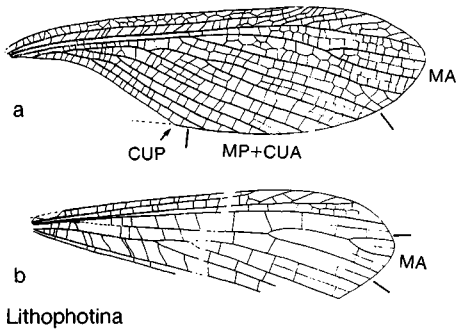


FIG. 84. Chaeteessidae (p. 143).

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

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

Family CHAETEESSIDAE Handlirsch, 1920

[Chaeteessidae HANDLIRSCH, 1920, p. 497]

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

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

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

Family MANTEIDAE Saussure, 1859

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

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

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

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

Order PROTELYTROPTERA Tillyard, 1931

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

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

terior margin of elytron; cluster of small setae commonly present near subcosta and another along basal part of sutural margin; in Megelytridae microtrichia covering entire elytron. Hind wings typically longer and much broader than elytra; anal area expanded, with longitudinal and, in some families, transverse folding. Abdomen broad, terminating in short but prominent cerci about as long as last 3 abdominal segments. Females with short external ovipositor. Immature stages unknown. CARPENTER & KUKALOVÁ, 1964. *Perm.–Cret.*

The fore wings in this extinct order of elytrophorous insects resemble those of the Coleoptera, but the general nature of the venation of both fore and hind wings and the presence of prominent cerci indicate relationship with the orthopteroids, especially the Blattaria and Dermaptera. Although few species of Protelytroptera are known at present, their diversity suggests that the order was a large and varied group, at least during the Permian. The relatively recent discovery of the family Umenocoleidae in a Cretaceous deposit (see below) indicates that the order may have continued to diversify throughout the Mesozoic.

In the more primitive species the fore wings tended to be tegminous and almost flat, with the costal expansion small, the sutural margin absent or weakly developed, and the crossveins numerous (e.g., Archelytridae, Apachelytridae). In the more specialized forms, in which the fore wings were convex and heavily sclerotized, the main veins were reduced or obsolescent distally, crossveins were virtually absent, and the surfaces of the elytra were granulate or rugose (e.g., Protelytridae, Permelytridae, Planelytridae, Umenocoleidae).

The hind wings, which are known in four families (Archelytridae, Protelytridae, Permelytridae, Apachelytridae), had a narrow remigium and a well-developed anal fan. However, there were substantial differences in the structure of the wings in these families. Those of the Protelytridae could fold at rest transversely as well as longitudinally (TILLYARD, 1931; CARPENTER, 1933a), but those of the Permelytridae and Apachelytridae could apparently fold only longitudinally (CARPENTER & KUKALOVÁ, 1964).

The body structure is known, very incompletely, in the families Protelytridae, Permelytridae, and Apachelytridae.

Family ELYTRONEURIDAE Carpenter, 1933

[Elytroneuridae CARPENTER, 1933a, p. 478]

Elytron nearly flat, not convex; sutural margin apparently absent; vein SC branched; M and CUA fused for considerable distance beyond wing base. *Perm.*

Elytroneura CARPENTER, 1933a, p. 478 [**E. permiana*; OD]. Costal margin convex, costal expansion very prominent; SC remote from anterior wing margin. *Perm.*, USA (Kansas).——FIG. 85,*4*. **E. permiana*; elytron, ×4 (Carpenter, 1933a).

Family ARCHELYTRIDAE Carpenter, 1933

[Archelytridae CARPENTER, 1933a, p. 477]

Elytron slightly convex; costal expansion weakly developed; stems of main veins independent; vein SC long, terminating about two-thirds of wing length from base; SC, R, M, CUP, and 1A unbranched; CUP strongly concave; sutural margin well developed, terminating before apex; weak crossveins over entire wing. *Perm.*

Archelytron CARPENTER, 1933a, p. 477 [**A. superbum*; OD]. Costal margin strongly arched. Vein SC weakly developed at base but strong distally; RS arising at level of termination of SC; CUA and CUP diverging about one-fifth wing length from base; CUA with 3 terminal branches; most crossveins unbranched. [The generic name *Archelytron* was subsequently proposed by HAUPT (1952, p. 248) for a Permian species, *priscus*, that he assigned to the Coleoptera. However, Dr. Jörg SCHNEIDER of the Bergakademie Freiberg, Germany, who recently examined the unique specimen for me, found that it is a plant fragment, not an insect. No homonymy is, therefore, involved.] CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).——FIG. 85,*2*. **A. superbum*; fore wing, ×8 (Carpenter & Kukalová, 1964).

Ortelytron KUKALOVÁ, 1965, p. 66 [**O. europaeum*; OD]. Similar to *Archelytron*, but fore wing with much shorter sutural margin and with crossveins

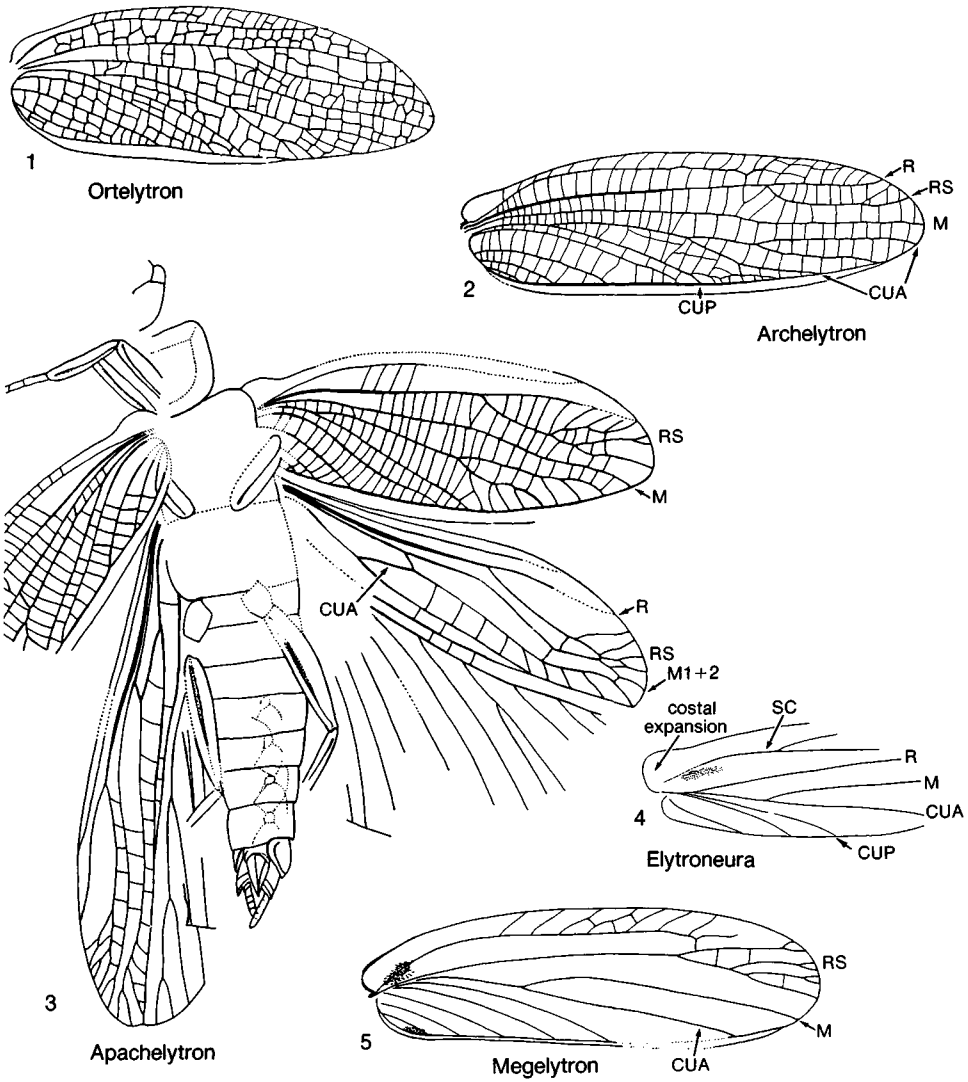


FIG. 85. Elytroneuridae, Archelytridae, Apachelytridae, and Megelytridae (p. 144–147).

more irregular. Hind wing with CUP and 1A close together and parallel from wing base to distal margin. *Perm.*, Europe (Czechoslovakia). ——FIG. 85,*1*. **O. europaeum*; fore wing, ×14 (Kukalová, 1965).

Family APACHELYTRIDAE Carpenter & Kukalová, 1964

[Apachelytridae CARPENTER & KUKALOVÁ, 1964, p. 185]

Related to Archelytridae. Fore wing weakly tegminous, similar to that of Archelytridae, but costal expansion larger and crossveins more numerous and virtually all unbranched. Hind wing with expanded anal area as in Protelytridae; stem of vein M independent of R; M forked near midwing; CUP coalesced with 1A. Body little known; eyes relatively small; pronotum rectangular; forelegs short, hind legs much longer, with well-developed femora; tarsi short, segmented. *Perm.*

Apachelytron CARPENTER & KUKALOVÁ, 1964, p. 187 [**A. transversum*; OD]. Costal margin of fore wing arched; RS arising slightly beyond

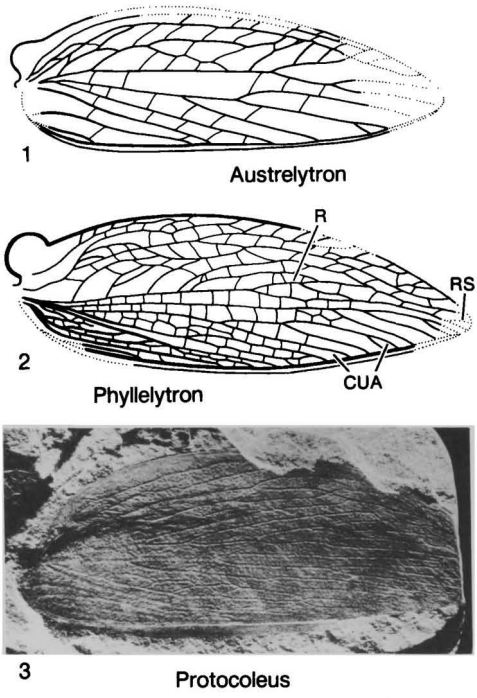


FIG. 86. Protocoleidae (p. 146).

midwing. *Perm.,* Europe (Moravia).——FIG. 85,*3*. **A. transversum*; holotype as preserved, ×9 (Carpenter & Kukalová, 1964).

Family PROTOCOLEIDAE Tillyard, 1924

[Protocoleidae TILLYARD, 1924b, p. 434]

Fore wing tegminous, only slightly convex; anterior margin strongly arched; sutural margin nearly straight and bordering entire posterior margin; wing surface granulate and with tubercles at least in some areas; setae commonly present in subcostal area; costal expansion large; vein SC long with several to many branches; RS arising near midwing; M and CUA with several branches, variable in form. Hind wing and body unknown. *Perm.*

Protocoleus TILLYARD, 1924b, p. 434 [**P. mitcheli*; OD]. Fore wing uniformly covered with flat tubercles; main veins and their branches parallel with longitudinal axis of wing; RS arising near midwing. KUKALOVÁ, 1966. *Perm.,* Australia (New South Wales).——FIG. 86,*3*. **P. mitcheli*; fore wing, holotype, ×3.2 (Tillyard, 1924b).

Austrelytron KUKALOVÁ, 1966, p. 96 [**A. tillyardi*; OD]. Similar to *Protocoleus* but with fewer branches of main veins and crossveins; tubercles few and pointed. *Perm.,* Australia (New South Wales).——FIG. 86,*1*. **A. tillyardi*; fore wing, ×5 (Kukalová, 1966).

Phyllelytron KUKALOVÁ, 1966, p. 94 [**P. folium*; OD]. Similar to *Protocoleus,* but main veins and their branches very irregular, not aligned or parallel with longitudinal axis of wing; granulation of wing surface coarse. *Perm.,* Australia (New South Wales).——FIG. 86,*2*. **P. folium*; fore wing, ×2.3 (Kukalová, 1966).

Family PROTELYTRIDAE Tillyard, 1931

[Protelytridae TILLYARD, 1931, p. 235]

Elytron convex, anterior margin strongly arched; vein SC short, not extending beyond midwing; venation and sutural margin well developed; RS and CUP unbranched; M free from CUA or coalesced with it basally for a short interval; 3 or 4 anal veins. Hind wing: anal area with about 10 anal veins; stem of M coalesced with R. Body apparently flattened; antenna well developed, with short, thick segments. *Perm.*

Protelytron TILLYARD, 1931, p. 239 [**P. permianum*; OD]. Vein CUA unbranched; patches of setae along SC and basal part of sutural margin. *Perm.,* USA (Kansas).——FIG. 87,*3a*. *P. furcatum* CARPENTER; elytron, ×8.8 (Carpenter, 1933a).——FIG. 87,*3b*. **P. permianum*; reconstruction, ×5.4 (Carpenter, 1933a).

Permelytropsis CARPENTER, 1933a, p. 474 [**P. cubitalis*; OD]. CU unbranched. *Perm.,* USA (Kansas).——FIG. 87,*1*. **P. cubitalis*; elytron, ×10 (Carpenter, 1933a).

Uralelytron ROHDENDORF, 1939, p. 506 [**U. martynovi*; OD]. Little-known elytron and body fragments. [Family assignment uncertain.] *Perm.,* USSR (Asian RSFSR).——FIG. 87,*2*. **U. martynovi*; elytron, ×8 (Rohdendorf, 1939).

Family MEGELYTRIDAE Carpenter, 1933

[Megelytridae CARPENTER, 1933a, p. 476]

Fore wing flat except for basal part of costal area; costal expansion very small; vein R very strong; RS arising in distal part of wing, branched; CUA and M coalesced basally, both unbranched; sutural margin complete; several oblique crossveins in costal area; entire

wing with a dense covering of fine hair. Hind wing unknown. *Perm.*

Megelytron TILLYARD, 1931, p. 247 [**M. robustum*; OD]. Vein RS with 4 terminal branches and several twigs; one cluster of setae at base of subcosta and another near inner margin of anal area. CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).——FIG. 85,5. **M. robustum*; fore wing, ×5 (Carpenter & Kukalová, 1964).

Family PLANELYTRIDAE Kukalová, 1965

[Planelytridae KUKALOVÁ, 1965, p. 75]

Fore wing almost flat; anterior margin strongly arched; costal expansion well developed; vein SC extending about two-thirds of wing length from base; veins M and CUA coalesced for about one-third wing length from base; sutural margin well developed. *Perm.*

Planelytron KUKALOVÁ, 1965, p. 75 [**P. planum*; OD]. SC strongly arched in costal area; weak crossveins in subcostal area. *Perm.*, Europe (Czechoslovakia).——FIG. 88,2. **P. planum*; fore wing, ×8 (Kukalová, 1965).

Family PERMELYTRIDAE Tillyard, 1931

[Permelytridae TILLYARD, 1931, p. 246] [=Blattelytridae TILLYARD, 1931, p. 249; Acosmelytridae TILLYARD, 1931, p. 252]

Fore wing convex; costal margin arched; veins weakly developed, commonly obsolescent distally; vein RS absent; MA commonly free from CU, rarely coalesced with it; sutural margin normally developed. Hind wing apparently like that of *Protelytron*, but SC much longer and terminating on RS. Body little known; head smaller than in Protelytridae and Apachelytridae; antenna, as preserved, about as long as abdomen; cerci short, segmented. *Perm.*

Permelytron TILLYARD, 1931, p. 246 [**P. schucherti*; OD]. Vein M of fore wing not coalesced with CUA. CARPENTER & KUKALOVÁ, 1964. *Perm.*, USA (Kansas).——FIG. 88,4. **P. schucherti*; elytron, ×6.7 (Carpenter, 1939).

Blattelytron TILLYARD, 1931, p. 250 [**B. permianum*; OD]. Little-known genus, based on fragment of elytron. *Perm.*, USA (Kansas).——FIG. 88,5. **B. permianum*; elytron, ×5 (Tillyard, 1931).

Parablattelytron TILLYARD, 1931, p. 251 [**P. subincisum*; OD] [=*Acosmelytron* TILLYARD, 1931, p. 253 (type, *A. elongatum*)]. Vein CUA coalesced with M basally; main veins commonly obsolescent in distal half of wing. *Perm.*, USA (Kansas).——FIG. 88,6. **P. subincisum*; dorsal view as preserved, ×7 (Carpenter & Kukalová, 1964).

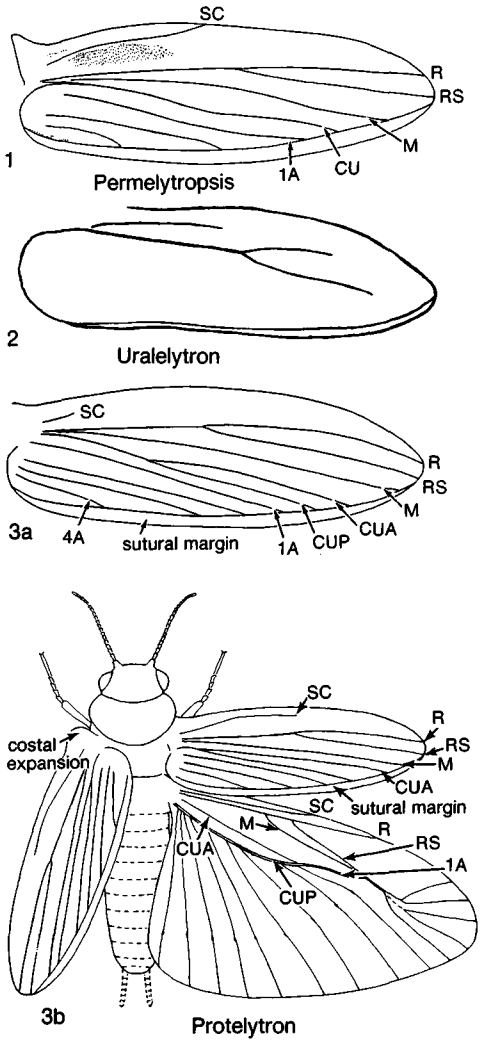


FIG. 87. Protelytridae (p. 146).

Family PERMOPHILIDAE Tillyard, 1924

[Permophilidae TILLYARD, 1924b, p. 430]

Fore wing tegminous, slightly convex; sutural margin distinct but narrow; wing surface with granulation and tubercles; costal

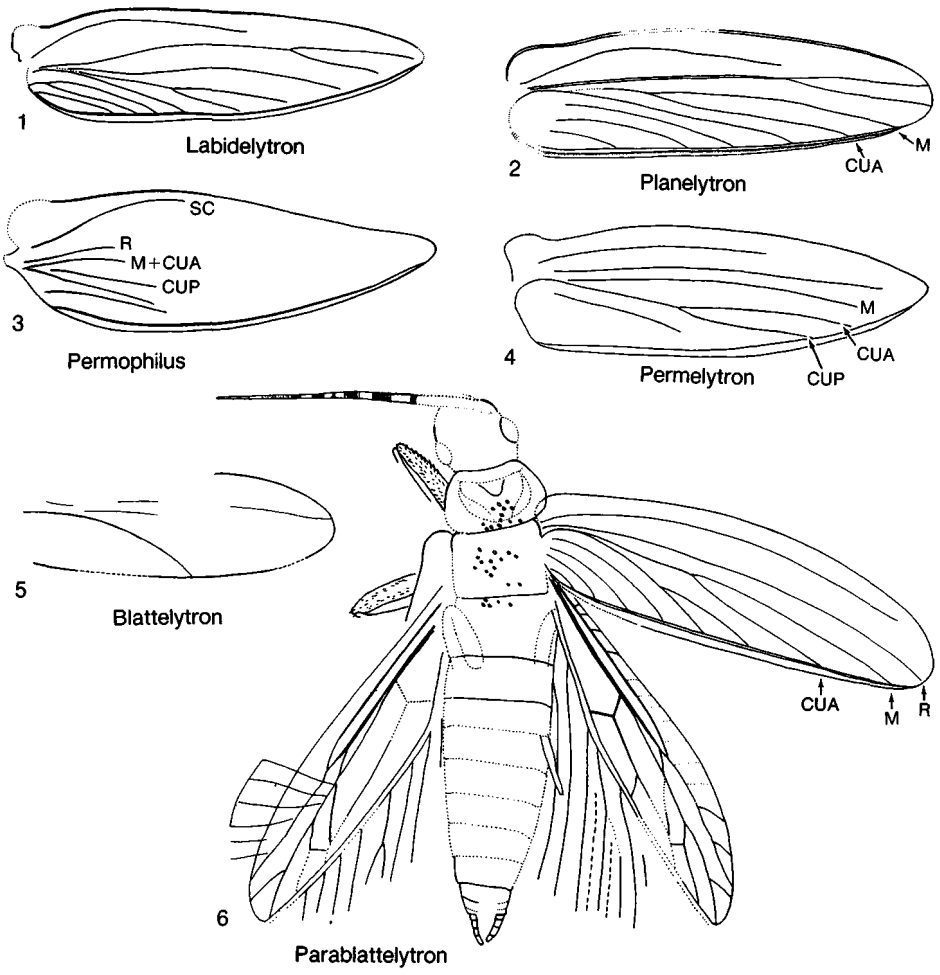


FIG. 88. Planelytridae, Permelytridae, Permophilidae, and Labidelytridae (p. 147–148).

expansion prominent; costal margin arched but asymmetrical; apex acute; main veins present in basal half of wing only. [Originally placed in Coleoptera.] *Perm.*

Permophilus TILLYARD, 1924b, p. 430 [**P. pincombei*; OD]. Fore wing with very narrow sutural margin; wing surface with dense granulation and indistinct tubercles; wing strongly narrowed in distal half. KUKALOVÁ, 1966. *Perm.*, Australia (New South Wales).——FIG. 88,*3*. *P. hirtus* KUKALOVÁ; fore wing, ×8 (Kukalová, 1966).

Elytrathrix KUKALOVÁ, 1966, p. 102 [**E. hirsuta*; OD]. Similar to *Permophilus* but with conspicuous tubercles and setae in basal half of wing, including costal expansion. *Perm.*, Australia (New South Wales).

Family LABIDELYTRIDAE Kukalová-Peck, 1988

[Labidelytridae KUKALOVÁ-PECK, 1988, p. 339, *nom. subst. pro* Stenelytridae KUKALOVÁ, 1966, p. 102]

Fore wing tegminous, nearly flat, long and slender; apex pointed; surface finely granulate; costal expansion large; venation as in Protelytridae. *Perm.*

Labidelytron KUKALOVÁ-PECK, 1988, p. 339, *nom subst. pro Stenelytron* KUKALOVÁ, 1966, p. 102, *non* HANDLIRSCH, 1906 [**Stenelytron enervatum* KUKALOVÁ, 1966; OD]. Vein M of fore wing unbranched, not coalesced with CU basally. *Perm.*, Australia (New South Wales).——FIG. 88,*1*. **L. enervatum*; fore wing, ×4 (Kukalová, 1966).

Xenelytron KUKALOVÁ, 1966, p. 105 [**X. ligula*; OD]. Similar to *Stenelytron,* but M coalesced with CU in basal half of wing. *Perm.,* Australia (New South Wales).

Family DERMELYTRIDAE Kukalová, 1966

[Dermelytridae KUKALOVÁ, 1966, p. 105]

Fore wing convex, apparently weakly sclerotized; anterior margin convex; sutural margin well developed; venation much reduced, at most with only basal parts of veins R, CU, and A present. *Perm.*

Dermelytron KUKALOVÁ, 1966, p. 106 [**D. conservativum*; OD]. Fore wing oval, apex directed posteriorly; costal expansion small. *Perm.,* Australia (New South Wales).

Chanoselytron KUKALOVÁ, 1966, p. 108 [**C. gingiva*; OD]. Similar to *Dermelytron,* but costal expansion much larger. *Perm.,* Australia (New South Wales).

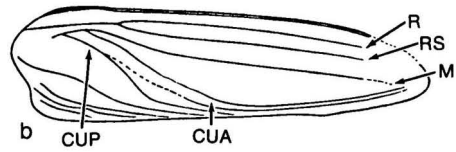
Psychelytron KUKALOVÁ, 1966, p. 108 [**P. progressivum*; OD]. Fore wing as in *Dermelytron,* but apex directed anterolaterally. *Perm.,* Australia (New South Wales).

Family UMENOCOLEIDAE Chen & T'an, 1973

[Umenocoleidae CHEN & T'AN, 1973, p. 174]

Elytron apparently only slightly convex, elongate, with well-developed longitudinal veins; vein SC very close to and paralleling anterior margin of wing; R nearly parallel to SC; RS arising about one-fifth of wing length from base; stems of M and CU coalesced; M diverging from common stem just before level of origin of RS, parallel to RS; CUA diverging posteriorly as far as midwing, then continuing parallel to posterior margin of wing; CUP apparently forked, with an anterior branch directed toward posterior margin of wing, then continuing parallel to CUA; 4 short anal veins; crossveins apparently absent, but surface of wing finely granulate. Hind wing little known, extending a short distance beyond end of fore wing. Body little known; antennae filiform, with at least 16 segments; pronotum broader than long, coarsely granulate. *Cret.*

The remarkable fossil on which this genus and family is based was placed by its authors in the order Coleoptera. However, the general structure of the elytra and of their venation in particular is so much like that of the Protelytroptera that I transferred the insect to that order. The filiform and segmented nature of the antennae and the peculiar vena-



Umenocoleus

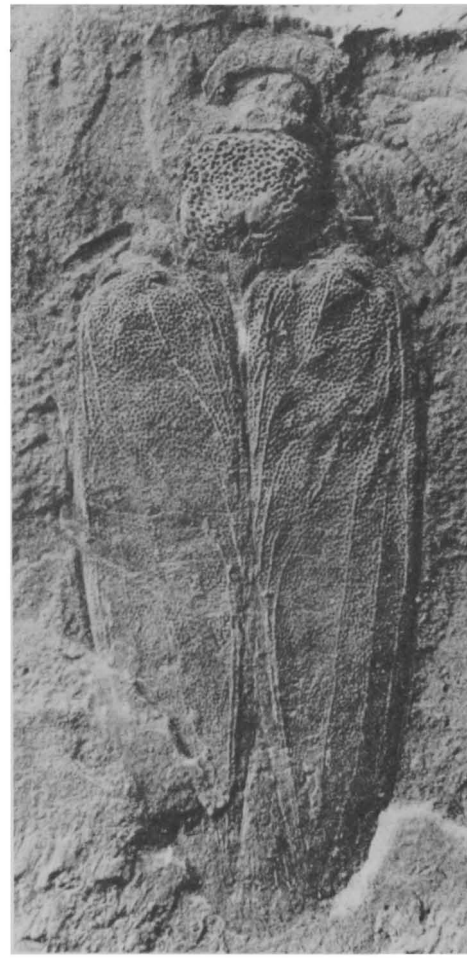


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FIG. 89. Umenocoleidae (p. 150).

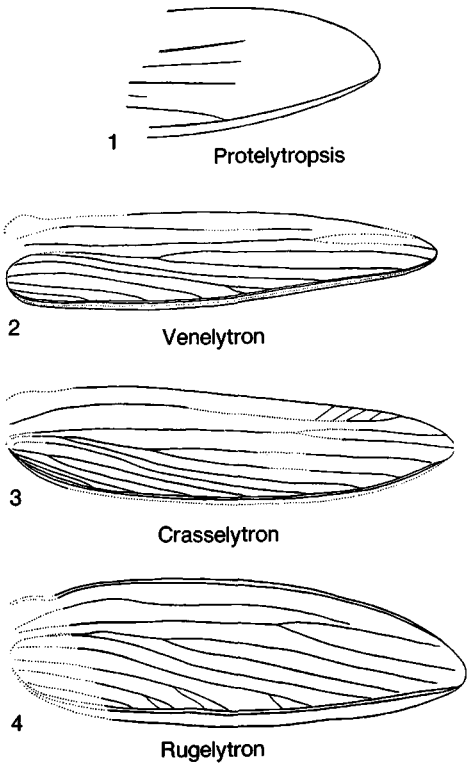


FIG. 90. Uncertain (p. 150).

tional pattern are not at all like those of the Coleoptera, as noted by the authors. Of course, since no Protelytroptera have been reported from deposits later than the Permian, this Cretaceous fossil extends the range of the order at least a hundred million years. It also suggests the possibility that some of the isolated and poorly preserved elytra found in Triassic or Jurassic deposits and identified as Coleoptera may actually be Protelytroptera.

Umenocoleus CHEN & T'AN, 1973, p. 169 [**U. sinuatus*; OD]. RS and CUA unbranched. *Cret.*, China (Kansu).——FIG. 89. **U. sinuatus; a*, dorsal view of holotype, ×7.0 (Chen & T'an, 1973); *b*, elytron, ×4.5 (after Chen & T'an, 1973).

Family UNCERTAIN

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

Artocoleus MARTYNOV, 1933b, p. 78 [**A. ivensis*; OD]. Little-known elytron. [Ordinal assignment doubtful.] *Perm.*, USSR (European RSFSR).

Crasselytron KUKALOVÁ, 1965, p. 70 [**C. convexum*; OD]. Fore wing very convex, slender and long; anterior margin nearly straight; SC extending nearly to wing apex; M coalesced with CUA for about one-third of wing length from base; wing surface granulate; sutural margin very narrow. *Perm.*, Europe (Czechoslovakia).——FIG. 90,*3*. **C. convexum*; fore wing, ×7 (Kukalová, 1965).

Glabelytron KUKALOVÁ, 1965, p. 77 [**G. lativenosum*; OD]. Fore wing flat; anterior margin arched; SC sigmoidal, unbranched, extending about two-thirds of wing length. *Perm.*, Europe (Czechoslovakia).

Protelytropsis TILLYARD, 1931, p. 245 [**P. grandis*; OD]. Distal fragment of large elytron. *Perm.*, USA (Kansas).——FIG. 90,*1*. **P. grandis*; elytron, ×7 (Tillyard, 1931).

Rugelytron KUKALOVÁ, 1965, p. 72 [**R. fuscum*; OD]. Fore wing convex, relatively long; anterior margin arched; sutural margin well developed, extending to wing apex; M coalesced with CUA for about one-third of wing length from base; wing surface granulate. *Perm.*, Europe (Czechoslovakia).——FIG. 90,*4*. **R. fuscum*; fore wing, ×7 (Kukalová, 1965).

Venelytron KUKALOVÁ, 1965, p. 73 [**V. tuberculatum*; OD]. Fore wing long and narrow; anterior margin nearly staight; SC long, extending nearly to apex; M and CUA coalesced for about one-third wing length from base; posterior margin of wing slightly concave distally; wing surface granulate. *Perm.*, Europe (Czechoslovakia).——FIG. 90,*2*. **V. tuberculatum*; fore wing, ×4.5 (Kukalová, 1965).

Order DERMAPTERA de Geer, 1773

[Dermaptera DE GEER, 1773, p. 399]

Head broad, with mandibulate mouthparts and conspicuous antennae, consisting of at least 10 segments, usually many more; compound eyes commonly very large; ocelli absent in recent species; fore wings forming short, convex tegmina or elytra, typically lacking veins; hind wings semicircular, with greatly expanded anal area; remigium much reduced, with at most vestiges of veins SC, R, M, and CU; at rest, hind wings folded radially and also transversely beneath tegmina; hind wings commonly absent; abdomen usually broad, first tergum fused with

metathorax; in typical species (suborder Forficulina) cerci forming pair of heavily sclerotized, unsegmented forceps; ovipositor present in primitive species, absent in others. Immature stages similar to adults in general characteristics; cerci usually styliform. Subsocial habits in several genera. Most species omnivorous. *Jur.–Holo.*

The Dermaptera share many features of the Orthoptera and Blattaria, and they almost certainly arose from related stock. However, their peculiarly modified wings and thorax indicate that they belong to a widely divergent line.

The most distinctive characteristics of the Dermaptera are found in the modifications of their wings and cerci. Although the tegmina of existing species lack veins, those of most Jurassic species (suborder Archidermaptera) have veins that are apparently homologous with R, RS, M, CUA, and CUP of other insects (VISHNIAKOVA, 1980a). Also, two Jurassic genera belonging to the existing family Pygidicranidae, considered to be the most primitive of existing families, have several simple veins in the tegmina. The hind wings are membranous and when expanded are large and semicircular. The anterior half of the remigium is at least slightly sclerotized, forming a leathery scale; several of the main veins seem to have been lost in the sclerotization, only their basal parts persisting (Fig. 91). The rest of the hind wing is supported by a series of radiating veins, which appear to arise from a fulcrum at the distal end of the scale (Fig. 91). The complicated folding of these hind wings has been described in detail by MARTYNOV (1938b) and VERHOEFF (1917).

The heavily sclerotized forceps, which are modified cerci, show much diversity of form and size in recent Dermaptera. Segmentation of the forceps is not visible in adults of recent Dermaptera but is clearly indicated in the nymphs of some of the Pygidicranidae. The cerci of the adults of the Archidermaptera, all Jurassic, are very diverse in form, some being long and setaceous, with as many as 40 segments (VISHNIAKOVA, 1980a). In others they are shorter, with a tendency for the basal segments to be more sclerotized and coalesced, forming incipient forceps (see Fig. 92,*3*).

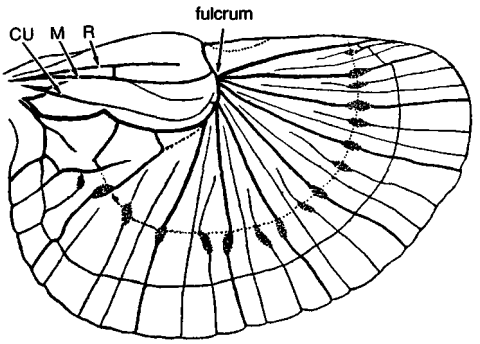


FIG. 91. Dermaptera; expanded hind wing of *Forficula auricularia* LINNÉ, Holocene (Bey-Bienko, 1936).

The order Dermaptera is generally considered to consist of four suborders: Archidermaptera, Forficulina, Arixeniina, and Diploglossata. The last two, which include only a very few species, have no geological record; they are apterous, with short, styliform, unsegmented cerci, and are associated with bats (Arixeniina) or are ectoparasites of rodents (Diploglossata). The Archidermaptera include the most generalized members of the order and are known at present only from the Jurassic. The Forficulina, consisting of several families of typical earwigs, extend back to the Jurassic.

