATIDAE

Brongniart, 1885

[*nom. correct.* CARPENTER, herein, *pro* Protophasmida BRONGNIART, 1885a, p. 59]

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

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

Family UNCERTAIN

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

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

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

Aenigmarella SHAROV, 1961c, p. 159 [**A. com-*

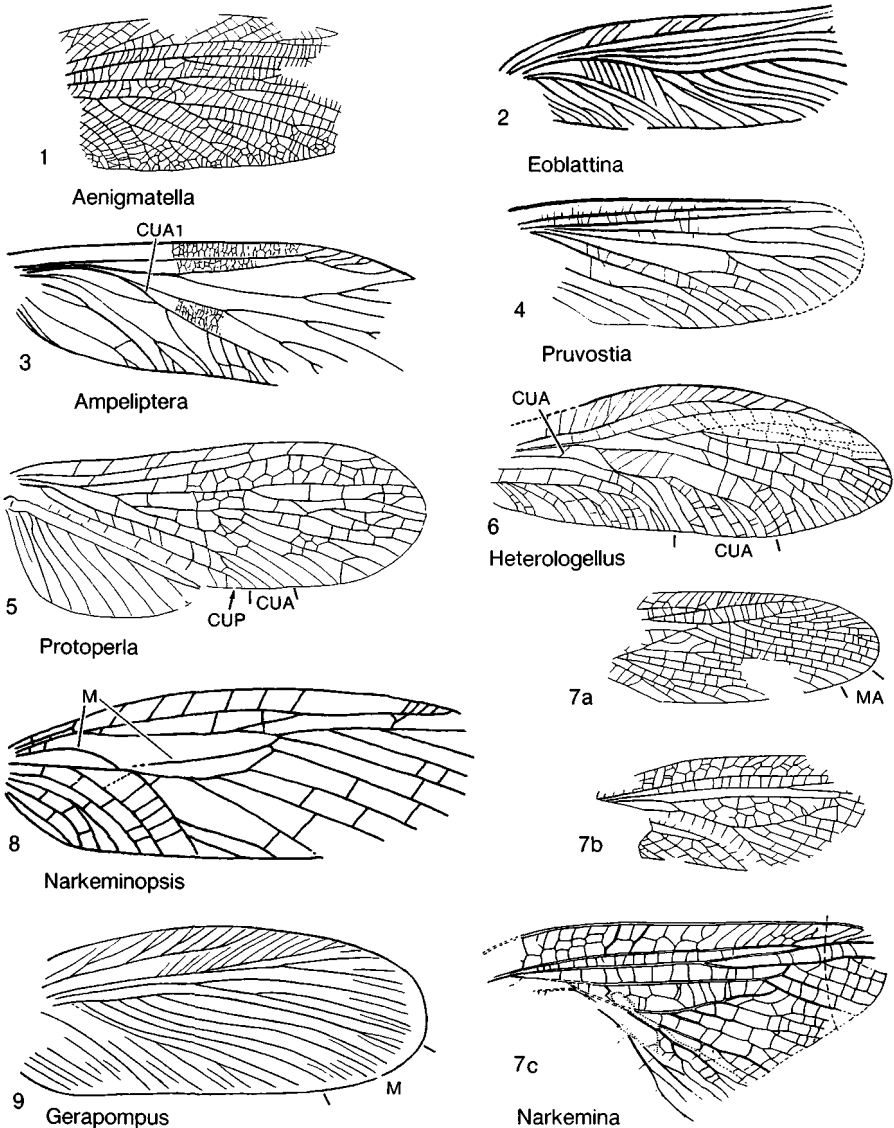


FIG. 77. Uncertain (p. 130–134).

parabilis; OD]. Costal area broad, with numerous veinlets; RS and M dividing at about same level; CUA very extensively developed. *U. Carb.*, USSR (Asian RSFSR).—FIG. 77.1. **A. comparabilis*; fore wing, $\times 1.4$ (Sharov, 1961c).

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

Aetophlebiopsis ZALESSKY, 1955b, p. 347 [**A. fusca*; OD]. Based on fragments of wings. *Perm.*, USSR (Asian RSFSR).

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

Ampeliptera PRUVOST, 1927, p. 76 [**A. limburgica*; OD]. Little-known genus, based on incomplete fore wing with fine archidictyon; CUA1 apparently anastomosed with M near wing base and diverging away before the level of the origin of RS, as in some Permian Orthoptera. [Placed in Hapalopteridae (order Hapaloptera) by PRUVOST (1927); in Palaeocixiidae (order Protor-

