

TREATISE ON
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Part R
ARTHROPODA 4

Volume 3: Superclass Hexapoda

By F. M. CARPENTER

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

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

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

Roger L. Kaesler
Lawrence, Kansas
May 1, 1992

AUTHOR'S PREFACE

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

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

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

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

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

Frank M. Carpenter
Cambridge, Massachusetts
January, 1992

SOURCES OF ILLUSTRATIONS

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

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

STRATIGRAPHIC DIVISIONS

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

- CENOZOIC ERATHEM**
- Quaternary System
- Holocene Series
- Pleistocene Series
- Tertiary System
- Pliocene Series
- Miocene Series
- Oligocene Series
- Eocene Series
- Paleocene Series
- MESOZOIC ERATHEM**
- Cretaceous System

- Jurassic System
- Triassic System
- PALEOZOIC ERATHEM**
- Permian System
- Carboniferous System
- Upper Carboniferous Subsystem
- Lower Carboniferous Subsystem
- Devonian System
- Silurian System
- Ordovician System
- Cambrian System
- PRECAMBRIAN** (undifferentiated herein)

PART R
ARTHROPODA 4

HEXAPODA

VOLUMES 3, 4

By FRANK M. CARPENTER

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SYSTEMATIC DESCRIPTIONS OF THE SUPERCLASS HEXAPODA

Superclass HEXAPODA

Latreille, 1825

[Hexapoda LATREILLE, 1825, p. 328]

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

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

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

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

Class and Order COLLEMBOLA

Lubbock, 1871

[Collembola LUBBOCK, 1871, p. 295]

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

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

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

THORAX

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

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

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

wings become functional in a surprisingly short time.

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

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

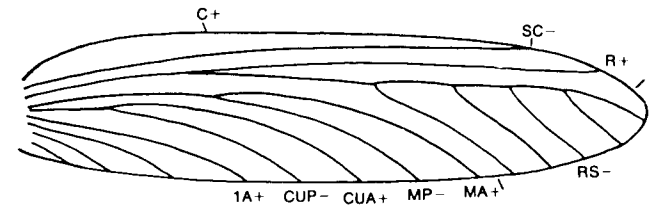


FIG. 4. Fore wing of *Stenodictya* sp., Palaeodictyoptera, Upper Carboniferous of France (Carpenter, new).

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

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

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

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

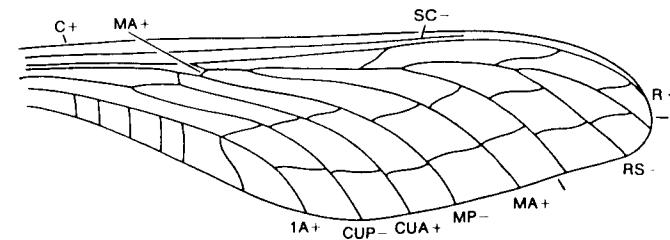


FIG. 5. Fore wing of *Psilotborax* sp., Megasecoptera, Upper Carboniferous of France (Carpenter, 1951).

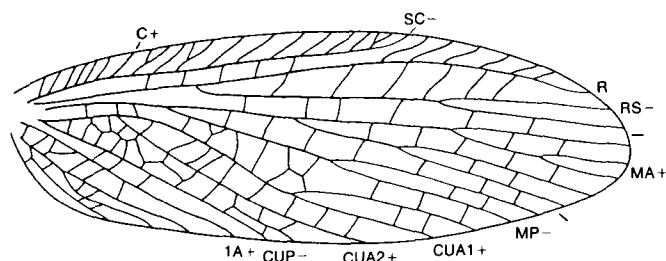


FIG. 6. Fore wing of *Liometopum* sp., Protorthoptera, Permian of Kansas (Carpenter, 1950).

ABDOMEN

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

REPRODUCTION AND DEVELOPMENT

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

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

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

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

ORIGIN OF INSECTS

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

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

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

EVOLUTION OF INSECTA

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

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

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

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

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

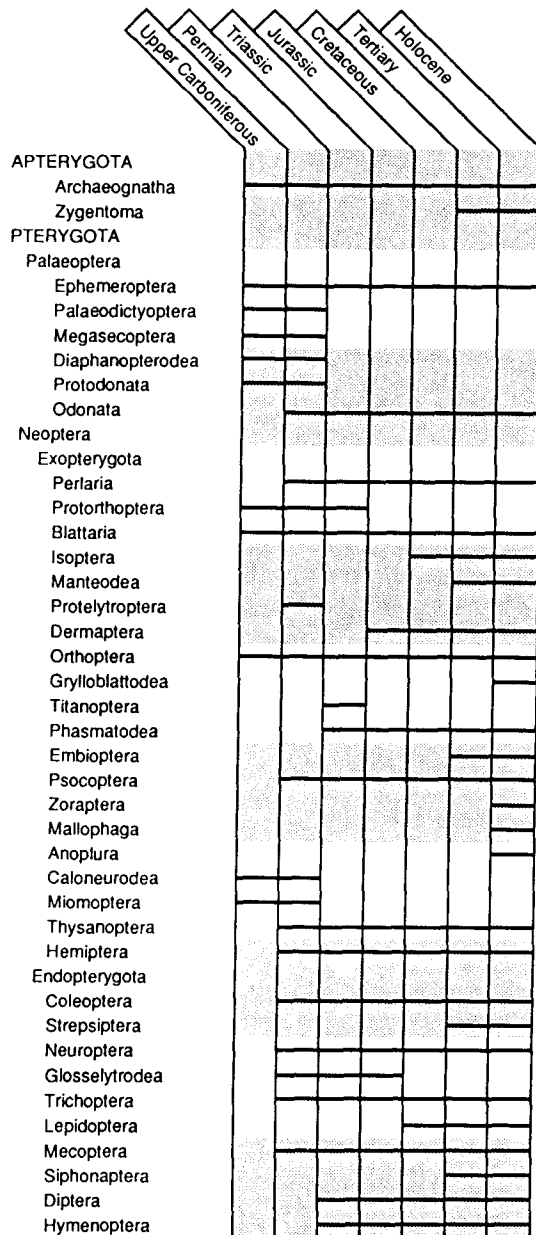


FIG. 9. Geological ranges of orders of insects (Carpenter, new).

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

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

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

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

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

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

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

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

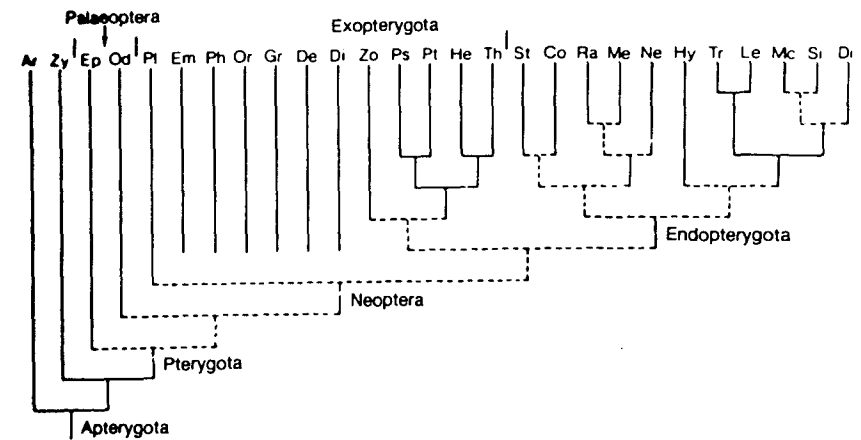


FIG. 10. Phylogeny of existing orders of insects. Higher categories: APTERYGOTA; Pterygota; Palaeoptera; Neoptera; Exopterygota; Endopterygota. Orders: Archaeognatha (Ar); Zygentoma (Zy); Ephemeroptera (Ep); Odonata (Od); Perlaria (Plecoptera) (Pl); Embioptera (Em); Phasmatodea (Ph); Orthoptera (Or);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

Subclass APTERYGOTA

Brauer, 1885

[Apterygota BRAUER, 1885, p. 290]

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

Order ARCHAEOGNATHA

Börner, 1904

[Archaeognatha BÖRNER, 1904, p. 523]

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

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

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

OD]. Similar to *Austrotrips* (recent), but eyes very large, protruding, and consisting of many facets. USINGER, 1942; PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Proleuwenia PRIESNER, 1924, p. 148 [**P. succini*; OD]. Wings reduced (female); similar to *Idiotrips* (recent), but antennae with 8 segments. USINGER, 1942; PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Schlechtendalia BAGNALL, 1929, p. 96 [**S. longisubus*; OD]. Similar to *Pblaeotrips*, but tenth abdominal segment substantially longer than head; fifth antennal segment with a projection; wing bristles blunt. PRIESNER, 1949. *Oligo.*, Europe (Baltic).

Symphothrips HOOD & WILLIAMS, 1915, p. 131. USINGER, 1924, 1949. *Oligo.*, Europe (Baltic)—*Holo.*

Treherniella WATSON, 1923, p. 81. PRIESNER, 1930, 1949. *Oligo.*, Europe (Baltic)—*Holo.*

Suborder UNCERTAIN

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

Family LIASSOTHRIPIDAE Priesner, 1949

[Liassothripidae PRIESNER, 1949, p. 34] [=Mesothripidae MARTYNOV, 1927b, p. 768]

Antennae thin, with at least 7 segments; head narrow; anterior femora very broad; wings unknown. *Jur.*

Liassothrips PRIESNER, 1949, p. 34, *nom. subst. pro Mesothrips* MARTYNOV, 1927b, p. 768, *non* ZIMMERMANN, 1900 [**Mesothrips crassipes* MARTYNOV, 1927b, p. 768; OD]. Little-known thysanopteron; abdomen apparently constricted basally. *Jur.*, USSR (Kazakh).—FIG. 133,3. **L. crassipes* (MARTYNOV); body, $\times 16$ (Martynov, 1927b).