Suborder ARCHIDERMAPTERA Bey-Bienko, 1936

[Archidermaptera BEY-BIENKO, 1936, p. 215]

Tarsi with 4 or 5 segments; tegmina with distinct but much reduced venation; cerci commonly long, slender, multisegmented, rarely short. Hind wings unknown. *Jur.*

Family PROTODIPLATYIDAE Martynov, 1925

[Protodiplatyidae MARTYNOV, 1925b, p. 573] [=Protodiplatidae ROHDENDORF, 1957, p. 78, unjustified emendation]

Antenna filiform, with 17 to 23 segments, the first segment enlarged and second at least

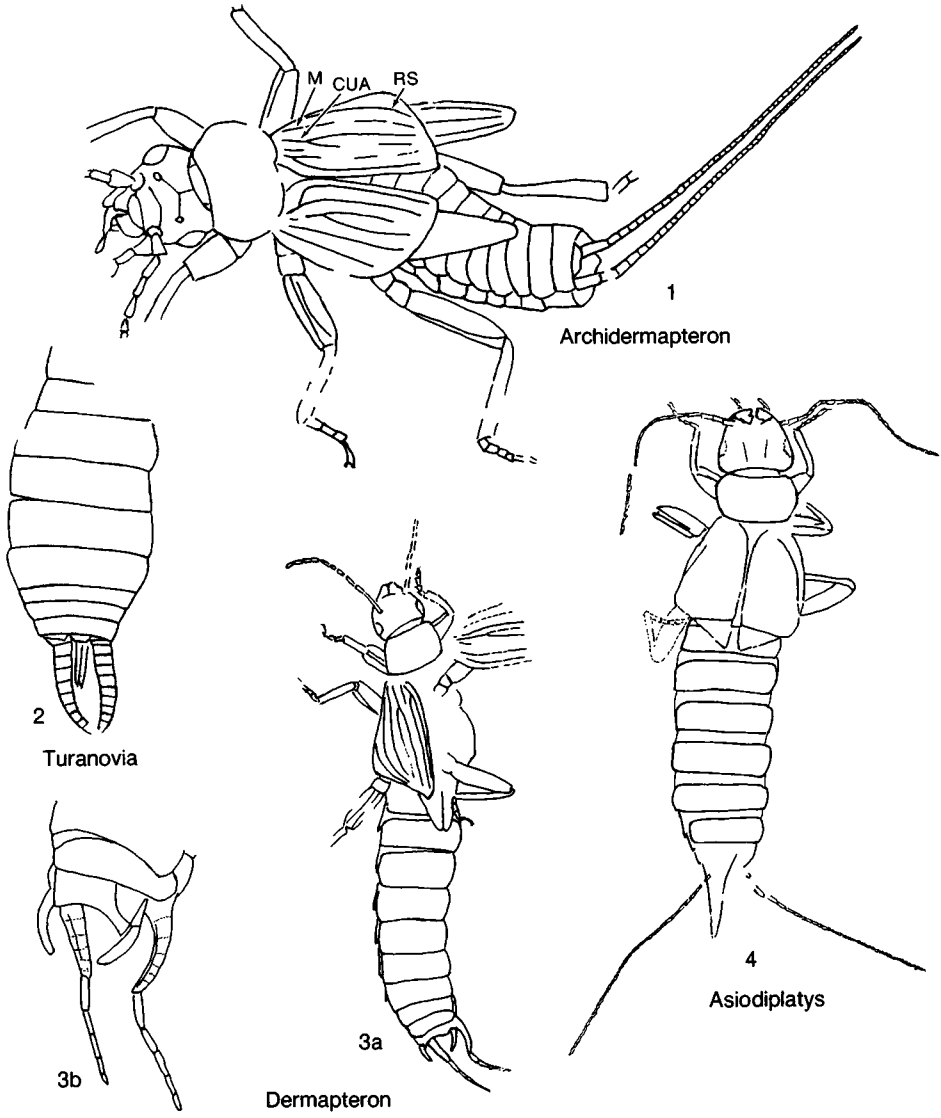


FIG. 92. Protodiplatyidae (p. 152–153).

as long as third; ocelli present; pronotum transverse; tegmina relatively long, apically dilated, and with veins RS and M unbranched, CUA and A forked, and CUP reduced; tarsi long; fore and middle tarsi with 4 segments, hind tarsi with 5; pretarsi with 2 claws and arolium; abdomen with 10 visible segments. Females with prominent, external ovipositor. *Jur.*

Protodiplatys MARTYNOV, 1925b, p. 573 [**P. fortis*; OD]. Head small; antenna with 17 to 19 segments; tegmina broad, not extending beyond second abdominal segment; cerci about half as long as body, with no more than 40 segments. VISHNIAKOVA, 1980a. *Jur.*, USSR (Kazakh).

Archidermapteron VISHNIAKOVA, 1980a, p. 82 [**A. martynovi*; OD]. Similar to *Protodiplatys* but with much larger and longer tegmina; cerci nearly as long as body, with more than 40 segments. *Jur.*, USSR (Kazakh).——FIG. 92,*1*. **A. martynovi*; lateral view of holotype as preserved, ×2.5 (after Vishniakova, 1980a).

Asiodiplatys VISHNIAKOVA, 1980a, p. 85 [**P. speciosus*; OD]. Similar to *Protodiplatys*, but head larger; antenna with 22 segments; tegmina api-

cally truncate in straight line; cerci about half length of body. *Jur.,* USSR (Kazakh).——Fig. 92,*4*. **A. speciosus*; dorsal view of holotype as preserved, ×5.5 (after Vishniakova, 1980a).

Dermapteron Martynov, 1925b, p. 575 [**D. incerta*; OD]. Similar to *Protodiplatys*; anterior margin of pronotum concave, posterior margin slightly convex; femora without spines; cerci short, with only 6 segments and only about one-fifth length of body; basal segment of cerci enlarged and falciform, with vestigial segmentation; ovipositor short. Vishniakova, 1980a. *Jur.,* USSR (Kazakh).——Fig. 92,*3*. **D. incerta; a,* paratype as preserved, ×3; *b,* apex of abdomen, ×6 (both after Vishniakova, 1980a).

Microdiplatys Vishniakova, 1980a, p. 85 [**V. campodeiformis*; OD]. Similar to *Protodiplatys* but smaller; antenna with 19 segments; pronotum with lateral margins almost parallel; cerci as long as body. *Jur.,* USSR (Kazakh).

Turanovia Vishniakova, 1980a, p. 88 [**T. incompleta*; OD]. Similar to *Dermapteron,* but anterior and posterior margins of pronotum nearly parallel; cerci short, about one-sixth length of body, weakly curved and converging, consisting of 9 more or less coalesced segments. *Jur.,* USSR (Kazakh).——Fig. 92,*2*. **T. incompleta*; distal part of abdomen and cerci, ×7 (after Vishniakova, 1980a).

Suborder FORFICULINA Newman, 1835

[Forficulina Newman, 1835, p. 424]

Tarsi with 3 segments; cerci forming heavy forceps, without segmentation in adults; eyes well developed. *Jur.–Holo.*

Family PYGIDICRANIDAE Verhoeff, 1902

[Pygidicranidae Verhoeff, 1902, p. 188]

Head depressed, truncate, concave, not emarginate posteriorly; femora commonly compressed and carinulate; body typically pubescent; tarsi commonly simple. Cerci of nymphs of two subfamilies segmented. [A diverse family generally considered to be the most primitive of the existing families of the order.] *Jur.–Holo.*

Pygidicrana Serville, 1831, p. 30. *Holo.*

Semenoviola Martynov, 1925c, p. 74 [**S. obliquotruncata*; OD]. Head large, transverse, posterior margin concave; antenna with 11 moniliform segments, first 2 segments of nearly identical length; ocelli present; tegmina with unbranched veins RS, M, and CUA; vein A forked; cerci short, strongly curved; ovipositor short, external. Vishniakova, 1980a. *Jur.,* USSR (Kazakh).

Semenovioloides Vishniakova, 1980a, p. 92 [**S. capitatus*; OD]. Similar to *Semenoviola* but larger; anterior margin of pronotum concave. *Jur.,* USSR (Kazakh).

Turanoderma Vishniakova, 1980a, p. 92 [**T. sepultum*; OD]. Similar to *Semenoviola,* but tegmina widened distally and truncate apically in a straight line; antenna with 12 segments; cerci short, strongly falciform. *Jur.,* USSR (Kazakh).——Fig. 93,*2*. **T. sepultum*; dorsal view of holotype as preserved, ×3.7 (after Vishniakova, 1980a).

Family LABIDURIDAE Verhoeff, 1902

[Labiduridae Verhoeff, 1902, p. 189]

Body usually convex; femora not flattened or carinulate; cerci of nymphs not segmented. *Paleoc.–Holo.*

Labidura Leach, 1815, p. 118. Cockerell, 1920e; Zeuner, 1962b. *Mio.,* Asia (Burma); *Pleist.,* St. Helena–*Holo.*

Carcinophora Scudder, 1876b, p. 291. Cockerell, 1925e; Bogachev, 1940. *Paleoc.–Plio.,* Argentina; *Mio.,* Europe (Germany)–*Holo.*

Labiduromma Scudder, 1890, p. 203 [**L. avia*; SD Townes, 1945, p. 350]. First segment of anterior tarsus stout and swollen; forceps very broad. [Family assignment doubtful.] Cockerell, 1924a; Brown, 1984. *Oligo.,* USA (Colorado).——Fig. 93,*1* **L. avia*; whole insect, ×2 (Scudder, 1890).

Family FORFICULIDAE Verhoeff, 1902

[Forficulidae Verhoeff, 1902, p. 190]

Body usually moderately flattened; antenna with 12 to 15 cylindrical or subcylindrical segments; elytra commonly present; legs short, flattened; second tarsal segment dilated on each side; abdomen with parallel sides, rarely tapering or dilated; forceps flattened or cylindrical. *Eoc.–Holo.*

Forficula Linné, 1758, p. 423. Bogachev, 1940. *Eoc.,* Europe (Italy); *Mio.,* Europe (Germany) –*Holo.*

Suborder UNCERTAIN

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

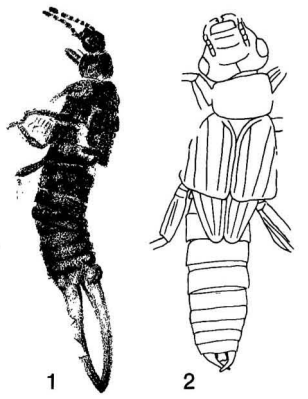


FIG. 93. Pygidicranidae and Labiduridae (p. 153).

Mesoforficula PING, 1935, p. 107 [**M. sinkianensis*; OD]. Little-known insect with short antennae and elytra. *Jur.*, China (Xinjiang).

Sinolabia ZHOU & CHEN, 1983, p. 62 [**S. longyouensis*; OD]. Little-known genus, based on poorly preserved specimen, apparently lacking tegmina. *Cret.*, China (Zhejing).

Order ORTHOPTERA Olivier, 1789

[*nom. transl. et correct.* OLIVIER, 1811, p. 550, *ex* Orthopteres OLIVIER, 1789a, p. 12] [=*Pruvostitoptera* ZALESSKY, 1928b, p. 381]

Fore wings typically tegminous, rarely membranous; costa submarginal, precostal area usually prominent; vein SC generally extending beyond midwing, with series of oblique veinlets directed to anterior margin beyond C; R with oblique veinlets or definite terminal branches; RS arising from R, usually having several branches; M typically with at least 2 main branches, which in some families may represent MA and MP; CUA well developed, commonly anastomosed with M or its branches; CUP and 1A nearly straight, unbranched. Hind wings membranous, with slender remigium and expanded anal lobe; costa reduced, usually marginal; anal lobe including several to many radiating anal veins. Crossveins usually well developed and numerous, in many forming reticulation, which may develop into series of weak intercalary veins. Fore wings or both fore and hind wings may be reduced or completely absent. Mouthparts mandibulate; antennae well developed, commonly long; prothorax prominent; tarsi usually with from 3 to 5 segments; hind legs modified for jumping; female usually with ovipositor; cerci small, usually inconspicuous and unsegmented. Stridulatory organs usually present (generally alary or femoroalary) at least in males; tympanal organs on either abdomen or fore tibiae. *U. Carb.–Holo.*

As usually treated and as presented here, the order Orthoptera includes only the saltatorial orthopteroids. Lack of knowledge of the leg structure of a few Permian orthopteroids has made their ordinal positions uncertain. In these cases I have accepted SHAROV's conclusions, as given in his detailed account of the phylogeny of the orthopteroids (1968).

The venation of the Orthoptera has some controversial features. The topography (i.e., convexity or concavity) of veins C, SC, R, and CUP is retained, but the branches of RS and M, as well as of CUA, are usually flat or neutral in the fore wings. In certain extinct families, such as the Oedischiidae, however, MP is clearly preserved as a strongly concave vein and CUA as convex. MA does not occur in any known Orthoptera as a distinctly convex vein; its presence, as in the Protorthoptera, can only be assumed on the basis of the proximal position of the first fork of M. One area of controversy is the relationship between M and CUA. In the fore wings of most Orthoptera there is some kind of connection between CUA and M (Fig. 94, *Oedischia williamsoni*; see also Fig. 95,*4b*). In others, CUA curves anteriorly from the stem of CU near the base of the wing and anastomoses with the stem of M for a brief interval before diverging posteriorly (see Fig. 110,*2, Mesoedischia madygenica*). In most families, CUA has merged with M at the very base of the wing and is usually no longer visible as a distinct vein (see Fig. 103,*1, Hagla gracilis*). Also, as noted by SHAROV (1968), some crossveins have tended to become relatively thick, functioning as struts (as in the Odonata), especially in the fore wings of the males,

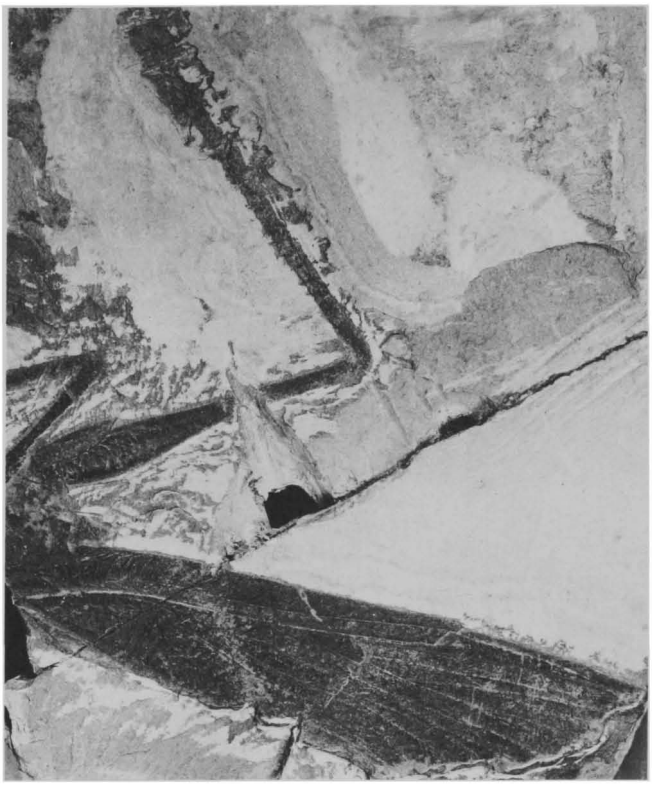


FIG. 94. Orthoptera; fore wing and hind leg of *Oedischia williamsoni,* Upper Carboniferous of France, ×1.6 (Carpenter, new).

in which the venation has been much modified by the development of the stridulatory apparatus.

The evolution of the Orthoptera has apparently involved (1) increasing specializations of the fore wings as tegmina or wing covers, (2) development of stridulatory organs on the fore wings at least of the males, (3) expansion of the anal lobes of the hind wings, and (4) development of tympanal organs. The ability of the Orthoptera to jump and to stridulate has placed them among the most conspicuous of the existing insects. The saltatorial legs were well developed in the Oedischiidae of the Upper Carboniferous (Fig. 94). Stridulatory organs were thought by SHAROV (1968) to have been present on the wings of some oedischiids; they were obviously well developed on the wings of several Triassic genera of the related, existing family Haglidae (see Figs. 104,*1, Archihagla* and 106,*2, Protshorkuphlebia*).

The order Orthoptera is here divided into two suborders, Ensifera and Caelifera.

Suborder ENSIFERA Chopard, 1920

[Ensifera CHOPARD, 1920, p. 56]

Antennae long, filiform, commonly longer than body and consisting of at least 30 segments; tympanal (auditory) organs, when present, located on fore tibiae; stridulatory structures (if present) on the overlapping, horizontal part of the fore wings in resting position; ovipositor, when present, sword-shaped. *U. Carb.–Holo.*

The morphological features included in the diagnosis of the Ensifera are only rarely preserved in fossils. However, there are other

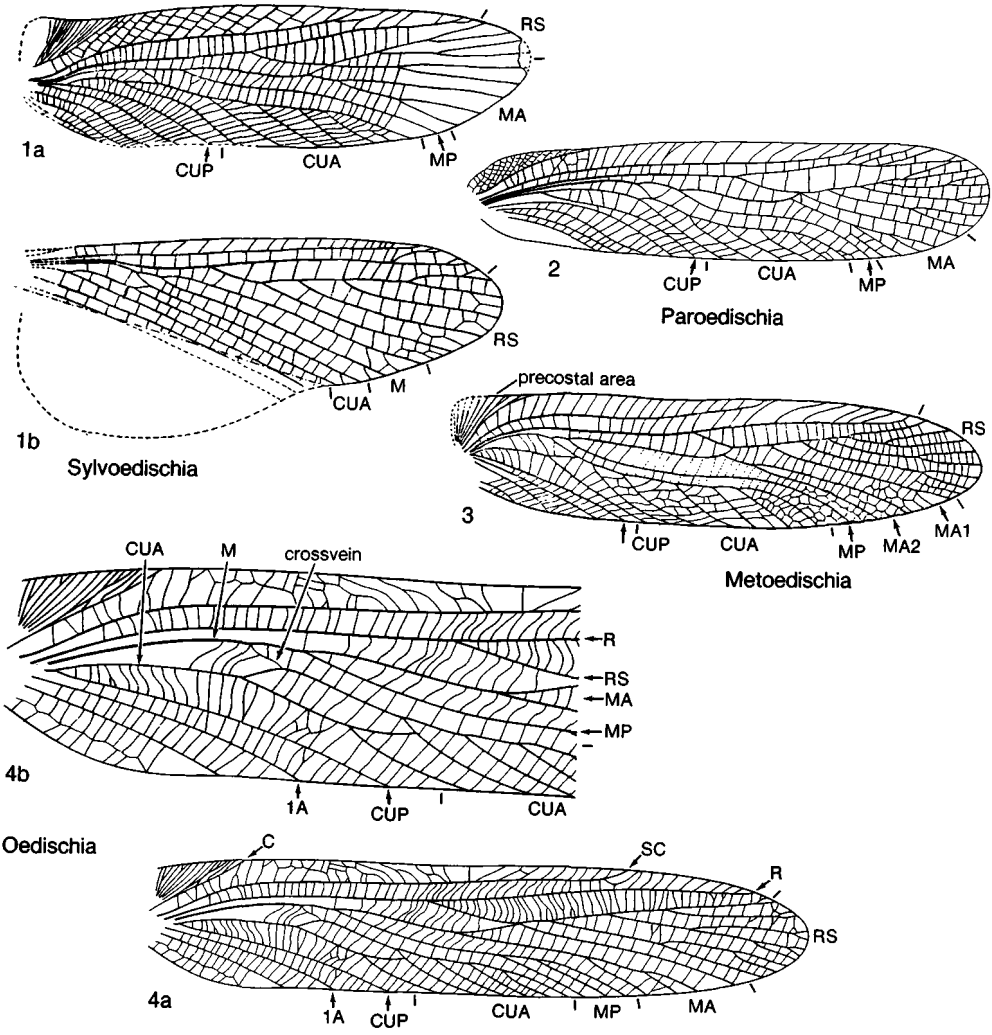


FIG. 95. Oedischiidae (p. 157–158).

characteristics, especially in the venational patterns, that are sufficiently associated with the body structures mentioned to enable suborder classification in most instances.

Family OEDISCHIIDAE Handlirsch, 1906

[Oedischiidae HANDLIRSCH, 1906a, p. 700] [=Anhomalophlebiidae HANDLIRSCH, 1919b, p. 547; Pruvostitidae ZALESSKY, 1928b, p. 381]

Fore wing weakly coriaceous; precostal area well developed; vein SC extending well beyond midwing; RS arising at about midwing, with several branches; stem of M independent basally, dividing into MA and MP after a short interval; MA with a distinct anterior branch (MA1) diverging toward RS and commonly at least touching it; MP commonly unbranched; CUA and CUP separating close to wing base; CUA1 directed toward stem of M and typically connected to it by a thickened crossvein, just before origin of MP; CUA with several long branches; CUP and anal veins unbranched. Hind wing incompletely known (in *Sylvoedischia* and *Macroedischia*); remigium about same size as in fore wing; MA not anastomosed with

RS; anal area unknown. Body known only in *Oedischia* and *Sylvoedischia*; head hypognathous; pronotum long; legs long, posterior pair with enlarged femora (Fig. 94), tarsi with 5 segments; cerci and ovipositor short. *U. Carb.–Perm.*

The oedischiids are generally considered to be the most primitive of the known Orthoptera. At present thirteen genera are known, two from the Upper Carboniferous and the rest from Permian strata. It should be noted here that I have excluded from the Oedischiidae the Triassic genus *Mesoedischia* SHAROV, which seems to me to represent a distinct family. It is here placed in the category of family Uncertain.

Oedischia BRONGNIART, 1885a, p. 58 [**O. williamsoni*; OD]. Fore wing with SC terminating at about one-quarter wing length from apex; MA1 touching or nearly touching RS; MP branched. ZEUNER, 1939; CARPENTER, 1966; SHAROV, 1968. *U. Carb.*, Europe (France).——FIG. 94. **O. williamsoni*; fore wing and hind leg, ×1.6 (Carpenter, new).——FIG. 95,*4*. **O. williamsoni; a,* fore wing, ×1.0; *b,* proximal half of fore wing, ×1.7 (both Carpenter, new).

Anhomalophlebia HANDLIRSCH, 1919b, p. 547 [**Homalophlebia couloni* MEUNIER, 1911a, p. 128; OD]. Fore wing as in *Oedischia* but relatively shorter and broader; MP unbranched; MA1 not quite reaching RS. [Type of family Anhomalophlebiidae HANDLIRSCH, 1919b.] *U. Carb.*, Europe (France).——FIG. 96,*1*. **A. couloni* (MEUNIER); fore wing, ×1.6 (Carpenter, new).

Jasvia ZALESSKY, 1934, p. 150 [**J. reticulata*; OD]. Little-known genus, apparently similar to *Oedischia,* but crossveins forming a dense reticulation over most of wing; MP unbranched. *Perm.*, USSR (Asian RSFSR).——FIG. 96,*2*. **J. reticulata*; fore wing, ×1.0 (Zalessky, 1934).

Macroedischia SHAROV, 1968, p. 159 [**M. elongata*; OD]. Fore wing as in *Jasvia,* but precostal area longer and more pointed; crossveins not forming a dense reticulation apically; anal area longer. *Perm.*, USSR (Asian RSFSR).——FIG. 96,*6*. **M. elongata*; fore wing, ×1.0 (Sharov, 1968).

Metoedischia MARTYNOV, 1928b, p. 45 [**M. magnifica*; OD]. Fore wing as in *Jasvia,* but relatively broader; MA1 anastomosed with RS for longer interval; crossveins between branches of RS more nearly straight. [The small wing fragment of an oedischiid from the Permian of Portugal and described by LAURENTIAUX & TEIXEIRA (1958b, p. 212) as *Metoedischia lusitanica* obviously does not belong to this genus.] SHAROV, 1968. *Perm.*, USSR (European RSFSR).——FIG. 95,*3*. **M. magnifica*; fore wing, ×1.8 (Martynov, 1928b).

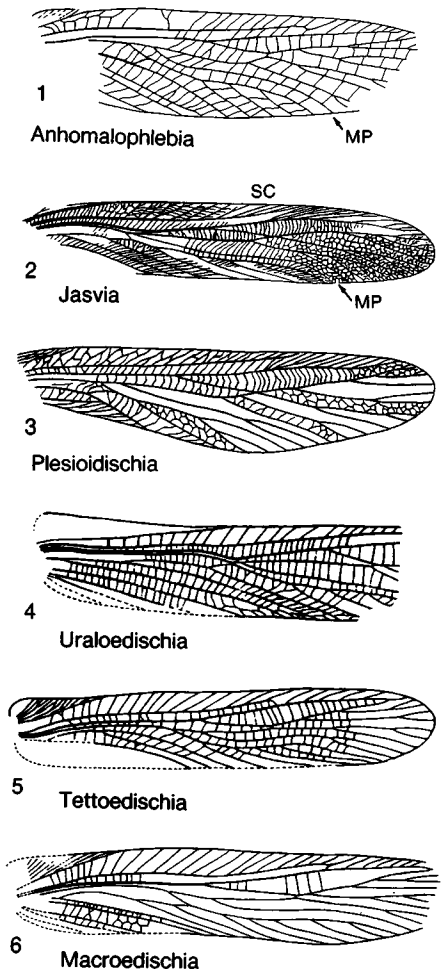


FIG. 96. Oedischiidae (p. 157–158).

Paroedischia CARPENTER, 1966, p. 79 [**P. recta*; OD]. Similar to *Metoedischia,* but precostal area very long; SC long; crossveins not reticulate. *Perm.*, USA (Kansas).——FIG. 95,*2*. **P. recta*; fore wing, ×1.8 (Carpenter, 1966).

Permoedischia KUKALOVÁ, 1955a, p. 542 [**P. moravica*; OD]. Little-known fore wing; precostal area more extensive than in *Oedischia*; MP unbranched. SHAROV, 1968. *Perm.*, Europe (Czechoslovakia).

Plesioidischia HANDLIRSCH, 1906b, p. 346 [**P. baentschi*; OD]. Fore wing as in *Oedischia* but markedly widened near middle; crossveins forming reticulation in region of RS. *Perm.*, Europe (Germany).——FIG. 96,*3*. **P. baentschi*; fore wing, ×1.0 (Guthörl, 1934).

Pruvostites ZALESSKY, 1928b, p. 381 [**P. takhtachurensis*; OD]. Little-known genus, based on wing fragment with broad costal area. [Type of family Pruvostitidae and order Pruvostitoptera.] SHAROV, 1968. *Perm.*, USSR (European RSFSR).

Rimnosentomon ZALESSKY, 1955b, p. 349 [**R. grande*; OD]. Little-known genus, based on distal fragment of fore wing. SHAROV, 1962c. *Perm.*, USSR (Asian RSFSR).

Sylvoedischia SHAROV, 1968, p. 158 [**S. uralica*; OD]. Fore wing with large precostal area, nearly as long as in *Macroedischia*; costal veinlets connected by crossveins; crossveins very dense over most of wing. Hind wing with SC nearly straight. *Perm.*, USSR (Asian RSFSR).——FIG. 95,*1*. **S. uralica*; *a*, fore and *b*, hind wings, both ×1.8 (Sharov, 1968).

Tettoedischia SHAROV, 1968, p. 159 [**T. minuta*; OD]. Fore wing slender; precostal area large, tapering; costal veinlets not connected by crossveins. *Perm.*, USSR (Asian RSFSR).——FIG. 96,*5*. **T. minuta*; fore wing, ×1.8 (Sharov, 1968).

Uraloedischia SHAROV, 1968, p. 157 [**U. permiensis*; OD]. Little-known genus, based on proximal fragment of fore wing. Precostal area long and narrow, extending about halfway to origin of RS; subcostal veinlets not reticulate. *Perm.*, USSR (Asian RSFSR).——FIG. 96,*4*. **U. permiensis*; fore wing, ×1.7 (Sharov, 1968).

Family TCHOLMANVISSIIDAE Zalessky, 1934

[Tcholmanvissiidae ZALESSKY, 1934, p. 153] [=Tillyardiellidae HANDLIRSCH, 1937, p. 82]

Fore and hind wings similar to those of the Oedischiidae. Fore wing with vein MA1 not anastomosed with RS and without a sharp bend toward RS; branches of CUA nearly parallel and close together. Hind wing with 1A forked distally; anal area with about 12 radiating veins. Body as in the Oedischiidae; ovipositor well developed and bearing many small spines. SHAROV, 1968. *Perm.*

Pinegia MARTYNOV, 1928b, p. 47 [**P. oknowae*; OD] [=*Thnetodes* MARTYNOV, 1928b, p. 5 (type, *T. craticus*); *Tcholmanvissia* ZALESSKY, 1929, p. 19 (type, *T. noinskii*); *Kamaites* ZALESSKY, 1929, p. 21 (type, *K. mirabilis*); *Tillyardiella* MARTYNOV, 1930a, p. 76 (type, *T. distincta*)]. Crossveins very numerous and close together, forming a reticulation only in distal part of wings; posterior margin of fore wing concave. SHAROV, 1962c, 1968. *Perm.*, USSR (Asian and European RSFSR).——FIG. 97,*1*. *P. longipes* (MARTYNOV); *a*, fore and *b*, hind wings, both ×1.0 (Sharov, 1968).

Jubilaeus SHAROV, 1968, p. 161 [**J. beybienkoi*; OD]. Fore wing as in *Pinegia*, but subcostal area broader; precostal area bulging; posterior margin of wing straight or slightly convex. *Perm.*, USSR (Asian RSFSR).——FIG. 97,*2*. **J. beybienkoi*; *a*, fore and *b*, hind wings, both ×0.8 (Sharov, 1968).

Family PERMELCANIDAE Sharov, 1962

[Permelcanidae SHAROV, 1962b, p. 112]

Fore wing more membranous than in Oedischiidae; vein SC extending at least to midwing; RS arising near midwing, with very short, oblique stem and anastomosed with MA for a considerable interval; MP diverging from MA before level of origin of RS; CUA separating from CUP near wing base; CUA forking before level of main fork of M; CUA diverging toward M and typically anastomosed with M and MP for a short interval; CUP arising from the common stem CU; several anal veins. Hind wing little known; costa submarginal; SC terminating near midwing; anal area apparently well developed; anal veins unknown. Body (known only in *Permelcana*): antennae long, filiform; legs slender, hind femora thick basally; tarsi with 4 segments. SHAROV, 1968. *Perm.*

Permelcana SHAROV, 1962b, p. 114 [**P. sojanense*; OD]. MA in fore wing anastomosed with RS for an interval almost equal to length of free part of MA. *Perm.*, USSR (European RSFSR).——FIG. 98,*1*. *P. kukalovae* SHAROV; *a*, fore and *b*, hind wings, both ×5.0 (Sharov, 1968).

Meselcana SHAROV, 1968, p. 162 [**P. madygenica*; OD]. Similar to *Permelcana*, but SC much longer; branches of CUA1 in fore wing strongly curved. *Perm.*, USSR (Asian RSFSR).——FIG. 98,*4*. **M. madygenica*; *a*, fore and *b*, hind wings, both ×5.3 (Sharov, 1968).

Proelcana SHAROV, 1962b, p. 113 [**P. uralica*; OD]. Little-known genus, based on fragment of fore wing. MA anastomosed with RS for a very short interval. *Perm.*, USSR (Asian RSFSR).

Promartynovia TILLYARD, 1937a, p. 99 [**P. venicosta*; OD]. Similar to *Permelcana*, but fore wing more broadly rounded distally; RS with only 2 terminal branches. Hind wing unknown. *Perm.*, USA (Kansas).——FIG. 98,*3*. **P. venicosta*; fore wing, ×7.3 (Carpenter, 1966).

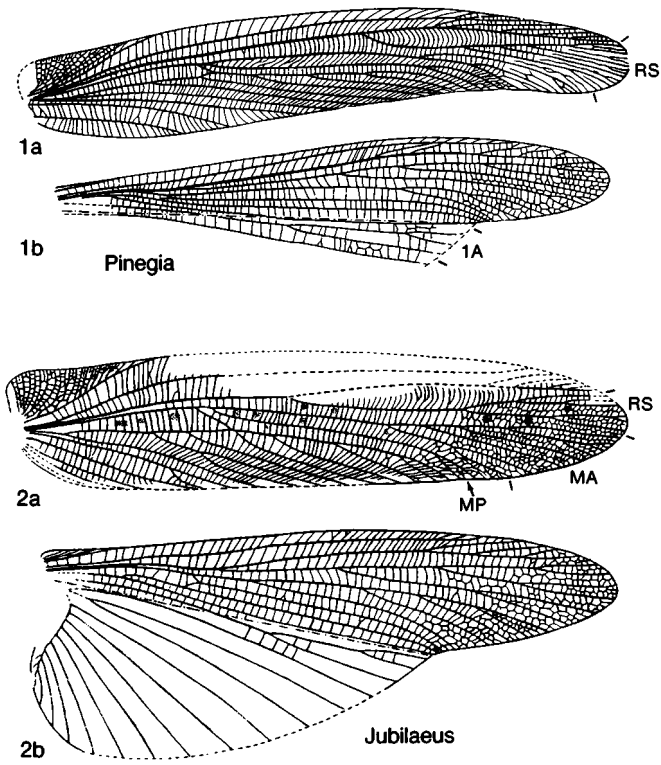


FIG. 97. Tcholmanvissiidae (p. 158).

Family ANELCANIDAE Carpenter, 1987

[Anelcanidae CARPENTER, 1987, p. 375, *nom. subst. pro* Parelcanidae CARPENTER, 1966, p. 84]

Fore wing as in Oedischiidae but more coriaceous; precostal area very large and very acute distally, extending about one-third wing length from wing base; vein SC remote from costal margin, terminating beyond midwing. Hind wing unknown. *Perm.*

Anelcana CARPENTER, 1987, p. 375, *nom. subst. pro Parelcana* CARPENTER, 1966, p. 84, *non* HANDLIRSCH, 1906b [**Parelcana dilatata*; OD]. Costal area about as wide as area between SC and R at midwing; crossveins numerous but not branched. *Perm.*, USA (Kansas).——FIG. 98,*2*. **A. dilatata* (CARPENTER); fore wing as preserved, ×2.8 (Carpenter, 1966).

Petrelcana CARPENTER, 1966, p. 85 [**P. elongata*; OD]. Fore wing elongate, with many irregular veinlets; precostal area not so long or so broad as in *Anelcana*; costal area much wider than area between SC and R; R with several irregular, oblique veinlets distally; basal piece of MA very long; crossveins forming a coarse reticulation in several areas of wing. *Perm.*, USA (Kansas).——FIG. 98,*5*. **P. elongata*; fore wing, ×2.2 (Carpenter, 1966).