- thoptera) by HANDLIRSCH (1937); in family uncertain (order Paraplecoptera) by MARTYNOV (1938b); in new family Ampelipteridae (order Protocicadida) by HAUPT (1941); and in Paoliidae (order Protorthoptera) by KUKALOVÁ (1958b).] *U. Carb.*, Europe (Holland).—FIG. 77,3. **A. limburgica*; fore wing, holotype, $\times 5$ (Kukalová, 1958b).
- Anergertus** HANDLIRSCH, 1911, p. 353 [**A. cubitalis*; OD]. Based on wing fragments. *U. Carb.*, USA (Illinois).
- Anthracomastax** HANDLIRSCH, 1904a, p. 17 [**A. furcifer*; OD]. Based on wing fragment. *U. Carb.*, Europe (Belgium).
- Archaeologus** HANDLIRSCH, 1906a, p. 807 [**A. falcatus*; OD]. Based on fore and hind wing fragments. *U. Carb.*, USA (Illinois).
- Archimastax** HANDLIRSCH, 1906a, p. 806 [**A. americanus*; OD]. Based on wing fragment. *U. Carb.*, USA (Arkansas).
- Asiopompus** SHAROV, 1961c, p. 160 [**A. tomicus*; OD]. Based on fragment of fore wing. [Type of Asiopompidae SHAROV, 1961d.] *U. Carb.*, USSR (Asian RSFSR).
- Atava** SELLARDS, 1909, p. 157 [**A. ovata*; OD]. Based on fragment of hind wing. *Perm.*, USA (Kansas).
- Axiologus** HANDLIRSCH, 1906a, p. 805 [**A. thoracicus*; OD]. Based on fragments of body and wings. *U. Carb.*, USA (Illinois).
- Balduriella** MEUNIER, 1925, p. 105 [**B. latissima*; OD]. Based on wing fragment. *U. Carb.*, Europe (Germany).
- Boutakovia** PRUVOST, 1934, p. 1 [**B. saleei*; OD]. Based on wing fragment. [Placed in Homalophlebiidae by PRUVOST.] *U. Carb./Perm.*, Africa (Zaire).
- Cacurgellus** PRUVOST, 1919, p. 125 [**C. barryi*; OD]. Based on wing fragment. *U. Carb.* Europe (France).
- Cheliphlebia** SCUDDER, 1885d, p. 328 [**C. carbonaria*; OD]. Little-known genus, based on fragments of fore wings. [Type of Cheliphlebiidae HANDLIRSCH, 1906a, p. 709.] *U. Carb.*, USA (Illinois).
- Chrestotes** SCUDDER, 1868b, p. 567 [**C. lapidea*; OD]. Based on fragments of wings. *U. Carb.*, USA (Illinois).
- Commentrya** LAMEERE, 1917b, p. 176 [**Oedischia maximae* BRONGNIART, 1893, p. 437; OD]. Little-known genus, based on body fragment. *U. Carb.*, Europe (France).
- Danielsiella** COCKERELL, 1916c, p. 100 [**D. priscula*; OD]. Based on fragments of wings and body. *U. Carb.*, USA (Illinois).
- Didymophleps** SCUDDER, 1885d, p. 330 [**Termes contusa* SCUDDER, 1878c, p. 300; OD]. Based on small fragment of wing. *U. Carb.*, USA (Illinois).
- Dieconeurites** HANDLIRSCH, 1906a, p. 699 [**Dieconeurina rigida* SCUDDER, 1885d, p. 336; OD]. Based on wing fragment. *U. Carb.*, USA (Pennsylvania).
- Distasis** HANDLIRSCH, 1904a, p. 17 [**D. rhipophora*; OD]. Based on distal fragment of hind wing. *U. Carb.*, Europe (Belgium).
- Endoiasmus** HANDLIRSCH, 1906a, p. 805 [**E. reticulatus*; OD]. Based on wing fragment. *U. Carb.*, USA (Illinois).
- Eoblattina** BOLTON, 1925, p. 19 [**E. complexa*; OD]. Little-known genus, based on fragments of wings and body; fore wing with extensive, sigmoidal CUA having several short, straight branches leading to CUP. *U. Carb.*, Europe (France). — FIG. 77,2. **E. complexa*; fore wing, $\times 1.3$ (Bolton, 1925).
- Gerapompus** SCUDDER, 1885d, p. 326 [**G. blattinoides*; SD HANDLIRSCH, 1906a, p. 711]. Little-known genus, based on poorly preserved fore wing; R and RS apparently with several long branches distally; M extensively branched. [Type of Gerapompidae HANDLIRSCH, 1906a, p. 711.] *U. Carb.*, USA (Illinois).—FIG. 77,9. *G. schucherti* HANDLIRSCH; fore wing, $\times 2$ (Handlirsch, 1906a).
- Gerarianus** HANDLIRSCH, 1919b, p. 551 [**G. commentryanus*; OD]. Based on wing fragments. *U. Carb.*, Europe (France).
- Gerarites** HANDLIRSCH, 1919b, p. 551 [**Gerarus commentryi* BRONGNIART, 1893, pl. 24, fig. 10; OD]. Based on wing fragment. *U. Carb.*, Europe (France).
- Geraroides** HANDLIRSCH, 1906a, p. 704 [**Dieconeurina maxima* MELANDER, 1903, p. 193; OD]. Little-known genus, based on fragments of wings and body. HANDLIRSCH, 1922. *U. Carb.*, USA (Illinois).
- Germanoprisca** ZEUNER, 1936a, p. 267 [**F. zimmermanni*; OD]. Little-known insect with prominent, slender cerci; fore wing fragment. [Type of Germanopriscidae ZEUNER, 1936a.] MÜLLER, 1978b. *Perm.*, Europe (Germany).
- Gyrophlebia** HANDLIRSCH, 1906a, p. 697 [**G. longicollis*; OD]. Little-known genus, based on poorly preserved fore wing and body. *U. Carb.*, USA (Illinois).
- Hadentomoides** RIEK, 1974a, p. 15 [**H. duykenensis*; OD]. Little-known genus, based on apical fragment of wing. [Originally placed in family Hadentomidae.] *Perm.*, South Africa (Natal).
- Haplopterum** MARTYNOV, 1928b, p. 84 [**H. majus*; OD]. Based on hind wing fragment. *Perm.*, USSR (European RSFSR).
- Hemeristia** DANA, 1864, p. 35 [**H. occidentalis*; OD] [= *Hemeristica* GOLDENBERG, 1877, p. 15, obj.]. Based on wing fragments. *U. Carb.*, USA (Illinois).
- Heterologellus** SCHMIDT, 1962, p. 843 [**H. teichmuelleriae*; OD]. Apparently similar to *Omalia*, but fore wing with SC terminating on R well before wing apex; MP dividing distally, near