HEMIPTEROID EXOPTERYGOTES

Order HEMIPTERA Linné, 1758

[Hemiptera LINNÉ, 1758, p. 434] [=Hemipsocoptera ZATSEVSKY, 1937c, p. 51; Palaeohemiptera HANDIRSUU, 1904b, p. 2]

Exopterygote Neoptera, mostly small to very small, with much morphological diversity. Head opisthognathous or prognathous; compound eyes usually present but diverse

in size; two ocelli commonly present, rarely three or none; antennae typically with five segments or less, rarely with as many as ten; mouthparts haustellate, consisting of two pairs of maxillary stylets in a segmented, rostrate labium. Pronotum of moderate size, often diversely modified; meso- and metathorax well developed. Legs usually cursorial, but forelegs of some genera raptorial, vestigial, or absent; tarsi commonly with three segments, rarely with two or one. Wings usually present, but very different in the two suborders. Wing venation quite generalized in primitive forms but much reduced in most families; fore wings of suborder Homoptera usually of uniform texture, those of suborder Heteroptera partly membranous and partly coriaceous. Abdomen well developed; ovipositor usually present. Nymphs resembling adults in basic body structure. *Perm.—Holo.*

This is the largest of the exopterygote orders, and it has apparently been a major order at least since the Triassic. All available evidence suggests that the Hemiptera are most closely related to the Psocoptera, which were well represented in the Permian. The order Hemiptera has traditionally been divided into two suborders, Homoptera and Heteroptera, the members of both groups having the same distinctive, haustellate mouthparts. Both suborders are also represented in the Permian, but the Homoptera have by far the more extensive record in that period.

The wings provide the best means of distinguishing the members of the two suborders. The homologies of the main veins are clear throughout both suborders, even in those in which the venation is much reduced. However, there has been much convergence in the reduction process. In part because of this, the family and generic classifications of the Hemiptera, especially of the Homoptera, have been based mainly on body features, such as the detailed structure of the rostrum, number and size of ocelli, tarsal segmentation, and integumentary details. Since fossils do not usually show such structures, the family position of many of the extinct genera is uncertain.

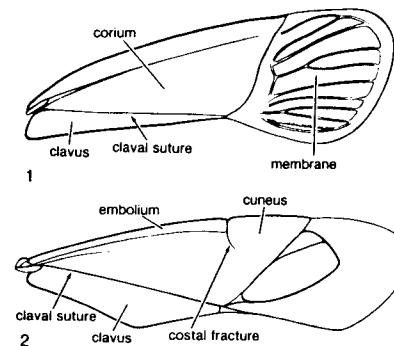


FIG. 134. Hemiptera; wing structure of the suborder Heteroptera.—1. *Nazara* sp., Pentatomidae. (adapted from CSIRO, 1970).—2. *Megacoelum* sp., Miridae (adapted from CSIRO, 1970).

The fore wings of the two suborders, except for a few primitive families in each one, differ mainly in texture. Those of the Homoptera are usually of a uniform or nearly uniform texture. Exceptions are found in a few primitive families, such as the Palaeontinidae and Prosbolidae, in which the fore wing is partly divided into two areas by an irregular nodal line (see Figs. 137,1 and 139,4a). The proximal area is usually more coriaceous than the distal part. A slight break (costal break or indentation) in the costal margin appears to be functionally associated with the nodal line. The anal area, commonly termed the clavus in the Hemiptera, is usually a distinct region of the fore wing. The fore wings of the Heteroptera, usually termed hemelytra, have a more complex structure. The distal portion of the wing is membranous, but the proximal part is coriaceous, consisting of a large, anterior, triangular section (corium) and a relatively small region (clavus), separated from the corium by the claval suture (Fig. 134,1). These areas are diverse in form and size in families and genera. The costal area of the corium may be separated from the rest of it by vein M+R, forming the embolium; and a more distal part (cuneus) of the corium may be separated by a costal fracture (Fig. 134,2). The hind wings of the Hemiptera

are generally more specialized than the fore pair, often with a very different shape. Polymorphism of wings, including aptery, occurs commonly in the order.

The great majority of the Hemiptera are phytophagous, but some Heteroptera are active predators. Immature stages have essentially the same feeding habits as the adults.

The geological record of the Hemiptera is very extensive, including almost a hundred families, two-thirds of which are Homoptera. A surprisingly large number of entomologists, specialists on the systematics of existing Hemiptera, have contributed to our knowledge of this fossil record and of the phylogeny of the order. There is, however, much difference of opinion among them about the systematic position of many of the extinct genera.

Suborder HOMOPTERA

Leach, 1815

[Homoptera LEACH, 1815, p. 124]

Fore wing of uniform texture or nearly so, not sharply differentiated into membranous and coriaceous areas; wings typically held sloping over the sides of the body at rest. *Perm.—Holo.*

Family DUNSTANIIDAE Tillyard, 1916

[Dunstaniidae TILLYARD in TILLYARD & DUNSTAN, 1916, p. 31]

Fore wing sharply separated into tegminous basal part and membranous distal area; nodal break prominent; vein SC long, terminating on costal margin; R and RS curved; RS unbranched; clavus broad, triangular; 1A and 2A long, extending to hind margin. Hind wing little known, smaller than fore wing, with rounded anal area. Head, compound eyes, and pronotum relatively large. Relatively large insects. Affinities uncertain, but apparently closely related to the Palaeontinidae. TILLYARD, 1918d; BECKER-MIGDISOVA, 1949b; EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965; RIEK, 1976b. *Trias.*

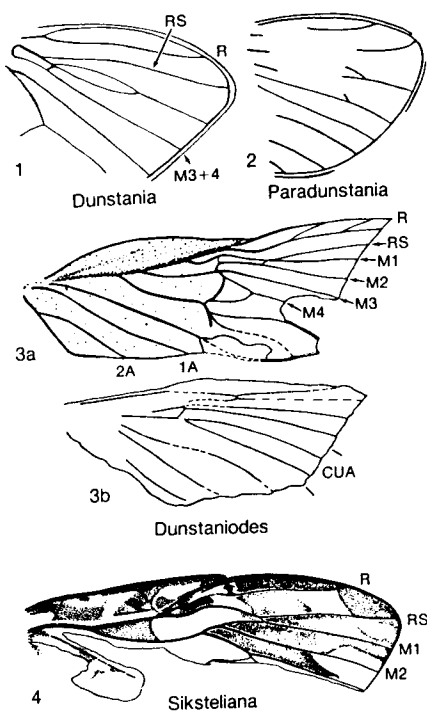


FIG. 135. Dunstaniidae (p. 214).

Dunstania TILLYARD in TILLYARD & DUNSTAN, 1916, p. 31 [**D. pulchra*; OD]. M3+4 not forked, RS apparently joined to M by a short, oblique cross-vein. [The genus has been reported from South Africa (RIEK, 1976b), but the generic position of the species described is very uncertain.] *Trias.*, Australia (Queensland).—FIG. 135, 1. **D. pulchra*; fore wing as preserved, $\times 1.5$ (Evans, 1956).

Dunstaniodes BECKER-MIGDISOVA & WOOTTON, 1965, p. 64 [**D. elongatus*; OD]. Fore wing elongate; costal margin of basal half of wing strongly convex. *Trias.*, USSR (Kirghiz).—FIG. 135, 3. **D. elongatus*; a, fore and b, hind wings as preserved, $\times 3.0$ (Becker-Migdisova & Wootton, 1965).

Dunstaniopsis TILLYARD, 1918d, p. 584 [**D. triassica*; OD]. Little-known genus, based on incomplete fore wing; apex apparently more pointed than in *Dunstania*. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Trias.*, Australia (Queensland).

Paradunstania TILLYARD, 1918d, p. 585 [**P. affinis*; OD]. Little-known genus, based on fragment of fore wing; probably a synonym of *Dunstania*. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON,

1965. *Trias.*, Australia (Queensland).—FIG. 135, 2. **P. affinis*; fore wing as preserved, $\times 1.5$ (Evans, 1956).

Siksteliana BECKER-MIGDISOVA & WOOTTON, 1965, p. 68 [**S. popovi*; OD]. Little-known genus, based on fore wing. Similar to *Dunstaniodes*, but costal margin of basal half nearly straight. *Trias.*, USSR (Kirghiz).—FIG. 135, 4. **S. popovi*; fore wing, $\times 3$ (Becker-Migdisova & Wootton, 1965).

Family PALAEONTINIDAE Handlirsch, 1906

[Palaeontinidae HANDLIRSCH, 1906b, p. 618] [=Cicadomorphae EVANS, 1956, p. 222]

Fore wing as in Dunstaniidae, with membranous, distal part of wing broader and longer than basal, tegminous part; vein SC usually weakly developed, commonly with branches or suggestions of branches; R and M separating before or close to midwing; R and RS nearly straight. Hind wing with a prominent indentation on costal margin; M1 commonly coalesced for short interval with RS; M with 4 branches. Head small, narrow, pronotum wide; body generally with numerous hairs. *Perm.—Jur.*

Palaeontina BUTLER, 1873, p. 126 [**P. oolitica*; OD]. Little-known genus, based on fore wing. M with 4 branches, M1+2 and M3+4 forking at about same level. [The genus was excluded from Homoptera by EVANS (1956) but included here by BECKER-MIGDISOVA (1962b) and POPOV (1980b)]. *Jur.*, England.—FIG. 136, 1. **P. oolitica*; fore wing, $\times 0.8$ (Handlirsch, 1906b).

Asiocossus BECKER-MIGDISOVA, 1962a, p. 89 [**A. subcostalis*; OD]. Little-known genus, based on fragment of fore wing. SC free from R+M except for very base, branched; R+M and stem of R very short. *Trias.*, USSR (Kirghiz).—FIG. 136, 3. **A. subcostalis*; fore wing base, $\times 2.5$ (Becker-Migdisova, 1962b).

Cicadomorpha MARTYNOV, 1926b, p. 1357 [**C. punctulata*; OD]. SC coalesced with R+M at base; area between M and CUA very broad, without crossveins; CU slightly arched at base. *Jur.*, USSR (Kazakh).—FIG. 136, 7. **C. punctulata*; fore wing, $\times 1.0$ (Becker-Migdisova, 1962b).

Fletcheriana EVANS, 1956, p. 224 [**F. triassica*; OD]. Fore wing as in *Pseudocossus*, but costal area much broader; SC lying alongside R basally; RS arising from R remote from wing base. [The assignment of a species from the Triassic of South Africa (RIEK, 1976b) to this genus is very uncertain.] *Trias.*, Australia (New South Wales).—FIG. 136, 2. **F. triassica*; a, fore wing; b, hind wing, $\times 1.0$ (Evans, 1956).