Family PERMORAPHIDIIDAE Tillyard, 1932

[Permoraphidiidae TILLYARD, 1932a, p. 5]

Similar to Permelcanidae. Fore wing apparently lacking precostal area; vein SC with an anterior basal branch, connected to costal margin of wing by crossveins; MA anastomosed for a short interval with RS; crossveins numerous. Hind wing with MA anastomosed with RS; CUA1 anastomosed with M; anal area unknown. *Perm.*

Permoraphidia TILLYARD, 1932a, p. 6 [**P. americana*; OD]. Costal area of fore wing much broader than subcostal area; CUP extending

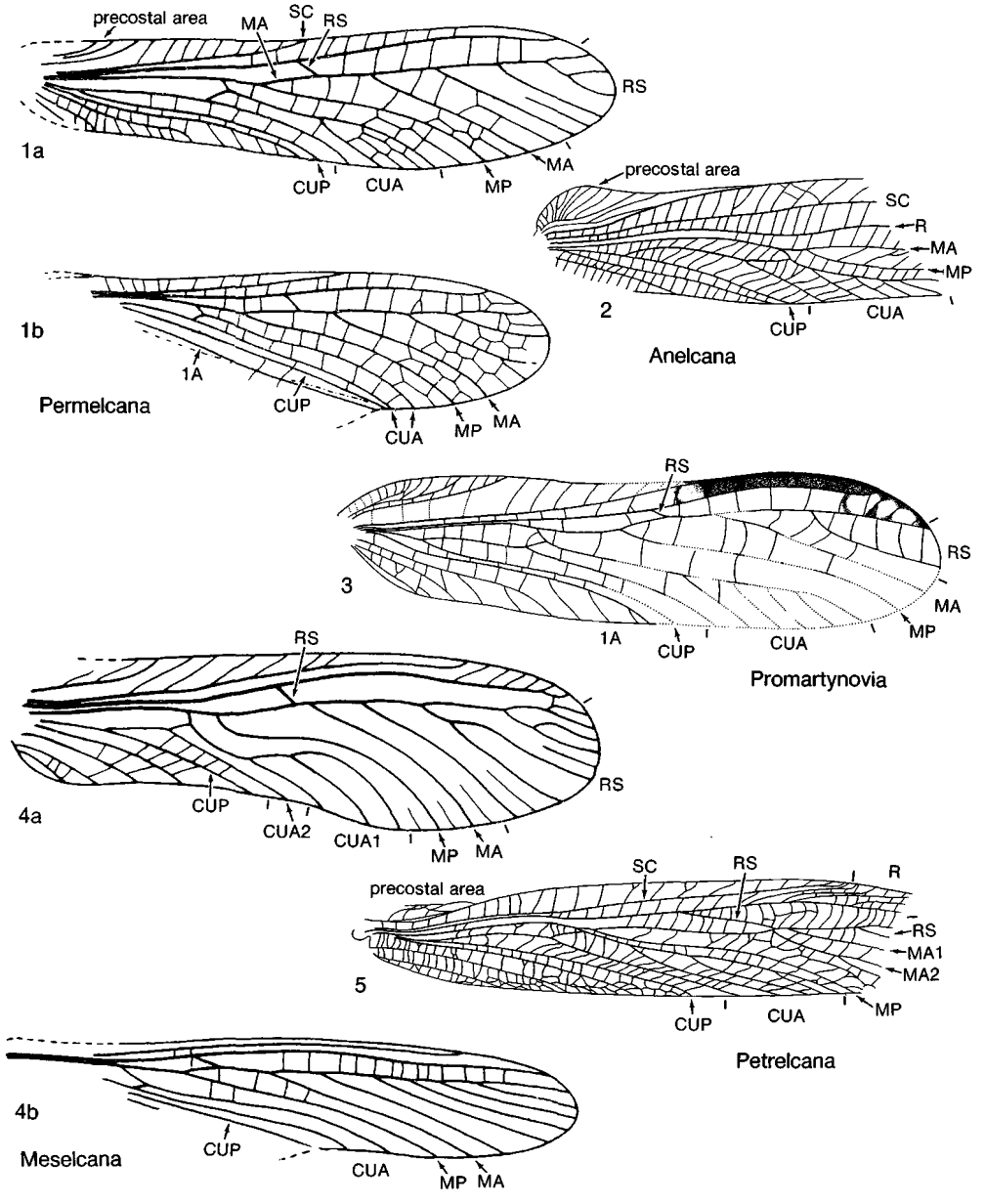


FIG. 98. Permelcanidae and Anelcanidae (p. 158–159).

beyond midwing. CARPENTER, 1943a; SHAROV, 1968. *Perm.*, USA (Kansas).——FIG. 99,*1*. **P. americana; a,* fore and *b,* hind wings, ×8.0 (Carpenter, 1943a).

Family ELCANIDAE Handlirsch, 1906

[Elcanidae HANDLIRSCH, 1906b, p. 412]

Similar to Permelcanidae, but fore wing with vein CUA forking much nearer wing base; RS and MA in brief contact. SHAROV, 1968. *Jur.–Cret.*

Panorpidium WESTWOOD, 1854, p. 394 [**P. tessellatum*; OD] [=*Elcana* GIEBEL, 1856, p. 259, obj.; *Rapha* GIEBEL, 1856, p. 290 (type, *R. liassina*); *Clathrotermes* HEER, 1865, p. 85 (type, *C. signatus*); *Parelcana* HANDLIRSCH, 1906b, p. 420 (type, *P. tenuis*)]. Fore wing: submarginal part

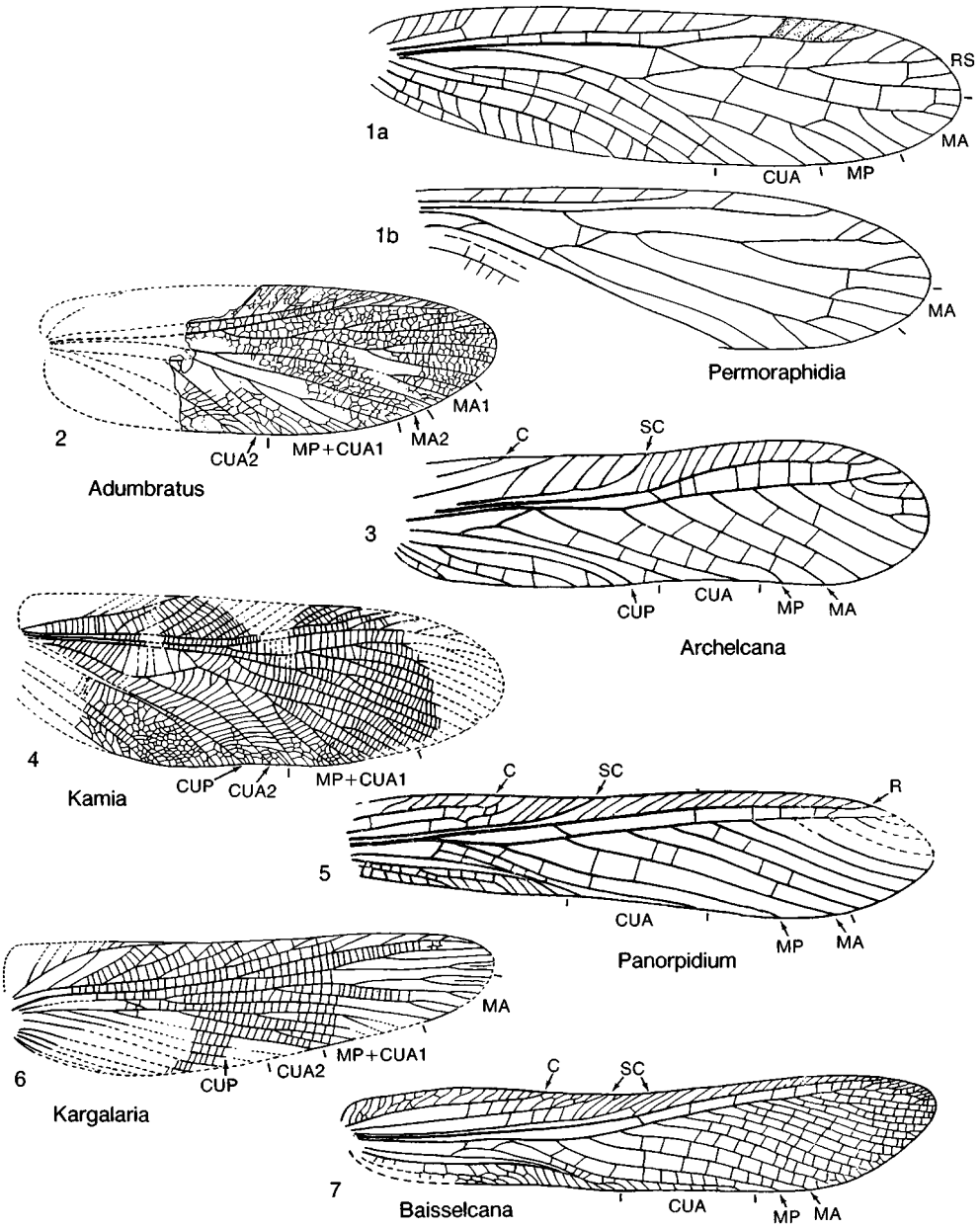


FIG. 99. Permoraphidiidae, Elcanidae, and Kamiidae (p. 159–162).

of C with several branches leading to front margin of wing; apex of wing rounded. ZEUNER, 1942d; BODE, 1953. *Jur.,* England, Europe (Germany, Switzerland), USSR (Kazakh).——FIG. 99,5. *P. karatavica* (SHAROV), USSR; fore wing, ×4.0 (Sharov, 1968).

Archelcana SHAROV, 1968, p. 163 [**Elcana britannica* HANDLIRSCH, 1906b, p. 414; OD]. Fore wing as in *Panorpidium,* but submarginal part of C without distinct branches. *Jur.,* England, USSR (Kirghiz).——FIG. 99,3. **A. britannica* (HANDLIRSCH), England; fore wing, ×4.5 (Sharov, 1968).

Baisselcana SHAROV, 1968, p. 164 [**B. sibirica*; OD]. Fore wing: precostal area long, with many veinlets; apex of wing pointed. *Cret.,* USSR (Asian RSFSR).——FIG. 99,7. **B. sibirica*; fore wing, ×2.5 (Sharov, 1968).

Family KAMIIDAE Sharov, 1968

[Kamiidae Sharov, 1968, p. 165]

Related to Oedischiidae. Costal area of fore wing very broad; area between veins SC and R very narrow; MA not anastomosed with RS or even curved toward it and with 3 or more branches; crossveins very numerous. *Perm.*

Kamia Martynov, 1928b, p. 4 [**K. angustovenosa*; OD] [=*Spongoneura* Martynov, 1928b, p. 6 (type, *S. incerta*); *Permacridites* Martynov, 1931c, p. 156 (type, *P. maximus*)]. Fore wing broad; crossveins mostly straight, not branched. Sharov, 1968. *Perm.*, USSR (European and Asian RSFSR).——Fig. 99,*4*. **K. angustovenosa*; fore wing as preserved, ×1.3 (Sharov, 1968).

Adumbratus Sharov, 1961f, p. 246 [**A. extentus*; OD]. Similar to *Kamia,* but crossveins forming a dense reticulation over most of fore wing. Sharov, 1968. *Perm.*, USSR (Asian RSFSR).——Fig. 99,*2*. **A. extentus*; fore wing as preserved, ×3.0 (Sharov, 1961f).

Kargalaria Sharov, 1968, p. 165 [**K. maculata*; OD]. Fore wing as in *Kamia* but more slender; crossveins not so dense; main veins and their branches nearly parallel. *Perm.*, USSR (Asian RSFSR).——Fig. 99,*6*. **K. maculata*; fore wing as preserved, ×1.0 (Sharov, 1968).

Family VITIMIIDAE Sharov, 1968

[Vitimiidae Sharov, 1968, p. 152]

Similar to Kamiidae, but anastomosis of MP and CUA in fore wing apparently occurring at base of wing; hind wing with large anal area. *Trias.–Cret.*

Vitimia Sharov, 1968, p. 167 [**V. evoluta*; OD]. Crossveins mostly simple, unbranched. *Cret.*, USSR (Asian RSFSR).——Fig. 100,*4*. **V. evoluta*; fore wing as preserved, ×3.5 (Sharov, 1968).

Fergania Sharov, 1968, p. 167 [**F. reducta*; OD]. Fore wing similar to that of *Vitimia,* but precostal area much larger and CUP diverging from CU more proximally. Hind wing with a concave anterior margin. *Trias.*, USSR (Kirghiz).——Fig. 100,*2*. **F. reducta*; *a,* fore and *b,* hind wings, both ×2.8 (Sharov, 1968).

Provitimia Sharov, 1968, p. 166 [**P. pectinata*; OD]. Little-known genus, similar to *Vitimia,* but SC with many forked branches. *Trias.*, USSR (Kirghiz).

Family BINTONIELLIDAE Handlirsch, 1939

[Bintoniellidae Handlirsch, 1939, p. 55]

Related to Vitimiidae. Fore wing with prominent precostal area; veinlets in costal area commonly unbranched, without connecting crossveins; vein MA not anastomosed with RS and remote from it; M with 3 main, parallel branches. *Trias.–Jur.*

Bintoniella Handlirsch, 1939, p. 55 [**B. brodiei*; OD]. Costal area of fore wing narrow, nearly as narrow as subcostal area; branches of vein RS curved and parallel. Remigium of hind wing relatively slender and pointed; crossveins very dense distally. Fore wings showing some sexual dimorphism, those of males being more sclerotized than those of females, as well as slightly larger. Whalley, 1982. *Jur.*, England.——Fig. 100,*1*. **B. brodiei; a,* fore and *b,* hind wings, both ×1.8 (Sharov, 1968).

Probintoniella Sharov, 1968, p. 168 [**P. triassica*; OD]. Fore wing as in *Bintoniella,* but costal area very broad, about twice as wide as subcostal area; branches of RS divergent and irregular. Remigium of hind wing broad, with rounded apex. *Trias.*, USSR (Kirghiz).——Fig. 100,*3*. **P. triassica; a,* fore and *b,* hind wings, both ×2.8 (Sharov, 1968).

Family TRIASSOMANTEIDAE Tillyard, 1922

[*nom. correct.* Brues, Melander, & Carpenter, 1954, p. 809, *ex* Triassomantidae Tillyard, 1922b, p. 449, *nom. imperf.*] [=Xenopteridae Riek, 1955, p. 687]

Apparently related to the Oedischiidae. Precostal area of fore wing small and narrow; costal area very broad, its veinlets unbranched; subcostal area narrow; vein M much reduced; crossveins unbranched, except in anal area. Hind wing with large anal area, with CUA extending farther distally than in fore wing. [I have followed Sharov (1968) in placing his genera *Ferganopterus, Ferganopterodes,* and *Triassomanteodes* in the family Triassomanteidae. However, because of the fragmentary nature of the unique specimen of the type genus, that placement is uncertain. The family diagnosis above is based in part on Sharov's genera.] *Trias.*

Triassomantis Tillyard, 1922b, p. 450 [**T. pygmaeus*; OD]. Little-known genus, based on fragment of fore wing. *Trias.*, Australia (Queensland).

Ferganopterodes Sharov, 1968, p. 169 [**F. reductus*; OD]. Fore wing as in *Ferganopterus,* but MA not anastomosed with RS. *Trias.*, USSR (Kirghiz).——Fig. 101,*1*. **F. reductus*; fore wing, ×4.0 (Sharov, 1968).

Ferganopterus Sharov, 1968, p. 169 [**F. clarus*; OD]. Fore wing with long and tapering costal area; SC extending well beyond midwing; MA

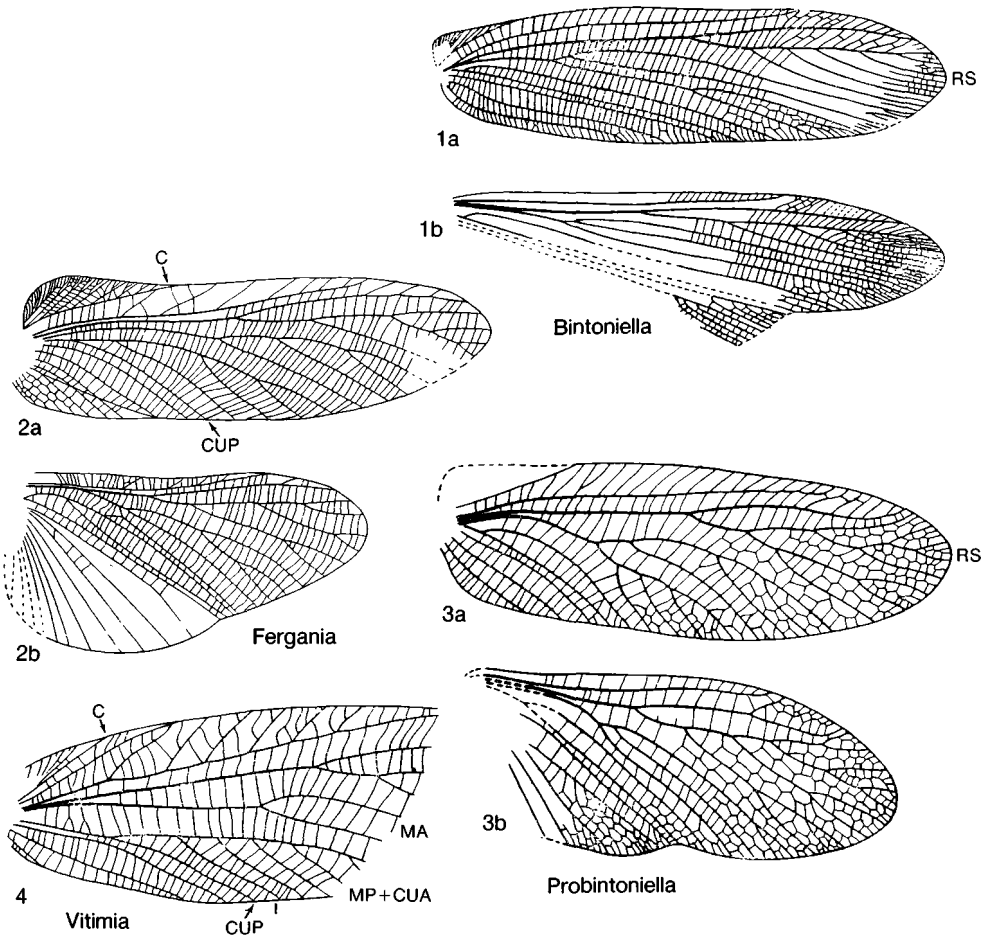


FIG. 100. Vitimiidae and Bintoniellidae (p. 162).

anastomosed with RS; crossveins between CUP and 1A very close together. Hind wing with MA and CUA close together and parallel. *Trias.*, USSR (Kirghiz).——FIG. 101,*4*. **F. clarus; a,* fore and *b,* hind wings, both ×3.0 (Sharov, 1968).

Triassomanteodes SHAROV, 1968, p. 170 [**T. madygenicus*; OD]. Similar to *Ferganopterodes,* but SC terminating at about midwing, MA anastomosed with RS, and stem of CUA much shorter. *Trias.*, USSR (Kirghiz).——FIG. 101,*3*. **T. madygenicus*; fore wing, ×7.0 (Sharov, 1968).

Xenopterum RIEK, 1955, p. 678 [**X. crosbyi*; OD]. Little-known genus, based on wing fragments. [Type of family Xenopteridae RIEK.] SHAROV, 1968. *Trias.*, Australia (Queensland).

Family TETTAVIDAE Sharov, 1968

[Tettavidae SHAROV, 1968, p. 171]

Wing venation similar to that of Oedischiidae; veins RS and MA anastomosed in hind wing but not in fore wing; R in fore wing with several branches distally. *Perm.–Trias.*

Tettavus SHAROV, 1968, p. 171 [**Pinegia fenestrata* MARTYNOV, 1931c, p. 208; OD]. Fore wing (presumably of female): distal branches of R very long; RS with pectinate branching; crossveins in radial field forming a reticulation distally. *Perm.*, USSR (Asian RSFSR).——FIG. 101,*5*. **T. fenestrata; a,* fore wing as preserved, *b,* hind wing, both ×2.0 (Sharov, 1968).

Madygenia SHAROV, 1968, p. 171 [**M. orientalis*; OD]. Female: fore wing as in *Tettavus,* but RS branched dichotomously; crossveins reticulate over most of wing; hind wing with branches of RS nearly parallel to MA, MP, and CUA. Male much smaller than female; venation little known. *Trias.*, USSR (Kirghiz).——FIG. 101,*2*. **M. orientalis; a,* fore and *b,* hind wings of female, *c,* fore wing of male as preserved, all ×2.0 (Sharov, 1968).

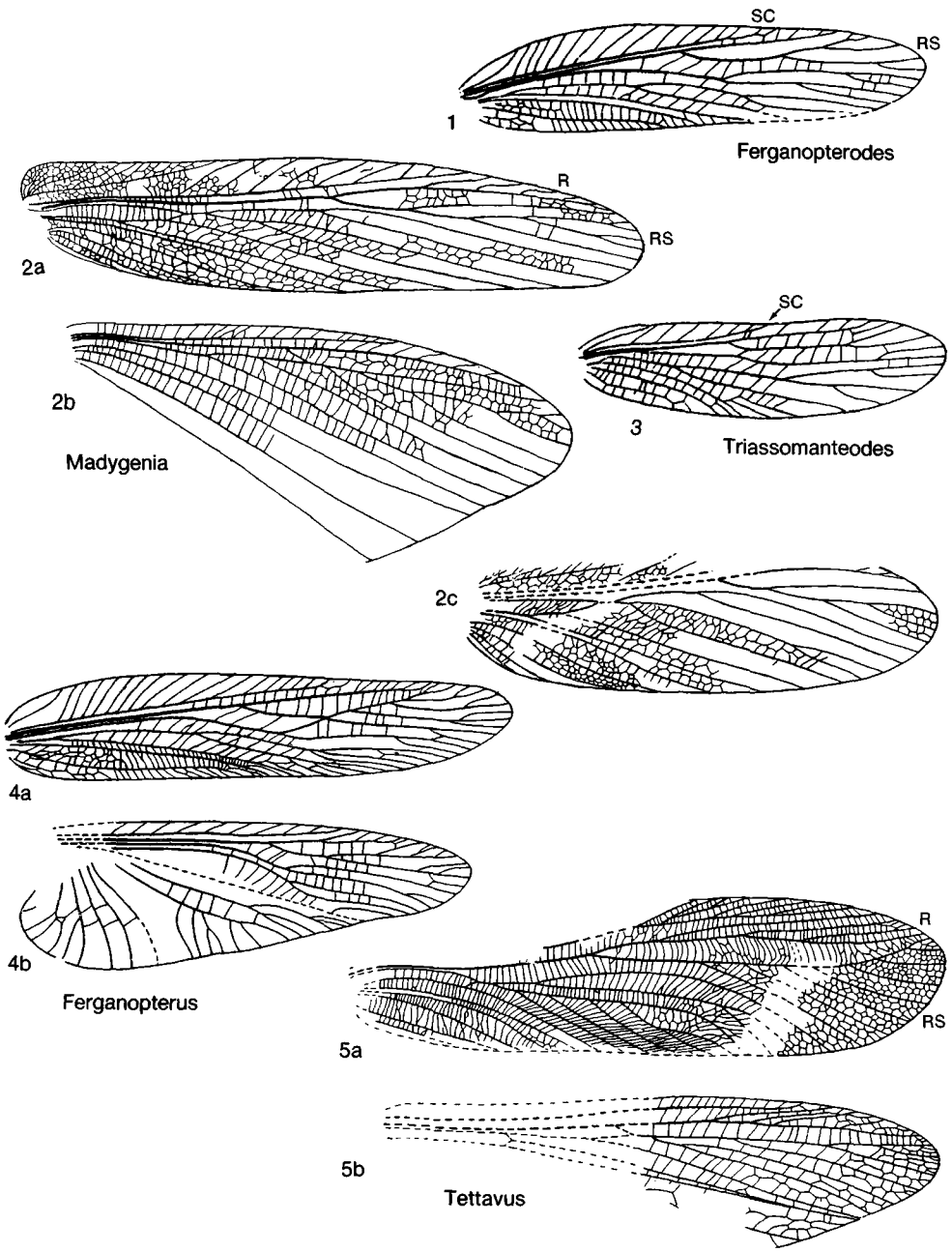


FIG. 101. Triassomanteidae and Tettavidae (p. 162–163).

Family TETTIGONIIDAE Krauss, 1902

[Tettigoniidae KRAUSS, 1902, p. 538]

Similar in appearance to Oedischiidae and Tettavidae. Fore wings tegminous, their apices folded together at rest; vein RS only rarely fused with MA, even for a short interval; CUA with an anterior branch coalescing with MP; stridulatory structures commonly well developed; right tegmen with a membranous

area between CUP and branches of CUA; left tegmen with a similar structure, but CUP larger and serrulate. Hind wings much as in Oedischiidae, but MA commonly anastomosed for a short interval; MP typically fused with an anterior branch of CUA. Body laterally compressed; antennae long, filiform; fore and middle legs relatively short; hind femora skittle-shaped; tarsi with 4 segments; ovipositor laterally flattened; auditory organs commonly present, situated on fore tibiae. *Eoc.–Holo.*

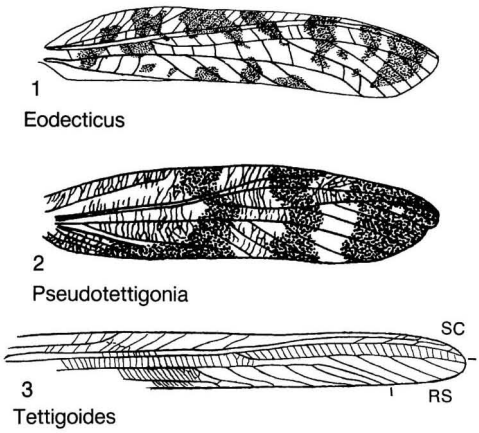


FIG. 102. Tettigoniidae (p. 165).

Tettigonia LINNÉ, 1758, p. 425. *Holo.* [A wing from the Miocene/Pliocene of France has been identified (BRICE & LAURENTIAUX, 1964) as belonging to a female of the existing species *Tettigonia viridissima* LINNÉ, but SHAROV (1968) reports that the wing is from a male and that the taxonomic identification is erroneous.]

Anabrus HALDEMANN, 1852, p. 372. Ovipositor only. [Generic position doubtful.] COCKERELL, 1908p. *Oligo.,* USA (Colorado)–*Holo.*

Arctolocusta ZEUNER, 1937, p. 157 [**Locusta groenlandica* HEER, 1883, p. 146; OD]. Little-known fore wing, female. SHAROV, 1968. *Eoc.,* Greenland.

Eodecticus PONGRÁCZ, 1928, p. 128 [**E. maculatus*; OD]. Fore wing similar to that of *Decticus* (recent) but with more branches of SC to costal margin and with irregular maculations. ZEUNER, 1939. *Mio.,* Europe (Austria).——FIG. 102,*1*. **E. maculatus*; fore wing, ×1.0 (Zeuner, 1939).

Eomortoniellus ZEUNER, 1936b, p. 291 [**E. handlirschi*; OD]. Similar to *Mortoniellus* (recent) but pronotum smaller. ZEUNER, 1944b. *Oligo.,* Europe (Baltic).

Lipotactes BRUNNER, 1898, p. 274. Nymphal male. ZEUNER, 1936b. *Oligo.,* Europe (Baltic)–*Holo.*

Lithymnetes SCUDDER, 1878a, p. 532 [**L. guttatus*; OD]. Little-known genus, based on fore wing. THÉOBALD, 1937a; ZEUNER, 1939; SHAROV, 1968; KEVAN & WIGHTON, 1983. *Oligo.,* USA (Colorado).

Nymphomorpha HENRIKSEN, 1922b, p. 13 [**N. medialis*; OD]. Little-known hind wing. ZEUNER, 1939. *Eoc.,* Europe (Denmark).

Orchelimum SERVILLE, 1839, p. 522. Complete male and female. SCUDDER, 1890. *Oligo.,* USA (Colorado)–*Holo.*

Orphania FISCHER, 1853, p. 222. Hind tibia. CHARPENTIER, 1825; ZEUNER, 1929, 1939. *Pleist.,* Europe (Poland)–*Holo.*

Platycleis FIEBER, 1852, p. 2. Fore wings, hind wings, and parts of body. ZEUNER, 1929, 1939. *Mio.,* Europe (Austria, Germany)–*Holo.*

Pseudotettigonia ZEUNER, 1937, p. 157 [**Tettigonia amoena* HENRIKSEN, 1929, p. 317; OD]. Similar to *Tettigonia,* but crossveins of fore wing more regular. SHAROV, 1968. *Eoc.,* Europe (Denmark). —— FIG. 102,*2*. **P. amoena* (HENRIKSEN); fore wing, ×0.8 (Zeuner, 1939).

Rammea ZEUNER, 1931, p. 253 [**R. laticeps*; OD]. Similar to *Decticus* but with a conelike process between meso- and metasternum. ZEUNER, 1939. *Mio.,* Europe (Germany).

Tettigoides RIEK, 1952b, p. 20 [**T. pectinata*; OD]. Elytron very narrow, with long SC; RS arising at midwing; M nearly parallel to R. [Family position uncertain.] *?Eoc.,* Australia (Queensland). ——FIG. 102,*3*. **T. pectinata*; elytron, ×2.0 (Riek, 1952b).

Family HAGLIDAE Handlirsch, 1906

[Haglidae HANDLIRSCH, 1906b, p. 425] [=Eospilopteronidae COCKERELL, 1915, p. 472; Pamphagopsidae MARTYNOV, 1925b, p. 577; Aboilidae MARTYNOV, 1925b, p. 581; Prophalangopsidae HANDLIRSCH, 1929, p. 724; Isfaropteridae MARTYNOV, 1937a, p. 61; Tshorkuphlebiidae MARTYNOV, 1937a, p. 72]

Related to Oedischiidae but with the venation of the fore wings conspicuously different in males and females; fore wings of males with a more or less elaborate stridulatory organ. Fore wing, male: costal area very broad, at least basally, with numerous veinlets and crossveins; costal vein submarginal in specialized species, forming a long precostal area; R typically with several terminal branches; RS with numerous branches in generalized genera, but few in genera having elaborate stridulatory organs; CUA coalesced with M basally but diverging posteriorly before M divides into MA and MP; MA not anastomosed with RS; MA and MP commonly unbranched but strongly curved in specialized genera; CUP unbranched. Fore wing,

female: MA not directed toward RS or in contact with it; MA and MP much as in males but without curves. Hind wing known in only a few species; venation as in Oedischiidae but with an enlarged anal area in some specialized genera. Antennae long, multisegmented; legs relatively short; 4 tarsal segments; auditory organs on fore tibiae; ovipositor broad and well developed. ZEUNER, 1939; SHAROV, 1968. *Trias.–Holo.*

SHAROV's account (1968) of the fossil Haglidae shows that the family was very large and diverse during the early half of the Mesozoic. In contrast, there are only two recent genera, *Prophalangopsis* WALKER (India) and *Cyphoderis* UHLER (western North America), neither of which is represented in the fossil record.

Hagla GIEBEL, 1856, p. 265 [**H. gracilis*; SD ZEUNER, 1939, p. 139] [=*Haglodes* HANDLIRSCH, 1906b, p. 425 (type, *Hagla similis* GIEBEL, 1856, p. 265)]. Male: fore wing broadest before midwing. Female: fore wing with 5 to 6 terminal branches on RS. Hind wing unknown. ZEUNER, 1939; SHAROV, 1968. *Jur.,* England.——FIG. 103,*1*. **H. gracilis*; fore wings of *a,* male and *b,* female, ×2.0 (Zeuner, 1939).

Aboilus MARTYNOV, 1925b, p. 581 [**A. fasciatus*; OD] [=*Pamphagopsis* MARTYNOV, 1925b, p. 578 (type, *P. maculata*); *Syndesmophyllum* MARTYNOV, 1934, p. 1004, *nom. nud.*]. Male: fore wing broadly oval; precostal area large; costal area very broad; RS arising just before midwing; MA and MP smoothly curved and parallel; hind wing with narrow costal area; RS arising nearer wing base than in fore wing; anal area unknown. Female: fore wing with nearly straight anterior margin, M forking before origin of RS. [Type of family Aboilidae MARTYNOV, 1925b.] ZEUNER, 1939; SHAROV, 1968. *Jur.,* USSR (Kazan).——FIG. 103,*2*. *A. columnatus* MARTYNOV; *a,* fore and *b,* hind wings of male, both ×1.7 (Rohdendorf, 1962a); *c,* fore wing of female, ×0.2 (Sharov, 1968).

Albertoilus KEVAN & WIGHTON, 1981, p. 1825 [**A. cerviruft*; OD]. Little-known genus, based on fragments of fore and hind wings, apparently related to *Aboilus.* KEVAN & WIGHTON, 1983. *Paleoc.,* Canada (Alberta).

Alloma HONG, 1982a, p. 79 [**A. facialata*; OD]. Female: fore wing as in *Hebeihagla* but broader near midwing. HONG, 1982b. *Jur.–Cret.,* China (Liaoning Province).

Archaboilus MARTYNOV, 1937a, p. 51 [**A. kisylkiensis*; OD]. Male: fore wing as in *Aboilus,* but costal veinlets more numerous and closer together; precostal area much smaller. ZEUNER, 1939; SHAROV, 1968. *Jur.,* USSR (Kirghiz, Tadzhik).——FIG. 104,*6*. *A. shurabicus* MARTYNOV; fore wing of male, ×0.8 (Rohdendorf, 1962a).

Archaeohagla LIN, 1965, p. 364 [**A. sinensis*; OD]. Little-known genus, based on proximal fragment of fore wing of female. [Probably a synonym of *Sinohagla.*] *Jur.,* China (Inner Mongolia).

Archihagla SHAROV, 1968, p. 175 [**A. zeuneri*; OD]. Male: fore wing very similar to that of *Hagla,* but front margin of fore wing smoothly curved and branching of R more extensive; subcostal veinlets mostly forked. Female unknown. *Trias.,* USSR (Kirghiz).——FIG. 104,*1*. **A. zeuneri*; fore wing, ×3.2 (Sharov, 1968).

Cyrtophyllites OPPENHEIM, 1888, p. 223 [**C. rogeri*; OD]. Little-known genus. Male: fore wing broadly oval, with very wide costal area; RS with 3 or 4 long branches; crossveins close together and forming cellules distally. SHAROV, 1968. *Jur.,* Europe (Germany).——FIG. 104,*2*. **C. rogeri*; fore wing, ×1.2 (Zeuner, 1939).

Eospilopteron COCKERELL, 1915, p. 472 [**E. ornatum*; OD]. Little-known genus, based on apical fragment of wing. [Family assignment doubtful. Type of family Eospilopteronidae.] SHAROV, 1968. *Jur.,* England.

Hebeihagla HONG, 1982b, p. 1121 [**H. songyingziensis*; OD]. Female: fore wing similar to that of *Parahagla,* but RS apparently with a few more branches; wing broadest basally. [Probably a synonym of *Parahagla.*] *Jur.,* China (Hebei Province).