- wing margin; CUA only just touching CUP, not coalesced with it; MP not as extensively branched as CUA. [Placed in Omaliidae by SCHMIDT.] *U. Carb.*, Europe (Germany).—FIG. 77,6. **H. teichmuelleriae*; fore wing, $\times 3$ (Schmidt, 1962).
- Heterologopsis** BRAUCKMANN & KOCH, 1982, p. 18 [**H. rubrensis*; OD]. Little-known genus, apparently related to the Cacurgidae, but SC much shorter and terminating on R. *U. Carb.*, Europe (Germany).
- Kaltanopterodes** SHAROV, 1961d, p. 223 [**K. vanus*; OD]. Based on hind wing of nymph. *Perm.*, USSR (Asian RSFSR).
- Kargalodes** MARTYNOV, 1937b, p. 33 [**K. incerta*; OD]. Based on wing fragment. *Perm.*, USSR (European RSFSR).
- Kelleropteron** BRAUCKMANN & HAHN, 1980, p. 308 [**K. kaelberbesense*; OD]. Little-known genus, based on small fragment of wing. *U. Carb.*, Europe (Germany).
- Khosarophlebia** MARTYNOV, 1940, p. 24 [**K. sylvaensis*; OD]. Based on hind wing fragment. *Perm.*, USSR (Asian RSFSR).
- Klebsiella** MEUNIER, 1908c, p. 242 [**K. exstincta*; OD]. Based on fragments of fore and hind wings. [Type of Klebsiellidae HANDLIRSCH, 1919b, p. 552.] *U. Carb.*, Europe (France).
- Lecopterum** SELLARDS, 1909, p. 161 [**L. delicosum*; OD]. Based on wing fragment. *Perm.*, USA (Kansas).
- Limburgina** LAURENTIAUX, 1950, p. 14 [**L. antiqua*; OD]. Based on wing fragment, with suggestions of convex MA. [Ordinal position doubtful.] *U. Carb.*, Europe (Netherlands).
- Macrophlebiom** GOLDENBERG, 1869, p. 164 [**M. hollebeni*; OD]. Based on wing fragment. *U. Carb.*, Europe (Germany).
- Megalometer** HANDLIRSCH, 1906a, p. 713 [**M. lata*; OD]. Based on fragments of wings. *U. Carb.*, USA (Illinois).
- Mesorthopteron** TILLYARD in TILLYARD & DUNSTAN, 1916, p. 14 [**M. locustoides*; OD]. Little-known genus, based on fragments of fore wing. Fore wing elongate-oval, with fine archidictyon; costal area broad, with numerous, parallel veinlets; SC straight and close to R and RS, with several distal branches; M weakly formed; CUA with numerous long, pectinate branches; anal area small. [Type of family Mesorthopteridae TILLYARD, 1922b.] RIEK, 1956. *Trias.*, Australia (New South Wales).
- Metacheliphlebia** HANDLIRSCH, 1906a, p. 698 [**Cheliphlebia elongata* SCUDDER, 1885d, p. 328; OD]. Little-known genus, based on small fragments of wings. HANDLIRSCH, 1906b. *U. Carb.*, USA (Illinois).
- Miamia** DANA, 1864, p. 34 [**M. bronsoni*; OD]. Little-known genus, based on wing fragments. [Possibly belonging to the Spanioideridae.] *U. Carb.*, USA (Illinois).
- Mitinovia** SHAROV, 1961d, p. 223 [**M. dubia*; OD]. Based on hind wing with extensive veinlets from R to costa beyond SC. *Perm.*, USSR (Asian RSFSR).
- Narkemina** MARTYNOV, 1931a, p. 81 [**N. angustata*; OD]. Fore wing elongate-oval; venation with some resemblance to that of the Narkemidae. RS forking near midwing; M dividing near base, MA continuing in a straight line and branching beyond origin of RS; MP diverging posteriorly and coalescing with CUA for a considerable interval before diverging anteriorly, its terminal branches joining some of those of MA; CUA with a few short, terminal branches; CUP unbranched. Hind wing very broad, with an enlarged anal area, but with the venation of the remigium much as in the fore wing. [PINTO & ORNELLAS (1978c) correctly recognized that the genus *Narkemina*, formerly placed in the Narkemidae, required a separate family, but they proposed the invalid family name, Narkemiparacurgidae, for the type genus *Narkemina*.] SHAROV, 1961e; PINTO & ORNELLAS, 1978c; LEWIS, 1979; RASNITSYN, 1980c. *U. Carb.*, USSR (Asian RSFSR), Brazil (Parana Basin), USA (Missouri).—FIG. 77,7a. **N. angustata*; fore wing, $\times 2.6$ (Sharov, 1961e).—FIG. 77,7b. *N. angustiformis* SHAROV; fore wing, $\times 2$ (Sharov, 1961e).—FIG. 77,7c. *N. rodendorfi* PINTO & ORNELLAS; hind wing, $\times 1.2$ (Pinto & Ornellas, 1978c).
- Narkeminopsis** WHALLEY, 1979, p. 87 [**N. eddi*; OD]. Little-known genus. Apparently similar to *Narkemina*, but fore wing with M diverging posteriorly near wing base, then anastomosing briefly with CUA before diverging anteriorly and joining RS at level of end of SC; few costal veinlets; archidictyon present in costal and CUA areas. *U. Carb.*, England.—FIG. 77,8. **N. eddi*; fore wing, $\times 2.5$ (Whalley, 1979).
- Ochetopteron** COCKERELL, 1927g, p. 414 [**O. cancellulatum*; OD]. Little-known genus, based on wing fragment. *U. Carb.*, USA (Maryland).
- Orthoneurites** MARTYNOV, 1928b, p. 49 [**O. regularis*; OD]. Based on distal wing fragment. *Perm.*, USSR (European RSFSR).
- Palaeocarrina** COCKERELL, 1917e, p. 80 [**P. ornata*; OD]. Based on fragment of wing. *U. Carb.*, USA (Illinois).
- Palaeoedischia** MEUNIER, 1914d, p. 364 [**P. boulei*; OD]. Based on fragment of fore wing. *U. Carb.*, Europe (France).
- Palaeomantopsis** MARTYNOV, 1928b, p. 83 [**P. furcatella*; OD]. Based on distal wing fragment. *Perm.*, USSR (European RSFSR).
- Paolekia** RIEK, 1976a, p. 764 [**P. perditae*; OD]. Little-known genus, based on small apical fragment of wing. [Placed originally in Paoliidae.] *Perm.*, South Africa (Natal).
- Paranarkemina** PINTO & ORNELLAS, 1980a, p. 288