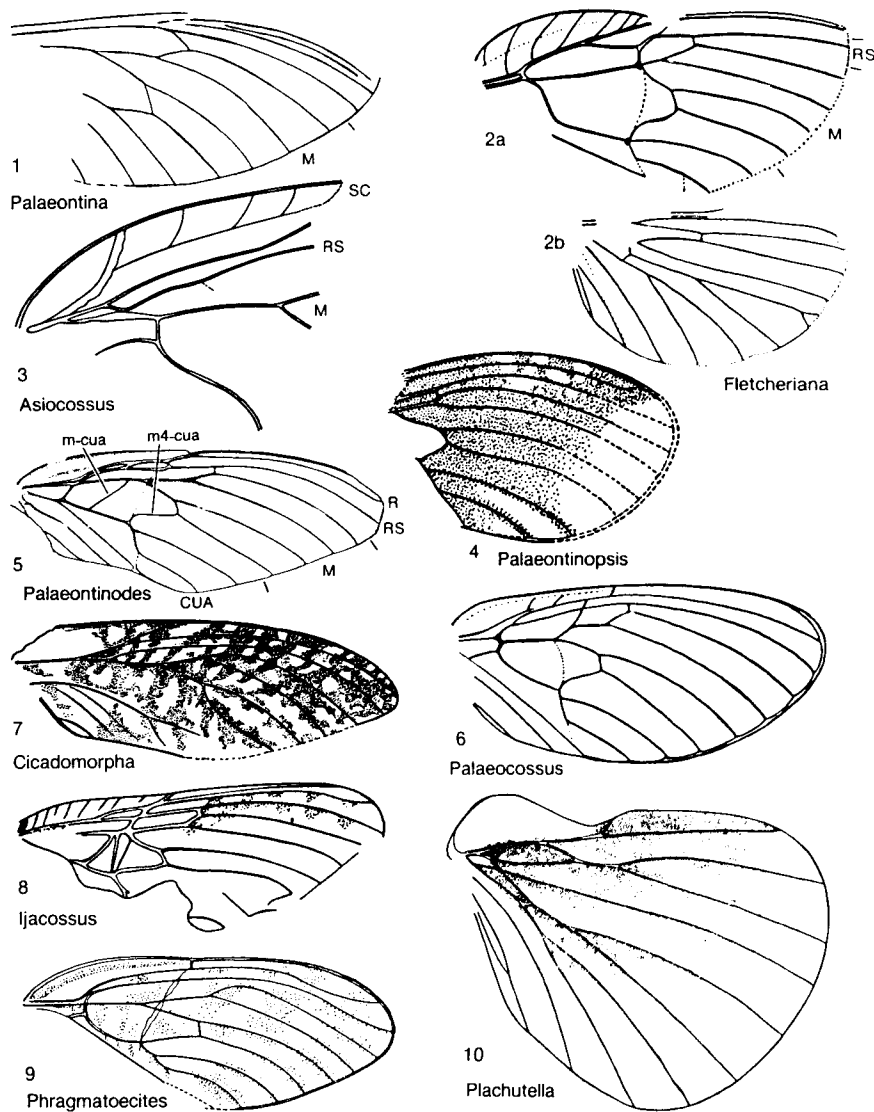


FIG. 136. Palaeontinidae (p. 214–216).

Ijacossus BECKER-MIGDISOVA, 1950, p. 1106 [**I. suchanovae*; OD]. Little-known genus, based on fore wing. Similar to *Palaeontinodes*, but SC with several branches. [Family assignment uncertain.] *Jur.*, USSR (Asian RSFSR).—FIG. 136, 8. **I. suchanovae*; fore wing, $\times 1$ (Becker-Migdisova, 1962b).

Palaeocicadopsis T'AN, 1980, p. 161 [**P. chinensis*; OD]. Fore wing similar to that of *Cicadomorpha*, but M branching near wing base. *Perm.*, China (Inner Mongolia).

Palaeocossus OPPENHEIM, 1885, p. 333 [**P. jurassicus*; OD]. Fore wing without nodal indentation; wing broadly oval; distal margin of basal median

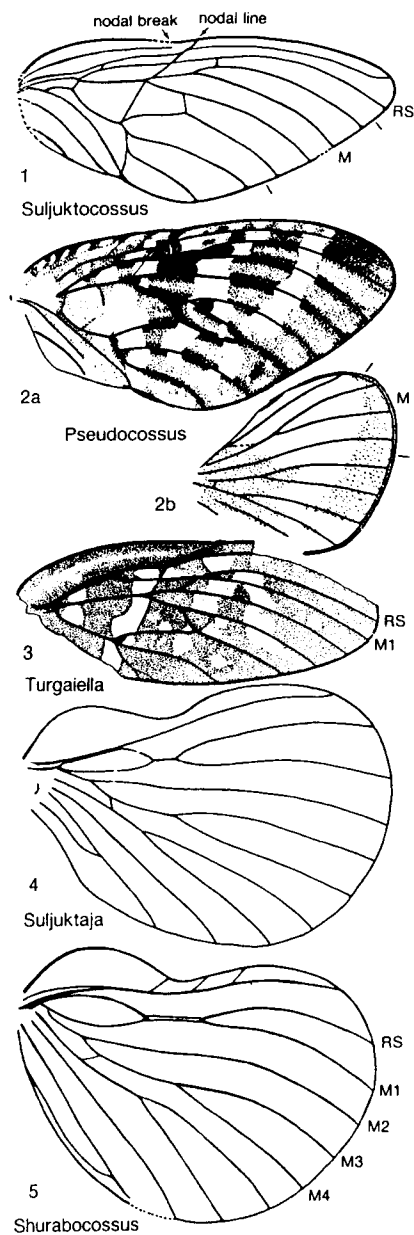


FIG. 137. Palaeontinidae (p. 216-217).

cell (between M and CUA) smoothly curved; hind margin strongly convex. *Jur.*, USSR (Asian RSFSR).—FIG. 136,6. **P. jurassicus*; fore wing, $\times 1.5$ (Evans, 1956).

Palaeontinodes MARTYNOV, 1937a, p. 166 [**P. shabarovii*; OD]. Fore wing triangular; costal indentation weak; SC without branches; crossvein m-cua long; basal median cell divided by crossveins (not shown in figure). BECKER-MIGDISOVA, 1949b; EVANS, 1956. *Jur.*, USSR (Tadzhik, Asian RSFSR).—FIG. 136,5. *P. angarensis* BECKER-MIGDISOVA & WOOTTON; fore wing, $\times 1$ (Becker-Migdisova & Wootton, 1965).

Palaeontinopsis MARTYNOV, 1937a, p. 167 [**P. latipennis*; OD]. Little-known genus. Fore wing apparently oval and with rounded apex. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Tadzhik).—FIG. 136,4. **P. latipennis*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Phragmatoecites OPPENHEIM, 1885, p. 333 [**P. damesi*; OD]. Fore wing with costal margin straight or only slightly curved; nodal indentation weak. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Asian RSFSR).—FIG. 136,9. **P. damesi*; fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).

Plachutella BECKER-MIGDISOVA, 1949b, p. 11 [**P. rotundata*; OD]. Little-known genus, based on hind wing. M2 close to M3+4 at one point but not coalesced with it. BECKER-MIGDISOVA, 1950; BECKER-MIGDISOVA & WOOTTON, 1965. *Jur.*, USSR (Kazakh, Tadzhik).—FIG. 136,10. **P. rotundata*; hind wing, $\times 2.5$ (Becker-Migdisova, 1949b).

Pseudocossus MARTYNOV, 1931d, p. 94 [**P. zemcuznicovi*; OD]. Fore wing triangular, with pronounced indentation of costal margin at nodal break; SC free from R+M at base, branched; RS arising from R near wing base; distinct bands of coloration. Hind wing rounded, much smaller than fore wing. *Jur.*, USSR (Asian RSFSR, Kazakh).—FIG. 137,2. *P. tugaiensis* BECKER-MIGDISOVA & WOOTTON, Kazakh; a, fore and b, hind wings, $\times 1.5$ (Becker-Migdisova & Wootton, 1965).

Shurabocossus BECKER-MIGDISOVA, 1949b, p. 15 [**S. gigas*; OD]. Hind wing similar to that of *Plachutella*, but M2 coalesced with M3+4 for a considerable interval before separating. *Jur.*, USSR (Tadzhik).—FIG. 137,5. **S. gigas*; hind wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Suljuktaja BECKER-MIGDISOVA, 1949b, p. 17 [**S. turkestanensis*; OD]. Hind wing as in *Shurabocossus* but with the coalesced parts of 1A and 2A at least as long as the free portions. *Jur.*, USSR (Kirghiz).—FIG. 137,4. **S. turkestanensis*; hind wing, $\times 2$ (Becker-Migdisova, 1962b).

Suljuktocossus BECKER-MIGDISOVA, 1949b, p. 8 [**S.*

prosboloides; OD]. Fore wing as in *Phragmatoecites* but more nearly triangular and with apex nearly pointed. *Jur.*, USSR (Kirghiz).—FIG. 137,1. **S. prosboloides*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Turgaiella BECKER-MIGDISOVA & WOOTTON, 1965, p. 70 [**T. pomerantsevae*; OD]. Fore wing as in *Palaeontinodes*, but wing oval and basal median cell not divided by crossveins; crossvein m-cua very short. *Jur.*, USSR (Kazakh).—FIG. 137,3. **T. pomerantsevae*; fore wing, $\times 1.5$ (Becker-Migdisova & Wootton, 1965).

Family MESOGEREONIDAE Tillyard, 1921b

[Mesogereonidae TILLYARD, 1921b, p. 272]

Fore wing slender, with well-developed submarginal (ambient) vein and coriaceous border; veins SC and R close together and to costal margin; RS arising before fork of M1+2; crossvein m4-cua near wing base and almost longitudinal in position. Hind wing little known, much smaller than fore wing. Body structure unknown. EVANS, 1956; BECKER-MIGDISOVA & WOOTTON, 1965. *Trias.*

Mesogereon TILLYARD in TILLYARD & DUNSTAN, 1916, p. 33 [**M. neuropunctatum*; OD]. RS joined to M1 by a short crossvein; M3+4 forking more basally than M1+2. *Trias.*, Australia (New South Wales).—FIG. 138,1a. *M. superbum* TILLYARD; fore wing, $\times 1.2$ (Evans, 1956).—FIG. 138,1b. *M. shepherdii* TILLYARD; hind wing, $\times 1.2$ (Evans, 1956).