Isfaroptera MARTYNOV, 1937a, p. 61 [**I. grylliformis*; OD]. Similar to *Cyrtophyllites*. Male: fore wing about as wide as long, almost circular; RS with only 1 or 2 branches. [Type of family Isfaropteridae MARTYNOV, 1937a.] ZEUNER, 1939; SHAROV, 1968. *Jur.,* USSR (Kirghiz).——FIG. 104,*3*. **I. grylliformis*; fore wing of male, ×2.0 (Martynov, 1937a).

Jurassobatea ZEUNER, 1937, p. 154 [**J. grillacroides*; OD]. Little-known genus, based on a poorly preserved specimen. Large species, similar to *Aboilus.* [Probably a synonym of *Pycnophlebia.* Placed by ZEUNER (1937, 1939) in Gryllacrididae; by SHAROV (1968) in Haglidae.] KEVAN & WIGHTON, 1981, 1983. *Jur.,* Europe (Germany).

Liassophyllum ZEUNER, 1935, p. 106 [**L. abbreviatum*; OD]. Little-known genus, based on distal fragment of fore wing of male; apex pointed; RS arising much nearer apex than in *Cyrtophyllites*; MA strongly arched anteriorly. [Family assignment doubtful.] ZEUNER, 1939; SHAROV, 1968. *Jur.,* England.——FIG. 104,*5*. **L. abbreviatum*; fore wing as preserved, ×0.8 (Zeuner, 1935).

Mesogryllus HANDLIRSCH, 1906b, p. 523 [**Blattidium achelous* WESTWOOD, 1854, p. 390; OD]. Little-known genus, based on poorly preserved

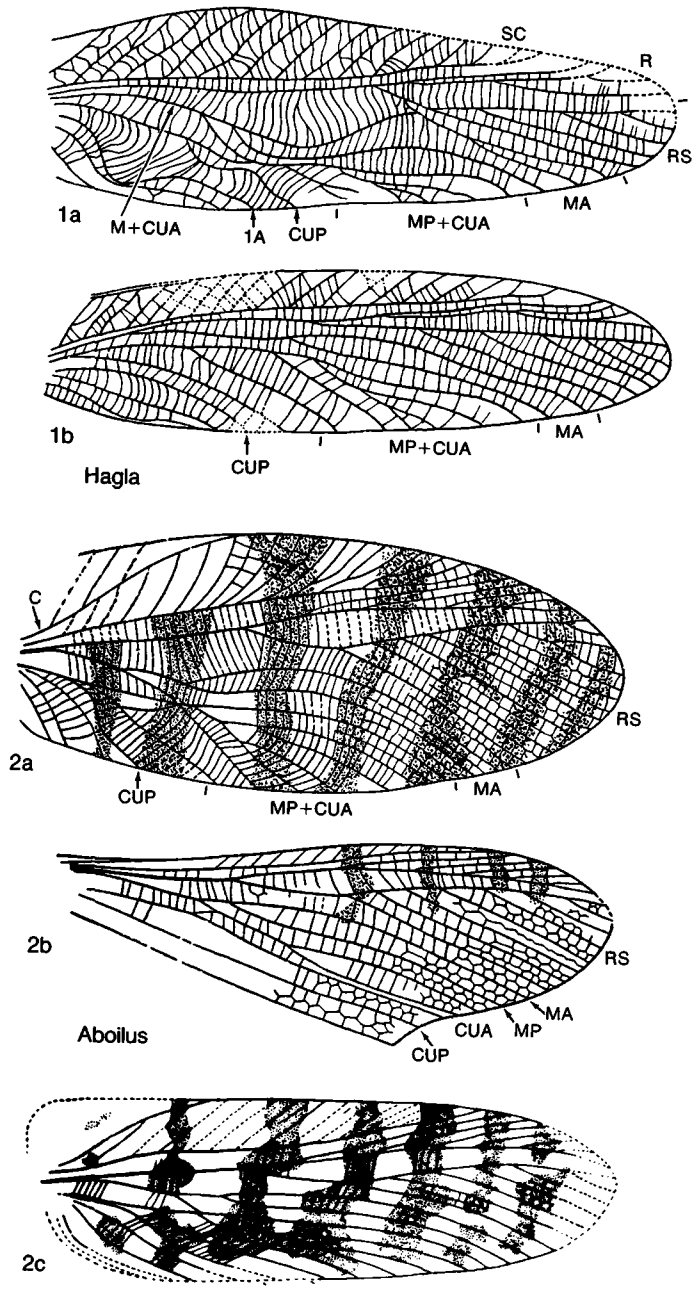


FIG. 103. Haglidae (p. 166).

wing. [Placed in Gryllidae by ZEUNER (1939) and in Haglidae by SHAROV (1968).] *Jur.*, England.

Neohagla RIEK, 1955, p. 683 [**N. sinuata*; OD]. Male: venation of fore wing as preserved similar to that of *Hagla*, but with fewer branches on R; crossveins between R and RS more sinuous. SHAROV, 1968. *Trias.*, Australia (Queensland).

Nipponohagla FUJIYAMA, 1978, p. 183 [**N. kaga*; OD]. Female: fore and hind wings apparently as

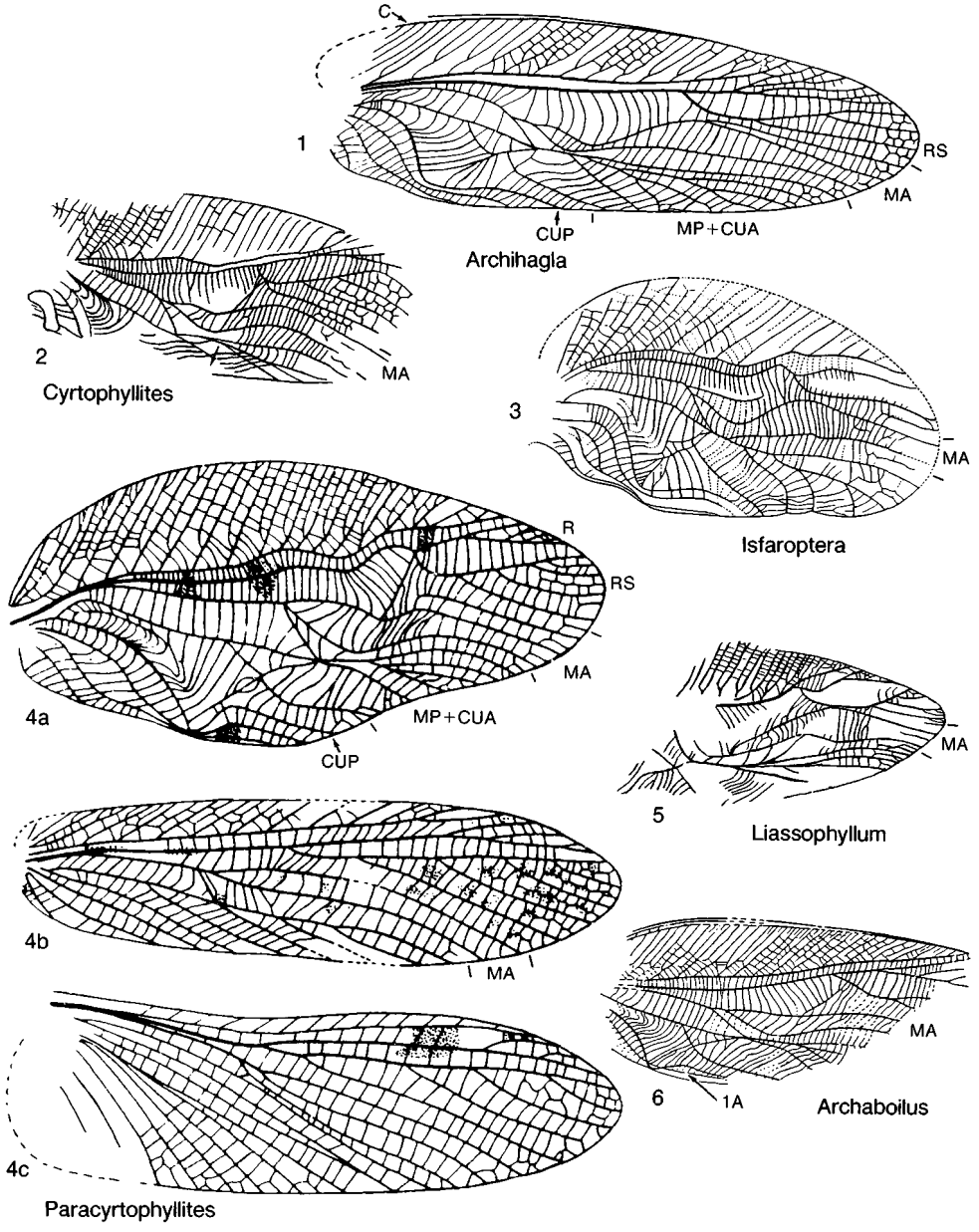


FIG. 104. Haglidae (p. 166–168).

in *Aboilus,* but fore wing much broader, with convex posterior margin. *Cret.,* Japan.

Notopamphagopsis CABRERA, 1928, p. 371 [**N. bolivari*; OD]. Little-known genus, based on apical fragment of wing. SHAROV, 1968. *Trias.,* Argentina (Mendoza).

Palaeorehnia COCKERELL, 1908t, p. 126 [**P. maculata*; OD] [=*Cymatomera maculata* SCUDDER, 1890, p. 230]. Little-known genus, based on small proximal fragment of fore wing of female. ZEUNER, 1939; SHAROV, 1968; KEVAN & WIGHTON, 1983. *Paleog.,* Scotland; *Oligo.,* USA (Colorado).

Paracyrtophyllites SHAROV, 1968, p. 177 [**P. undulatus*; OD]. Similar to *Cyrtophyllites,* but male with stem MA of fore wing more remote from MP and deeply forked. Fore wing of female with normal costal area and shape. Hind wing

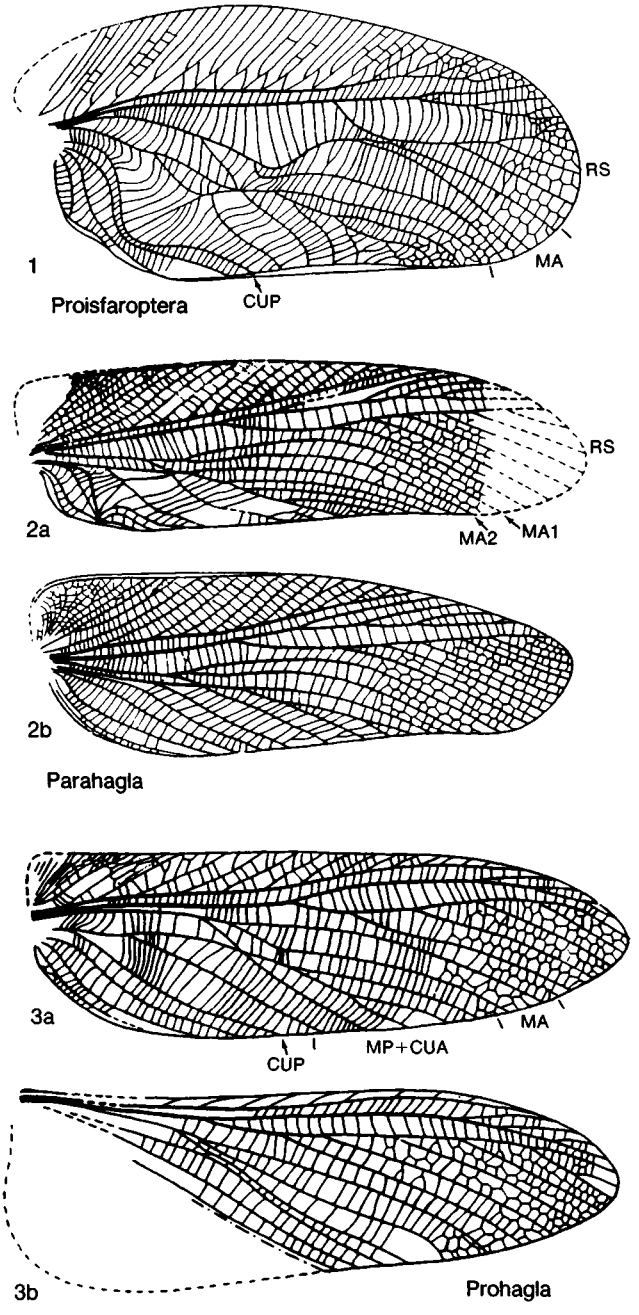


FIG. 105. Haglidae (p. 169–170).

with enlarged anal area. *Jur.*, USSR (Kazakh). ——FIG. 104,*4*. **P. undulatus; a,* fore wing of male, ×4.0; *b,* fore wing of female, ×3.2; *c,* hind wing of female, ×4.0 (Sharov, 1968).

Parahagla SHAROV, 1968, p. 178 [**P. sibirica*; OD]. Similar to *Hagla,* but fore wing of male with MA1 and MA2 almost parallel and with a strong bend at midwing. *Cret.*, USSR (Asian RSFSR).

——Fig. 105,*2*. **P. sibirica; a,* fore wing of male, ×2.3; *b,* fore wing of female, ×1.8 (Sharov, 1968).

Paratshorkuphlebia Sharov, 1968, p. 176 [**P. multivenosa*; OD]. Similar to *Tshorkuphlebia.* Male: costal area of fore wing very broad; MA curved anteriorly near midwing. *Jur.,* USSR (Kirghiz). —— Fig. 106,*3*. **P. multivenosa*; fore wing of male as preserved, ×1.6 (Sharov, 1968).

Procyrtophyllites Zeuner, 1935, p. 106 [**P. britannicus*; OD]. Little-known genus, based on small wing fragment of male; similar to *Archaboilus,* but crossveins between RS and M more sigmoidal. Zeuner, 1939; Sharov, 1968. *Jur.,* England.

Prohagla Riek, 1954c, p. 164 [**P. superba*; OD]. Female: fore wing relatively broad, with prominent precostal area; oblique costal veinlets as in *Protshorkuphlebia.* RS with only 5 terminal branches; vein 2A serrate. Riek, 1955; Sharov, 1968. *Trias.,* Australia (New South Wales, Queensland).——Fig. 105,*3*. **P. superba; a,* fore and *b,* hind wings of female, ×2.0 (Sharov, 1968).

Proisfaroptera Sharov, 1968, p. 173 [**P. martynovi*; OD]. Male: fore wing broadly oval, with wide costal area; MA strongly curved; stridulatory organ well developed. Female: fore wing similar to that of *Turkestania,* but branches of R much shorter. *Trias.,* USSR (Kirghiz).—— Fig. 105,*1*. **P. martynovi*; fore wing of male, ×3.0 (Sharov, 1968).

Prophalangopseides Sharov, 1968, p. 178 [**P. vitimicus*; OD]. Similar to *Prophalangopsis* (recent), but fore wing of male with branching of RS more extensive and that of M more reduced. *Cret.,* USSR (Asian RSFSR).——Fig. 106,*7*. **P. vitimicus*; fore wing of male, ×2.5 (Sharov, 1968).

Protohagla Zeuner, 1962a, p. 165 [**P. langi*; OD]. Little-known genus, based on proximal fragment of fore wing of male. Precostal area well developed; subcostal area with dense, parallel crossveins; longitudinal veins straight, except CUP. Sharov, 1968. *Jur.,* England.

Protshorkuphlebia Sharov, 1968, p. 174 [**P. triassica*; OD]. Male: fore wing elongate, pointed; R and RS branching at same level, almost symmetrically. Female: fore wing very similar to that of *Turkestania. Trias.,* USSR (Kirghiz).——Fig. 106,*2*. **P. triassica*; fore wing of male, ×2.0 (Sharov, 1968).

Pseudohagla Sharov 1962g, p. 152 [**Hagla pospelovi* Martynova, 1949b, p. 923; OD]. Female: fore wing broader than in *Hagla* and precostal area longer; crossveins numerous but not reticulate. Sharov, 1968. *Jur.,* USSR (Asian RSFSR). ——Fig. 106,*6*. **P. pospelovi* (Martynova); fore wing of female, ×1.4 (Sharov, 1962g).

Pycnophlebia Deichmüller, 1886, p. 20 [*Locusta speciosa* Germar, 1839, p. 198; OD]. Little-known genus, based on numerous but poorly preserved specimens; apparently similar to *Aboilus.* Large species; remigium of fore wing subtriangular; RS with about 10 parallel branches. Tympanal organ on fore tibia. [Placed by Martynov (1937a) in Haglidae, by Zeuner (1939) in Ensifera, *incertae sedis,* and by Sharov (1968) in Haglidae.] *Jur.,* Europe (Germany).

Sinohagla Lin, 1965, p. 363 [**S. anthoides*; OD]. Little-known genus, based on distal portion of fore wing of female. Venation as in *Aboilus,* with some reticulate crossveins distally. Sharov, 1968. *Jur.,* China (Inner Mongolia).

Sunoprophalangopsis Hong, 1982b, p. 1124 [**S. elegantis*; OD]. Similar to *Aboilus,* but fore wing with CUA more abruptly curved. [Probably a synonym of *Aboilus.*] *Jur.,* China (Hebei Province).

Tshorkuphlebia Martynov, 1937a, p. 154 [**T. compressa*; OD]. Related to *Hagla,* but with fewer branches on RS. Male: costal area very broad basally; precostal area wide but short; stridulatory organ as in *Hagla.* Female: fore wing with branches of M and CUA parallel. [Type of family Tshorkuphlebiidae.] Sharov, 1968. *Jur.,* USSR (Tadzhik).——Fig. 106,*1*. *T. shurabica* Sharov; *a,* fore wing of male as preserved; *b,* fore wing of female, ×1.5 (Sharov, 1968).

Turkestania Sharov, 1968, p. 173 [**T. deviata*; OD]. Female: fore wing as in *Zeunerophlebia,* but CUP nearly straight basally; crossveins very dense over entire wing. *Trias.,* USSR (Kirghiz). ——Fig. 106,*4*. **T. deviata*; fore wing of female, ×0.75 (Sharov, 1968).

Zalmona Giebel, 1856, p. 266 [**Z. brodiei*; OD]. Little-known genus, based on small fragment of fore wing of female, probably related to *Paracyrtophyllites.* Zeuner, 1939; Sharov, 1968. *Jur.,* England.

Zalmonites Handlirsch, 1906b, p. 422 [**Z. geinitzi*; OD]. Little-known genus, based on small distal fragment of wing. [Placed in Locustidae by Handlirsch (1906b) and in Haglidae by Sharov (1968).] *Jur.,* Europe (Germany).

Zeunerophlebia Sharov, 1968, p. 172 [**Z. gigas*; OD]. Male: costal area of fore wing very broad; RS with at least 7 branches; CUA with at least 6 branches; stridulatory organs present. Female: costal area of fore wing less broad; CUP curved basally, serrate. *Trias.,* USSR (Kirghiz).——Fig. 106,*5*. **Z. gigas; a,* fore wing of male, ×1.0; *b,* fore wing of female, ×0.7 (Sharov, 1968).

Family PHASMOMIMIDAE Sharov, 1968

[Phasmomimidae Sharov, 1968, p. 179]

Related to the Haglidae. Fore wing elongate; precostal area small or absent; costal area narrow, with few veinlets; vein RS typ-

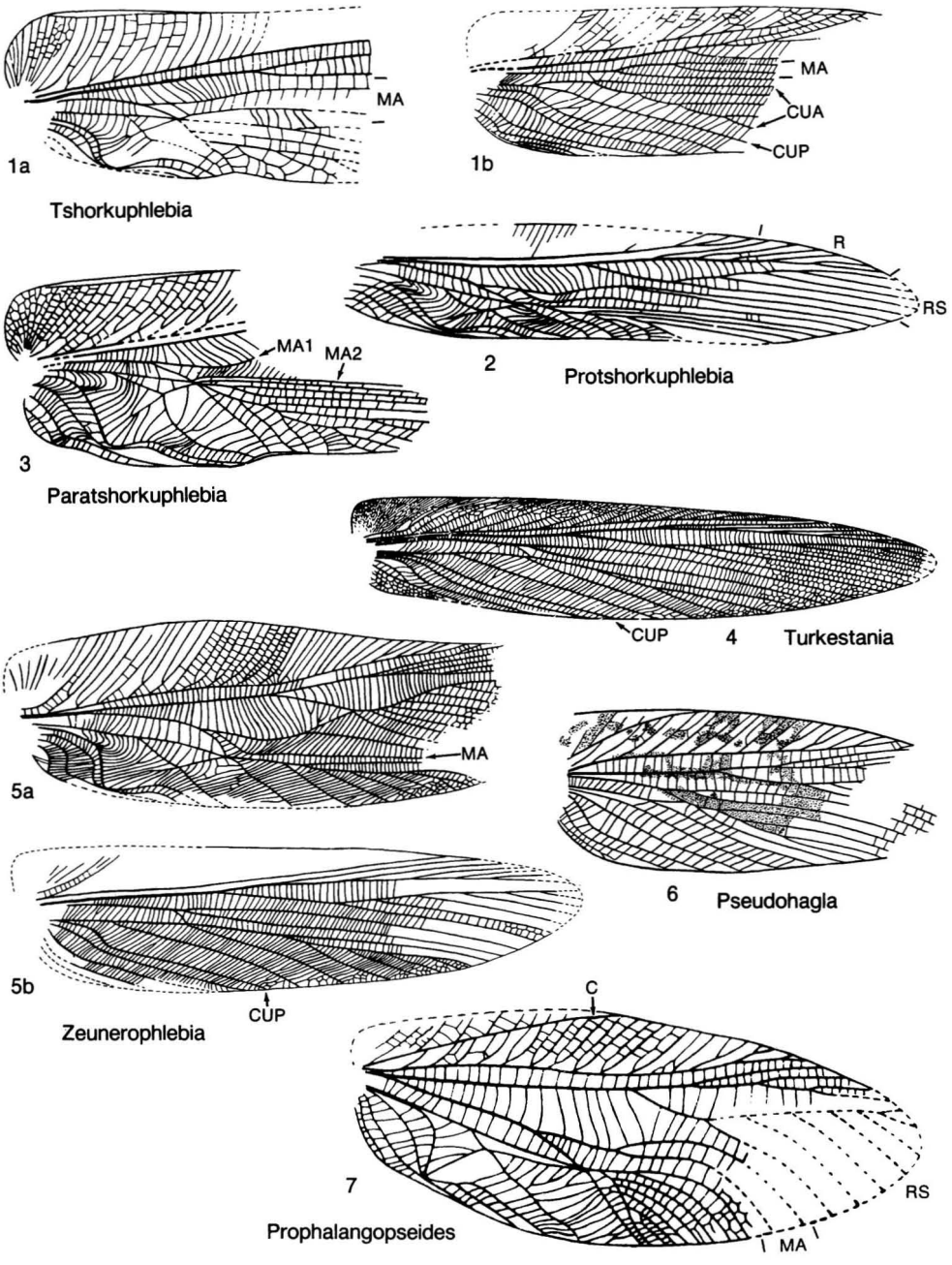


FIG. 106. Haglidae (p. 170).

ically with 2 or 3 terminal branches; MA and MP commonly unbranched; CUA not attached to stem of M. Hind wing much as in Haglidae but with a large anal fan. Ovipositor long, curved. *Jur.–Paleoc.*

Phasmomima SHAROV, 1968, p. 179 [**P. maculomarginata*; OD]. Fore wing: R and RS branched distally only; MA and MP ending almost at wing apex. *Jur.*, USSR (Kazakh).——FIG. 107,*2*. **P. maculomarginata*; *a*, fore and *b*, hind wings, both ×2.0 (Sharov, 1968).

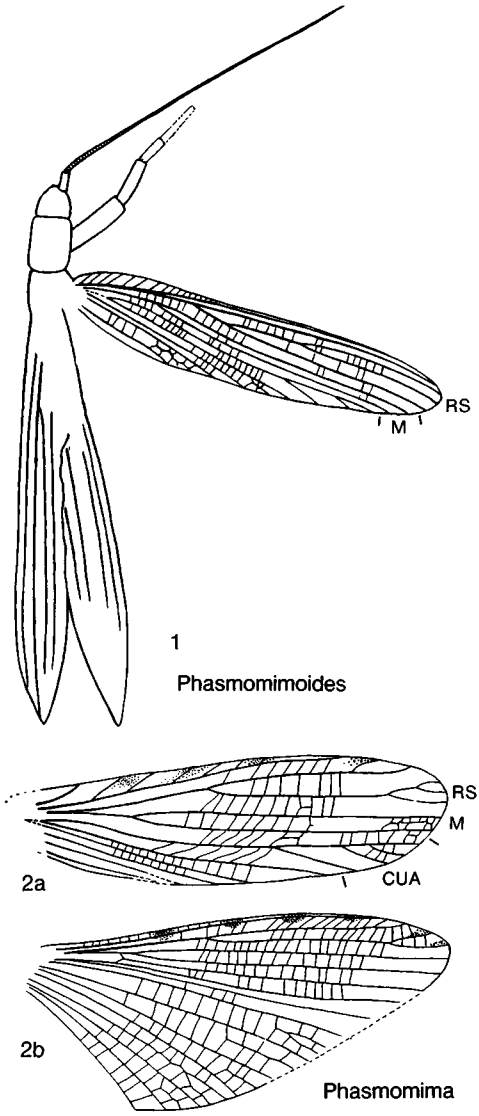


FIG. 107. Phasmomimidae (p. 171–172).

Palaeopteron RICE, 1969, p. 7 [**P. complexum*; OD]. Little-known genus, based on a fore wing fragment; similar to *Phasmomimella,* with veins SC, R, and RS1 convergent apically. [Originally placed in order Perlaria.] KEVAN & WIGHTON, 1983. *Cret.,* Canada (Labrador).

Phasmomimella KEVAN & WIGHTON, 1981, p. 1826 [**P. paskapoensis*; OD]. Little-known genus, based on fragments of fore and hind wings. Fore wing apparently as in *Phasmomimoides,* but stem of RS much longer; M apparently unbranched. *Paleoc.,* Canada (Alberta).

Phasmomimoides SHAROV, 1968, p. 180 [**P. lineatus*; OD]. Fore wing as in *Phasmomima,* but RS deeply forked and MA and MP ending below wing apex. *Jur.,* USSR (Kazakh); *Cret.,* USSR (Asian RSFSR).——FIG. 107,*1*. **P. lineatus,* Jur.; fore wing, part of body, and antenna, ×1 (Sharov, 1968).

Phasmomimula KEVAN & WIGHTON, 1981, p. 1828 [**P. enigma*; OD]. Little-known genus, based on fragments of fore and hind wings. Apparently similar to *Phasmomimella,* but RS unbranched in fore wing. *Paleoc.,* Canada (Alberta).

Family GRYLLACRIDIDAE Stål, 1874

[Gryllacrididae STÅL, 1874, p. 4]

Related to the Haglidae. Fore wing with precostal area very long, submarginal costa extending typically beyond midwing; branches of main veins more or less parallel; few branches on vein RS. Hind wing with M apparently unbranched; anal fan larger than remigium. Stridulatory organs absent from both pairs of wings, but tympanal organs present on fore tibiae of some existing species. Tarsi with 4 segments; ovipositor as in Haglidae. *Paleoc.–Holo.*

Gryllacris SERVILLE, 1831, p. 138. *Holo.*

Macrelcana KARNY, 1932, p. 67 [**Gryllacris ungeri* HEER, 1849, p. 8; OD]. Little-known genus, based on poorly preserved fore wing and hind legs; apparently related to *Gryllacris* (recent), but spines in hind femora broadened to form flat plates. ZEUNER, 1939, SHAROV, 1968. *Mio.,* Europe (Germany).

Prorhaphidophora CHOPARD, 1936a, p. 163 [**P. antiqua*; OD]. Similar to *Rhaphidophora* (recent), but fore and middle femora armed only with a small geniculate spine. ZEUNER, 1939. *Oligo.,* Europe (Baltic).

Zeuneroptera SHAROV 1962g, p. 153 [**Palaeorehnia scotica* ZEUNER, 1939, p. 126; OD]. Little-known genus, based on fore wing fragment. Vein C terminating slightly before midwing. SHAROV, 1968; KEVAN & WIGHTON, 1983. *Paleoc.,* Scotland.

Family GRYLLIDAE Latreille, 1802a

[Gryllidae LATREILLE, 1802a, p 274]

Related to the Haglidae. Male: fore wing tegminous, each tegmen with a longitudinal line of folding; tegmina at rest forming a boxlike cover over meso- and metanotum, hind wings, and abdomen; posterior branches of vein CUA modified as part of stridulatory

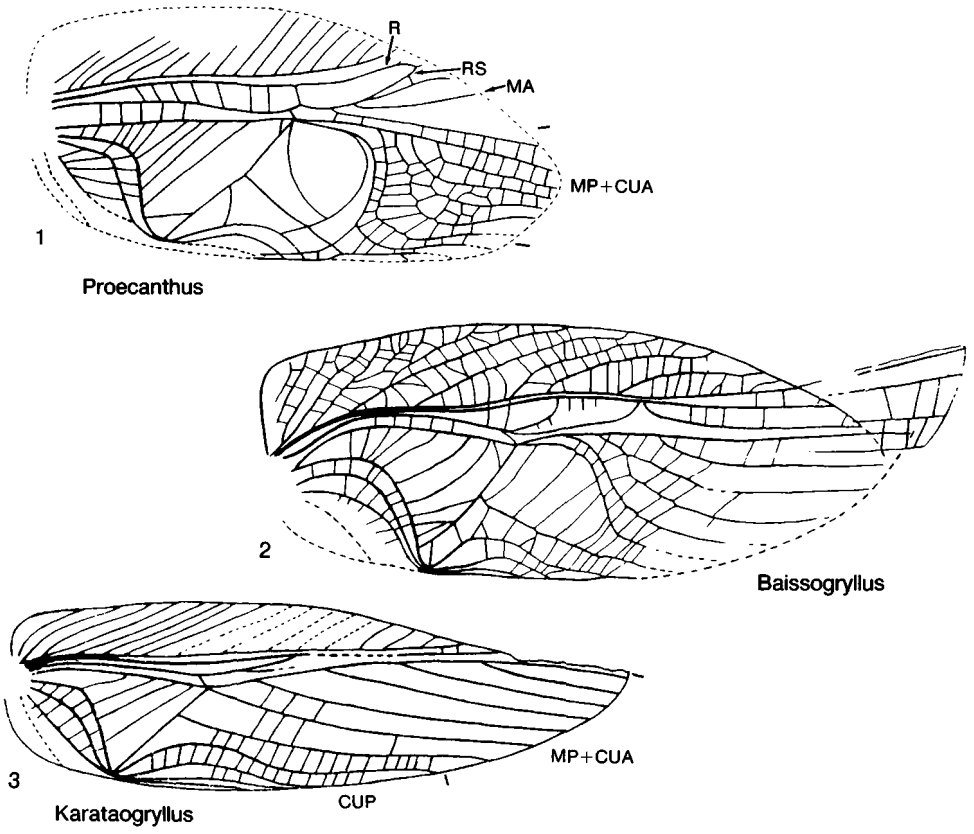


FIG. 108. Gryllidae (p. 173–174).

organ, extending almost to wing apex; stridulatory organ expanded distally and anteriorly, commonly occupying at least half of wing area, with an oblique secondary vein extending diagonally across central part of wing; CUP curving posteriorly, serrulate. Hind wing typically with an enlarged anal fan, as in Haglidae. Female: fore wing as in male in most respects, but lacking modifications of veins associated with stridulatory organ; branching of R and RS reduced, with loss of RS in highly specialized genera. Tarsi with 3 segments; cerci long, flexible; ovipositor cylindrical. ZEUNER, 1939, SHAROV, 1968. *Trias.–Holo.*

Gryllus LINNÉ, 1758, p. 425. Specimens of fore wings only. COCKERELL, 1925e; THÉOBALD, 1937a; ZEUNER, 1937, 1939; SHAROV, 1968. *Paleoc.–Plio,* Argentina (Jujuy); *Oligo.,* England, Europe (France, Germany)–*Holo.*

Allopterites COCKERELL, 1920a, p. 275 [**A. multilineatus*; OD]. Little-known genus; similar to *Gryllus,* but M with more branches. *Oligo.,* England.

Baissogryllus SHAROV, 1968, p. 183 [**B. sibiricus*; OD]. Male: fore wing nearly oval in shape; costal area long and nearly of uniform width; branches of SC long, oblique. *Jur.,* USSR (Asian RSFSR). ——FIG. 108,*2*. **B. sibiricus*; fore wing of male, ×4 (Sharov, 1968).

Eneopterotrypus ZEUNER, 1937, p. 156 [**E. chopardi*; OD]. Little-known genus, based on fragment of fore wing of male. ZEUNER, 1939. *Oligo.,* England.

Gryllavus SHAROV, 1968, p. 181 [**G. madygenicus*; OD]. Male: fore wing relatively slender; R with a few, short terminal branches; RS with a shallow fork; MA and MP parallel and nearly straight, terminating at wing apex; CUA with 8 terminal branches. Female: fore wing similar to that of male except for details in region of stridulatory organ; RS unbranched. *Trias.,* USSR (Kirghiz). ——FIG. 109,*1*. **G. madygenicus*; fore wings of *a,* male and *b,* female, both ×4 (Sharov, 1968).