- [**P. kurtzi*; OD]. Little-known genus, based on incomplete wing. SC ending on R beyond level of midwing; RS arising basally and forking at about level of end of SC, with numerous branches; M forking before origin of RS; MA with 2 distal branches; CUA anastomosed briefly with MP before terminating in many branches. *U. Carb.*, Argentina (San Luis).
- Polyernus** SCUDDER, 1885d, p. 343 [**D. complanatus*; OD]. Based on fragments of wings and body. *U. Carb.*, USA (Illinois).
- Polyetes** HANDLIRSCH, 1906a, p. 715 [**P. furcifer*; OD]. Based on small wing fragment. *U. Carb.*, USA (Illinois).
- Protoperla** BRONGNIART, 1893, p. 407 [**P. westwoodi*; OD]. Little-known genus, based on hind wing. SC ending on costal margin near midwing; M apparently coalesced with R and RS basally; RS with 2 main branches; M with numerous irregular branches; CUA with 3 very short terminal branches; CUP unbranched. Anal area enlarged, with a series of long pectinate branches from 2A. [Placed in the family Protoperlidae by BRONGNIART.] LAMEERE, 1917b. *U. Carb.*, Europe (France).—FIG. 77,5. **P. westwoodi*; hind wing, $\times 4$ (Carpenter, new).
- Prototettix** GIEBEL, 1856, p. 306 [**Gryllacris lithantraca* GOLDENBERG, 1854, p. 24; OD]. Based on fore wing fragment. [Type of Prototettigidae HANDLIRSCH, 1906b, p. 135.] *U. Carb.*, Europe (Germany).
- Pruvostia** BOLTON, 1921, p. 48 [**P. spectabilis*; OD]. Little-known wing (probably hind) with basal origin of RS. *U. Carb.*, Europe (England).—FIG. 77,4. **P. spectabilis*; wing, $\times 0.9$ (Bolton, 1921).
- Pseudetoblattina** HANDLIRSCH, 1906a, p. 714 [**Etoblattina reliqua* SCUDDER, 1893b, p. 18; OD]. Based on wing fragment. *U. Carb.*, USA (Rhode Island).
- Pseudogerarus** HANDLIRSCH, 1906a, p. 804 [**P. scudderi*; OD]. Based on small fragments of wings. *U. Carb.*, USA (Illinois).
- Pseudopolyernus** HANDLIRSCH, 1906a, p. 803 [**Polyernus laminarum* SCUDDER, 1885d, p. 343; OD]. Little-known genus, based on wing fragments. *U. Carb.*, USA (Pennsylvania).
- Ptenodera** BOLTON, 1922, p. 90 [**P. dubius*; OD]. Based on distal wing fragment. *U. Carb.*, England.
- Rhipidoptera** BRONGNIART, 1893, p. 447 [**R. elegans*; OD]. Little-known genus, based on small fragment of wing. *U. Carb.*, Europe (France).
- Roomeria** MEUNIER, 1914e, p. 388 [**R. carbonaria*; OD]. Based on little-known fore wing. [Type of Roomeriidae HANDLIRSCH, 1919.] *U. Carb.*, Europe (France).
- Schuchertiella** HANDLIRSCH, 1911, p. 311 [**S. gracilis*; OD]. Little-known genus, based on small wing fragment. [Type of Schuchertiellidae HANDLIRSCH, 1911.] *U. Carb.*, USA (Illinois).
- Sellardsiopsis** ZALESKY, 1939, p. 51 [**S. conspicua*; OD]. Little-known fore wing. *Perm.*, USSR (Asian RSFSR).
- Sharovia** PINTO & ORNELLAS, 1978b, p. 100, *junior homonym*, *Sharovia* SINITSHENKOVA, 1977 [**S. permiafricana*; OD]. Little-known genus, based on wing fragment. [Originally placed in Lemmatophoridae.] *Perm.*, South Africa (Cape of Good Hope).
- Sindonopsis** MARTYNOV, 1928b, p. 61 [**S. subcostalis*; SD SHAROV, 1962c, p. 117]. Little-known wing with short SC. *Perm.*, USSR (European RSFSR).
- Thaumatophora** RIEK, 1976d, p. 147 [**T. pronotalis*; OD]. Little-known genus, based on nymph with lateral abdominal gills. *Perm.*, South Africa (Natal).

Order BLATTARIA Latreille, 1810

[Blattaria LATREILLE, 1810, p. 246] [=Blatodea BRUNNER, 1882, p. 26; Protofulgorida HAUPT (in part), 1941, p. 75]

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

These are primitive orthopteroids, probably most closely related to the Isoptera among existing orders (McKITTRICK, 1965). The order is now a relatively small one, containing less than 4,000 species (M. J. MAC-

KERRAS, 1970), but the geological record indicates that it was one of the largest orders of insects during the late Paleozoic.

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

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

Unfortunately, such details of structure are rarely preserved in fossil roaches, with the exception of those in amber. The vast majority of fossil Blattaria, close to 90 percent, consist of isolated wings or wing fragments. Furthermore, most of the specimens with bodies preserved have the two pairs of wings folded back over the body in the usual resting position, obscuring most of the body structures that are preserved (Fig. 78). Study of extensive series of Paleozoic roaches has shown that their venational variability was at least as great as that of existing species (SCHNEIDER, 1977, 1978a, 1978b). The tendency in

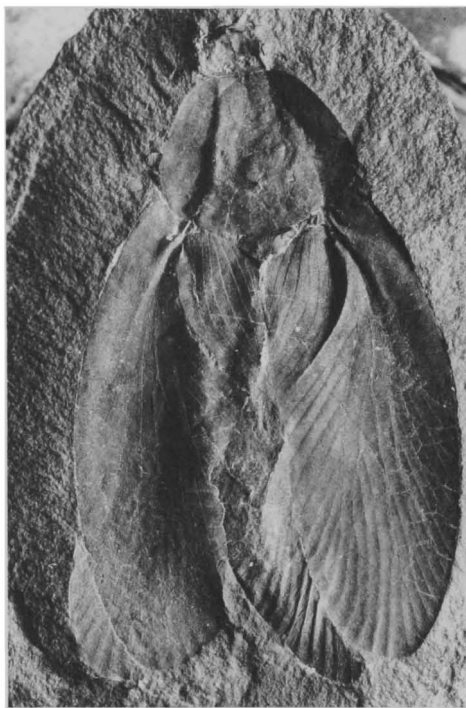


FIG. 78. Blattaria; dorsal view of an archimylacrid roach from the Upper Carboniferous of Illinois in its normal resting posture, $\times 3.4$ (Carpenter, new).

publications on these fossils has been to place emphasis on slight differences in venation, resulting in many families and genera. At least 25 extinct families and 370 extinct genera have been named from Paleozoic and early Mesozoic deposits, and fully half of these are based on single specimens.

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

Quite apart from the wings, the geological record has provided some interesting data bearing on the reproduction of the Blattaria.

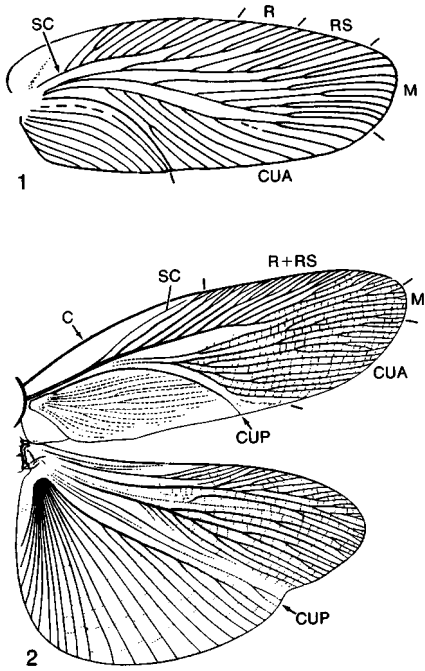


FIG. 79. Blattaria; typical venation.—1. Tegmen of *Phyloblatta manebachensis* GOLDENBERG, Upper Carboniferous of Germany, Archimyliacridae, $\times 2.2$ (Schneider, 1978b).—2. Tegmen and hind wing of *Periplaneta brunnea*, Holocene of Australia, Blattidae, $\times 2.3$ (CSIRO, 1970).