Triassogereon RIEK, 1976b, p. 808 [**T. distinctum*; OD]. Fore wing as in *Mesogereon*, but fork of M3+4 close to fork of M1+2. *Trias.*, South Africa.—FIG. 138,2. **T. distinctum*; fore wing, $\times 1.6$ (Riek, 1976b).

Family PROSBOLIDAE Handlirsch, 1906

[Prosbolidae HANDLIRSCH, 1906b, p. 390] [=Sojanecuridae BECKER-MIGDISOVA, 1946, p. 750]

Fore wing: distal part commonly membranous; costal area broad; vein SC usually forming an anterior branch submarginal to costal margin and more rarely an indistinct, short branch that parallels R+M and even part of R; forks of M and CUA usually shallow. Hind wing: costal margin usually deeply excised near middle, convex basally and dis-

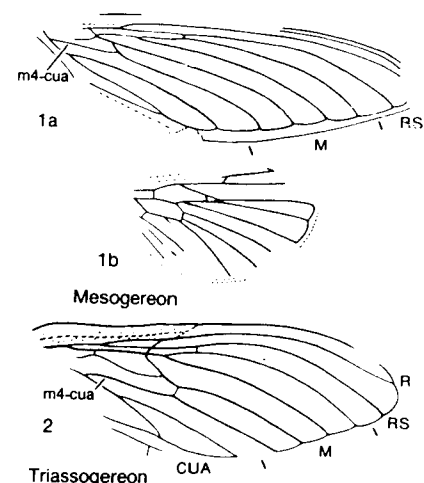


FIG. 138. Mesogereonidae (p. 217).

tally; anal region extended posteriorly. Body structure unknown. BECKER-MIGDISOVA, 1940, 1947, 1962b; EVANS, 1956. *Perm.*—*Trias.*

Prosbolus HANDLIRSCH, 1904b, p. 2 [**P. hirsuta*; OD] [=Prosbolina HANDLIRSCH, 1937, p. 132 (type, *Prosbolus biexcisa* MARTYNOV, 1928b, p. 7)]. Fore wing: nodal break and nodal line present; R, M, and CUA dividing at about same level. Hind wing: M with at least 4 branches. *Perm.*, USSR (European and Asian RSFSR).—FIG. 139,4a. **P. hirsuta*; fore wing, $\times 1.6$ (Evans, 1956).—FIG. 139,4b. *P. reducta* MARTYNOV; fore wing, $\times 3.5$ (Becker-Migdisova, 1940).—FIG. 139,4c. *P. breviata* BECKER-MIGDISOVA; hind wing, $\times 2.6$ (Becker-Migdisova, 1940).

Austroprosbolus EVANS, 1943b, p. 181 [**A. maculata*; OD]. Fore wing with nodal break and nodal line; RS curved posteriorly, touching M1+2 at point of fork; CUA with a shallow, distal fork. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 139,5. **A. maculata*; fore wing, $\times 4$ (Evans, 1943b).

Austroprosboloides RIEK, 1973, p. 527 [**A. vandijki*; OD]. Little-known genus; fore wing similar to *Austroprosbolus*, but RS touching M1 beyond fork and M3+4 connected to CUA distally. RIEK, 1976a. *Perm.*, South Africa.—FIG. 140,6. **A. vandijki*; fore wing, $\times 4$ (Riek, 1973).

Beaufortiscus RIEK, 1976a, p. 779 [**B. dixi*; OD]. Fore wing very similar to that of *Prosbolus*; anal

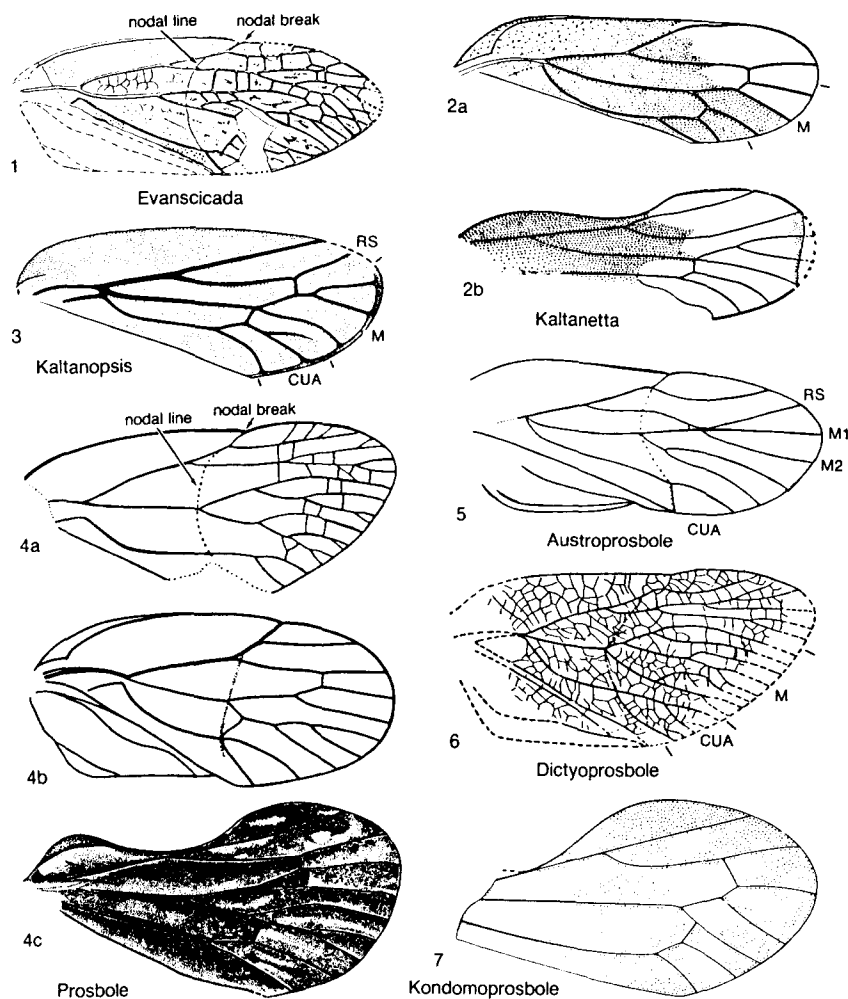


FIG. 139. Prosbolidae (p. 217-220).

area with 3 veins. [Probably a synonym of *Prosbole*.] *Perm.*, South Africa.
Dictyoprosbole MARTYNOV, 1935d, p. 443 [**D. membranosa*; OD]. Fore wing membranous, covered with a network of crossveins; M and CUA dividing at level of origin of RS; RS, M, and CUA with branching as in *Orthoprosbole*. EVANS, 1956. *Perm.*, USSR (Asian RSFSR). —FIG. 139.6. **D. membranosa*; fore wing, $\times 1.5$ (Becker-Migdisova, 1960).
Evanscicada BECKER-MIGDISOVA, 1962b, p. 170,

nom. subst. pro Evansia BECKER-MIGDISOVA, 1961c, p. 323, *non* CAMBRIDGE, 1900 [**Evansia speciosa* BECKER-MIGDISOVA, 1961c, p. 323; OD]. Fore wing narrow; basal part tegminous; RS arising at level of forking of M; numerous crossveins distally and indication of network near basal-central part of wing. *Perm.*, USSR (Asian RSFSR). —FIG. 139.1. **E. speciosa*; fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).
Falsia BECKER-MIGDISOVA, 1946, p. 750 [**F. chimaera*; OD]. Similar to *Sojanoneura*, but first

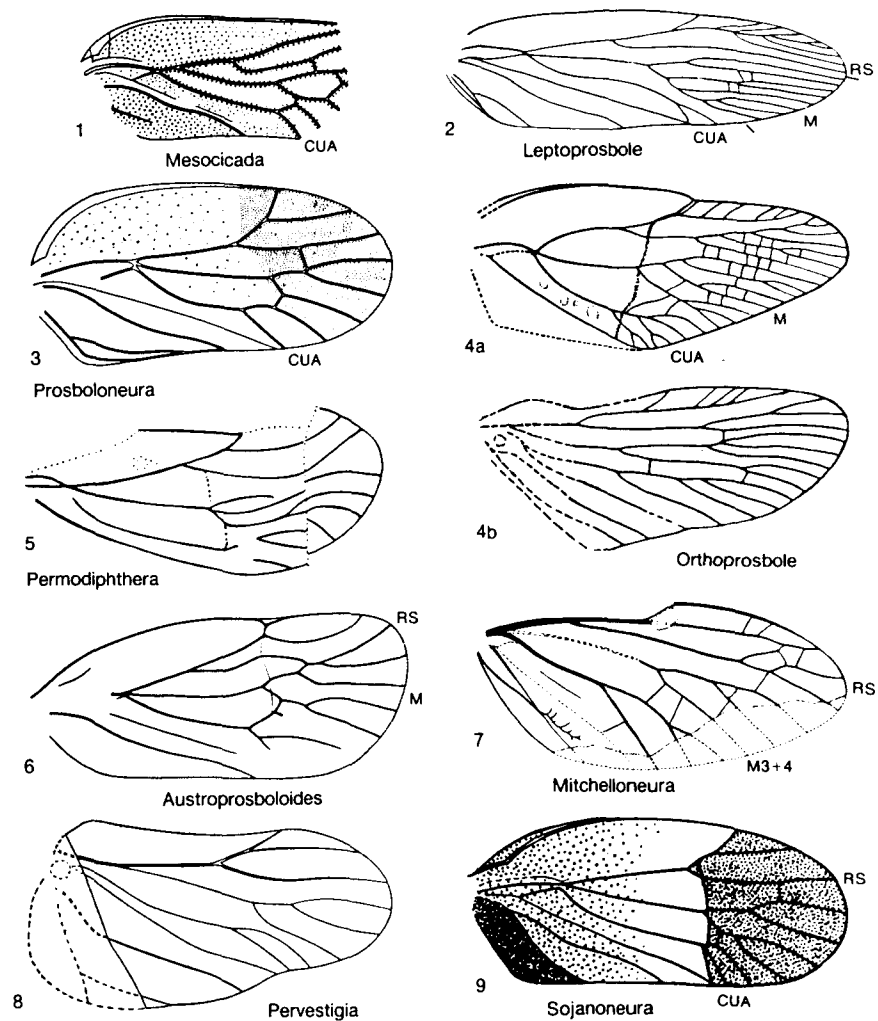


FIG. 140. Prosbolidae (p. 217-221).