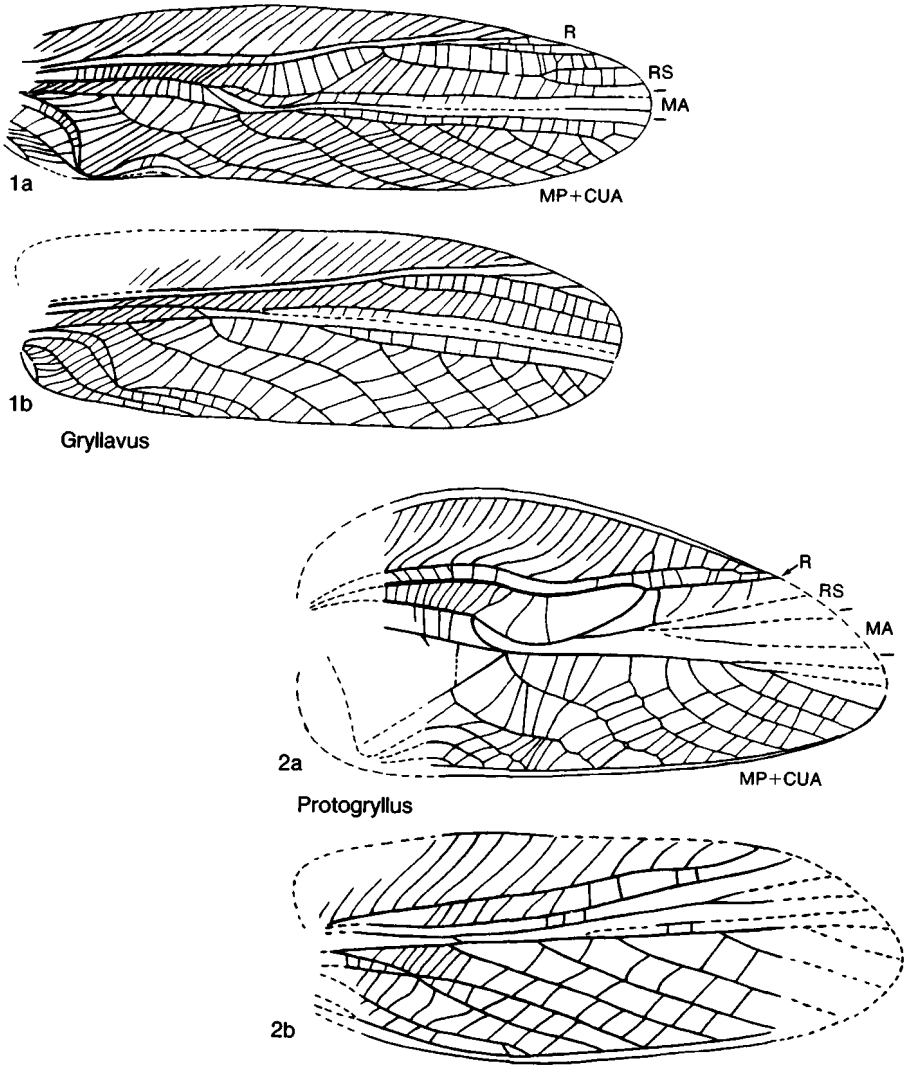


FIG. 109. Gryllidae (p. 173–175).

Heterotrypus SAUSSURE, 1878, p. 537. Whole adult male. CHOPARD, 1936b; WEIDNER, 1956. *Oligo.*, Europe (Baltic)–*Holo.*

Karataogryllus SHAROV, 1968, p. 182 [**K. gryllotalpiformis*; OD]. Male: fore wing as in *Protogryllus* but more elongate; anterior margin not so convex; branches of M and CUA parallel. *Jur.*, USSR (Kazakh).——FIG. 108,*3*. **K. gryllotalpiformis*; fore wing of male, ×4 (Sharov, 1968).

Liassogrylloides BODE, 1953, p. 105 [**L. basifastigatus*; OD]. Little-known fore wing. [Family assignment doubtful.] *Jur.*, Europe (Germany).

Lithogryllites COCKERELL, 1908p, p. 64 [**L. lutzii*; OD]. Little-known genus, based on apterous male, probably immature. ZEUNER, 1939. *Oligo.*, USA (Colorado).

Madasumma WALKER, 1869, p. 64. Female adult. CHOPARD, 1936b; ZEUNER, 1939, 1944b. *Oligo.*, Europe (Baltic)–*Holo.*

Paroecanthus SHAROV, 1968, p. 184 [**P. caucasicus*; OD]. Little-known genus, based on fragment of fore wing of male. Similar to *Proecanthus*, but costal area much narrower. *Mio.*, USSR (Asian RSFSR).

Proecanthus SHAROV, 1968, p. 183 [**P. anatolicus*; OD]. Little-known genus, based on incomplete fore wing of male. Similar to *Baissogryllus* but with fewer crossveins in the stridulatory area. *Cret.*, USSR (Kazakh).——FIG. 108,*1*. **P. anatolicus*; fore wing of male as preserved, ×5 (Sharov, 1968).

Pronemobius SCUDDER, 1890, p. 234 [**Nemobius*

tertiarius SCUDDER, 1878b, p. 774; SD ZEUNER, 1939, p. 227]. Related to *Nemobius* (recent), but hind tibiae without spines. ZEUNER, 1939. *Eoc.*, USA (Wyoming, Colorado).

Protogryllus HANDLIRSCH, 1906b, p. 424 [**Gryllus dobbertinensis* GEINITZ, 1880, p. 523; OD] [=*Achaetites* HANDLIRSCH, 1906b, p. 523 (type, *Acheta sedgwicki* BRODIE, 1845, p. 32); *Archaegryllodes* HAUGHTON, 1924, p. 336 (type, *A. stormburgensis*)]. Male: fore wing very broad, about half as wide as long; anterior border of wing very convex; R unbranched; distal branches of CUA more curved than in *Gryllavus*. ZEUNER, 1939; SHAROV, 1968. *Trias.*, South Africa; *Jur.*, USSR (Kirghiz, Kazakh), England, Europe (Germany). —— FIG. 109,*2*. *P. asiaticus* SHAROV, USSR; fore wings of *a*, male and *b*, female, both ×6 (Sharov, 1968).

Stenogryllodes CHOPARD, 1936b, p. 382 [**S. brevipalpis*; OD]. Little-known genus, based on a male nymph. Similar to *Stenogryllus*, but spines of hind tibiae less numerous but more closely arranged. ZEUNER, 1939. *Oligo.*, Europe (Baltic).

Trichogryllus CHOPARD, 1936b, p. 378 [**Gryllus macrocercus* GERMAR & BERENDT, 1856, p. 36; OD]. Related to the recent *Pteroplistes*. Posterior tibiae with 4 widely separated spines on each side. ZEUNER, 1939. *Oligo.*, Europe (Baltic).

Family GRYLLOTALPIDAE Leach, 1815

[Gryllotalpidae LEACH, 1815, p. 119]

Fore wing short, with a simple stridulatory organ on that of male; hind wing typically functional, but apterous species not uncommon. Forelegs well developed, adapted for digging; femora and tibiae broad and compressed; middle legs small; hind legs relatively short, with prominent femora; tarsi with 3 segments; external ovipositor absent. *Oligo.–Holo.*

Gryllotalpa LATREILLE, 1802, p. 275. Fore wing and whole specimen. COCKERELL, 1921d; ZEUNER, 1931, 1939; WEIDNER, 1968a. *Oligo.*, England; *Mio.*, Europe (Germany); *Plio.*, Europe (Germany)–*Holo.*

Neocurtilla KIRBY, 1906, p. 2. Foreleg only. ZEUNER, 1937, 1939. *Mio.*, Europe (Germany)–*Holo.*

Family PROPARAGRYLLACRIDIDAE Riek, 1956

[*nom. transl.* SHAROV, 1968, p. 185, *ex* Proparagryllacridinae RIEK, 1956, p. 106]

Male: fore wing with vein C submarginal; precostal area long, as in Oedischiidae; R with several branches, some arising close to origin of RS; RS with only 3 terminal branches; branches of RS, MA, MP, and CUA close together and parallel; stridulatory organ absent. Female: fore wing as in male, but RS with several long branches. Antennae long, filiform; prothorax of moderate length; hind legs long, with femora only slightly thickened; tarsi with 5 segments; arolium present; ovipositor broad, serrate; cerci long and thin. SHAROV, 1968. *Trias.*

The relationships of this family with others in the Ensifera are uncertain. The type genus is known only by small fragments. The preceding family diagnosis is based on SHAROV's account (1968) of the family, which was based mainly on two other genera that he placed in the family, *Mesogryllacris* RIEK and *Gryllacrimima* SHAROV.

Proparagryllacris RIEK, 1956, p. 106 [**P. crassifemur*; OD]. Little-known genus, based on fragments of wings and body. Venation apparently similar to that of *Gryllacrimima*. SHAROV, 1968. *Trias.*, Australia (Queensland).

Gryllacrimima SHAROV, 1968, p. 185 [**G. perfecta*; OD]. Similar to *Proparagryllacris*. Both MA and MP+CUA forked in fore wing of male. Body structure discussed under family. *Trias.*, USSR (Kirghiz).——FIG. 110,*3*. **G. perfecta*; fore wing of male, ×2.0 (Sharov, 1968).

Mesogryllacris RIEK, 1955, p. 685 [**M. giganteus*; OD]. Large species. Costal area of fore wing broader than in *Proparagryllacris*; M forked in basal half of wing; MA and MP apparently not forked. SHAROV, 1968. *Trias.*, Australia (Queensland).

Family UNCERTAIN

The following genera, apparently belonging to the Orthoptera, suborder Ensifera, are too poorly known to permit assignment to families.

Huabeius HONG, 1982b, p. 1128 [**H. suni*; OD]. Little-known genus, possibly related to the Haglidae. Cubital and anal areas of fore wing of female very narrow. *Cret.*, China (Hebei Province).

Lithymnetoides KEVAN & WIGHTON, 1983, p. 220, footnote [**Lithymnetes laurenti* THÉOBALD, 1937a, p. 113; OD]. Little-known genus, based on poorly preserved specimens. *Oligo.*, Europe (France).

Mesoedischia SHAROV, 1968, p. 160 [**M. madygenica*; OD]. Fore wing of male: precostal area very short; costal veinlets widely spaced, not reticulate; area between SC and R very narrow; crossveins numerous but reticulate only near wing

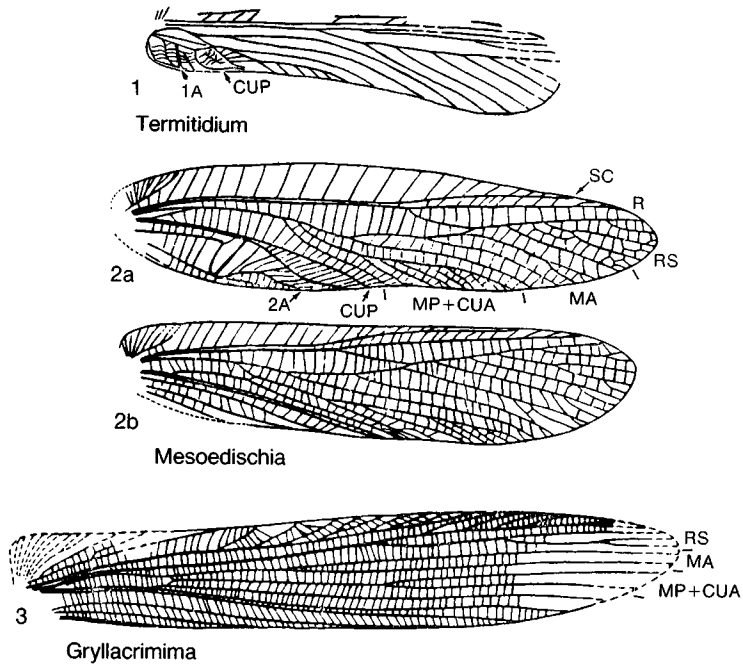


FIG. 110. Proparagryllacrididae and Uncertain (p. 175–176).

apex; CUA diverging basally from CUP and anastomosed with M for a considerable interval, before diverging off, usually in combination with MP; CUA with several branches; stridulatory apparatus well develped at base of wing. Fore wing of female similar to that of male but without local specializations near wing base. [This genus was placed by SHAROV (1968) in the Oedischiidae. The anastomosis of CUA with the stem of M, clearly shown at the base of the wing of the type specimen, and the presence of an advanced stridulatory apparatus at the base of the wing of the male seem to me to require a separate family. With regard to the structures mentioned, the genus seems more closely related to the Haglidae than to the Oedischiidae. So far as I am aware, however, this is the only extinct genus that shows the actual anastomosis of CUA1 with M at the base of the wing.] *Trias.*, USSR (Tadzhik).——FIG. 110,*2*. **M. madygenica*; fore wings of *a*, male and *b*, female, ×2.5 (Sharov, 1968).

Proedischia PINTO & ORNELLAS, 1978c, p. 309 [**P. mezzalirai*; OD]. Little-known genus, possibly related to the Oedischiidae. Fore wing elongate; costal area slender; precostal area very small or absent, the main veins not curved posteriorly near wing base; anal area unknown. [Type of family Proedischiidae PINTO & ORNELLAS]. *U. Carb.*, Brazil (São Paulo).

Protachaeta HANDLIRSCH, 1939, p. 55 [**P. masculina*; OD]. Little-known genus, based on poorly preserved fore wing. ZEUNER, 1939. *Jur.*, Europe (Germany).

Pseudohumbertiella HANDLIRSCH, 1906b, p. 522 [**Humbertiella grandis* BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 13; OD]. Little-known genus, based on distal fragment of wing. [Placed in Locustidae by HANDLIRSCH (1906b), and in Haglidae by SHAROV (1968).] *Jur.*, USSR (Asian RSFSR).

Termitidium WESTWOOD, 1854, p. 394 [**T. ignotum*; OD]. Fore wing with CUP remote from 1A. [Placed in Tettigoniidae by ZEUNER (1939) and in Haglidae by SHAROV (1968).] *Jur.*, England.——FIG. 110,*1*. **T. ignotum*; fore wing, ×1.5 (Zeuner, 1939).

Thuringopteryx KUHN, 1937, p. 191 [**T. gimmi*; OD]. Little-known genus, based on hind wing fragment, possibly belonging to Haglidae. ZEUNER, 1939. *Trias.*, Europe (Germany).

Zhemengia HONG, 1982b, p. 1123 [**Z. sinica*; OD]. Little-known genus, based on wing fragment. *Jur.*, China (Inner Mongolia).

Suborder CAELIFERA Ander, 1936

[Caelifera ANDER, 1936, p. 93]

Antennae shorter than body, with not more than 30 segments; tympanal organs, when present, on first abdominal segment; strid-

ulatory mechanism diverse (rarely absent), hind tibiae or femora commonly scraped across ridges on abdomen or fore wings; ovipositor, when present, typically short. *Trias.–Holo.*

Family LOCUSTOPSEIDAE Handlirsch, 1906

[*nom. correct* Rohdendorf, 1957, p. 83, *pro* Locustopsidae Handlirsch, 1906b, p. 421]

Related to Acrididae. Fore wings long, commonly twice as long as body, typically broader distally than proximally; apex rounded; vein SC terminating near apex; M forking into MA and MP near level of origin of RS; MA typically with 2 long, parallel branches; CUA commonly with 3 terminal branches; CUP unbranched; crossveins not so numerous as in Acrididae. Stridulatory apparatus apparently absent. Hind wing as in Acrididae; M anastomosed with R basally. Body structures apparently similar to those of the Acrididae. Zessin, 1983a. *Trias.–Cret.*

Locustopsis Handlirsch, 1906b, p. 421 [**L. elegans*; SD Cockerell, 1915, p. 473] [=*Brodiana* Zeuner, 1942d, p. 13 (type, *B. cubitalis*)]. Fore wing: RS with 3 to 5 branches; M with 3, rarely 2; crossveins forming an irregular network over at least part of wing. Sharov, 1968; Zessin, 1983a. *Jur.,* England, Europe (Germany), USSR (Kazakh, Tadzhik, Kirghiz, Asian RSFSR). ——Fig. 111,*1. L. karatavica* Sharov; *a,* fore wing, *b,* hind wing, both ×3.5; *c,* entire specimen, ×2.5 (Sharov, 1968).

Conocephalella Strand, 1926, p. 46, *nom. subst. pro Conocephalites* Handlirsch, 1906b, p. 518, *non* Barrande, 1852 [**Conocephalus capito* Deichmüller, 1886, p. 24; OD] [=*Conocephalopsis* Handlirsch, 1939, p. 154, obj.]. Large species; RS of fore wing with 6 or 7 branches. Strong spines on hind tibiae. Zeuner, 1942d; Sharov, 1968. *Jur.,* Europe (Germany).

Parapleurites Brauer, Redtenbacher, & Ganglbauer, 1889, p. 13 [**P. gracilis*; OD]. Fore wing as in *Locustopsis* but with a double row of cells between M and CU basally. Zeuner, 1942d; Sharov, 1968. *Jur.,* USSR (Asian RSFSR).—— Fig. 111,*4. P. sibirica* Sharov; fore wing, ×4.0 (Sharov, 1968).

Praelocustopsis Sharov, 1968, p. 187 [**P. mirabilis*; OD]. Fore wing: SC short; precostal area with very few veinlets and narrower than costal area below it; crossveins widely spaced distally. *Trias.,* USSR (Asian RSFSR).——Fig. 111,*2. *P. mirabilis*; fore wing, ×9.0 (Sharov, 1968).

Schwinzia Zessin, 1983a, p. 180 [**S. sola*; OD]. Fore wing similar to that of *Triassolocusta,* but CUA with 4 terminal branches. *Jur.,* Europe (Germany).

Triassolocusta Tillyard, 1922b, p. 451 [**T. leptoptera*; OD]. Little-known genus, based on part of a fore wing; M with 4 terminal branches, CUA with 2. Sharov, 1968. *Trias.,* Australia (Queensland).

Zeunerella Sharov, 1968, p. 189 [**Z. arborea*; OD]. Fore wing as in *Locustopsis* but C longer, extending almost to level of origin of RS; C strongly curved anteriorly near wing base. Kevan & Wighton, 1983. *Cret.,* USSR (Kazakh).—— Fig. 111,*3. *Z. arborea*; fore wing, ×4.5 (Sharov, 1968).

Family LOCUSTAVIDAE Sharov, 1968

[Locustavidae Sharov, 1968, p. 185]

Fore wing as in Locustopseidae, but vein CUA with 4 or 5 terminal branches. Body unknown. [Provisionally placed in Caelifera by Sharov; lack of knowledge of body structure prevents definite assignment to either Caelifera or Ensifera.] *Trias.*

Locustavus Sharov, 1968, p. 186 [**L. madygensis*; OD]. RS arising near midwing; forking of M at level of end of C. *Trias.,* USSR (Kirghiz).—— Fig. 112,*2. *L. madygensis*; fore wing, ×2.5 (Sharov, 1968).

Ferganopsis Sharov, 1968, p. 186 [**F. lanceolatus*; OD]. Fore wing as in *Locustavus,* but RS arising much nearer wing base; M forking well before origin of RS. *Trias.,* USSR (Kirghiz).——Fig. 112,*4. *F. lanceolatus; a,* fore and *b,* hind wings, both ×3.0 (Sharov, 1968).

Family EUMASTACIDAE Burr, 1899

[Eumastacidae Burr, 1899, p. 75]

Small species, with great diversity of structure. Fore and hind wings commonly reduced or absent; stridulatory structures and tympanal organs apparently absent; fore wing (when fully formed) with an unbranched CUA. *Cret.–Holo.*

Eumastax Burr, 1899, p. 94. *Holo.*

Archaeomastax Sharov, 1968, p. 189 [**A. jurassicus*; OD]. Similar to *Erucius* (recent), but subcostal area broader and branches of M shorter. *Cret.,* USSR (Kazakh).——Fig. 112,*1. *A. jurassicus*; fore wing, ×8.0 (Sharov, 1968).

Taphacris Scudder, 1890, p. 226 [**T. reliquata*; OD] [=*Eobanksia* Cockerell, 1909h, p. 384 (type, *E. bittaciformis*)]. Little-known genus, based on fragments of wings and body. [Family

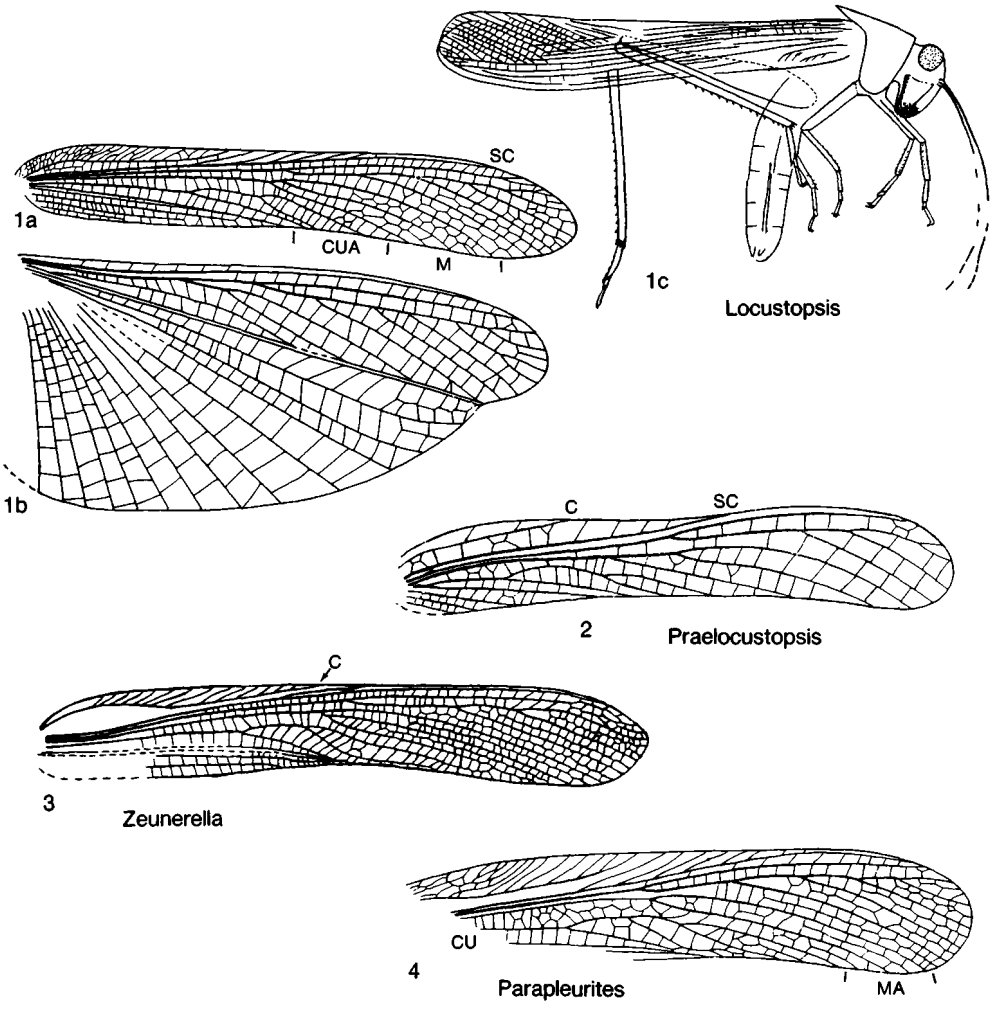


FIG. 111. Locustopseidae (p. 177).

assignment uncertain.] ZEUNER, 1944b. *Oligo.,* USA (Colorado).

Family PROMASTACIDAE Kevan & Wighton, 1981

[Promastacidae KEVAN & WIGHTON, 1981, p. 1834]

Apparently similar to Erucidae (recent), but fore wings broader and less constricted near middle; stems of veins SC, R, RS, and M more widely separated from each other. *Paleoc.–Eoc.*

Promastax HANDLIRSCH, 1910b, p. 97 [**P. archaicus*; OD]. Little-known genus, based on distal fragment of fore wing. Branches of RS arising in distal third of wing; RS with 3 terminal branches; MA unbranched. KEVAN & WIGHTON, 1981. *Eoc.,* Canada (British Columbia).——FIG. 112,*3*. **P. archaicus*; fore wing, ×2.6 (Handlirsch, 1910b).

Promastacoides KEVAN & WIGHTON, 1981, p. 1834 [**P. albertae*; OD]. Little-known genus, based on poorly preserved fore wing. Similar to *Promastax,* but branches of RS arising before midwing; RS with 5 terminal branches; MA forked. *Paleoc.,* Canada (Alberta).

Family TETRIGIDAE Rambur, 1838

[Tetrigidae RAMBUR, 1838, p. 64]

Small species. Fore wings short and thick, commonly scalelike or absent in existing species. Hind wings of moderate size, if present.

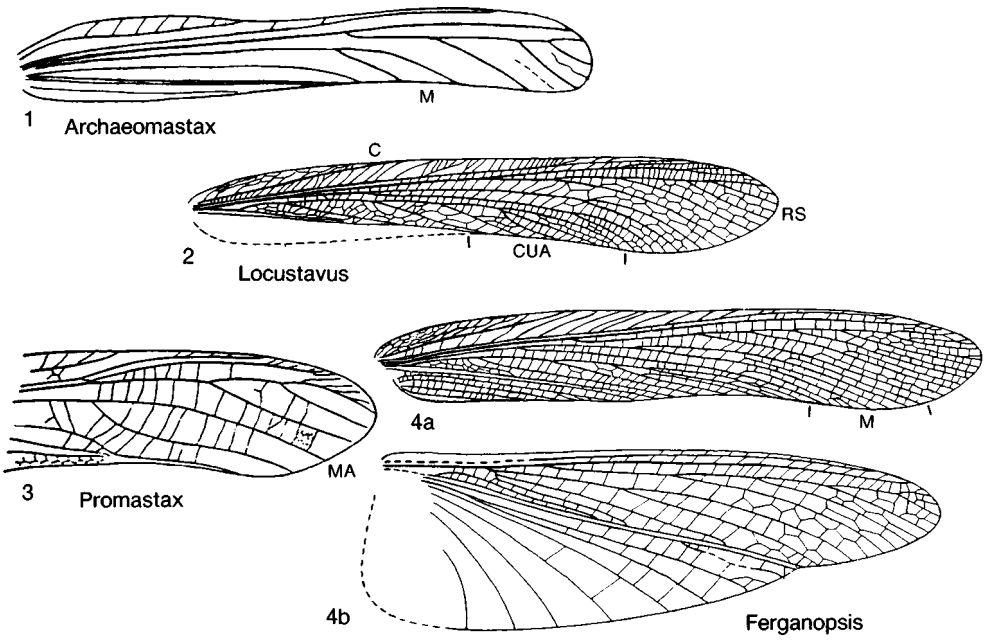


FIG. 112. Locustavidae, Eumastacidae, and Promastacidae (p. 177–178).

Pronotum projecting posteriorly at least to base of abdomen and commonly to or beyond apex of abdomen. Tympanal and stridulatory structures absent. *Cret.–Holo.*

Tetrix LATREILLE, 1802, p. 284. Adult male. ZEUNER, 1937. *Oligo.,* Europe (Baltic)–*Holo.*

Archaeotetrix SHAROV, 1968, p. 190 [**A. locustopseiformis*; OD]. Fore and hind wings fully formed. Fore wing tegminous, unusually thick; crossveins forming a coarse reticulation between longitudinal veins; precostal and costal areas nearly equally broad, the two combined about half width of wing; SC and stem of R very close together and parallel; M and CUA unbranched. Hind wing with MA and MP present. *Cret.,* USSR (Asian RSFSR).——FIG. 113,*3*. **A. locustopseiformis; a,* fore and *b,* hind wings, both ×6.5 (Sharov, 1968).

Prototetrix SHAROV, 1968, p. 190 [**P. reductus*; OD]. Fore wing with precostal area forming a small basal lobe; SC, R, and RS distinct; M and CU much reduced; CUA absent. *Cret.,* USSR (Asian RSFSR).——FIG. 113,*1*. **P. reductus*; fore wing, ×13.0 (Sharov, 1968).

Succinotettix PITON, 1938, p. 227 [**S. chopardi*; OD]. Little-known genus, apparently related to *Paratettix* (recent). Antennae with 19 segments; pronotum extending posteriorly slightly beyond end of abdomen. *Oligo.,* Europe (Baltic).

Tettigidea SCUDDER, 1862, p. 476. Whole insect. [Generic assignment doubtful.] HEER, 1865; SCUDDER, 1890. *Mio.,* Europe (Germany)–*Holo.*

Family TRIDACTYLIDAE Brunner, 1882

[Tridactylidae BRUNNER, 1882, p. 453]

Small, highly specialized species. Fore wing tegminous and short, commonly not reaching apex of abdomen; venation in existing species reduced to 2 or 3 veins (SC, R, 1A). Hind wing with remigium reduced to narrow strip; all veins unbranched; anal fan very large. Hind femora greatly enlarged; hind tibiae of recent species with a pair of articulated plates. *Cret.–Holo.*

Tridactylus OLIVIER, 1789, p. 26. *Holo.*

Monodactyloides SHAROV, 1968, p. 191 [**M. curtipennis*; OD]. Similar to *Monodactylus,* but fore wings short, extending only to middle of abdomen. SC of fore wing with short branches. *Cret.,* USSR (Asian RSFSR).

Monodactylus SHAROV, 1968, p. 191 [**M. dolichopterus*; OD]. Fore wing well developed and long, with apices reaching end of abdomen; SC extending about three-fourths wing length from base, with several long branches; M and CUA unbranched. Pronotum with broad lateral lobes.

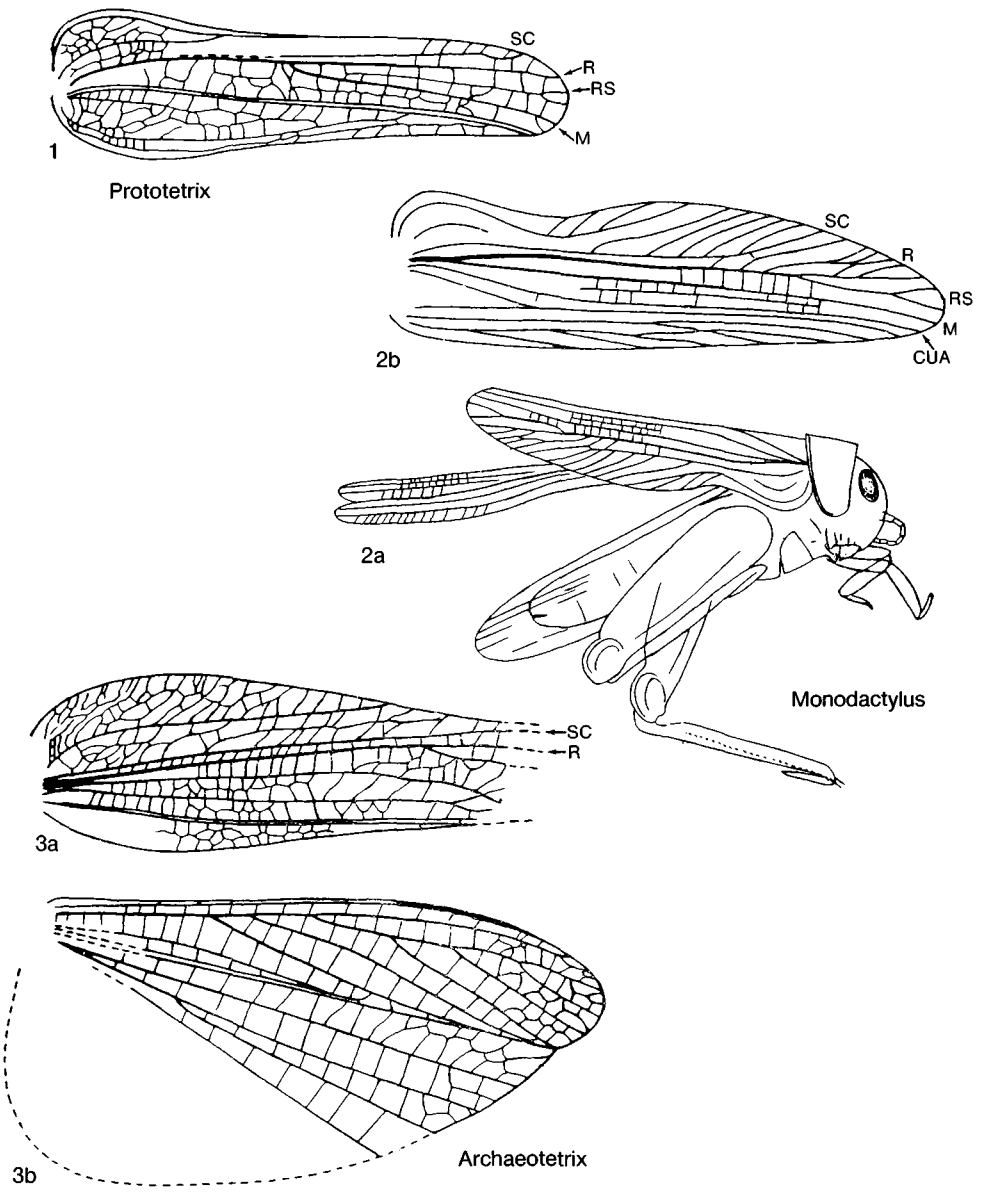


FIG. 113. Tetrigidae and Tridactylidae (p. 178–180).

Cret., USSR (Asian RSFSR).——FIG. 113,*2*. **M. dolichopterus; a,* entire specimen as preserved, ×4.5; *b,* fore wing, ×7.3 (Sharov, 1968).

Family ACRIDIDAE Latreille, 1825

[Acrididae LATREILLE, 1825, p. 414]

Both pairs of wings typically well developed. Fore wing with basal parts of veins SC, R, and M very close together; RS with numerous branches. Hind wing with R and M anastomosed basally. Tympanal organs on first abdominal segment. Stridulation by rubbing hind femora across posterior margin of fore wings, or by snapping hind wings in flight. *Eoc.–Holo.*

Acrida LINNÉ, 1758, p 425. *Holo.*

Bryodema FIEBER, 1853, p. 129. Parts of wings and body. PONGRÁCZ, 1928; ZEUNER, 1942a. *Mio.,* Europe (Hungary)–*Holo.*

Heeracris ZEUNER, 1937, p. 159 [**Acridium oeningense* SCUDDER, 1895a, p. 118; OD]. Little-known genus, based on part of fore wing. [Possibly related to *Catanops* (recent).] *Mio.,* Europe (Germany).

Mentacridium PITON, 1936b, p. 78 [**M. eocenicum*; OD]. Little-known genus, based on poorly preserved fore wing. [Family assignment doubtful.] ZEUNER, 1944b. *Eoc.,* Europe (France).

Miocaenacris ZEUNER, 1931, p. 275 [**M. soergeli*; OD]. Little-known genus, based on general body form; probably related to *Catanops* (recent). ZEUNER, 1941b. *Mio.,* Europe (Germany).

Nanthacia SCUDDER, 1890, p. 224 [**N. torpida*; OD]. Little-known genus, based on single hind wing. ZEUNER, 1944b. *Oligo.,* USA (Colorado).

Oedipoda LATREILLE, 1829, p. 188. Fore wings and body. [Generic assignment of fossils uncertain.] ZEUNER, 1942a. *Mio.,* Europe (Hungary)–*Holo.*

Proschistocerca ZEUNER, 1937, p. 158 [**P. oligocaenica*; OD]. Similar to *Schistocerca* (recent), but costal area of fore wing abruptly narrowed just before first branch of RS. *Oligo.,* England.

Protocatanops ZEUNER, 1931, p. 262 [**P. gracilis*; OD]. Little-known genus, based on head and prothorax. [Probably synonymous with *Catanops* (recent).] *Mio.,* Europe (Germany).

Taeniopodites COCKERELL, 1909q, p. 283 [**T. pardalis*; OD]. Little-known genus, based on fragment of fore wing; probably related to *Catanops* (recent). ZEUNER, 1941b. *Oligo.,* USA (Colorado).

Tyrbula SCUDDER, 1885b, p. 768 [**T. russelli*; OD]. Little-known genus, based on body only. ZEUNER, 1944b. *Eoc.,* USA (Wyoming); *Oligo.,* USA (Colorado).