The females of existing roaches lack a true ovipositor but commonly possess short internal valves that serve only to guide the fertilized eggs (several to many) into the genital atrium, where the ootheca is formed. In some species the oothecae are deposited within a few days, the embryos developing outside the body of the female. In others, the oothecae are first extruded, then retracted, and finally deposited in the brood sac, where the embryos continue their development. When they are mature, the ootheca is extruded again and the nymphs emerge from it (ROTH, 1967; M. J. MACKERRAS, 1970). Several small and obscure fossils, presumed to be oothecae, have been reported from Paleozoic deposits, but these are not very convincing as oothecae, and all are now considered to be fragments

of other organisms (BROWN, 1957; VISHNIAKOVA, 1968). Furthermore, numerous specimens of female Blattaria with long, external ovipositors are known from Upper Carboniferous and Permian deposits of Europe, Asia, and North America (BRONGNIART, 1889; SELLARDS, 1904; ZALESSKY, 1939, 1940, 1953b). In more recent years Dr. V. N. VISHNIAKOVA of the Paleontological Institute in Moscow has described similar ovipositors on specimens from Triassic and Jurassic deposits of the USSR (VISHNIAKOVA, 1965, 1968, 1973) (Fig. 80, 1–3). From her detailed study of these remarkable fossils, Dr. VISHNIAKOVA concluded that these ovipositors were derived from the eighth and ninth abdominal sternites and that they were therefore homologous with the ovipositors of the Orthoptera but not with the short internal valves of the existing Blattaria, which are derived from the seventh sternite (NEL, 1929; SHAROV, 1966b). It is noteworthy that in some of the Jurassic species the ovipositor is very short (Fig. 80, 1). The gradual shortening and ultimate loss of the long external ovipositors apparently took place toward the end of the Mesozoic.

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

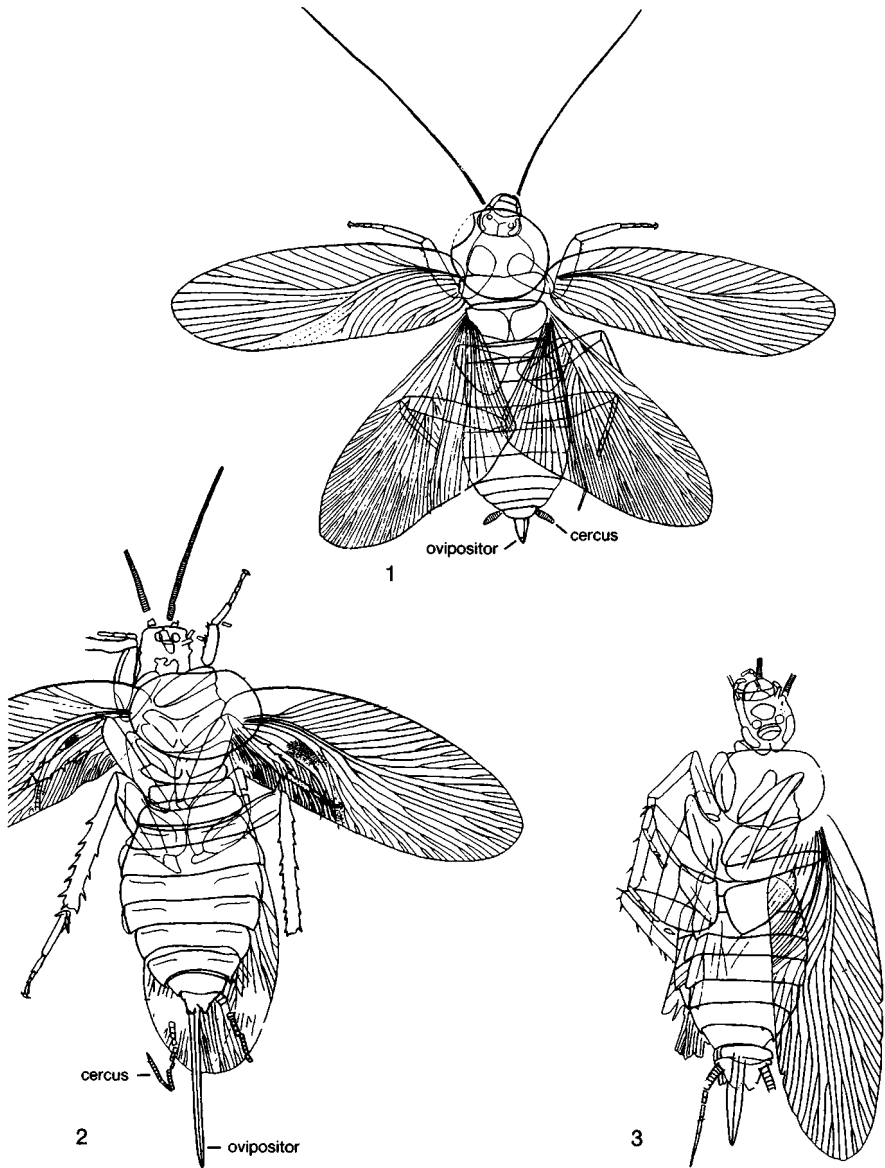


FIG. 80. Blattaria; wings and body of several female specimens from the family Mesoblattinidae.—1. *Artitocoblatta asiatica* VISHNIAKOVA, Jurassic of the USSR, $\times 3.5$.—2. *Karatavoblatta longicaudata* VISHNIAKOVA, Jurassic of the USSR, $\times 1$.—3. *Rhipidoblatta brevisvalvata* VISHNIAKOVA, Jurassic of the USSR, $\times 2$ (all Vishniakova, 1968).

Order ISOPTERA Brullé, 1832

[Isoptera BRULLÉ, 1832, p. 66]

Wings membranous, usually very similar, held flat over abdomen at rest, and possessing a transverse humeral or basal suture; veins

in anterior part of wings more strongly sclerotized than in remainder; crossveins very weakly developed, commonly forming delicate reticulation covering all or greater part of wing surface; vein C marginal; SC simple or branched, in some species very short or



FIG. 81. Isoptera; holotype specimen of *Cretatermes carpenteri*, Hodotermitidae, Cretaceous of Labrador, $\times 16.5$ (Carpenter, new).

completely absent as distinct vein; radial system usually consisting of distinct R of variable length, equally distinct RS1+2 arising from R very near base of wing, and more highly developed RS3+4 arising about at origin of RS1+2 and forming a series of branches extending to apical or subapical region of wing (with much variation in degree of development of these radial veins); M weak but often extensively branched, no indication of division into MA and MP; CUA also weak, tending to be extensively branched along posterior margin; CUP usually weak and commonly short; anal fold formed along CUP in some; 1A usually short and reduced. Mouthparts mandibulate; antennae moniliform; cerci distinct in all castes. All species social and polymorphic, their communities composed of reproductive forms and numerous workers and soldiers. *Cret.-Holo.*

The Isoptera, commonly known as termites, are clearly related to the orthopteroids and show closest affinities with the Blattodea (McKITTICK, 1964, 1965). The known range of the existing family Mastotermitidae, universally regarded as the most primitive family, is only from the late Oligocene or early Miocene. The earliest records of the order, however, consist of two genera from the Cretaceous (EMERSON, 1967; JARZEMBOWSKI, 1981). Both belong to the existing

family Hodotermitidae, which, although less specialized than the Termitidae, is distinctly more advanced than the Mastotermitidae with respect to both morphology and social behavior. It seems almost certain, therefore, that some species closely related to the Mastotermitidae will eventually be found in Jurassic or even Triassic deposits.