and second tarsal segments of same size. BECKER-MIGDISOVA, 1946. *Perm.*, USSR (European RSFSR).
Kaltanetta BECKER-MIGDISOVA, 1961c, p. 303 [**K. nigra*; OD]. Fore wing slender, apex symmetrically curved; RS arising well before level of forking of M and of CUA; M with 3 branches. Hind wing slender distally; marginal indentation deep and wide; M with 3 branches. *Perm.*, USSR (Asian RSFSR). —FIG. 139.2. **K. nigra*; a,

fore and b, hind wings, $\times 6.5$ (Becker-Migdisova, 1961c).
Kaltanopsis BECKER-MIGDISOVA, 1961c, p. 300 [**K. ornata*; OD]. Fore wing similar to that of *Kaltanetta*, but costal margin strongly curved and R continuing in a straight line from its stem; longitudinal veins unusually thick. *Perm.*, USSR (Asian RSFSR). —FIG. 139.3. **K. ornata*; fore wing, $\times 8$ (Becker-Migdisova, 1961c).
Kondomoprosbole BECKER-MIGDISOVA, 1961c, p.

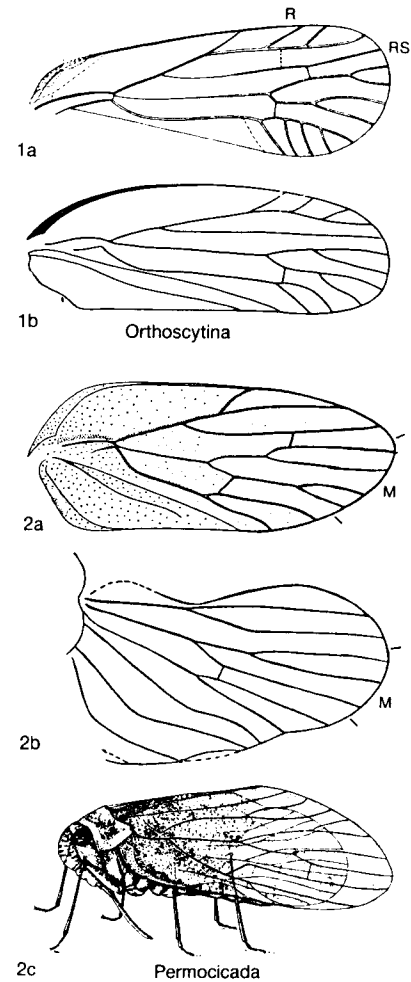


FIG. 141. Prosbolidae (p. 220).

315 [**K. pictata*; OD]. Hind wing: anterior margin with prominent bulge distally; R a straight continuation of stem R; M with 3 short branches. *Perm.*, USSR (Asian RSFSR).—FIG. 139,7. **K. pictata*; hind wing, $\times 8.5$ (Becker-Migdisova, 1962b).

Leptoprosbole RIEK, 1976b, p. 812 [**L. lepida*; OD]. Fore wing elongate; M with 8 terminal branches. [Family assignment doubtful.] *Trias.*, South Africa.—FIG. 140,2. **L. lepida*; fore wing, $\times 1.5$ (Riek, 1976b).

Mesocicada BECKER-MIGDISOVA, 1962a, p. 90 [**M.*

verrucosa; OD]. Little-known fore wing; nodal break absent; M with 4 branches; CUA with small fork. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).—FIG. 140,1. **M. verrucosa*; fore wing, $\times 14$ (Becker-Migdisova, 1962a).

Mitchelloneura TILLYARD, 1921c, p. 414 [**M. permiana*; OD]. Little-known hind wing; RS with irregular distal branches; M with M1, M2, and M3+4; CUA deeply forked. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 140,7. **M. permiana*; hind wing, $\times 3.2$ (Tillyard, 1921c).

Neurobole RIEK, 1976a, p. 779 [**N. ramosa*; OD]. Little-known genus, based on small apical fragment of wing. [Family assignment doubtful.] *Perm.*, South Africa.

Orthoprosbole MARTYNOV, 1935d, p. 445 [**O. congesta*; OD]. Fore wing strongly narrowed in distal half; RS and M with numerous branches; nodal break prominent. Hind wing little known; distal part elongate; M and CUA with numerous branches. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 140,4a. **O. triangularis* (MARTYNOV); fore wing, $\times 2.5$ (Becker-Migdisova, 1962b).—FIG. 140,4b. **O. congesta*; hind wing, $\times 3.5$ (Becker-Migdisova, 1962b).

Orthoscytina TILLYARD, 1926a, p. 9 [**O. mitchelli*; OD]. Fore wing slender, oval; anal area long; RS arising just before midwing; M and CUA forked at distal third of wing; R with several oblique branches to costal margin. Hind wing little known. EVANS, 1956; RIEK, 1976a. *Perm.*, Australia (New South Wales), Africa (South Africa), USSR (Asian RSFSR).—FIG. 141,1a. **O. mitchelli*, Australia; fore wing, $\times 6$ (Tillyard, 1926a).—FIG. 141,1b. **O. suchovi* BECKER-MIGDISOVA, USSR; fore wing, $\times 6$ (Becker-Migdisova, 1961c).

Permocicada MARTYNOV, 1928b, p. 19 [**P. umbrata*; SD BECKER-MIGDISOVA, 1940, p. 29] [= *Permocicadopsis* BECKER-MIGDISOVA, 1940, p. 54 (type, *Permocicada angusta* MARTYNOV, 1935c, p. 15)]. Fore wing with weak venation; RS arising before forking of M and CUA; M with 3 or 4 branches. Hind wing with deeply indented costal margin having nearly symmetrical slopes. ZALESSKY, 1929, 1932b; EVANS, 1956; BECKER-MIGDISOVA, 1961c, 1962b. *Perm.*, USSR (European and Asian RSFSR).—FIG. 141,2. **P. integra* BECKER-MIGDISOVA; a, fore wing, $\times 4$; b, hind wing, $\times 4$; c, reconstruction, $\times 3$ (Becker-Migdisova, 1940).

Permodiphthera TILLYARD, 1926a, p. 24 [**P. robusta*; OD]. Little-known genus. Fore wing with RS unbranched; branches of M apparently strongly curved. *Perm.*, Australia (New South Wales).—FIG. 140,5. **P. robusta*; fore wing, $\times 6$ (Evans, 1956).

Pervestigia BECKER-MIGDISOVA, 1961c, p. 318 [**P.*

veteris; OD]. Hind wing: anterior margin without distal hump; M with 3 branches; CUA with narrow fork distally. *Perm.*, USSR (Asian RSFSR).—FIG. 140,8. **P. veteris*; hind wing, $\times 3$ (Becker-Migdisova, 1961c).

Prosbolomorpha RIEK, 1974c, p. 21 [**P. clara*; OD]. Fore wing as in *Austroprosbolole*, but RS not coalesced with M; M3+4 forking at its point of origin. [Probably a synonym of *Austroprosbolole*.] *Trias.*, South Africa.

Prosboloneura BECKER-MIGDISOVA, 1961c, p. 305 [**P. colorata*; OD]. Fore wing shaped as in *Sojanoneura*, but CUA more deeply forked and M with 3 branches. *Perm.*, USSR (Asian RSFSR).—FIG. 140,3. **P. kondonensis* BECKER-MIGDISOVA; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Sojanoneura MARTYNOV, 1928b, p. 22 [**S. edemskii*; SD BECKER-MIGDISOVA, 1940, p. 44]. Fore wing oval, bluntly rounded; RS arising nearer wing apex than in *Dictyoprosbole*; M with 3 or 4 branches. Hind wing little known, with only a slight bulging of the costal margin basally; M with 2 or 3 branches. MARTYNOV, 1935c; EVANS, 1956. *Perm.*, USSR (European and Asian RSFSR).—FIG. 140,9. **S. stigmata* MARTYNOV; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Family CICADOPROSBOLIDAE Evans, 1956

[Cicadoprosbolidae EVANS, 1956, p. 222]

Apparently related to Prosbolidae. Fore wing with vein M forking at midwing; RS arising before midwing; short, supplementary veins between branches of R; nodal line distinct, crossing RS remote from origin of RS and crossing M beyond its first fork. *Trias.*

Cicadoprosbole BECKER-MIGDISOVA, 1947, p. 445 [**C. sogutensis*; OD]. Fore wing oval, apex slightly asymmetrical; branches of M and CUA slightly curved and parallel. [Originally placed in the family Prosbolidae but transferred to a new family, Cicadoprosbolidae, by EVANS (1956) and later to the Tettigarctidae by BECKER-MIGDISOVA, 1962b.] *Trias.*, USSR (Kirghiz).—FIG. 142,4. **C. sogutensis*; fore wing, $\times 3.5$ (Becker-Migdisova, 1947).