Family UNCERTAIN

The following genera, apparently belonging to the Orthoptera, suborder Caelifera, are too poorly known to permit assignment to families.

Chresmoda GERMAR, 1839, p. 201 [**C. obscura*; OD] [=*Locusta prisca* GERMAR, 1839, p. 200]. Little-known genus, probably related to Acrididae. [Type of family Chresmodidae HAASE, 1890a, p. 11. Placed in the Orthoptera by GERMAR and in the Hemiptera (Hydrometridae or Gerridae) by most entomologists before 1900; placed by HANDLIRSCH (1906b) and almost everyone else since then in the Phasmatodea. Frequently confused with *Pygolampis gigantea* (GERMAR). See HAGEN, 1862; VISHNIAKOVA, 1980b, p. 173, footnote; and CARPENTER, 1992.] *Jur.,* Europe (Germany).

Miopyrgomorpha KEVAN in KEVAN & AKBAR, 1964, p. 1526, footnote [**Oedipoda fischeri* HEER, 1865, p. 367; OD]. Little-known genus, based on poorly preserved specimen. ZEUNER, 1944b; KEVAN, 1965. *Mio.,* Europe (Germany).

Suborder UNCERTAIN

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

Locustopsites THÉOBALD, 1937a, p. 116 [**L. gigantea*; OD]. Little-known genus, based on fore wing fragment. ZEUNER, 1942d. *Oligo.,* Europe (France).

Phaneropterites HANDLIRSCH, 1906b, p. 519 [**Phaneroptera germari* MÜNSTER in GERMAR, 1842, p. 81; OD]. Little-known genus, based on a poorly preserved specimen. ZEUNER, 1942d. *Jur.,* Europe (Germany).

Order GRYLLOBLATTODEA Brues & Melander, 1915

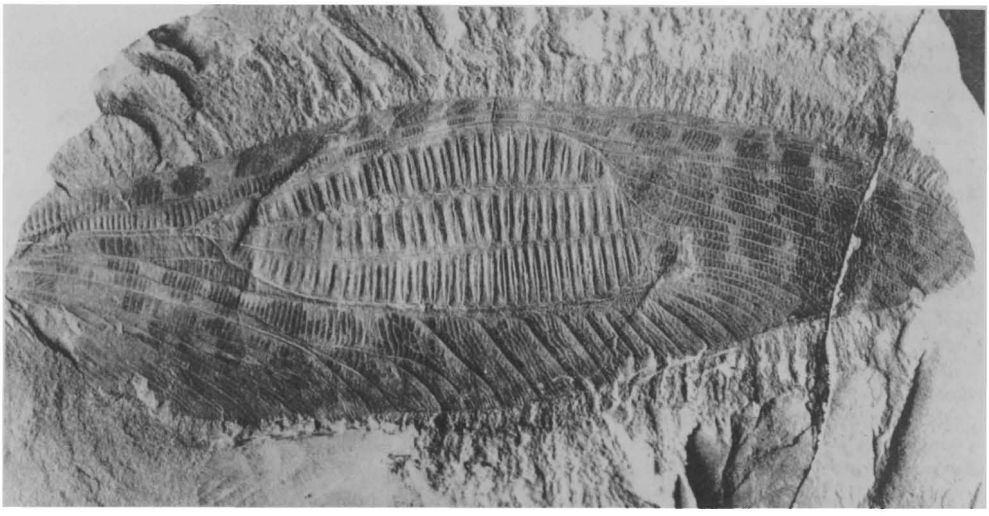
[*nom. correct.* BRUES & MELANDER, 1932, *pro* Grylloblattoidea BRUES & MELANDER, 1915, p. 13]

Wingless; antennae long, multisegmented; compound eyes absent or small; ocelli absent; legs cursorial; tarsi five-segmented; cerci well developed, segmented; ovipositor conspicuous. *Holo.*

Order TITANOPTERA Sharov, 1968

[Titanoptera SHAROV, 1968, p. 122]

Orthopteroid insects of moderate to large size. Fore wing with or without a precostal area; spaces between veins RS, MA, and MP commonly wide, in some genera much enlarged and forming a stridulatory area, apparently in both sexes; CUP commonly branched; 2A with pectinate branching for its entire length, directed posteriorly. Hind wing with MP+CUA1 branched; 2A branched much as in fore wing; anal area large and forming a lobe in some genera but relatively small in others. Antennae very long, slender, and filiform; head hypognathous, with long, serrate mandibles; prothorax relatively short; forelegs prehensile, spinose; hind



Mesotitan

FIG. 114. Mesotitanidae (p. 182).

legs cursorial, relatively short; all tarsi with 5 segments; arolium present; cerci short, unsegmented; ovipositor also short. Wings at rest folded flat over abdomen, not inclined as in the Orthoptera (Saltatoria). Nymphs unknown. *Trias.*

TILLYARD (in TILLYARD & DUNSTAN, 1916) originally placed the genus *Mesotitan* in the Protorthoptera, but he later (TILLYARD, 1925c) transferred it to the Protohemiptera, where it was also placed by MCKEOWN (1937), who had much better specimens for study (Fig. 114). ZEUNER (1939) transferred the genus and its family to the Orthoptera, in which they were also later placed by RIEK (1954c). SHAROV (1962b) assigned the Mesotitanidae to the Paraplecoptera, but in 1968, after study of a very extensive collection of Mesotitanidae and related families from the Triassic of the USSR, he designated the new order Titanoptera for their reception. More recently, RASNITSYN (1980c) treated the Titanoptera as a suborder of the Orthoptera. However, since in the present work the order Orthoptera is restricted to the saltatorial orthopteroids, the Titanoptera have ordinal status.

Family MESOTITANIDAE Tillyard, 1925

[Mesotitanidae TILLYARD, 1925c, p. 376] [=Clathrotitanidae RIEK, 1954c, p. 165]

Large insects. Fore wing with areas between veins RS and MA1, MA1 and MA2, MA2 and MP+CUA1 commonly broad; crossveins in those areas straight, unbranched, alternately convex and concave, and forming a stridulatory apparatus; RS arising from R about one-third wing length from base and very close to R for most of its length; MA forking at about level of origin of RS. Venation of hind wing similar to that of fore wing except for the stridulatory area. *Trias.*

Mesotitan TILLYARD in TILLYARD & DUNSTAN, 1916, p. 40 [**M. giganteus*; OD] [=*Clatrotitan* MCKEOWN, 1937, p. 32 (type, *C. andersoni*, =*M. scullyi* TILLYARD, 1925c, p. 376)]. Fore wing broadest at level of midwing; precostal area apparently absent; stridulatory area about half the width of entire wing. SHAROV, 1968. *Trias.*, Australia (New South Wales).——FIG. 114. *M. scullyi* TILLYARD (type specimen of *C. andersoni* MCKEOWN); fore wing, ×1 (McKeown, 1937).

Mesotitanodes SHAROV, 1968, p. 197 [**M. tillyardi*; OD]. Fore wing very broad, especially medially; precostal area present; area between MA1 and MA2 about twice as wide as that

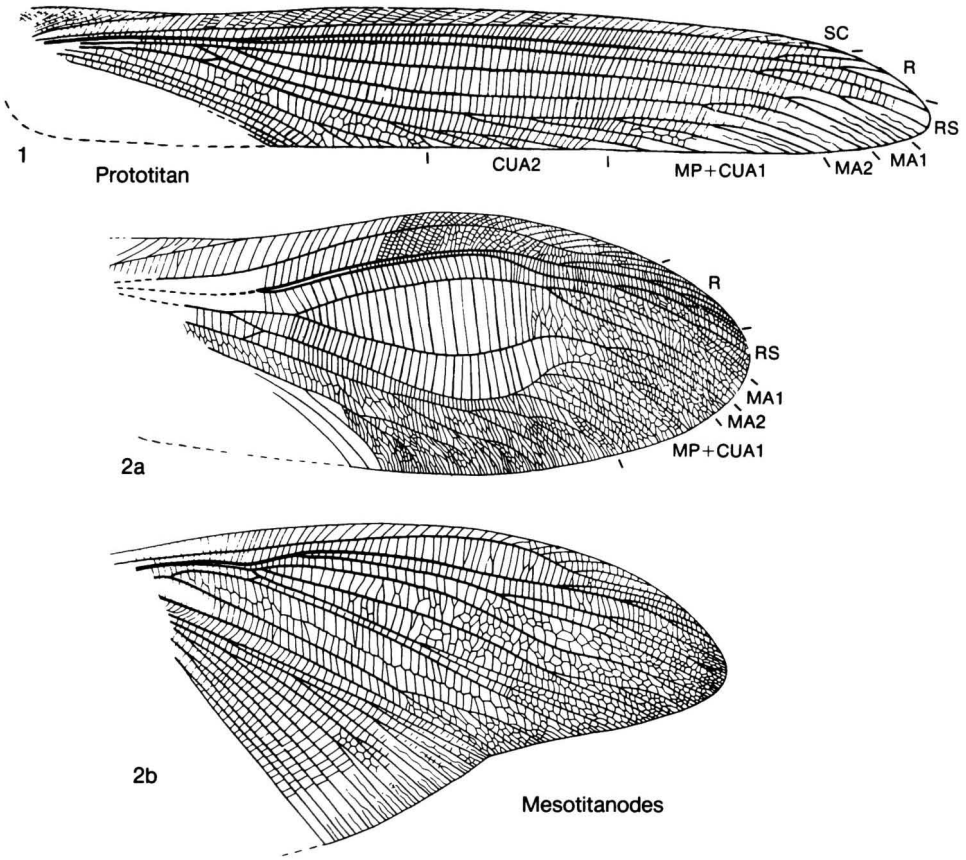


FIG. 115. Mesotitanidae (p. 182–183).

between RS and MA1. *Trias.*, USSR (Kirghiz). ——FIG. 115,*2*. **M. tillyardi*; *a*, fore and *b*, hind wings, ×1 (Sharov, 1968).

Prototitan SHAROV, 1968, p. 196 [**P. primitivus*; OD]. Fore wing nearly uniform in width, not increased medially; precostal area present; areas between RS and MP+CUA1 only slightly widened. *Trias.*, USSR (Kirghiz).——FIG. 115,*1*. **P. primitivus*; fore wing, ×1.5 (Sharov, 1968).

Ultratitan SHAROV, 1968, p. 198 [**U. superior*; OD]. Little-known genus, based on distal fragment of wing. Stridulatory area extending nearly to wing apex. *Trias.*, USSR (Kirghiz).

Family PARATITANIDAE Sharov, 1968

[Paratitanidae SHAROV, 1968, p. 198]

Fore wing with anterior margin uniformly curved; space between veins MA2 and MP+CUA1 very narrow; precostal area present; base of M anastomosed with R; RS arising from R in distal third of wing. Hind wing with enlarged anal lobe. *Trias.*

Paratitan SHAROV, 1968, p. 199 [**P. libelluloides*; OD]. Fore wing with subcostal area nearly as broad as costal area; M branching from R nearer to forking of M than to wing base; MA2 slightly sigmoidal in distal half. *Trias.*, USSR (Kirghiz). ——FIG. 116,*a,b*. **P. libelluloides; a*, fore and *b*, hind wings, ×1.6 (Sharov, 1968).——FIG. 116,*c*. *P. ovalis* SHAROV; fore wing, ×1.5 (Sharov, 1968).

Family GIGATITANIDAE Sharov, 1968

[Gigatitanidae SHAROV, 1968, p. 199]

Very large species. Fore wing with precostal area present; vein RS arising basally or near midwing; area between MA2 and

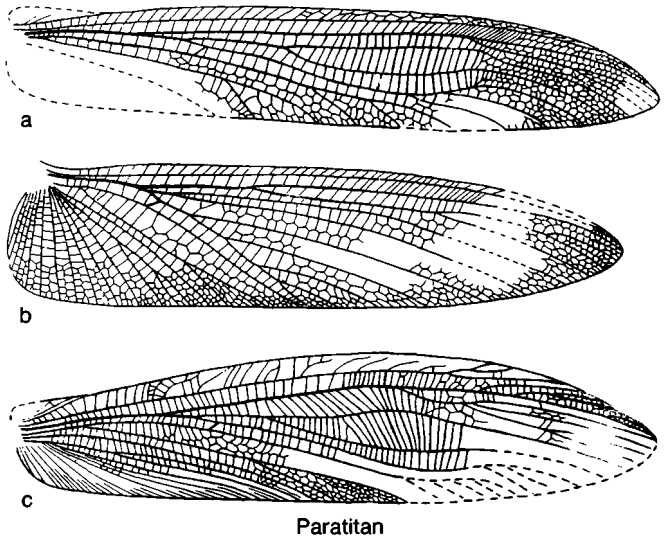


FIG. 116. Paratitanidae (p. 183).

MP+CUA1 the only broad space in the stridulatory area of the wing. *Trias.*

Gigatitan SHAROV, 1968, p. 200 [**G. vulgaris*; OD]. Fore wing: SC with basal branch extending about one-third wing length from base; RS arising from R near wing base. *Trias.*, USSR (Kirghiz).——FIG. 117,*3*. **G. vulgaris*; *a*, reconstruction, ×0.8; *b*, fore wing, ×0.6; *c*, hind wing, ×0.6; *d*, foreleg, ×2.0; *e*, head, antennae, pronotum, ×1 (all Sharov, 1968).

Nanotitan SHAROV, 1968, p. 202 [**N. magnificus*; OD]. Fore wing with large precostal area; RS arising near wing base; MA1 and MA2 unbranched; MA2 and MP+CUA1 anastomosed at base of wing. *Trias.*, USSR (Kirghiz).——FIG. 117,*1*. *N. extensus* SHAROV; fore wing, ×1 (Sharov, 1968).

Ootitan SHAROV, 1968, p. 201 [**O. curtis*; OD]. Fore wing very short and broad; RS arising at about midwing. *Trias.*, USSR (Kirghiz).——FIG. 117,*2*. **O. curtis*; fore wing, ×1 (Sharov, 1968).

Order PHASMATODEA Brunner, 1893

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 102, *pro* Phasmodea BRUNNER, 1893, p. 76] [=Aeroplanoptera TILLYARD, 1923b, p. 481]

Moderate-sized to large insects, with much diversity of wing and body form. Mouthparts mandibulate, mandibles strong; eyes small; antennae typically long, slender, and multisegmented, less commonly short, with few to many segments; legs gressorial, long, and diversely modified; 5 tarsomeres. Fore wings typically reduced or absent in existing species but normally developed in some Mesozoic families. Hind wings of existing species rarely absent, commonly large; remigium tegminous; anal area greatly enlarged, fan-shaped. Venation of fore wings and of remigium of hind wings of existing species reduced, with dense reticulation, and a series of strong, parallel longitudinal veins, with very few branches. Abdomen long, slender, and cylindrical in Phasmatidae and most Mesozoic species, shorter and dorsoventrally compressed in Phylliidae; cerci unsegmented, typically short. Existing species foliage-feeders. Eggs deposited in ground litter or more rarely inserted in soil. *Trias.–Holo.*

For many years the Phasmatodea were considered to be a family within the order Orthoptera. However, their gressorial hind legs, five-segmented tarsi, unsegmented cerci, as well as several venational features, support the conclusion of BEIER (1967) that they represent a separate order within the orthopteroid complex. The order is now relatively small, with only two families, Phasmatidae and Phylliidae, generally recognized. The

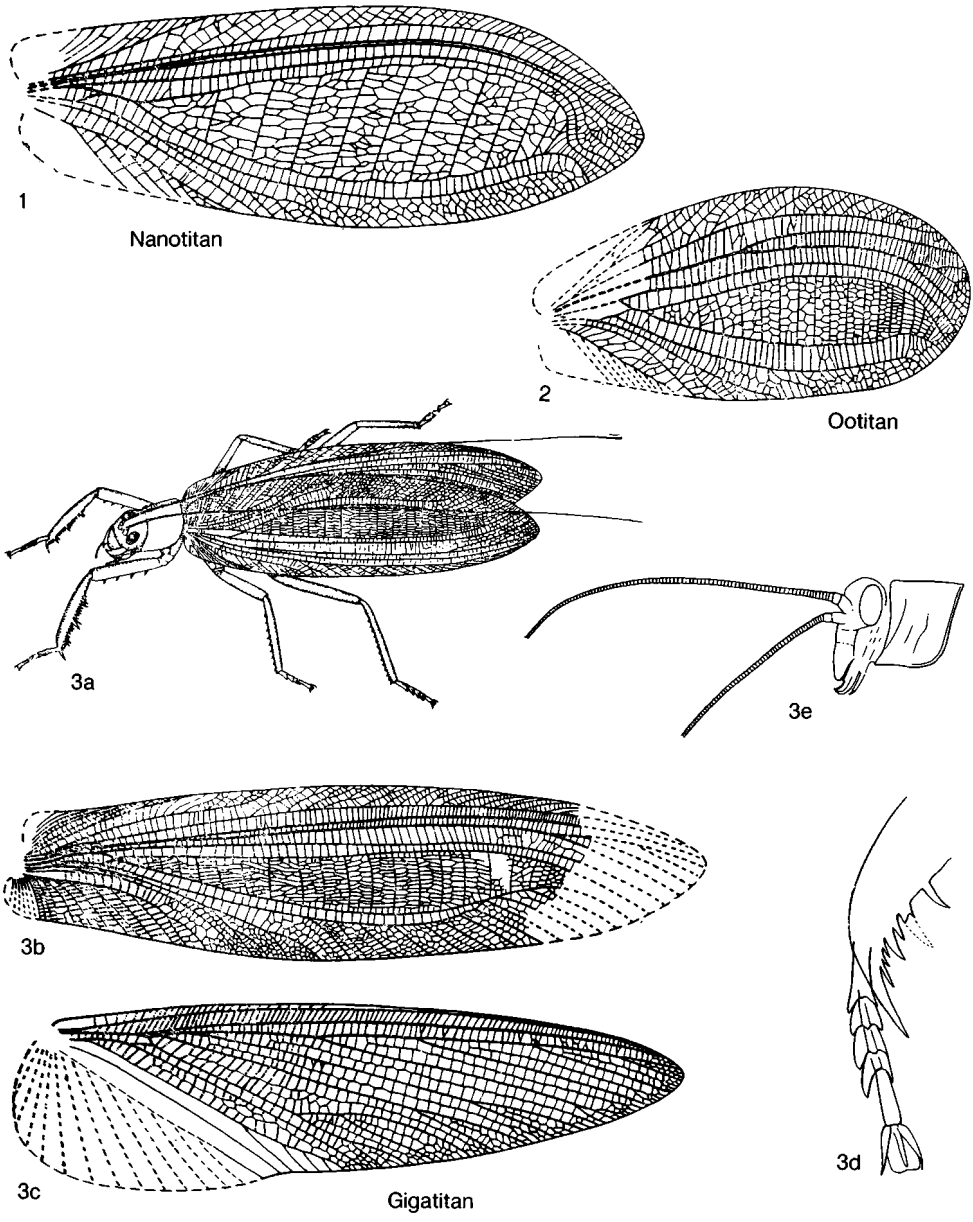


FIG. 117. Gigatitanidae (p. 184).

phasmatids, with long and cylindrical bodies, resemble twigs and small sticks; the phylliids, with dorsoventrally compressed bodies and flat extensions of the legs, resemble leaves.

SHAROV (1968) has made the most significant contribution to our knowledge of the geological record of the order, and in particular to what appears to have been its early stages, with a study of a series of Mesozoic specimens. The geological record of the two existing families is limited to nymphs of one species of each family in Baltic amber. The early Mesozoic members of the order bear little resemblance, in general form, to the

Phasmatidae or Phylliidae. They do, however, have very long and narrow fore wings, with the longitudinal veins straight and parallel as in the phasmatids. Similarly, the remigium of the hind wing is long, narrow, and tegminous, with the longitudinal veins as in the fore wings. The compound vein, MP+CUA1, is present in the Mesozoic species and similar in form to that in both Phasmatidae and Phylliidae. The cerci in the Mesozoic fossils are unsegmented, as in the existing Phasmatodea. These features are indeed indicative of relationship, but more structural details are probably needed for conviction. At present, the Mesozoic record includes only five small families of these insects.

Family XIPHOPTERIDAE Sharov, 1968

[Xiphopteridae SHAROV, 1968, p. 192]

Little-known family. Fore wing membranous; precostal area well developed; vein C with many fine branches; RS arising from R in distal half of wing, branched; MA forked; MP+CUA1 with a comb of branches directed posteriorly. Hind wing unknown. [Ordinal assignment doubtful.] *Trias.*

Xiphopterum SHAROV, 1968, p. 192 [*X. *curvatum*; OD]. Fore wing broadest distally and curved posteriorly in distal area; precostal area forming a prominent bulge basally; MA forking in proximal part of wing. *Trias.*, USSR (Kirghiz).——FIG. 118,*2*. *X. *curvatum*; fore wing, ×1.3 (Sharov, 1968).

Family AEROPLANIDAE Tillyard, 1918

[Aeroplanidae TILLYARD, 1918c, p. 425]

Fore wing: precostal area long, but vein C without branches; longitudinal veins mostly parallel; crossveins unbranched, except in the anal area; RS arising from R near wing base; MP+CUA1 forked near level of origin of RS, with at most 5 branches. Hind wing unknown. MARTYNOV, 1928a; SHAROV, 1968; VISHNIAKOVA, 1980b. *Trias.*

Aeroplana TILLYARD, 1918c, p. 426 [*A. *mirabilis*; OD]. Little-known genus, based on basal half of fore wing; CUA2, CUP, and 1A sigmoidal. [Originally placed in Protodonata, later in new order Aeroplanoptera (TILLYARD, 1923b).] *Trias.*, Australia (New South Wales).——FIG. 118,*1*. *A. *mirabilis*; fore wing, ×2 (Sharov, 1968; after Tillyard, 1923b).

Paraplana SHAROV, 1968, p. 193 [*P. *affinis*; OD]. Fore wing similar to that of *Aeroplana*, but the short, oblique base of CUA1 absent; MP+CUA1 with 3 branches. *Trias.*, USSR (Kirghiz).——FIG. 118,*4*. *P. *affinis*; fore wing, ×1.5 (Sharov, 1968).

Family AEROPHASMATIDAE Martynov, 1928

[*nom. correct.* BRUES, MELANDER, & CARPENTER, 1954, p. 809, *pro* Aerophasmidae MARTYNOV, 1928a, p. 320]

Similar to Aeroplanidae, but fore wing lacking precostal area; vein MP+CUA1 with only 3 branches. Hind wing with RS and M anastomosed near wing base. *Jur.*

Aerophasma MARTYNOV, 1928a, p. 320 [*A. *prynadai;* OD]. Fore wing with dense covering of hair; MA with 2 branches. SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur.*, USSR (Kazakh).——FIG. 118,*3*. *A. *prynadai*; *a*, fore and *b*, hind wings, ×1.3 (Sharov, 1968).

Family PROCHRESMODIDAE Vishniakova, 1980

[Prochresmodidae VISHNIAKOVA, 1980b, p. 173, footnote]

Apparently related to Aeroplanidae. Antennae long and filiform. Fore wing: precostal area broad, with fine archedictyon; vein SC extending to wing apex; MP+CUA1 and branches of MA curved; 2A ending well before midwing. Hind wing: anal area very broad, branches of 2A directed to posterior margin of wing. Legs very long; male apparently with broad and spiny hind femora. *Trias.*

Prochresmoda SHAROV, 1968, p. 194 [*P. *longipoda*; OD]. Precostal area extending nearly to midwing; crossveins very numerous, mostly straight, rarely branched. VISHNIAKOVA, 1980b. *Trias.*, USSR (Kirghiz).——FIG. 119. *P. *longipoda*; *a*, fore and *b*, hind wings, ×2; *c*, whole insect, ×1 (Sharov, 1968).

Family CRETOPHASMATIDAE Sharov, 1968

[Cretophasmatidae SHAROV, 1968, p. 193]

Fore wing much as in Aeroplanidae, but precostal area extending nearly to level of midwing; archedictyon present between veins

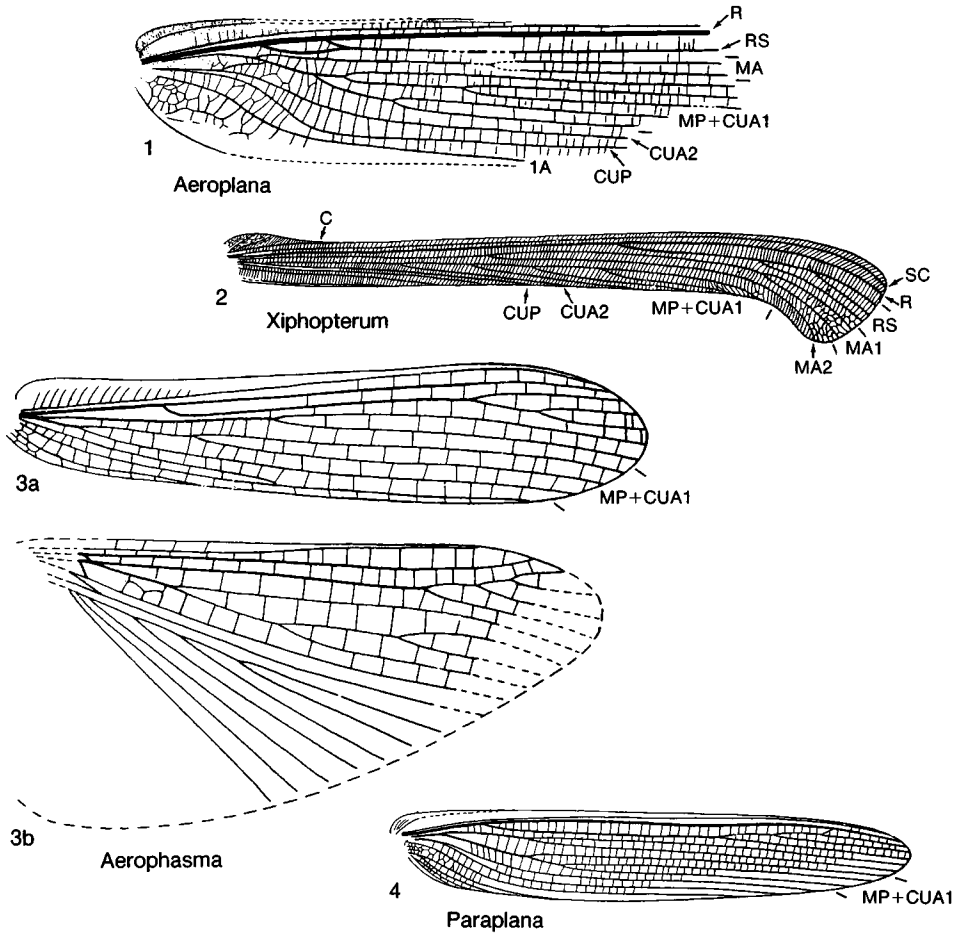


FIG. 118. Xiphopteridae, Aeroplanidae, and Aerophasmatidae (p. 186).

C and SC; RS unbranched; MA with 3 branches. *Cret.*

Cretophasma SHAROV, 1968, p. 193 [**C. raggei*; OD]. RS arising from R near base of wing. Anterior margin of wing slightly concave. *Cret.*, USSR (Kazakh).——FIG. 120,*4*. **C. raggei*; fore wing, ×2 (Sharov, 1968).

Family PHASMATIDAE Leach, 1815

[*nom. correct.* ROBERTS, 1941, p. 16, *pro* Phasmidae LEACH, 1815, p. 119]

Antennae commonly short and slender; fore wings coriaceous, commonly reduced or absent; hind wing typically well developed, with small coriaceous remigium and large anal fan, folded over the abdomen at rest; fore wing venation reduced, with a few, weakly developed, parallel veins; remigium of hind wings with a series of well-developed, parallel veins and numerous crossveins. Body commonly elongate; legs typically long, often spinose; middle and hind tibiae with a ventral, triangular, areolate area distally. *Oligo.–Holo.*

Phasma LICHTENSTEIN, 1796, p. 49. *Holo.*

Pseudoperla PICTET, 1854, p. 364 [**P. gracilipes*; OD]. Nymph, with small wing pads. Mesothorax slightly longer than pronotum. BACHOFFEN-ECHT, 1949. *Oligo.*, Europe (Baltic).——FIG. 120,*2*. **P. gracilipes*; whole insect, ×2.5 (Germar & Berendt, 1856).

Family PHYLLIIDAE Brunner, 1893

[Phylliidae BRUNNER, 1893, p. 101]

Similar to Phasmatidae, but body flattened dorsoventrally; legs and abdominal

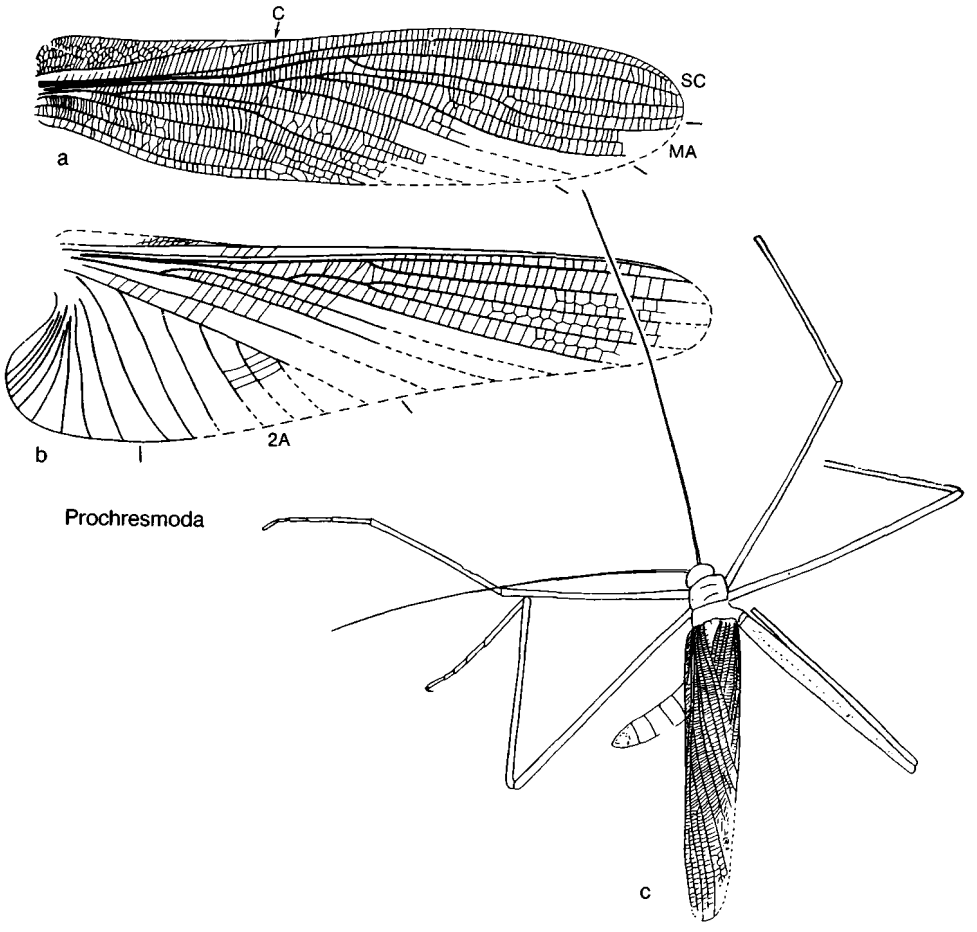


FIG. 119. Prochresmodidae (p. 186).

segments with lamellate extensions; fore wings reduced; hind wings commonly well developed, resting flat, not folded, over abdomen. *Oligo.,* Europe (Baltic)–*Holo.*

Phyllium ILLIGER, 1798, p. 499. *Holo.*

Electrobaculum SHAROV, 1968, p. 195 [**E. gracile*; OD]. Little-known genus, based on nymph. Ovipositor and cerci longer than those of other genera in family. *Oligo.,* Europe (Baltic).——FIG. 120,*3*. **E. gracile*; whole insect, ×3 (Sharov, 1968).

Family UNCERTAIN

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

Chresmodella BODE, 1953, p. 108 [**C. integra*; OD]. Little-known genus, based on fore wings, but details not clear; probably related to Halometridae (recent). SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur.,* Europe (Germany).——FIG. 120,*1*. **C. integra*; fore wing, ×2.5 (after Bode, 1953).

Coniphasma BIRKET-SMITH, 1981, p. 245 [**C. rosenkrantzi*; OD]. Little-known genus, based on incomplete fore wing. R, RS, MA, MP, CUA, and CUP nearly straight and parallel; costa marginal; SC ending just beyond midwing; MA, MP, CUA, and CUP unbranched. [Ordinal assignment doubtful.] *Cret.,* Greenland.

Propygolampis WEYENBERGH, 1874, p. 84 [**P. bronni*; OD] [=*Halometra* OPPENHEIM, 1888, p. 230 (type, *Pygolampis gigantea* GERMAR, 1839, p. 207); *Sternarthron* HAASE, 1890b, p. 655 (type, *S. zitteli*)]. Little-known genus, similar to *Prochresmoda,* but antennae very short; longitudinal veins of fore wing straight and close together, much as in Aeroplanidae. Hind wing unknown. [*Propygolampis* and *Halometra* were originally placed in the order Hemiptera and have been confused with *Chresmoda* (Orthoptera). *Sternarthron* was placed by HAASE in the Araneae, but

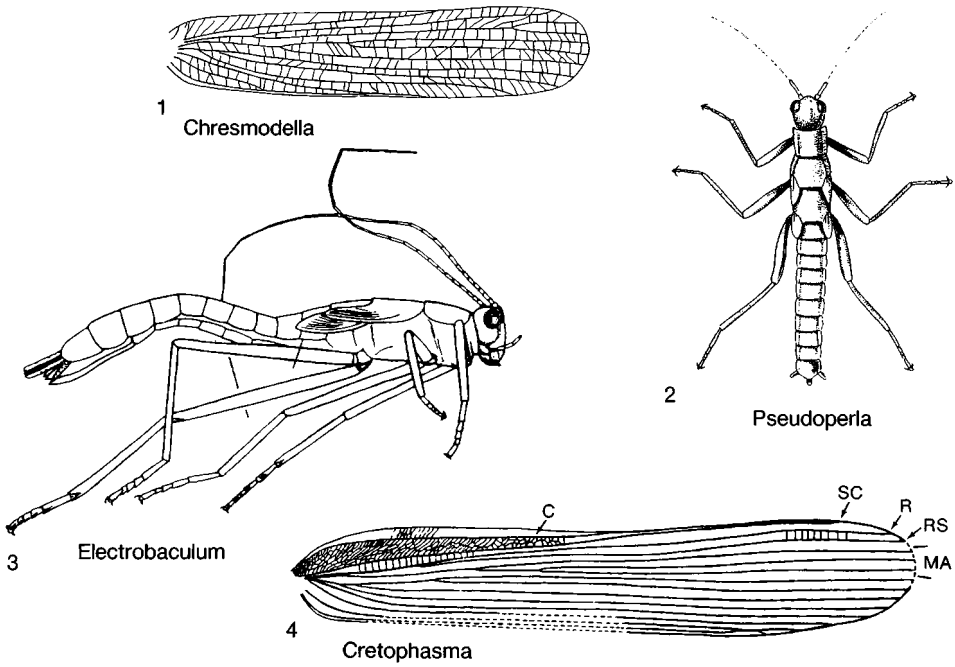


FIG. 120. Cretophasmatidae, Phasmatidae, Phylliidae, and Uncertain (p. 187–188).

as noted by HANDLIRSCH (1906b) the type specimens were insects; they were probably nymphs of *Propygolampis*.] HAGEN, 1862; HANDLIRSCH, 1906b, 1920; MARTYNOV, 1928a; CARPENTER, 1932a, 1992; ESAKI, 1949; SHAROV, 1968; VISHNIAKOVA, 1980b. *Jur.*, Europe (Germany); *Cret.*, China (Inner Mongolia).——FIG. 121. **Propygolampis gigantea* (GERMAR), *Jur.*, Germany; ventral view of whole insect, including antennae and cerci, specimen in Museum of Comparative Zoology, MCZ 6105, ×0.9 (Carpenter, new).