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

That some degree of social behavior was present among the Isoptera as far back as the Cretaceous is also apparent. In all existing termites the main part of the wing is separated from its base by a line of fracture, the humeral or basal suture (Fig. 81, *Cretatermes*; see also Fig. 82, 2a, *Mastotermes*, and Fig. 83, 7a, *Proelectrotermes*); shortly after the adult's flight from the parent colony, the

wings break off at the suture, leaving a stub or scale. The dropping of the wings after nuptial flight is obviously related to the founding of a new colony, the wings no longer being useful. The presence of humeral sutures in the Cretaceous specimens is therefore convincing evidence that colony founding had already been developed in the family Hodotermitidae by the Early Cretaceous.

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

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

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

Family MASTOTERMITIDAE

Desneux, 1904

[Mastotermitidae DESNEUX, 1904a, p. 284]

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

Mastotermes FROGGATT, 1896, p. 517 [= *Pliotermes* PONGRÁ CZ, 1926, p. 26 (type, *P. hungaricus*)]. EMERSON, 1965; JARZEMBOWSKI, 1980; KRISHNA & EMERSON, 1983. *Eoc.*, England; *Oligo.*, Europe (Germany), England; *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*—FIG. 82.2. *M. darwiniensis* FROGGATT, recent; *a*, fore and *b*, hind wings (humeral suture absent), $\times 2$ (CSIRO, 1970).

Blattotermes RIEK, 1952b, p. 17 [**B. neoxenus*; OD]. Similar to *Mastotermes* but with less consolidation of RS. COLLINS, 1925; EMERSON, 1965. ?*Eoc.*, Australia (Queensland); *Eoc.*, USA (Tennessee).—FIG. 82.3a. **B. neoxenus*, ?*Eoc.*, Australia; fore wing, $\times 2.4$ (Riek, 1952a).—FIG. 82.3b. *B. wheeleri* (COLLINS), *Eoc.*, Tennessee; wing, $\times 2.0$ (Collins, 1925).

Miotermes VON ROSEN, 1913, p. 325 [**M. procerus* HEER; OD]. Wing venation as in *Mastotermes* but with more extensively developed M. [Family assignment doubtful.] *Mio.*, Europe (Germany, Yugoslavia).—FIG. 82.1. **M. procerus* (HEER); hind wing, $\times 1.8$ (Pongrácz, 1926).

Spargotermes EMERSON, 1965, p. 19 [**S. costalimai*; OD]. Hind wings: RS diffuse, with several main branches forking to form additional branches reaching to wing tip. *Mio./Plio.*, Brazil.—FIG. 82.4. **S. costalimai*; hind wing with anal area folded under rest of wing, $\times 3.4$ (Emerson, 1965).

Family KALOTERMITIDAE

Froggatt, 1896

[Kalotermitidae FROGGATT, 1896, p. 516]

Wing membrane reticulate; vein R short and almost always unbranched; pronotum as wide as head or nearly so; 4 tarsal segments. KRISHNA, 1961; EMERSON, 1969. *Eoc.*—*Holo.*

Kalotermes HAGEN, 1853, p. 479. HAGEN, 1861–1863; HANDLIRSCH, 1907; COCKERELL, 1917a; SNYDER, 1949; KRISHNA, 1961; EMERSON, 1969; JARZEMBOWSKI, 1980. *Eoc.*, Europe (France); *Oligo.*, England, Europe (Baltic, Germany); *Mio.*, Europe (Germany, Italy), Asia (Burma)—*Holo.*

Calcaritermes SNYDER, 1925, p. 155. EMERSON, 1969. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Cryptotermes BANKS, 1906, p. 336. [Generic position of fossil uncertain.] PIERCE, 1958. *Mio.*, USA (California)—*Holo.*

Electrotermes VON ROSEN, 1913, p. 331 [**Termes*

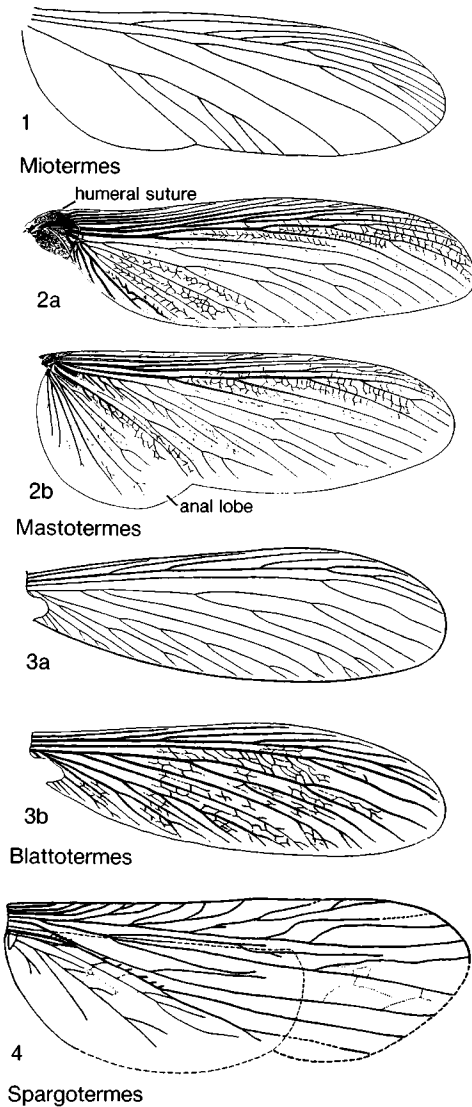


FIG. 82. Mastotermitidae (p. 139).

affinis HAGEN in PICTET & HAGEN, 1856, p. 49; OD]. Similar to *Kaloterмес*, but middle tibiae with 2 outer spines distally. KRISHNA, 1961; EMERSON, 1969. *Oligo.*, Europe (Baltic).—FIG. 83,6. *E. affinis* (HAGEN); a, fore wing, $\times 7.0$; b, right middle leg, $\times 1.2$ (both Krishna, 1961).