Family TETTIGARCTIDAE Distant, 1905

[Tettigarctidae DISTANT, 1905, p. 280]

Fore wing with transparent membranous area; costa broadly sclerotized; apical border narrow; venation much as in *Cicadidae*; vein SC with a short, hook-shaped anterior branch

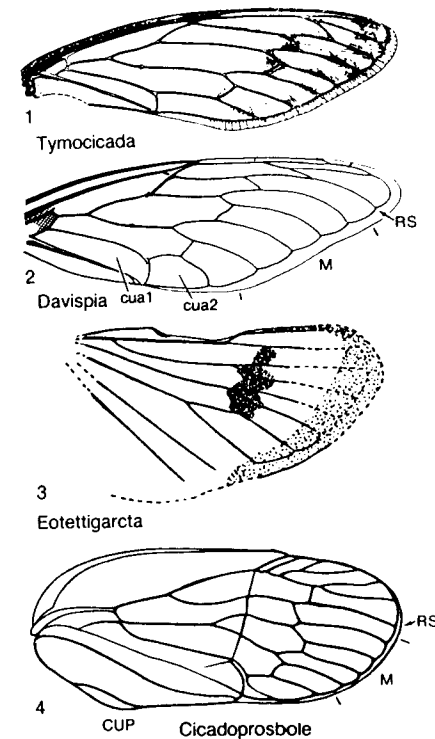


FIG. 142. Cicadoprosbolidae, Tettigarctidae, and Cicadidae (p. 221-222).

basally and a posterior branch coalesced with R+M and R. Hind wing: front margin with shallow indentation and convex area. Body structure: stridulatory organ present in both sexes. [This family is known by only one living genus, *Tettigarcta*, occurring in Australia. There is a reliable Tertiary record of the family, but the several Mesozoic genera that have been placed here are very poorly known and are assigned in this account to the category, family uncertain.] EVANS, 1956; WHALLEY, 1983. *Eoc.-Holo.*

Tettigarcta WHITE, 1845, p. 412. *Holo.*

Eotettigarcta ZEUNER, 1944a, p. 110 [**E. scotica*; OD]. Hind wing similar to that of *Tettigarcta* (recent), but indentation of costal margin much longer; origin of posterior branch of RS more remote from base of wing. Fore wing unknown.

WHALLEY, 1983. *Eoc.*, Scotland.—FIG. 142,3. **E. scotica*; hind wing, $\times 2.5$ (Zeuner, 1944a).

Family CICADIDAE Leach, 1815

[Cicadidae LEACH, 1815, p. 124]

Fore wing with costal area reduced to a narrow strip or absent; apical parts of distal forks of veins aligned to form a submarginal vein along the outer and hind margins; anal area narrow and short. Hind wing much smaller than fore wing; anterior margin smooth; submarginal vein formed as in fore wing; anal-jugal area slightly broader than in fore wing. Stridulatory organs (tymbals) present on dorsum of first abdominal segment, at least in males. [A fragmented specimen from the Eocene of France was described as *beauchampi* by Piton (1940a); this species was placed in the existing genus *Chemsitica* STÅL (= *Ribana* DISTANT). However, the fossil does not show enough structural detail for family assignment. See also *Liassocicada* under Homoptera, family Uncertain.] COOPER 1941; WHALLEY, 1983. *Paleoc.*—*Holo.*

Cicada LINNÉ, 1758, p. 434. COOPER, 1941; WHALLEY, 1983. *Oligo.*, USA (Colorado); *Mio.*, Europe (Yugoslavia, Germany)—*Holo.*

Davisia COOPER, 1941, p. 288 [**D. bearcreekensis*; OD]. Similar to *Tibicen*; cell *cua2* broad but slightly more than twice as long as wide; apical margin of cell *cua1* evenly and shallowly curving into cell *cua2*. WHALLEY, 1983. *Paleoc.*, USA (Montana).—FIG. 142,2. **D. bearcreekensis*; fore wing, $\times 1.0$ (Cooper, 1941).

Lithocicada COCKERELL, 1906c, p. 457 [**L. perita*; OD]. Similar to *Cicada*, but cubital cell of fore wing with pointed or narrowly truncate apex. COOPER, 1941. *Oligo.*, USA (Colorado).

Platypedia UHLER, 1888, p. 23. COCKERELL, 1908a; COOPER, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Tibicen LATREILLE, 1825, p. 426. SCUDDER, 1892; COOPER, 1941. *Oligo.*, USA (Colorado)—*Holo.*

Tymocicada BECKER-MIGDISOVA, 1954, p. 799 [**T. gorbunovi*; OD]. Fore wing similar to that of *Cosmopsaltivia* (recent), but CUA with longer anterior branch; cell between R and RS slightly broader. *Mio.*, USSR (Asian RSFSR).—FIG. 142,1. **T. gorbunovi*; fore wing, $\times 1.4$ (Becker-Migdisova, 1954).

Family SCYTIPTERIDAE Handlirsch, 1906b

[Scytipteridae HANDLIRSCH, 1906b, p. 391]

Fore wing regminous; costal margin commonly thickened basally; veins usually thin;

vein SC obsolescent; branches of M and CUA short; crossveins few; only a few closed cells between R, M, and CUA. Hind wing with costal margin with at most a shallow convexity at base of wing; RS unbranched; M and CUA distally branched. Body little known, apparently as in Cicadellidae. *Perm.*—*Trias.*

Scytiptera HANDLIRSCH, 1904b, p. 3 [**S. kokeni*; OD] [= *Anomascysta* MARTYNOV, 1928b, p. 34 (type, *A. reducta*); *Permocixius* MARTYNOV, 1928b, p. 36 (type, *P. kasanensis*); *Scytiptera curta* ZALESSKY, 1929, p. 28]. Fore wing with posterior branch of SC short, forming a sharp curve at level of R+M, or absent; M and CUA with distal forks, forming series of small, marginal cells, usually subequal; anal-jugal region strongly widened. Hind wing with costal margin with conspicuous but gradual convexity near base; no prominent marginal concavity or excision. Pronotum with lateral projections. [RIEK (1976b) has described a late Triassic species (*distorta*) in the genus *Scytiptera*, but there is really no evidence to justify that placement.] *Perm.*, USSR (European and Asian RSFSR).—FIG. 143,5a,b. *S. kaltanica* BECKER-MIGDISOVA; a, fore and b, hind wings, $\times 10$ (Becker-Migdisova, 1962b).—FIG. 143,5c. *S. picturata* BECKER-MIGDISOVA; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Anaprosbole BECKER-MIGDISOVA, 1960, p. 28 [**A. ivensis*; OD]. Fore wing with costal margin relatively broad basally; RS arising well beyond midwing; branches of M1+2 much longer than branches of M3+4; CUA with 3 terminal branches. [Family assignment uncertain.] *Perm.*, USSR (European RSFSR).—FIG. 143,6. **A. ivensis*; fore wing, $\times 5.0$ (Becker-Migdisova, 1960).

Anomaloscystina DAVIS, 1942, p. 112 [**A. metapteryx*; OD]. Hind wing with costal margin with distinct but gentle concavity; SC short but distinct; anal area extensive. [Family position uncertain.] *Perm.*, Australia (New South Wales).—FIG. 143,7. **A. metapteryx*; hind wing, $\times 6.5$ (Davis, 1942).

Elliptoscarta TILLYARD, 1926a, p. 16 [**E. ovalis*; OD]. Fore wing oval, with apex evenly rounded; costal area (between C and R) broad; R dichotomously forked; M with 5 branches; CUA forked. *Perm.*, Australia (New South Wales).—FIG. 143,1. **E. ovalis*; fore wing, $\times 8.2$ (Tillyard, 1926a).

Homaloscystina TILLYARD, 1926a, p. 16 [**H. plana*; OD]. Fore wing as in *Anaprosbole*, but CUA with only 2 terminal branches and connected to M by a crossvein; apex of wing bluntly rounded. EVANS, 1943b. *Trias.*, Australia (New South Wales).—FIG. 143,4. **H. plana*; fore wing, $\times 8$ (Evans, 1943b).

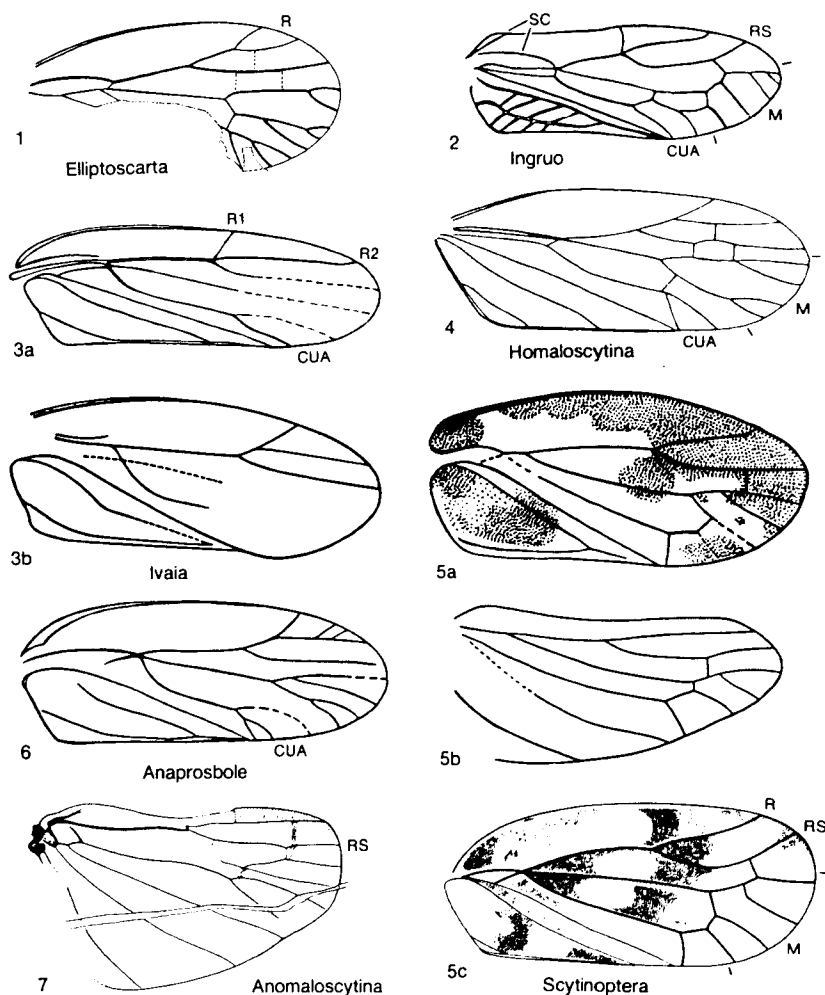


FIG. 143. Scytipteridae (p. 222–223).

Ingruo BECKER-MIGDISOVA, 1960, p. 19 [**I. lanceolata*; OD]. Fore wing very narrow; posterior branch of SC short, merging with R; CUA dividing at level of origin of RS; fork of CUA large. [Family assignment doubtful.] *Perm.*, USSR (European RSFSR).—FIG. 143,2. **I. lanceolata*; fore wing, $\times 16$ (Becker-Migdisova, 1960).