Order EMBIOPTERA Shipley, 1904

[Embioptera SHIPLEY, 1904, p. 261]

Small, subsocial insects with mandibulate mouthparts; tarsi with 3 segments, first segment of fore tarsi containing silk glands and much enlarged; hind femora enlarged; females apterous; males commonly winged; wings homonomous; veins except R and CUP usually weak; R and CUP thickened; SC short and not reaching midwing; RS typically forked before midwing; M simple or branched; CU usually with weak anterior branch and stronger CUP; anal lobes absent; cerci typically with 2 segments, generally asymmetrical in males. Ross, 1970. *Oligo.–Holo.*

The Embioptera are orthopteroids, apparently closely related to the Isoptera, although their precise ancestry is far from clear. Their morphological specializations, such as the slender body, short legs, and tendency for aptery, are adaptations to living in galleries. Lined with silk, produced by glands in the fore tarsi, the galleries are made on irregular surfaces of trees, rocks, moss, and even termite mounds. All existing Embioptera are subsocial, the female guarding the eggs and newly hatched nymphs in her galleries. The homonomous condition of the fore and hind wings is obviously secondary and the venation is much reduced.

The geological history of the Embioptera is poorly known. Two Permian genera, *Protembia* TILLYARD (1937b) and *Tillyardembia* ZALESSKY (1937d), originally placed in the order Embioptera, have been shown to be members of the Protorthoptera (MARTYNOV, 1940; CARPENTER, 1950; Ross, 1956); and another Permian genus, *Sheimia* MARTYNOVA

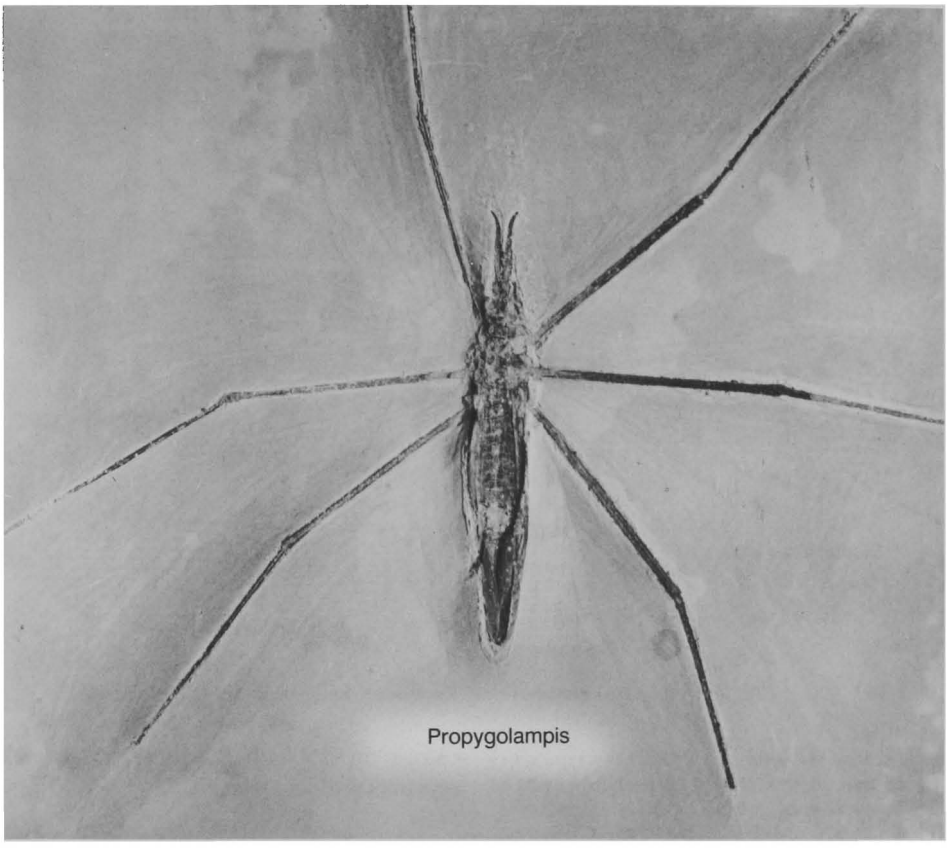


FIG. 121. Phasmatodea, Uncertain (p. 188–189).

(1958), also placed in the Embioptera, is known only by a poorly preserved wing that does not show sufficient structural features to justify assignment to the order (CARPENTER, 1976; ROSS, personal communication, 1977). The earliest record of the Embioptera, in the Baltic amber, consists of two apterous males belonging to the genus *Electroembia*. The genus is extinct but it is more specialized than some living genera. In all probability Embioptera will eventually be found in Cretaceous deposits.

Family EMBIIDAE Burmeister, 1838

[Embiidae BURMEISTER, 1838 in BURMEISTER, 1838–1839, p. 768]

Male wing (if present) with vein RS3+4 forked; hind tarsi with 1 or 2 ventral papillae (sole-bladders) on first segment; left cercus with 2 segments. *Oligo.–Holo.*

Embia LATREILLE, 1829, p. 257. *Holo.*

Electroembia ROSS, 1956, p. 77 [**Embia antiqua* PICTET, 1854, p. 370; OD]. Male apterous; basal segment of left cercus spiculate; hind basitarsus elongate and having 2 ventral papillae. *Oligo.*, Europe (Baltic).——FIG. 122,*2*. **E. antiqua* (PICTET); *a*, abdominal terminalia, *b*, hind basitarsus, ×30 (Ross, 1956).

Lithembia ROSS, 1984, p. 83 [**Embia florissantensis* COCKERELL, 1908e, p. 230; OD]. Little-known genus, based on relatively large male, with typical embiid venation. DAVIS, 1939b. *Oligo.*, USA (Colorado).

Family NOTOLIGOTOMIDAE Davis, 1940

[Notoligotomidae DAVIS, 1940a, p. 681]

Male left cercus with 1 segment. *Mio.–Holo.*

Notoligotoma DAVIS, 1936, p. 244. *Holo.*

Burmitembia COCKERELL, 1919d, p. 194 [**B. ve-*

nosa; OD]. Male winged; veins strong; RS3+4 and M single; several strong oblique crossveins. DAVIS, 1939b, 1940a. *Mio.*, Burma.——FIG. 122,*1*. **B. venosa; a*, right fore wing, ×20; *b*, hind legs and abdomen from below, ×16 (both Davis, 1939b).

Order PSOCOPTERA Shipley, 1904

[Psocoptera SHIPLEY, 1904, p. 261]

Small or minute insects, with short body; head relatively large; eyes large, ocelli usually present; antennae slender and commonly long, with numerous segments (12 to 50); mandibles well developed; laciniae forming sclerotized rods partially sunk into head and moved by muscles; labial palps vestigial in recent species; prothorax ordinarily small; meso- and metathorax usually distinct but may be fused to form compact unit; wings commonly present, reduced or absent in some, membranous and transparent, with distinct pterostigma. Fore wing commonly bearing conspicuous setae or scales; vein SC usually very short or absent; R and RS strongly developed, R enclosing distal end of pterostigma; RS usually forked; M arising from base, and in existing genera commonly coalesced with CUA basally and in contact with stem of R for short distance, terminating in several branches distally; CUA ordinarily forking near wing margin to form prominent cell, areola postica; CUP weakly developed, unbranched; usually only 1 anal vein. Hind wing generally smaller than fore wing, markedly so in some; in recent species, M, CUA, and CUP generally unbranched. Legs mostly homonomous, cursorial; tarsi in recent forms with 2 or 3 segments, in Permian Psocidiidae with 5 segments; abdomen with 9 or 10 distinct segments; cerci absent in recent forms, obsolescent in some Permian species. *Perm.–Holo.*

The Psocoptera constitute a very distinct and homogeneous group at present. Numerous recent families are now usually recognized, based on wing venation as well as tarsal and antennal segmentation, but much difference of opinion exists about characteristics of the families. The classification used here is based on the systems of ROESLER (1944) and SMITHERS (1965, 1972). The families of Psocoptera are usually grouped into three or four suborders; but since there is little agreement among specialists regarding characteristics of the suborders or about the families included, the subordinal grouping is omitted here. In any case, most characteristics on which suborders are based are actually known in very few of the extinct genera.

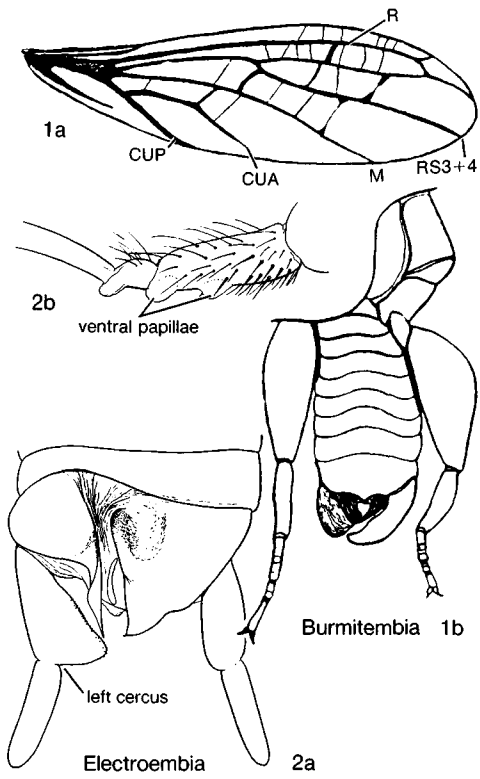


FIG. 122. Embiidae and Notoligotomidae (p. 190–191).

The venation of the Psocoptera presents no problems in homology, except for the median system, which shows neither convexity nor concavity and which is accordingly designated here as the media (M). The evolution of the Psocoptera has involved extensive modifications of the wing venation; these have included varying degrees of anastomosis of RS and M, the branching of the media,

and especially the form of the areola postica and its relationship to the media. Similar patterns have been developed independently in various lines of evolution within the order. Moreover, the Permian species seem to have evolved along lines very unlike those of recent families; none of the Permian groups seems to suggest an approach to any living family.

The discovery of Psocoptera in Permian deposits of Kansas in 1926 (TILLYARD, 1926f) was followed by finds of a similar nature in Australian and Russian beds. These fossils have revealed a fauna that is surprisingly diverse for Permian age and have indicated some lines of psocopterous evolution. On the basis of all evidence now available, the Permian Psocidiidae seem to be the most primitive members of the order known; they had homonomous wings, a relatively generalized venational pattern, five-segmented tarsi, and short but distinct cerci. Little is known of Mesozoic Psocoptera, but the order is well represented in the Oligocene of the Baltic amber. Fortunately, also, the amber species have been studied by several major workers on recent Psocoptera (HAGEN, ENDERLEIN, ROESLER), with the result that the systematics of the amber fauna is on as firm a basis as that of the recent one. It is clear that the Psocoptera in Baltic amber, although including several extinct genera, are remarkably modern, some of the species being as highly specialized as the most extensively modified recent species.

The Psocoptera are usually regarded as more closely related to the Hemiptera than to any other order. The mouthparts, although of a chewing type, are modified in several respects that are suggestive of the hemipterous pattern. In this connection, the prolongation of the head in *Dichentomum* (BECKER-MIGDISOVA, 1962a, p. 103) is especially interesting; it suggests the possibility that in these Permian species there was a tendency for the formation of a beaklike extension of the head. Relationship to the Hemiptera is also suggested by the close resemblance between the venation of the Psocidiidae and that of the Permian Archescytinidae (Hemiptera). In any event, although the Psocoptera as now known were almost certainly not ancestral to the Hemiptera, in all probability these two orders did arise from common ancestral stock.

Family PSOCIDIIDAE Tillyard, 1926

[Psocidiidae TILLYARD, 1926f, p. 319] [=Dichentomidae CARPENTER, 1932b, p. 6]

Fore wing usually slender; vein SC terminating on R; pterostigma commonly distinct; RS with 2 or 3 branches; M with at least 4 branches; length of areola postica about 3 times as long as its height. Hind wing similar to fore wing, usually about same size. Body structure known in *Dichentomum* only; head relatively large; antennae long, filamentous, with about 50 segments; head forming short rostrum; maxillary palpi long, with 3 segments; labial palpi shorter; fore tarsi with 4 segments; ovipositor prominent. *Perm.*

Dichentomum TILLYARD, 1926f, p. 320 [**D. tinctum*; OD] [=*Psocidium* TILLYARD, 1926f, p. 321 (type, *P. permianum*); *Chaetopsocidium* TILLYARD, 1926f, p. 331 (type, *C. sellardsi*); *Metapsocidium* TILLYARD, 1926f, p. 333 (type, *M. loxineurum*); *Pentapsocidium* TILLYARD, 1926f, p. 334 (type, *P. indistinctum*); *Permentomum* TILLYARD, 1926f, p. 335 (type, *P. tenuiforme*); *Parapsocidium* ZALESSKY, 1937d, p. 847 (type, *P. uralicum*)]. Pterostigma oval; M with 4 branches. *Perm.*, USA (Kansas), USSR (European RSFSR), Australia (New South Wales).——FIG. 123,*2*. **D. tinctum*, Perm., Kansas; *a*, whole insect, ×7 (Laurentiaux, 1953); *b*, fore wing, ×12 (Carpenter, 1933a).

Austropsocidium TILLYARD, 1935a, p. 267 [**A. pincombei*; OD]. R more remote from costa than in *Dichentomum*; pterostigma triangular. *Perm.*, Australia (New South Wales).——FIG. 123,*1*. **A. pincombei*; *a*, fore and *b*, hind wings, ×6 (Tillyard, 1935a).

Megapsocidium TILLYARD, 1935a, p. 269 [**M. australe*; OD]. Little-known wing apex; crossvein between base of pterostigma and RS. [Family assignment doubtful.] *Perm.*, Australia (New South Wales).

Stenopsocidium TILLYARD, 1935a, p. 270 [**S. elongatum*; OD]. Similar to *Dichentomum*, but M with 5 branches; pterostigma small. *Perm.*, Australia (New South Wales).——FIG. 123,*5*. **S. elongatum*; fore wing, ×9 (Tillyard, 1935a).

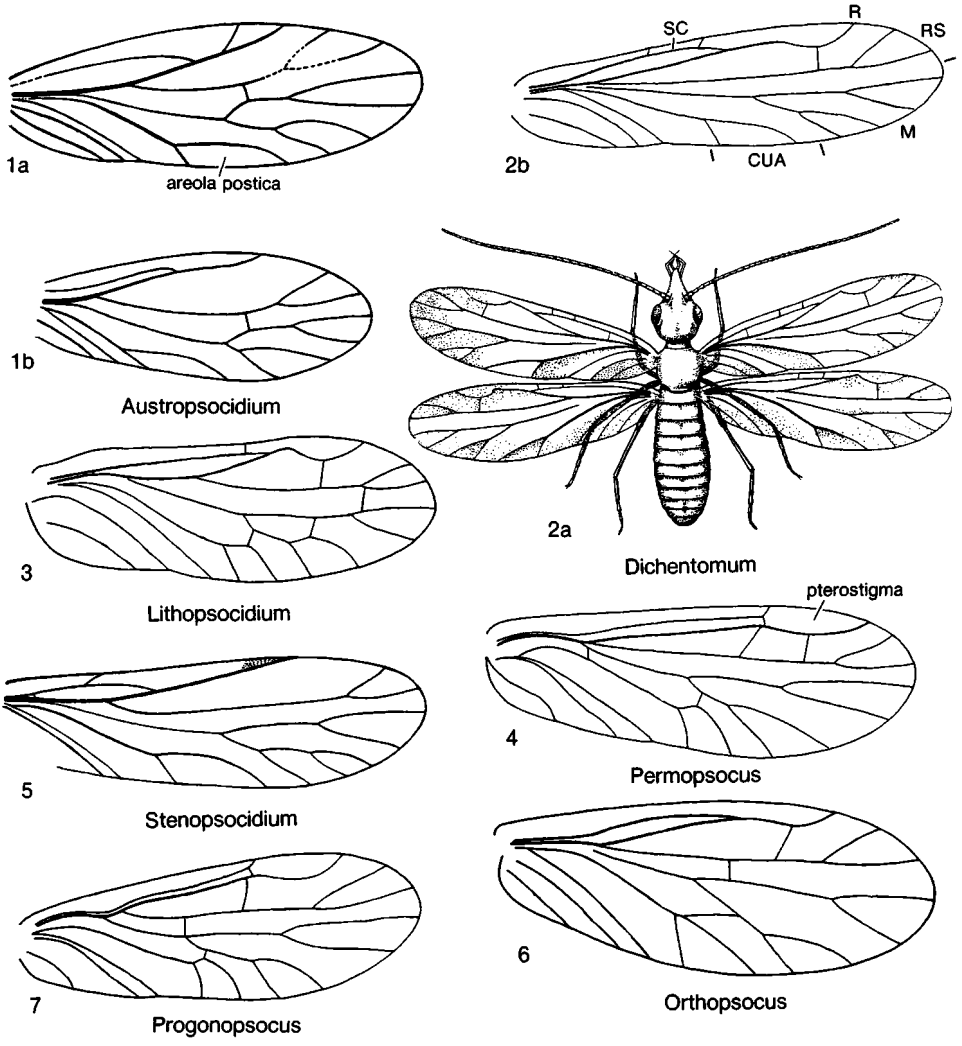


FIG. 123. Psocidiidae and Permopsocidae (p. 192–194).

Family PERMOPSOCIDAE Tillyard, 1926

[Permopsocidae TILLYARD, 1926f, p. 340]

Fore wing broader than in Psocidiidae; veins SC and R close together and parallel; pterostigma well developed; fork of CUA high, with crossvein between CUA1 and M3+4. Hind wing similar to fore wing; fork of CUA slightly higher. Body structure little known; antennae much shorter than in Psocidiidae. *Perm.*

Permopsocus TILLYARD, 1926f, p. 339 [**P. latipennis*; OD] [=*Ancylopsocus* TILLYARD, 1926f, p. 344 (type, *A. insolitus*)]. End of SC connected to base of pterostigma by short crossvein; RS and stem of M divergent; fore wing with small sclerotized lobe near base of posterior margin. *Perm.*, USA (Kansas).—— FIG. 123,*4*. **P. latipennis*; hind wing, ×11 (Carpenter, 1932b).

Lithopsocidium CARPENTER, 1932b, p. 14 [**L. permianum*; OD]. Hind wing: SC clearly terminating on R near pterostigma; RS arising near middle of wing. *Perm.*, USA (Kansas). —— FIG. 123,*3*. **L. permianum*; hind wing, ×17 (Carpenter, 1933a).

Orthopsocus CARPENTER, 1932b, p. 15 [**O. singularis*; OD]. Hind wing: SC terminating on R near pterostigma; RS arising nearer wing base than in *Lithopsocidium*; fork of CUA triangular. *Perm.*, USA (Kansas).——FIG. 123,6. **O. singularis*; hind wing, ×12 (Carpenter, 1933a).

Progonopsocus TILLYARD, 1926f, p. 337 [**P. permianus*; OD]. Very similar to *Permopsocus*, but RS and stem of M parallel. *Perm.*, USA (Kansas). —— FIG. 123,7. **P. permianus*; hind wing, ×14 (Carpenter, 1933a).

Family MARTYNOPSOCIDAE Karny, 1930

[Martynopsocidae KARNY, 1930, p. 446, *nom. subst. pro* Dinopsocidae MARTYNOV, 1928b, p. 40]

Fore wing with vein SC terminating on R; pterostigma very slender; RS and M each with 3 branches. Hind wing and body unknown. *Perm.*

Martynopsocus KARNY, 1930, p. 446, *nom. subst. pro Dinopsocus* MARTYNOV, 1928b, p. 39, *non* BANKS, 1920 [**Dinopsocus arcuatus* MARTYNOV, 1928b, p. 40; OD] [=*Idelopsocus* ZALESSKY, 1929, p. 17 (type, *I. tartaricus*)]. RS with RS1, RS2, and RS3+4; fork of CUA shallow. *Perm.*, USSR (European RSFSR).——FIG. 124,1. **M. arcuatus* (MARTYNOV); fore wing, ×6 (Martynov, 1928b).

Family ARCHIPSYLLIDAE Handlirsch, 1906

[Archipsyllidae HANDLIRSCH, 1906b, p. 502]

Antennae filiform, with at least 13 segments; mandibles elongate; fore and hind wings slender, very similar in shape and venation; vein SC short, coalesced with stem R at wing base, but almost immediately diverging towards and fusing with C, finally diverging back and joining R more distally; pterostigma well developed; RS forked distally; M with 4 branches; CU dividing basally; CUA forked distally; CUP well developed. VISHNIAKOVA, 1976. *Perm.–Cret.*

Archipsylla HANDLIRSCH, 1906b, p. 503 [**A. primitiva*; SD ENDERLEIN, 1909, p. 772]. Fore wing with pterostigma relatively short, about as long as wide; crossvein between RS and M1+2 near midwing. ENDERLEIN, 1929; VISHNIAKOVA, 1976. *Jur.*, Europe (Germany), USSR (Kazakh). —— FIG. 124,2. *A. turanica* MARTYNOV, USSR; fore wing, ×10 (adapted from Martynov, 1926b and Vishniakova, 1976).

Archipsyllodes VISHNIAKOVA, 1976, p. 83 [**A. speciosis*; OD]. Pterostigma short; crossvein rs+m as in *Eopsylla*; areola postica very slender. *Cret.*, USSR (Asian RSFSR).

Archipsyllopsis VISHNIAKOVA, 1976, p. 83 [**A. baisica*; OD]. Very similar to *Archipsyllodes*, but pterostigma longer. *Cret.*, USSR (Asian RSFSR).

Eopsylla VISHNIAKOVA, 1976, p. 78 [**Dichentomum sojanensis* BECKER-MIGDISOVA, 1962a, p. 102; OD]. Similar to *Archipsylla*, but pterostigma more slender and crossvein from RS joining M before it divides into M1+2 and M3+4. *Perm.*, USSR (European RSFSR).

Family SURIJOKOPSOCIDAE Becker-Migdisova, 1961

[Surijokopsocidae BECKER-MIGDISOVA, 1961b, p. 284]

Fore wing much wider distally than basally; vein M with 5 branches; basal parts of CUA and R+M thickened, forming cell at wing base; anal area very narrow. Hind wing and body unknown. *Perm.*

Surijokopsocus BECKER-MIGDISOVA, 1961b, p. 284 [**S. radtshenkoi*; OD]. SC close to R; costal area very wide at base; distal branches of CUA recurved. *Perm.*, USSR (Asian RSFSR). —— FIG. 124,3. **S. radtshenkoi*; fore wing, ×7 (Becker-Migdisova, 1961b).

Family LOPHIONEURIDAE Tillyard, 1921

[Lophioneuridae TILLYARD, 1921c, p. 417] [=Cyphoneuridae CARPENTER, 1932b, p. 18; Zoropsocidae TILLYARD, 1935a, p. 273]

Fore wing with vein SC short or absent, extending at most slightly beyond level of origin of RS and terminating on costal margin; RS with 2 branches; stem of M coalesced with stem R; M with 2 branches; CUA with weak posterior branch or unbranched. Hind wing little known, only about two-thirds length of fore wing; CUP and 1A apparently absent. Head broad, without prolongation as in Psocidiidae; antennae reaching only to about midwing. *Perm.*

Lophioneura TILLYARD, 1921c, p. 417 [**L. ustulata*; OD]. RS3+4 directed posteriorly, terminating at wing apex; M forked more deeply than RS. *Perm.*, Australia (New South Wales).—— FIG. 124,4. **L. ustulata*; fore wing, ×10 (Tillyard, 1921c).

Austrocypha TILLYARD, 1935a, p. 277 [**A. abrupta*; OD]. Fore wing with SC apparently absent; distal part of R strongly bent anteriorly; stems of RS, M, and CUA arising from stem R and continuing nearly parallel; CUA strongly curved sigmoidally. Hind wing about half length of fore wing; RS and M forked; CU and 1A

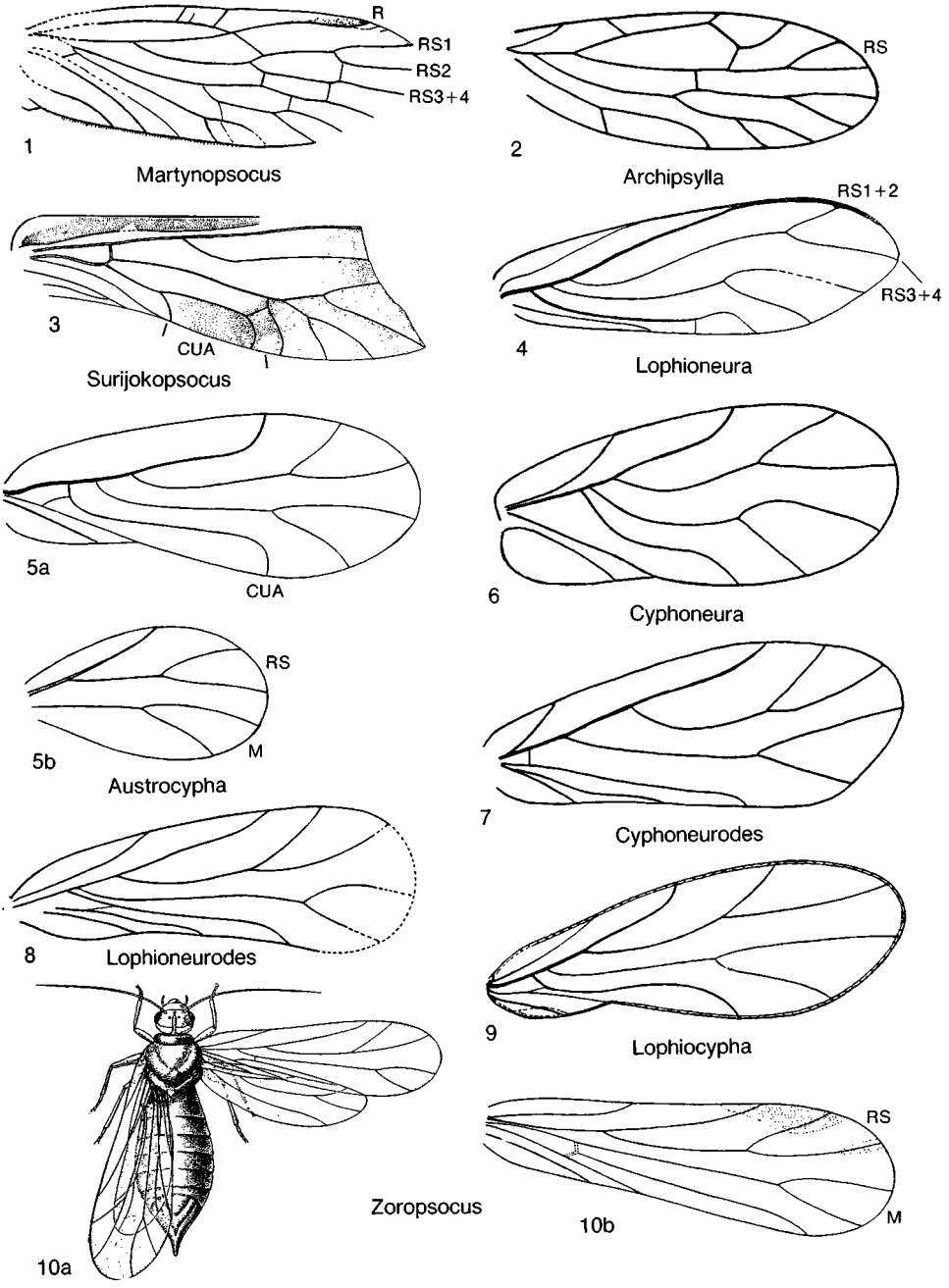


FIG. 124. Martynopsocidae, Archipsyllidae, Surijokopsocidae, and Lophioneuridae (p. 194–197).

absent. *Perm.,* Australia (New South Wales). ——FIG. 124,5. **A. abrupta; a,* fore and *b,* hind wings, ×18 (Tillyard, 1935a).

Cyphoneura CARPENTER, 1932b, p. 18 [**C. permiana*; OD]. Fore wing nearly oval; R curved strongly toward anterior margin; branches of M directed posteriorly; CUA unbranched, sigmoidally curved. *Perm.,* USA (Kansas). —— FIG. 124,6. **C. permiana*; fore wing, ×26 (Carpenter, 1932b).

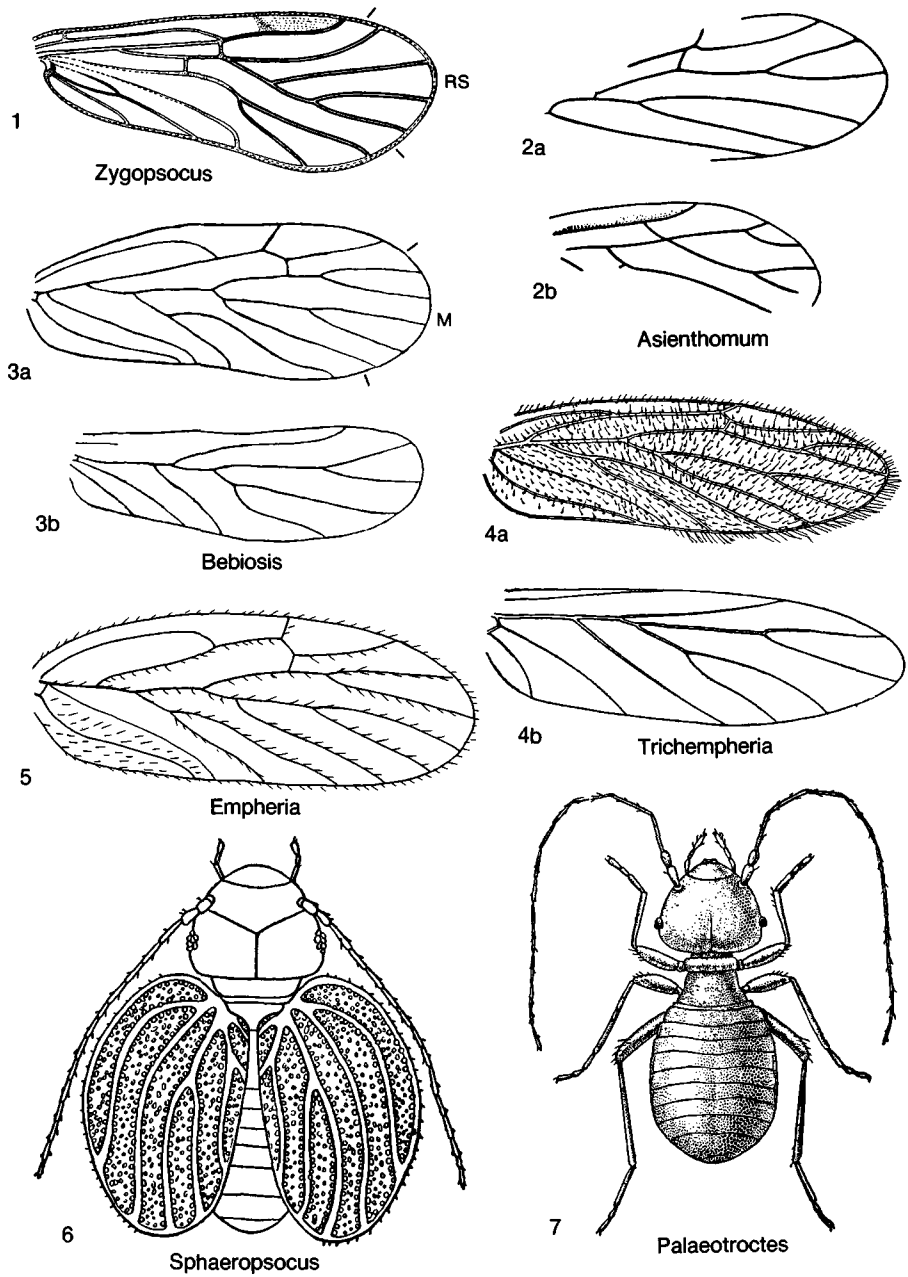


FIG. 125. Zygopsocidae, Asienthomidae, Trogiidae, and Pachytroctidae (p. 197–198).

Cyphoneurodes BECKER-MIGDISOVA, 1953b, p. 281 [**Cyphoneura reducta* CARPENTER, 1932b, p. 19; OD]. Fore wing subtriangular; R not so strongly curved as in *Cyphoneura*; branches of M directed distally; CUA straight. *Perm.*, USA (Kansas). ——FIG. 124,7. **C. reducta* (CARPENTER); fore wing, ×22 (Carpenter, 1932b).

Lophiocypha TILLYARD, 1935a, p. 274 [**L. permiana*; OD]. Similar to *Lophioneura* but with RS arising much farther from base of wing, and SC extending about to level of origin of RS. *Perm.*, Australia (New South Wales).——FIG. 124,9. **L. permiana*; fore wing, ×18 (Tillyard, 1935a).

Lophioneurodes Becker-Migdisova, 1953b, p. 280 [**L. sarbalensis*; OD]. CUA arising from stem of R+M; both branches of RS directed anteriorly; RS forked more deeply than M. *Perm.*, USSR (Asian RSFSR). —— Fig. 124,*8*. **L. sarbalensis*; fore wing, ×18 (Becker-Migdisova, 1962a).

Zoropsocus Tillyard, 1935a, p. 273 [**A. delicatulus*; OD]. CUA independent of R+M, arising from common CU stem and connected to M by short crossvein; branches of RS directed anteriorly. *Perm.*, USSR (Asian RSFSR), Australia (New South Wales).——Fig. 124,*10a*. *Z. tomiensis* Becker-Migdisova, USSR; whole insect, ×22 (Becker-Migdisova, 1962a). —— Fig. 124,*10b*. **Z. delicatulus*, Australia; fore wing, ×22 (Tillyard, 1935a).