Eotermes STATZ, 1939–1940, p. 13 [**E. grandaeva*; OD]. Similar to *Proelectrotermes* but much larger; lateral spines on middle tibiae relatively shorter; M weak, its main stem close and parallel to RS. EMERSON, 1969. *Oligo.*, Europe (Germany).—FIG. 83,8. **E. grandaeva*; fore wing, $\times 1.5$ (Emerson, 1969).

Incisitermes KRISHNA, 1961, p. 353. EMERSON, 1969. *Oligo./Mio.*, Mexico (Chiapas)—*Holo.*

Neotermes HOLMGREN, 1911, p. 53. PITON, 1940a; EMERSON, 1969. *Eoc.*, Europe (France)—*Holo.*

Proelectrotermes VON ROSEN, 1913, p. 331 [**Kaloterмес berendtii* PICTET in PICTET & HAGEN, 1856, p. 49; OD]. Similar to *Kaloterмес*, but middle tibiae with a single inner-lateral spine and 2 outer-lateral spines; fore wing with a very short SC; branches of RS directed anteriorly and terminating on anterior margin; M slightly nearer to RS than to CU at midwing. SCUDDER, 1883a; KRISHNA, 1961; EMERSON, 1969. *Oligo.*, Europe (Baltic).—FIG. 83,7. **P. berendtii* (PICTET); a, fore wing as preserved, $\times 5.5$; b, right middle leg, $\times 6.0$ (both Krishna, 1961).

Prokaloterмес EMERSON, 1933, p. 189 [**Paroterмес hageni* SCUDDER, 1883a, p. 139; OD]. Similar to *Proelectrotermes* but with 24 to 26 antennal segments. EMERSON, 1969; LEWIS, 1977a. *Oligo.*, USA (Colorado, Montana).

Family HODOTERMITIDAE

Desneux, 1904

[Hodotermitidae DESNEUX, 1904b, p. 14]

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

Hodoterмес HAGEN, 1853, p. 480. *Holo.*

Archotermopsis DESNEUX, 1904b, p. 13. VON ROSEN, 1913. *Oligo.*, Europe (Baltic)—*Holo.*

Cretaterмес EMERSON, 1967, p. 284 [**C. carpenteri*; OD]. Fore wing small, humeral suture evenly curved; RS area gradually widened from base to apical quarter of wing; M about midway between RS and CU; CU short, not reaching beyond basal half of posterior margin of wing. *Cret.*, Canada (Labrador).—FIG. 81. **C. carpenteri*; holotype, $\times 16.5$ (Carpenter, new).—FIG. 83,5. **C. carpenteri*; venation of fore wing, $\times 8.0$ (Emerson, 1967).

Paroterмес SCUDDER, 1883a, p. 135 [**P. insignis*; OD]. Second marginal tooth of left mandible slightly shorter than first marginal tooth; posterior edge of second marginal tooth and anterior edge of third marginal tooth not symmetrical. *Oligo.*, USA (Colorado).—FIG. 83,4. **P. insignis*; outline of left mandible, $\times 26$ (Emerson, 1933).

Termopsis HEER, 1849, p. 23 [**T. breinii*; SD HAGEN, 1858c, p. 74] [= *Xestotermopsis* VON ROSEN, 1913, p. 330, obj.]. Similar to *Zootermopsis* but having 5 hind tarsal segments visible above and below; humeral suture in fore wing only slightly curved. EMERSON, 1933. *Oligo.*,

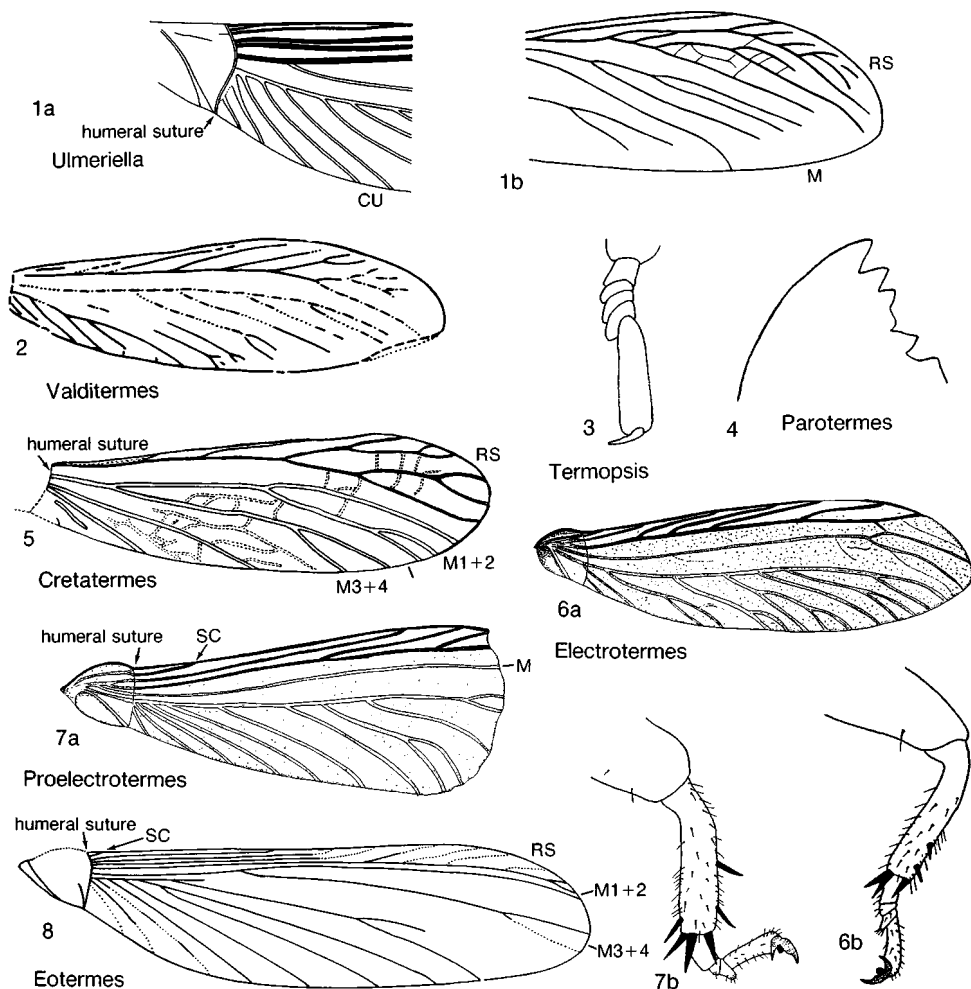


FIG. 83. Kalotermitidae and Hodotermitidae (p. 139-141).