Ivaia BECKER-MIGDISOVA, 1960, p. 25 [**I. indistincta*; OD]. Fore wing moderately broad; costal area (between C and R) broad; R straight; CUA in brief contact with M, then diverging; M apparently unbranched. *Perm.*, USSR (European RSFSR).—FIG. 143,3a. *I. proacropoides* BECKER-MIGDISOVA; fore wing, $\times 6.5$ (Becker-

Migdisova, 1960).—FIG. 143,3b. **I. indistincta*; fore wing, $\times 8$ (Becker-Migdisova, 1962b). *Kaltanospes* BECKER-MIGDISOVA, 1961c, p. 344 [**K. kuznetskiensis*; OD]. Fore wing as in *Ingruo*, but CUA dividing much further distally of origin of RS. *Perm.*, USSR (Asian RSFSR).—FIG. 144,6. **K. kuznetskiensis*; fore wing and body, $\times 10$ (Becker-Migdisova, 1961c).

Mesonirvana EVANS, 1956, p. 191 [**M. abrupta*; OD]. Fore wing: R with several branches; crossvein m-cu joined to CUA1; RS unbranched. *Trias.*, Australia (Queensland).—FIG. 144,7. **M. abrupta*; fore wing, $\times 5$ (Evans, 1956).

Mesothymbris EVANS, 1956, p. 191 [**M. perkinsi*;

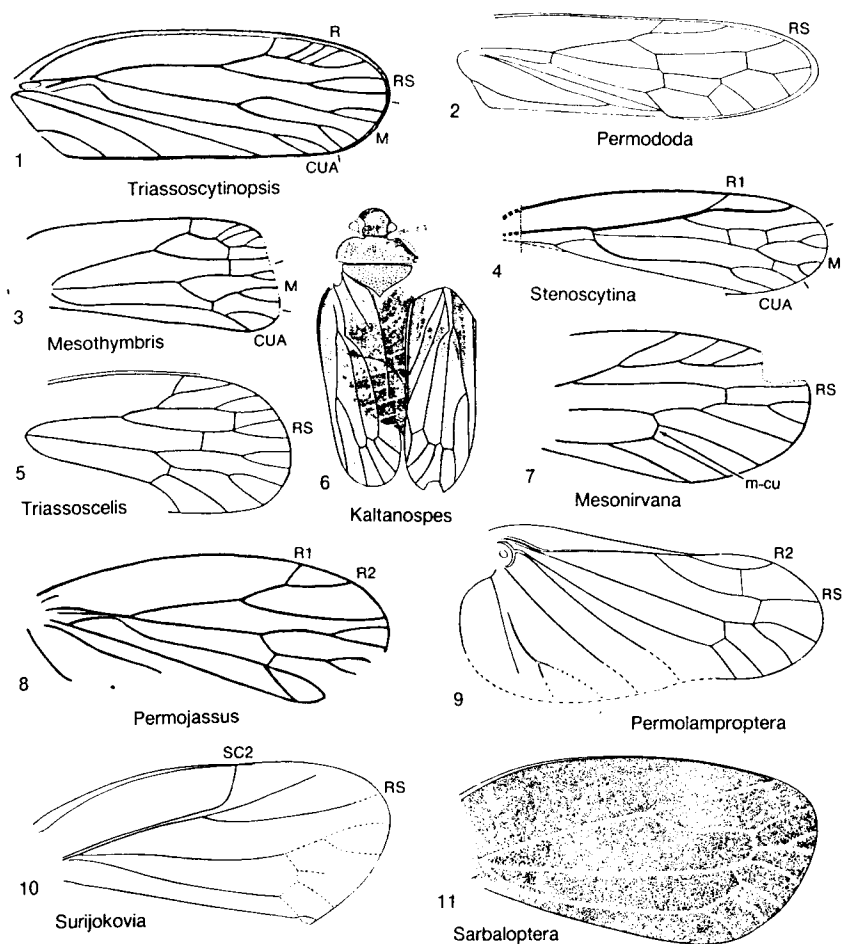


FIG. 144. Scytinopteridae (p. 223–225).

OD]. Fore wing as in *Triassoscytinopsis*, but M1+2 forming almost straight continuation of M; M3+4 bent towards CUA; crossvein m-cu joined to CUA. *Trias.*, Australia (Queensland).—FIG. 144,3. **M. perkinsi*; fore wing, X6 (Evans, 1956).

Permododa BECKER-MIGDISOVA, 1961c, p. 347 [**P. membracoides*; OD]. Fore wing very slender; several closed cells between RS and M and between M and CUA. *Perm.*, USSR (Asian RSFSR).—FIG. 144,2. **P. membracoides*; fore wing, X10 (Becker-Migdisova, 1961c).

Permojassus TILLYARD, 1926a, p. 7 [**P. australis*; OD] [= *Permojassula* HANDLIRSCH, 1937, p. 115, obj.] Fore wing similar to that of *Homaloscytina*, but anal area apparently much narrower. EVANS,

1956. *Perm.*, Australia (New South Wales).—FIG. 144,8. **P. australis*; fore wing, X8 (Evans, 1956).

Permolanproptera BECKER-MIGDISOVA, 1961c, p. 340 [**P. grandis*; OD]. Hind wing similar to that of *Scytinoptera* but with R2 curved distally; anal area extended. *Perm.*, USSR (Asian RSFSR).—FIG. 144,9. **P. grandis*; hind wing, X5.7 (Becker-Migdisova, 1961c).

Sarbaloptera BECKER-MIGDISOVA, 1961c, p. 328 [**S. sarbalensis*; OD]. Fore wing with asymmetrical apex; costal area (between C and R) very broad. *Perm.*, USSR (Asian RSFSR).—FIG. 144,11. **S. sarbalensis*; fore wing, X6.5 (Becker-Migdisova, 1961c).

Stenoscytina TILLYARD, 1926a, p. 15 [**S. aus-*

traliensis; OD]. Little-known genus. Fore wing narrow; M with 4 branches; CUA curving abruptly posteriorly after diverging from M. [Family assignment uncertain.] *Perm.*, Australia (New South Wales).—FIG. 144,4. **S. australiensis*; fore wing, X6.5 (Tillyard, 1926a).

Surijokovia BECKER-MIGDISOVA, 1961c, p. 342 [**S. lata*; OD]. Little-known fore wing; posterior branch of SC long, mostly parallel to R, then diverging anteriorly to termination on costal margin; RS apparently unbranched. *Perm.*, USSR (Asian RSFSR).—FIG. 144,10. **S. lata*; fore wing, X16 (Becker-Migdisova, 1961c).

Triassoscelis EVANS, 1956, p. 192 [**T. anomala*; OD]. Fore wing as in *Mesonirvana*, but RS forked. *Trias.*, Australia (Queensland).—FIG. 144,5. **T. anomala*; fore wing, X5 (Evans, 1956).

Triassoscytina EVANS, 1956, p. 179 [**T. incompleta*; OD]. Fore wing as in *Homaloscytina*, but M forking just beyond level of origin of RS. [Family position uncertain.] *Trias.*, Australia (Queensland).

Triassoscytinopsis EVANS, 1956, p. 190 [**T. stenulata*; OD]. Fore wing with apex evenly rounded; R with at least 4 parallel branches distally; RS with from 2 to 4 branches; M with 4 branches. *Trias.*, Australia (Queensland).—FIG. 144,1. **T. aberrans* EVANS; fore wing, X6 (Evans, 1956).

Tychoscytina BECKER-MIGDISOVA, 1952, p. 179 [**T. kuznetskiensis*; OD]. Fore wing little known, with wide costal area; R1 straight. *Perm.*, USSR (Asian RSFSR).

Family BITURRITIIDAE Metcalf, 1951

[Biturritiidae METCALF, 1951, p. 111]

Fore wing sclerotized; no marginal border; vein M unbranched; radial cell divided by a crossvein. Hind wing nearly of uniform width, with very slight concavity of costal margin. *Trias.*—*Holo.*

Biturritia GODING, 1930, p. 39. *Holo.*

Absoluta BECKER-MIGDISOVA, 1962a, p. 92 [**A. distincta*; OD]. Hind wing with base of CUA nearly or completely coalesced with stem of M. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).—FIG. 145,1. **A. distincta*; hind wing, X12 (Becker-Migdisova, 1962b).

Family CICAPELLIDAE Latreille, 1802

[Cicadellidae LATREILLE, 1802a, p. 257] [= Jassopidae HAMILTON, 1971, p. 943]

Fore wing tegminous; several to many closed cells; CUA usually with wide distal fork. Hind wing narrowed distally; submar-

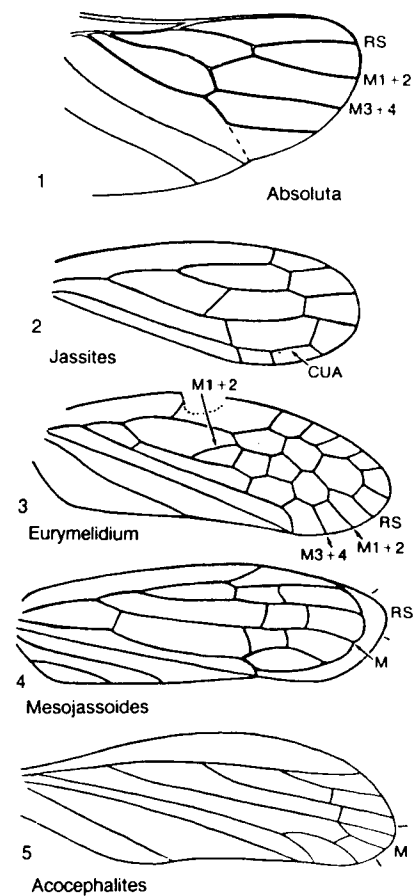


FIG. 145. Biturritiidae and Cicadellidae (p. 225–227).

ginal vein conspicuous, with relatively wide margin; ano-jugal area broad. *Trias.*—*Holo.*

Cicadella DUMÉRIE, 1806, p. 266. BIRVOULTS, 1910; COCKERELL, 1920c; BECKER-MIGDISOVA, 1951. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Baltic); *Mio.*, USSR (European RSFSR)—*Holo.*

Acocephalites MEUNIER, 1904e, p. 119 [**A. bred-dini*; OD]. Little-known genus, based on fore wing with strongly arched costal margin and a venation similar to that of *Mesojassoides*; M with distal fork. *Jur.*, Europe (Spain).—FIG. 145,5. **A. bred-dini*; fore wing, X14 (Handlirsch, 1907).