Family ZYGOPSOCIDAE Tillyard, 1935

[Zygopsocidae Tillyard, 1935a, p. 271]

Fore wing membranous with heavy veins; vein RS with 4 branches; M with 2 branches; CUA unbranched. Hind wing unknown. *Perm.*

Zygopsocus Tillyard, 1935a, p. 271 [**Z. permianus*; OD]. SC terminating on R near midwing; CUA strongly curved distally; wing margin thick. *Perm.*, Australia (New South Wales). ——Fig. 125,*1*. **Z. permianus*; fore wing, ×14 (Tillyard, 1935a).

Family ASIENTHOMIDAE Martynov, 1926

[Asienthomidae Martynov, 1926b, p. 1364, footnote, *nom. subst. pro* Lithentomidae Martynov, 1926b, p. 1364]

Fore wing with vein CUA unbranched, M deeply forked, and RS forked. *Jur.*

Asienthomum Martynov, 1926b, p. 1364, footnote, *nom. subst. pro Lithentomum* Martynov, 1926b, p. 1364, *non* Scudder, 1867 [**Lithentomum praecox* Martynov, 1926b, p. 1364; OD] [=*Lithopsocus* Karny, 1930, p. 435, obj.]. Little-known wings. Fore wing with pterostigma about 4 times longer than wide; RS connected to R by an oblique crossvein at base of pterostigma. *Jur.*, USSR (Kazakh).——Fig. 125,*2*. **A. praecox* (Martynov); *a*, fore and *b*, hind wings, ×24 (Rohdendorf, 1962a).

Family TROGIIDAE Enderlein, 1911

[Trogiidae Enderlein, 1911, p. 295]

Antennae with more than 20 segments; tarsi with 3 segments, claws smooth, without teeth; scales absent from body and wings; fore wing commonly broadly rounded distally, rarely absent. *Oligo.–Holo.*

Trogium Illiger, 1798, p. 500. *Holo.*

Bebiosis Enderlein, 1911, p. 344 [**B. pertinens*; OD]. Similar to *Empheria*, but last segment of maxillary palpus much enlarged and broadened. *Oligo.*, Europe (Baltic). —— Fig. 125,*3*. **B. pertinens; a*, fore and *b*, hind wings, ×3 (Enderlein, 1911).

Empheria Hagen, 1854, p. 225 [**E. reticulata*; OD]. Hairs on membrane of fore wing restricted to area between CUP and anal margin. Pictet & Hagen, 1856. *Oligo.*, Europe (Baltic).——Fig. 125,*5*. **E. reticulata*; fore wing, ×35 (Enderlein, 1911).

Trichempheria Enderlein, 1911, p. 345 [**Empheria villosa* Hagen, 1882, p. 221; OD]. Hairs generally distributed on fore wing membrane. *Oligo.*, Europe (Baltic).——Fig. 125,*4*. **T. villosa* (Hagen); *a*, fore and *b*, hind wings, ×26 (Becker-Migdisova & Vishniakova, 1962).

Family LEPIDOPSOCIDAE Enderlein, 1903

[Lepidopsocidae Enderlein, 1903, p. 206]

Antennae and tarsi as in Trogiidae, but claws with preapical tooth; scales usually present on wings and body. *Pleist.–Holo.*

Lepidopsocus Enderlein, 1903, p. 328. *Holo.*

Thylacella Enderlein, 1911, p. 349 [**T. eversiana*; OD]. Wings and body without scales; hind margin of fore wing evenly curved for its entire length. *Pleist.*, Africa.

Thylax Hagen, 1866b, p. 172 [**T. fimbriatum*; OD]. Similar to *Thylacella*, but hind margin of fore wing angular near middle. Enderlein, 1911. *Pleist.*, Africa.

Family PSYLLIPSOCIDAE Kolbe, 1884

[*nom. transl.* Enderlein, 1903, p. 208, *ex* Psyllipsocini Kolbe, 1884, p. 38]

Antennae and tarsi as in Trogiidae, but veins CUP and 1A meeting at point at wing margin. *Mio.–Holo.*

Psyllipsocus Selys-Longchamps, 1872, p. 136. Parts of fore and hind wings. [Generic assignment doubtful.] Cockerell, 1916a. *Mio.*, Burma–*Holo.*

Family PACHYTROCTIDAE Enderlein, 1905

[*nom. transl.* Pearman, 1936, p. 60, *ex* Pachytroctinae Enderlein, 1905a, p. 46]

Antennae usually with 15 segments; tarsi with 3 segments; body normally convex,

short; legs long and slender; hind femur not broadened. Wings often reduced or absent. *Oligo.–Holo.*

Pachytroctes ENDERLEIN, 1905, p. 46. *Holo.*

Palaeotroctes ENDERLEIN, 1911, p. 350 [**Atropos succinica* HAGEN, 1882, p. 231; OD]. Eyes very small; meso- and metathorax fused. *Oligo.,* Europe (Baltic).——FIG. 125,7. **P. succinicus* (HAGEN); complete insect, ×60 (Becker-Migdisova, 1962b).

Psylloneura ENDERLEIN, 1903, p. 317. Complete insect. [Generic assignment doubtful.] COCKERELL, 1919e. *Mio.,* Burma–*Holo.*

Sphaeropsocus HAGEN, 1882, p. 226 [**S. kunowi*; OD]. Fore wings forming short, broad elytra extending to end of abdomen; venation much reduced. *Oligo.,* Europe (Baltic).——FIG. 125,6. **S. kunowi*; complete insect, ×54 (Becker-Migdisova & Vishniakova, 1962).

Family LIPOSCELIDAE Enderlein, 1911

[Liposcelidae ENDERLEIN, 1911, p. 350]

Similar to Pachytroctidae, but body flattened and long; legs short; hind femur broad and flat; commonly wingless. *Oligo.–Holo.*

Liposcelis MOTSCHULSKY, 1852, p. 19. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Family AMPHIENTOMIDAE Enderlein, 1903

[Amphientomidae ENDERLEIN, 1903, p. 332]

Antennae with 12 or 13 segments; tarsi with 3 segments; body and wings usually scaled; fore femora with row of teeth; vein CUA attached to M. *Oligo.*

Amphientomum PICTET, 1854, p. 376 [**A. paradoxum*; OD]. Claws with 2 teeth; abdomen with very small scales. *Oligo.,* Europe (Baltic).——FIG. 126,1. **A. paradoxum; a,* fore and *b,* hind wings; ×35 (Enderlein, 1911).

Electrentomum ENDERLEIN, 1911, p. 337 [**E. klebsianum*; OD]. Wings and body entirely without scales. SMITHERS, 1972. *Oligo.,* Europe (Baltic).——FIG. 126,2. **E. klebsianum*; fore wing, ×15 (Enderlein, 1911).

Parelectrentomum ROESLER, 1940a, p. 228 [**P. priscum*; OD]. Similar to *Electrentomum,* but hind wing with closed middle cell; microtrichia on wing membranes very weakly developed. SMITHERS, 1972. *Oligo.,* Europe (Baltic).——FIG. 126,4. **P. priscum; a,* fore and *b,* hind wings, ×15 (Roesler, 1940a).

Family EPIPSOCIDAE Pearman, 1936

[Epipsocidae PEARMAN, 1936, p. 60]

Antennae usually with 13 segments; tarsi with 2 segments; fore wing completely lacking a crossvein from vein R to RS below pterostigma; 1 anal vein. *Oligo.–Holo.*

Epipsocus HAGEN, 1866c, p. 203. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Family PSOCIDAE Leach, 1815

[*nom. transl.* STEPHENS, 1829a, p. 312, *ex* Psocides LEACH, 1815, p. 139]

Antennae usually with 13 segments; tarsi with 2 segments; vein CUA1 in fore wing united with M by brief coalescence or by short crossvein. *Oligo.–Holo.*

Psocus LATREILLE, 1796, p. 99. ENDERLEIN, 1911; COCKERELL, 1921d. *Oligo.,* Europe (Baltic), England–*Holo.*

Copostigma ENDERLEIN, 1903, p. 229. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Trichadenotecnum ENDERLEIN, 1909, p. 329. ENDERLEIN, 1911, 1929. *Oligo.,* Europe (Baltic)–*Holo.*

Family MESOPSOCIDAE Enderlein, 1903

[Mesopsocidae ENDERLEIN, 1903, p. 206]

Similar to Psocidae, but tarsi with 3 segments; vein CUA1 not united with M or absent. *Oligo.–Holo.*

Mesopsocus KOLBE, 1880, p. 184. *Holo.*

Elipsocus HAGEN, 1866, p. 207. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Philotarsus KOLBE, 1880, p. 184. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Family PSEUDOCAECILIIDAE Pearman, 1936

[Pseudocaeciliidae PEARMAN, 1936, p. 60]

Similar to Mesopsocidae, but tarsi with 2 segments. *Oligo.–Holo.*

Pseudocaecilius ENDERLEIN, 1903, p. 260. *Holo.*

Archipsocus HAGEN, 1882, p. 222. ENDERLEIN, 1911. *Oligo.,* Europe (Baltic)–*Holo.*

Electropsocus ROESLER, 1940b, p. 244 [**E. unguidens*; OD]. Veins and margin of fore wing hairy; antennae shorter than body; 3 pairs of gonapophyses in female; hypandrium of male evenly rounded. SMITHERS, 1972. *Oligo.,* Europe (Baltic).

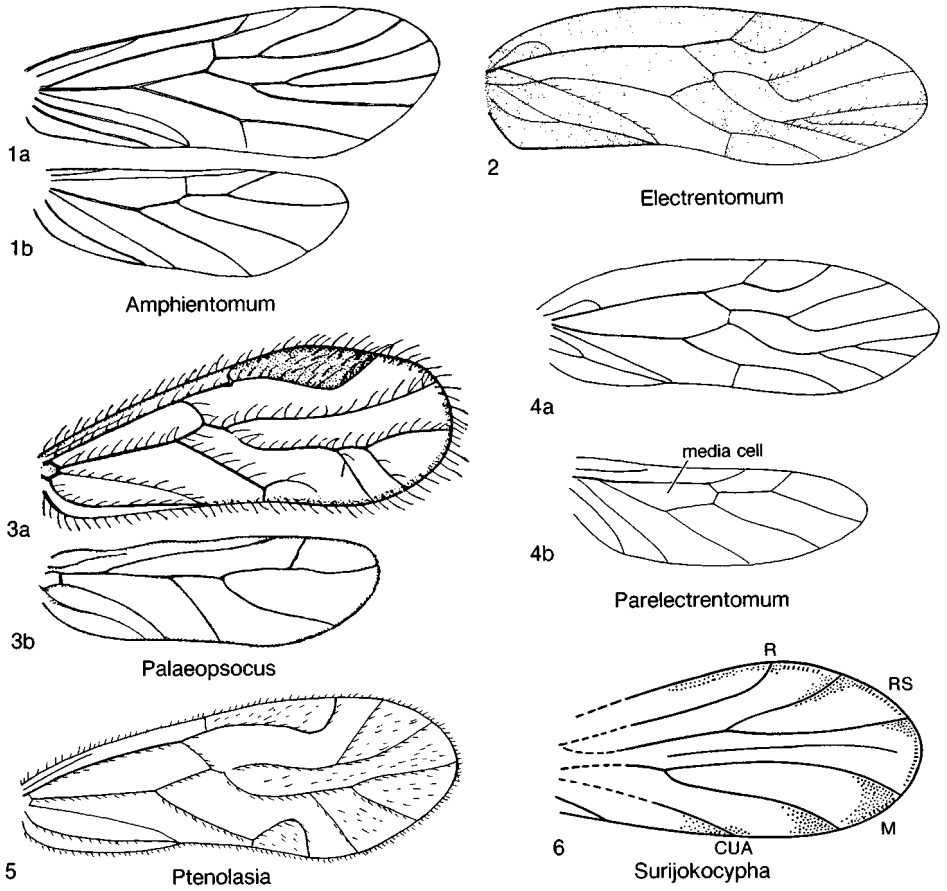


FIG. 126. Amphientomidae, Pseudocaeciliidae, Polypsocidae, and Uncertain (p. 198–200).

Palaeopsocus KOLBE, 1883, p. 190 [**Psocus tener* HAGEN in PICTET & HAGEN, 1856, p. 60; OD]. Veins of fore wing each with single row of hairs; antennae twice as long as fore wing. *Oligo.*, Europe (Baltic).——FIG. 126,*3*. **P. tener* (HAGEN); *a*, fore and *b*, hind wings, ×40 (Becker-Migdisova & Vishniakova, 1962).

Family POLYPSOCIDAE Pearman, 1936

[Polypsocidae PEARMAN, 1936, p. 60]

Antennae usually with 13 segments; tarsi with 2 or 3 segments; vein CUA2 of fore wing very short. *Oligo.–Holo.*

Polypsocus HAGEN, 1866, p. 211. *Holo.*

Caecilius CURTIS, 1837, p. 648. ENDERLEIN, 1911; NAVÁS, 1914. *Oligo.*, Europe (Baltic)–*Holo.*

Kolbea BERTKAU, 1883, p. 128. ENDERLEIN, 1911. *Oligo.*, Europe (Baltic)–*Holo.*

Ptenolasia ENDERLEIN, 1911, p. 321 [**Caecilius pilosus* HAGEN, 1882, p. 283; OD]. Distal half of fore wing membrane covered with hairs. *Oligo.*, Europe (Baltic). —— FIG. 126,*5*. **P. pilosa* (HAGEN); fore wing, ×15 (Enderlein, 1911).

Family UNCERTAIN

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

Parapsocus SCUDDER, 1890, p. 117 [**P. disjunctus*; OD]. Little-known insect, probably psocopterous. SMITHERS, 1972. *Eoc.*, USA (Colorado).

Psococicadellopsis BECKER-MIGDISOVA, 1962a, p. 101 [**P. primitiva*; OD]. Little-known wing; RS apparently unbranched. *Trias.*, USSR (Issik-Kul).

Surijokocypha BECKER-MIGDISOVA, 1961b, p. 280 [**S. surijokovensis*; OD]. Little-known wings;

M forked more deeply than RS; CUA unbranched. SMITHERS, 1972. *Perm.*, USSR (Asian RSFSR). —— FIG. 126,6. **S. surijokovensis*; fore wing, ×20 (Becker-Migdisova, 1961b).

Vitriala BECKER-MIGDISOVA, 1961b, p. 282 [**V. nigriapex*; OD]. Little-known wing; M apparently unbranched. *Perm.*, USSR (Asian RSFSR).

Order ZORAPTERA Silvestri, 1913

[Zoraptera SILVESTRI, 1913b, p. 205]

Very small insects, with mandibulate, chewing mouthparts; antennae moniliform, with 9 segments; maxillae and labium normal; prothorax well developed, larger than mesothorax and metathorax; legs well developed; tarsi with 2 segments; most individuals apterous, but winged individuals of both sexes appear in nearly all species; fore wing with greatly reduced venation, consisting of 3 unbranched veins (R, RS, and M) and a forked CUA; hind wing much smaller and with only 2 veins (RS and M); both wings may be shed along basal fracture lines; abdomen with 11 distinct segments and a pair of short cerci. Nymphs similar to adults in general form, some with developing wing buds. Adults and nymphs occur chiefly in decaying wood and rich humus and are apparently fungivorous. *Holo.*

This is a very small order, all known species belonging to one genus, *Zorotypus*. They appear to be highly specialized relicts of a basically primitive group, probably related to the Psocoptera.

Order MALLOPHAGA Nitzsch, 1818

[Mallophaga NITZSCH, 1818, p. 280]

Small, apterous insects, with body dorsoventrally compressed; head large but diversely shaped; eyes reduced; antennae with 3 to 5 segments, either filiform or capitate; mouthparts with prominent, biting, dentate mandibles; prothorax well developed; mesothorax and metathorax small and frequently fused; legs moderately short, the tarsi with 1 or 2 segments and usually with 2 claws; abdomen with 8 to 10 segments. Nymphs and adults similar in general appearance, both ectoparasites on birds or, more rarely, mammals; they feed on fragments of epidermal products, such as feathers or hairs. *Holo.*

This is a small order of ectoparasites, with somewhat fewer specializations than the Anoplura. They appear to be related to the Anoplura and Psocoptera.

Order ANOPLURA Leach, 1815

[Anoplura LEACH, 1815, p. 64]

Small, apterous insects, the body dorsoventrally compressed; head relatively small; eyes usually much reduced or absent; antennae short, with 3 to 5 segments; mouthparts highly modified for sucking blood, with 3 piercing stylets; thorax small, segmentation indistinct; legs short but well developed, the single tarsal segment bearing a strong claw; abdomen with 9 segments; cerci absent. The nymphs and adults, which are similar in general appearance, are ectoparasites on mammals and feed on blood. *Holo.*

This is a small order of highly specialized ectoparasites, often treated as a suborder of the order Phthiraptera, with the Mallophaga constituting a second suborder. In either case, the ancestral stock of the Anoplura is uncertain, although the Psocoptera are probably nearer to that ancestral line than any other known order (KRISTENSEN, 1981).

Although the Anoplura are not known prior to the Holocene, two well-preserved males of *Neohaematopinus relictus* DUBININ have been found on the frozen body of a gopher (*Citellus*) in Indigirka, USSR (Asian RSFSR). The age of the gopher was determined as about 10,000 years (DUBININ, 1948).

Order CALONEURODEA Handlirsch, 1937

[*nom. transl.* MARTYNOV, 1938a, p. 75, *ex* Caloneuroidea HANDLIRSCH, 1937, p. 64]

Fore and hind wings commonly similar in venation and texture, hind wings lacking an

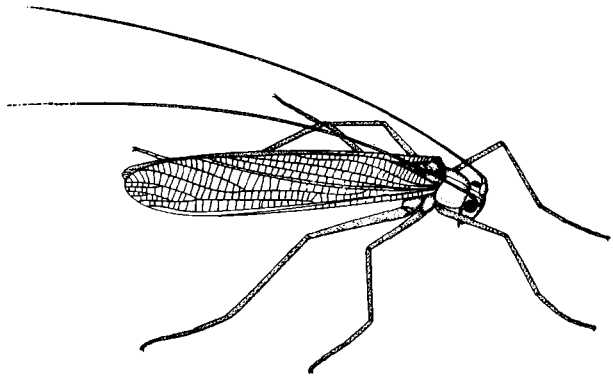


FIG. 127. Caloneurodea; restoration of *Paleuthygramma tenuicornis* MARTYNOV, Paleuthygrammatidae, Permian of USSR, ×1.8 (Sharov, 1966a).

expanded anal area; base of vein CUA coalesced with stem of M for short distance; M commonly with 2 branches; CUA and CUP typically very close together, parallel, and unbranched; 2 or more unbranched anal veins; crossveins numerous, evenly distributed. Body slender; antennae filiform, multisegmented (Fig. 127); head hypognathous or prognathous; mouthparts mandibulate; legs long and slender; tarsi with 5 segments. Females with short, one-segmented cerci. Immature stages unknown. *U. Carb.–Perm.*

The Caloneurodea have generally been regarded as relatives of the Protorthoptera (HANDLIRSCH, 1906b; MARTYNOV, 1938a; CARPENTER, 1943a, 1961, 1970; MARTYNOVA, 1962b; BURNHAM, 1984). However, SHAROV (1966a) and RASNITSYN (1980b) consider them to have been endopterygote insects, close to the base of the neuropteroids and the Coleoptera. Evidence for the affinities of the Caloneurodea is admittedly inconclusive and will probably remain so until much more is known about their body structure. At present, the few morphological features of the body mentioned above are known only in two genera (*Paleuthygramma* and *Synomaloptila*). However, since the case for the endopterygote status of the Caloneurodea seems to me to be very weak, I have followed here the more generally accepted view of the order's position.

Although the fore and hind wings do not usually show much difference in texture, in one family, the Caloneuridae, the fore wings are at least slightly tegminous, both membrane and veins being thicker than those of the hind wings. The wing venation throughout the order is considerably more reduced than that of the Protorthoptera and most other generalized orthopteroids. The convexities and concavities of the veins are unusually strong except for the media. The media is neutral, nearly flat, as in most other neopterous insects. The most prominent feature of the venation in most species is the close proximity of the strongly convex CUA and the strongly concave CUP.

This is one of the small extinct orders of insects, including only 16 genera distributed among 9 families. The genus *Genopteryx* SCUDDER (1885d), placed by RICHARDSON (1956) in the Caloneurodea, has recently been synonymized by BURNHAM (1983) with *Gerarus* SCUDDER (1885d) of the order Protorthoptera.

Family CALONEURIDAE Handlirsch, 1906

[Caloneuridae HANDLIRSCH, 1906b, p. 140]

Wings with vein SC terminating well before apex of wing; CUA and CUP very close together and nearly parallel. M forked dichotomously; 4 anal veins; crossveins numerous. *U. Carb.*

Caloneura BRONGNIART, 1885a, p. 59 [**C. dawsoni*; OD] [=*Confusio* HANDLIRSCH, 1919b, p. 547 (type, *Homaloneura royeri* MEUNIER, 1911a, p. 119)]. Fore wing with costal space abruptly narrowed basally; RS with 5 or 6 main branches; CUA and CUP unbranched. *U. Carb.*, Europe (France).——FIG. 128,*8*. **C. dawsoni; a,* fore and *b,* hind wings, ×1.2 (Carpenter, 1961).

Family ANOMALOGRAMMATIDAE Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Anomalogrammidae CARPENTER, 1943a, p. 74]

Vein SC terminating at midwing; M deeply forked; 3A absent. *Perm.*

Anomalogramma CARPENTER, 1943a, p. 75 [**A. parvum*; OD]. RS forked to about half length of fork of M. *Perm.*, USA (Kansas).——FIG. 128,*10*. **A. parvum*; wing, ×6 (Carpenter, 1943a).

Family APSIDONEURIDAE Carpenter, 1961

[Apsidoneuridae CARPENTER, 1961, p. 151]

Wings with vein SC extending about to wing apex; M forked broadly, the anterior branch (M1+2) arching strongly away from posterior branch; 3 anal veins. *U. Carb.–Perm.*

Apsidoneura CARPENTER, 1943a, p. 72 [**A. flexa*; OD]. Fore wing much more slender than in *Caloneura* and narrowed basally; RS with 2 or 3 main branches. BURNHAM, 1984. *U. Carb.*, Europe (France); *Perm.*, USA (Kansas).——FIG. 128,*9*. **A. flexa*; fore wing, ×2 (Carpenter, 1943a).

Homaloptila HANDLIRSCH, 1919b, p. 546 [**Homaloneura similis* MEUNIER, 1911a, p. 118; OD]. Fore wing nearly as broad as in *Caloneura*; RS with 4 main branches. *U. Carb.*, Europe (France).——FIG. 128,*7*. **H. similis* (MEUNIER); *a,* fore and *b,* hind wings, ×2 (Carpenter, 1961).

Family EUTHYGRAMMATIDAE Martynov, 1928

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Euthygrammidae MARTYNOV, 1928b, p. 49]

Similar to Paleuthygrammatidae but with vein CUA remote from CUP and CUP very close to 1A. *Perm.*

Euthygramma MARTYNOV, 1928b, p. 50 [**E. parallelum*; OD]. RS unbranched. *Perm.*, USSR (European RSFSR).——FIG. 128,*6*. **E. parallelum*; wing, ×2.7 (Martynov, 1938a).

Family PALEUTHYGRAMMATIDAE Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Paleuthygrammidae CARPENTER, 1943a, p. 70]

Wings long and slender; vein SC terminating not far from wing apex; RS arising near midwing, with 2 or 3 branches; M separating from stem R well before origin of RS; CUA and CUP straight and very close together. *Perm.*

Paleuthygramma MARTYNOV, 1930b, p. 42 [**P. tenuicornis*; OD]. RS branched only at wing apex. *Perm.*, USSR (Asian RSFSR), USA (Kansas).——FIG. 128,*5a*. **P. tenuicornis,* USSR; wing of holotype as preserved, ×2.5 (Martynov, 1930b) (see also Fig. 127).——FIG. 128,*5b,c*. *P. acutum* CARPENTER, Kansas; *b,* fore and *c,* hind wings, ×3 (Carpenter, 1943a).

Pseudogramma CARPENTER, 1943a, p. 70 [**Euthygramma aberrans* MARTYNOV, 1938a, p. 73; OD]. M unbranched. *Perm.*, USSR (European RSFSR).——FIG. 128,*4*. **P. aberrans* (MARTYNOV); wing, ×3 (Martynov, 1938a).

Vilvia ZALESSKY, 1933, p. 137 [**V. densinervosa*; OD]. Crossveins numerous and very close together. *Perm.*, USSR (Asian RSFSR).

Vilviopsis MARTYNOV, 1938a, p. 73 [**V. extensa*; OD]. RS with 2 long branches. [Probably synonymous with *Paleuthygramma.*] *Perm.*, USSR (European RSFSR).——FIG. 128,*3*. **V. extensa*; wing, ×2 (Martynov, 1938a).

Family PERMOBIELLIDAE Tillyard, 1937

[*nom. transl.* MARTYNOV, 1938b, p. 76, *ex* Permobiellinae TILLYARD, 1937a, p. 101]

Wings moderately slender; vein SC terminating slightly beyond midwing; RS with 3 branches; CUA and CUP close together proximally but diverging distally. *U. Carb.–Perm.*

Permobiella TILLYARD, 1937a, p. 101 [**P. perspicua*; OD]. R extending to wing apex; M forking well beyond origin of RS; crossveins strongly convex. CARPENTER, 1943a. *Perm.*, USA (Kansas).——FIG. 129,*3*. **P. perspicua*; wing as preserved, ×5 (Carpenter, 1943a).

Pseudobiella CARPENTER, 1970, p. 407 [**P. fasciata*; OD]. Similar to *Permobiella,* but crossveins relatively weak, not strongly convex; front margin of wing concave near end of SC; wings with dark transverse band. *U. Carb.*, USA (New Mexico).——FIG. 129,*1*. **P. fasciata*; fore wing, ×5 (Carpenter, 1970).

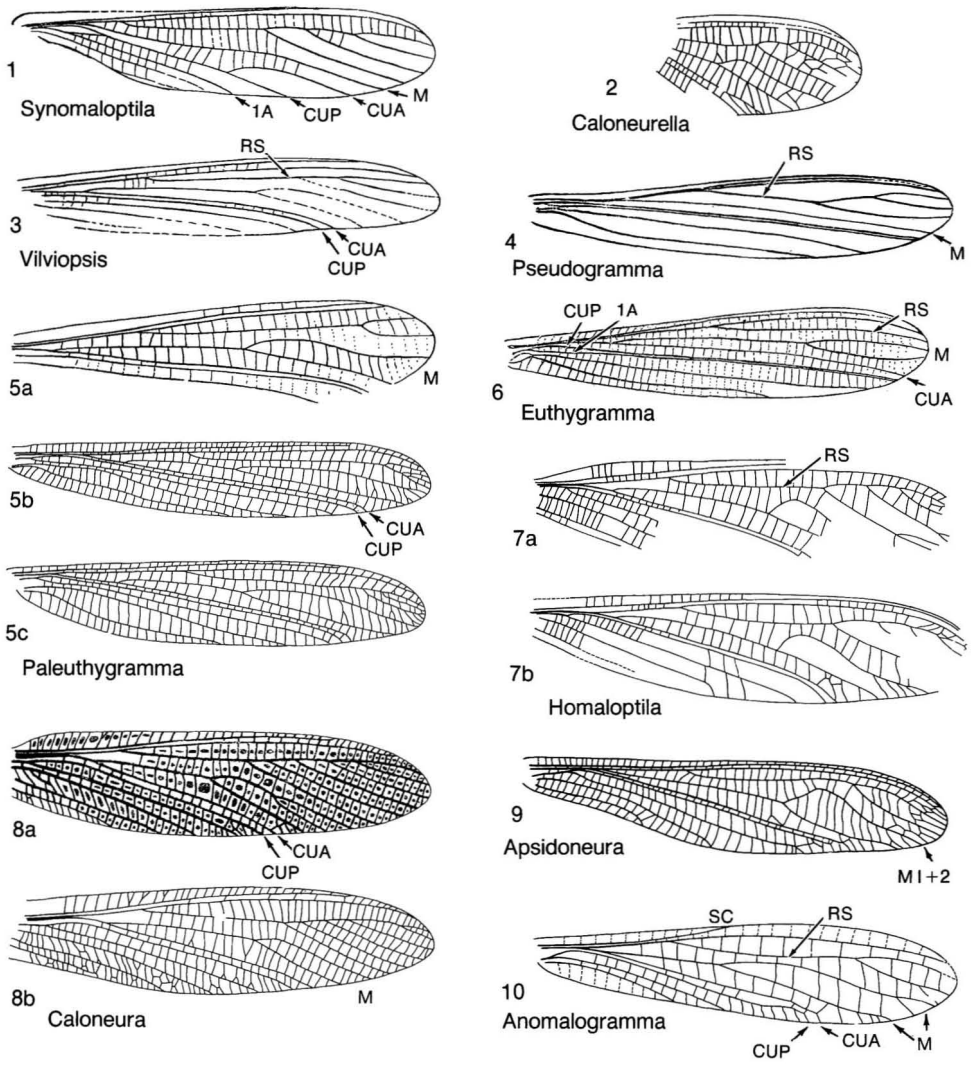


FIG. 128. Caloneuridae, Anomalogrammatidae, Apsidoneuridae, Euthygrammatidae, Paleuthygrammatidae, Synomaloptilidae, and Uncertain (p. 202–204).

Family AMBONEURIDAE Carpenter, 1980

[Amboneuridae CARPENTER, 1980, p. 111]

Apparently related to the Permobiellidae, but veins CUA and CUP not close together; crossveins forming a coarse network in strong relief over the wing. [Ordinal assignment uncertain.] *U. Carb.*

Amboneura CARPENTER, 1980, p. 112 [**A. klosei*; OD]. Vein RS with 5 terminal branches; M forked to level of midwing. *U. Carb.*, USA (Pennsylvania). ——FIG. 129,*4a,b*. **A. klosei; a,* photograph of wing showing strong relief of crossveins, ×2.4; *b,* drawing of venation as preserved in holotype, ×2.4 (both Carpenter, 1980).

Family PLEISIOGRAMMATIDAE Carpenter, 1943

[*nom. correct.* ROHDENDORF, 1957, p. 82, *pro* Pleisiogrammidae CARPENTER, 1943a, p. 73]

Wings nearly oval, broader than in Paleuthygrammatidae, narrowed basally; vein

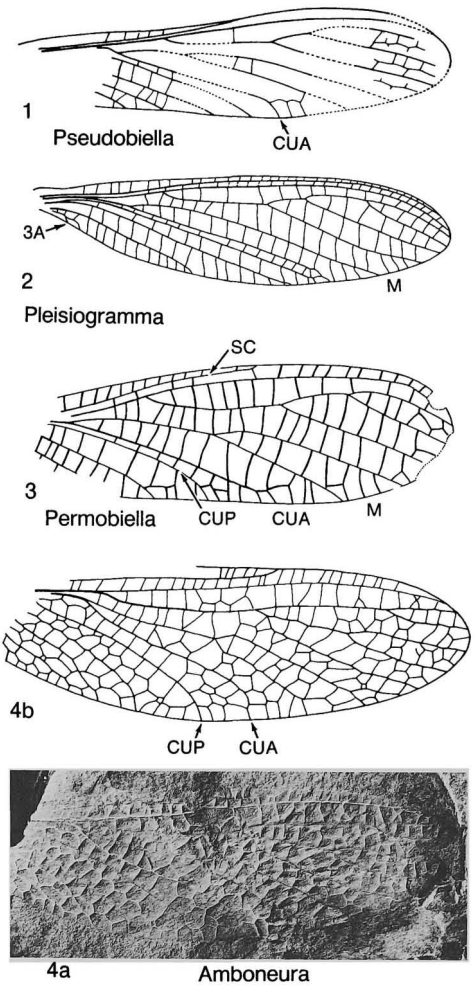


FIG. 129. Permobiellidae, Amboneuridae, and Pleisiogrammatidae (p. 202–204).

SC extending well beyond midwing; 3A vestigial or absent. *Perm.*

Pleisiogramma CARPENTER, 1943a, p. 73 [**P. mediale*; OD]. M unbranched. *Perm.*, USA (Kansas). ——FIG. 129,*2*. **P. mediale*; wing, ×3.2 (Carpenter, 1943a).

Family SYNOMALOPTILIDAE Martynov, 1938

[Synomaloptilidae MARTYNOV, 1938a, p. 76]

Related to Euthygrammatidae, but veins CUA and CUP anastomosed for a considerable distance. *Perm.*

Synomaloptila MARTYNOV, 1938a, p. 76 [**S. longipennis*; OD]. SC terminating well before wing apex; separation of CUA and CUP at about level of midwing. *Perm.*, USSR (Asian RSFSR).——FIG. 128,*1*. **S. longipennis*; wing, ×2 (Martynov, 1938a).

Family UNCERTAIN

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

Caloneurella CARPENTER, 1934, p. 324 [**C. carbonaria*; OD]. Apical wing fragment, probably related to *Caloneura*. *U. Carb.*, USA (Pennsylvania).——FIG. 128,*2*. **C. carbonaria*; ×1.8 (Carpenter, 1934).

Pruvostiella HANDLIRSCH, 1922, p. 82 [**Euthyneura lecomtei* PRUVOST, 1919, p. 115; OD]. Small wing fragment. *U. Carb.*, Europe (France).

Order MIOMOPTERA Martynov, 1927

[Miomoptera MARTYNOV, 1927d, p. 101, *emend.* MARTYNOV, 1938b, p. 138]

Small to very small insects, with wings nearly homonomous. Fore wing with vein SC ending before or at midwing; R commonly with a distal twig; RS arising before midwing, with at least 3 terminal branches; M commonly coalesced with CUA basally to varying amounts, but diverging in basal third of wing; M deeply forked; CUA with 2 or 3 terminal branches; CUP unbranched; 2 anal veins typically present. Hind wing similar in form to fore wing, without an anal lobe or fan; M usually arising from CU very near wing base. Body structure little known; head of moderate size; mouthparts apparently mandibulate; antennae conspicuous, relatively thick, with 15 to 20 segments; tarsi with 4 segments (*Palaeomantis*); cerci short. Immature stages unknown. *U. Carb.–Perm.*

The status of this order is uncertain. As originally proposed by MARTYNOV (1927d) it included five Permian families, previously placed in the order Protorthoptera, but it was based mainly on one of them, the Palaeomanteidae (=Delopteridae). The following year TILLYARD (1928b), obviously unaware of MARTYNOV's article, proposed the new order Protoperlaria for the same series of families except the Palaeomanteidae. Subsequent studies of extensive collections of