Europe (Baltic).—FIG. 83,3. **T. breinii*; hind tarsus, $\times 7$ (Emerson, 1933).
Ulmeriella MEUNIER, 1920a, p. 728 [**U. bauckborni*; OD] [= *Diatermes* MARTYNOV, 1929, p. 178 (type, *D. cockerelli*)]. Vein RS with several branches directed posteriorly and terminating on hind margin. MARTYNOV, 1929; ZEUNER, 1938; STATZ, 1939-1940; SNYDER, 1949; WEIDNER, 1967, 1968b, 1971; EMERSON, 1968. *Oligo.*, Europe (Germany), USSR (Kazakh); *Mio.*, Europe (Germany), USA (Washington); *Plio.*, Europe (Germany).—FIG. 83,1. **U. bauckborni*; a, base of fore wing, $\times 8$; b, distal half of fore wing, $\times 6$ (both Emerson, 1968).
Valditermes JARZEMBOWSKI, 1981, p. 92 [**V. brenanae*; OD]. Similar to *Cretatermes* but larger; fore wing more elongate; branching of RS and CU more complex. *Cret.*, England.—FIG. 83,2.

**V. brenanae*; fore wing, $\times 5.5$ (Jarzembowski, 1981).
Zootermopsis EMERSON, 1933, p. 182. [Generic assignment doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Family RHINOTERMITIDAE
Froggatt, 1896

[*Rhinotermitidae* FROGGATT, 1896, p. 518]

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

- Rhinotermes** HAGEN, 1858, p. 233. *Holo.*
Coptotermes WASMANN, 1896, p. 629. SNYDER, 1960; EMERSON, 1971. *Oligo./Mio.*, Dominican Republic, Mexico (Chiapas)—*Holo.*
Heterotermes FROGGATT, 1896, p. 518. Adult. SNYDER, 1960. *Mio.*, Mexico (Chiapas)—*Holo.*
Parastylotermes SNYDER & EMERSON in SNYDER, 1949, p. 378 [**Stylotermes washingtonensis* SNYDER, 1931, p. 317; OD]. Similar to *Reticulitermes*, but wing membrane and veins almost without hairs; eyes relatively larger than in *Reticulitermes*; ocelli distinct; stump of fore wing (basal scale) proportionately large. SNYDER, 1950, 1955; PIERCE, 1958. *Oligo.*, Europe (Baltic); *Mio.*, USA (Washington, California).
Reticulitermes HOLMGREN, 1913, p. 60. ARMBRUSTER, 1941; WEIDNER, 1955, 1971; PIERCE, 1958; EMERSON, 1971. *Oligo.*, Europe (Baltic, Germany), USA (Colorado); *Mio.*, USA (California), Europe (Germany); *Plio.*, Europe (Germany)—*Holo.*
Rhinotermes ARMBRUSTER, 1941, p. 21 [**R. dzierzoni*; OD]. Little-known genus, based on wing and body fragments. EMERSON, 1971. *Mio.*, Europe (Germany).

Family TERMITIDAE

Westwood, 1840

[Termitidae WESTWOOD, 1840, p. 11]

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

- Termes** LINNÉ, 1758, p. 609. *Holo.*
Gnathamitermes LIGHT, 1932, p. 390. PIERCE, 1958. *Mio.*, USA (California)—*Holo.*
Macrotermes HOLMGREN, 1909, p. 193. [Generic assignment of fossil doubtful.] CHARPENTIER, 1843; SNYDER, 1949. *Mio.*, Europe (Yugoslavia)—*Holo.*

Family UNCERTAIN

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

- Architermes** HAUPT, 1956, p. 28 [**A. simplex*; OD]. Little-known wing. *Eoc.*, Europe (Germany).
Mastotermes ARMBRUSTER, 1941, p. 13 [**M. stuttgartensis*; OD]. Little-known genus, possibly a synonym of *Miotermes*. EMERSON, 1971. *Plio.*, Europe (Germany).
Metatermes ARMBRUSTER, 1941, p. 26 [**M. statzi*; OD]. Little-known genus. EMERSON, 1971. *Mio.*, Europe (Germany).

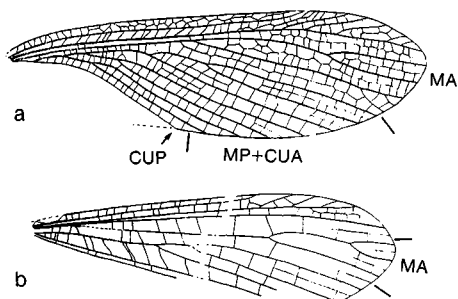
Order MANTEODEA

Burmeister, 1838

[Manteodea BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 517, as Mantodea]

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

The Manteodea, although clearly related to the Orthoptera, are less specialized in some respects (e.g., five-segmented tarsi, segmented cerci). In all probability they are even more closely related to the Blattaria (McKITTRICK, 1964, 1965) but appear to have been derived independently from a protorthopterous stock and to have evolved



Lithophotina

FIG. 84. Chaeteessidae (p. 143).

entirely as predators; the raptorial forelegs, present in all known species, show several types of modification. Although the oldest known Manteodea are from the Baltic amber (Oligocene), the group probably existed in the Mesozoic and even in the Permian. Some of the Late Carboniferous Protorthoptera are known to have possessed raptorial forelegs, but they do not appear to be related closely to the Manteodea.

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

Family CHAETEESIDAE
Handlirsch, 1920

[Chaeteessidae HANDLIRSCH, 1920, p. 497]

Fore wing having vein R with several distinct, anteriorly pectinate branches distally;

fore tarsus attached to distal end of tibia; tibia lacking terminal projecting hook. *Oligo.*—*Holo.*

Chaeteessa BURMEISTER, 1838, p. 527. [Generic assignment very dubious.] GIEBEL, 1862. *Oligo.*, Europe (Baltic)—*Holo.*

Lithophotina COCKERELL, 1908s, p. 343 [**L. floccosa*; OD]. Similar to *Chaeteessa* (recent) but with more pectinate branches on R in fore wing. SHAROV, 1962a. *Oligo.*, USA (Colorado).—FIG. 84. **L. floccosa*; a, fore wing and b, remigium of hind wing, $\times 2.5$ (Cockerell, 1908s).

Family MANTEIDAE Saussure, 1859

[*nom. correct.* ROBERTS, 1941, p. 15, *pro* Mantidae SAUSSURE, 1859, p. 59]

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

Mantis LINNÉ, 1758, p. 425. ZEUNER, 1931. *Mio.*, Europe (Germany)—*Holo.*

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

Order PROTELYTROPTERA

Tillyard, 1931

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

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