Agallia CURTIS, 1833, p. 193. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Aphrodes CURTIS, 1833, p. 193. SCUDDER, 1890;

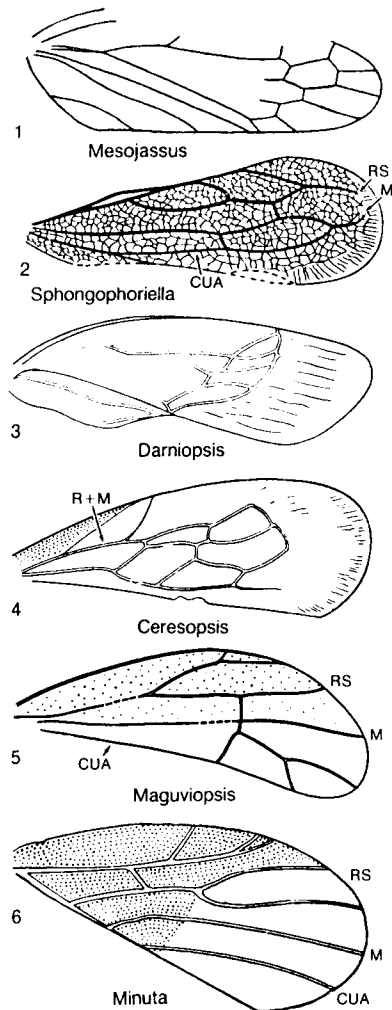


FIG. 146. Eurymelidae and Membracidae (p. 227-228).

STATZ, 1950a. *Eoc.*, USA (Wyoming); *Oligo.*-*Mio.*, Europe (Germany)-*Holo.*
Batrachomorpha LEWIS, 1834, p. 51, *nom. correct.* AGASSIZ, 1846, ex *Batrachomorpha* LEWIS, 1834. STATZ, 1950a. *Oligo.*, Europe (Germany)-*Holo.*
Cicadula ZETTERSTEDT, 1838, p. 296. SCUDDER, 1890. *Eoc.*, USA (Wyoming)-*Holo.*
Coelidia GERMAR, 1821, p. 75. SCUDDER, 1890, 1895b. *Eoc.*, USA (Wyoming), Canada (British Columbia); *Oligo.*, USA (Colorado)-*Holo.*

Deltocephalus BURMEISTER, 1838, p. 5. STATZ, 1950a. *Oligo.*, Europe (Germany)-*Holo.*
Durgades DISTANT, 1912, p. 608. BECKER-MIGDISOVA & MARTYNOVA, 1951. *Mio.*, USSR (Kirghiz)-*Holo.*
Eurymelidium TILLYARD, 1919c, p. 884 [**E. australe*; OD]. SC apparently absent; M1+2 anastomosed with part of RS. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 145, 3. **E. australe*; fore wing, $\times 10$ (EVANS, 1956).
Euscelis BRULLÉ, 1832, p. 109. STATZ, 1950a; PIERCE, 1963. *Oligo.*, Europe (Germany); *Mio.*, USA (California)-*Holo.*
Gypona GERMAR, 1821, p. 73. [Generic assignment of fossil doubtful.] SCUDDER, 1890. *Oligo.*, USA (Colorado)-*Holo.*
Gyponites STATZ, 1950a, p. 10 [**G. pronota*; OD]. Little-known cicadellid; head short and broad; ocelli large; pronotum long, with parallel sides; scutellum shorter than pronotum. *Oligo.*, Europe (Germany).
Homopterulum HANDLIRSCH, 1907, p. 641 [**Cercoptidium signoretti* WESTWOOD, 1854, p. 396; SD CARPENTER, herein]. Little-known genus, based on fore wing. [Family assignment doubtful.] EVANS, 1956. *Jur.*, England.
Idiocerus LEWIS, 1834, p. 47. STATZ, 1950a. *Oligo.*, Europe (Germany)-*Holo.*
Jascopus HAMILTON, 1971, p. 944 [**J. notabilis*; OD]. Little-known genus, based on nymph. [Type of family *Jascopidae* HAMILTON.] EVANS, 1972. *Cret.*, Canada (Manitoba).
Jassites HANDLIRSCH, 1907, p. 642 [**Cicada punctatus* BRODIE, 1845, p. 33; OD]. Little-known genus, based on fore wing. CUA with very short branches. EVANS, 1956. *Jur.*, England.—FIG. 145, 2. **J. punctatus*; fore wing, $\times 5.5$ (EVANS, 1956).
Jassopsis SCUDDER, 1890, p. 312 [**J. evidens*; OD]. Little-known genus, similar to *Thamnotettix*. Scutellum not more than half the length of thorax. *Oligo.*, USA (Colorado).
Jassus FABRICIUS, 1803, p. 85. BERVOETS, 1910; MEUNIER, 1920c; PITON, 1940a; STATZ, 1950a. *Eoc.*, Europe (France); *Oligo.*, Europe (Baltic, Germany)-*Holo.*
Lavrushinia COCKERELL, 1925g, p. 10 [**L. elegantula*; OD]. Little-known genus, based on long and narrow fore wing; marginal vein very close to wing margin. *Mio.*, USSR (Asian RSFSR).
Macropsis LEWIS, 1834, p. 49. BERVOETS, 1910; STATZ, 1950a. *Oligo.*, Europe (Baltic, Germany)-*Holo.*
Maleojassus ZEUNER, 1941a, p. 90 [**M. primitivus*; OD]. Fore wing as in *Stonasia* (recent), but RS smoothly curved, not bent at junction with M1; M almost straight. *Eoc.*, Scotland.
Megophthalmus CURTIS, 1833, p. 193. STATZ, 1950a. *Oligo.*, Europe (Germany)-*Holo.*
Mesojassoides OMAN, 1937, p. 38 [**M. gigantea*; OD]. Fore wing as in *Coelidia* but with additional crossveins; M unbranched. *Cret.*, USA (Colorado).—FIG. 145, 4. **M. gigantea*; fore wing, $\times 4.5$ (EVANS, 1956).
Miochlorotettix CARPENTER, herein [**M. gibroni* PIERCE, 1963, p. 73; OD]. Similar to *Chlorotettix* (recent), but prothorax strongly arched forward and scutellum extending back between wings about as far as forwards. The original generic name, *Miochlorotettix*, was a *nomen nudum* (PIERCE, 1963).] *Mio.*, USA (California).
Miomesamia PIERCE, 1963, p. 81 [**M. juliae*; OD]. Similar to *Ulope* (recent). Face wide, eyes prominent; antennae at sides of front sutures, opposite outer corners of eyes. *Mio.*, USA (California).
Oligogypona STATZ, 1950a, p. 8 [**O. haupti*; OD]. Similar to *Gypona*, but head broad, somewhat narrower than pronotum; costal margin of fore wing strongly arched. *Oligo.*, Europe (Germany).
Oligoidiocerus STATZ, 1950a, p. 15 [**O. pronotumalis*; OD]. Similar to *Idiocerus* but with richer venation and unmarked fore wing. *Oligo.*, Europe (Germany).
Oligopenthimia STATZ, 1950a, p. 9 [**O. ovalis*; OD]. Similar to *Penthimia* (recent). Head short, as wide as pronotum; scutellum long, reaching to the middle of the abdomen. *Oligo.*, Europe (Germany).
Phlepsius FIEBER, 1866, p. 503. PIERCE, 1963. *Mio.*, USA (California)-*Holo.*
Protochlorotettix PIERCE, 1963, p. 78 [**P. calico*; OD]. Similar to *Chlorotettix* (recent), but with last sternum completely divided. *Mio.*, USA (California).
Tetignia BLANCHARD, 1852, p. 282. STATZ, 1950a. *Oligo.*, Europe (Germany)-*Holo.*
Tettigella CHINA & FENNAH, 1945, p. 711. SCUDDER, 1890; STATZ, 1950a. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado), Europe (Germany)-*Holo.*
Thamnotettix ZETTERSTEDT, 1838, p. 292. COCKERELL, 1920c, 1924a, 1925a; STATZ, 1950a. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany); *Mio.*, USA (Colorado)-*Holo.*
Typhlocyba GERMAR, 1833, p. 180. GERMAR & BERENDT, 1856. *Oligo.*, Europe (Baltic)-*Holo.*

Family EURYMELIDAE Amyot & Serville, 1843

[Eurymelidae AMYOT & SERVILLE, 1843, p. 554]

Fore wing hyaline or opaque and coriaceous; venation often reticulate; vein RS absent; M1+2 retained as separate vein, extending to apex; M3+4 usually unbranched; CUA forked. *Trias.*-*Holo.*

Eurymela LE PELETIER & SERVILLE, 1828, p. 603. *Holo.*
Mesojassus TILLYARD in TILLYARD & DUNSTAN, 1916,

p. 34 [**M. ipsviciensis*; OD]. Little-known genus, based on fore wing. Fork of CUA marginal, very shallow. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 146, 1. **M. ipsviciensis*; fore wing, $\times 8.4$ (EVANS, 1956).

Family MEMBRACIDAE Rafinesque, 1815

[Membracidae RAFINESQUE, 1815, p. 121]

Fore wing usually membranous, except for basal region; clavus distinct, claval suture along vein 1A; ends of veins usually forming a scalloped submarginal line, the terminal marginal membrane (limbus) extending beyond the veins; veins usually clear and marked by punctures; M either free basally or coalesced in part with stem of R or CUA; cells usually irregular; venation highly diverse. Hind wing well developed, but usually shorter than fore wing; limbus usually present; venation usually similar to that of fore wing. Pronotum extensively developed, often prolonged posteriorly and concealing the scutellum, the wings, and even the entire abdomen; antennae minute, bristlelike; tarsi with 3 segments. *Trias.*-*Holo.*

This is a very large and diversified family. Fossil forms, which are usually known only from wings, are often difficult to classify because of the variability in the venation, especially that of the fore wings. Much difference of opinion exists among specialists in Homoptera about the generic lines. The taxonomic groups used here are essentially those employed in the *General Catalogue of the Homoptera* (METCALF & WADE, 1966).

Membracis FABRICIUS, 1775, p. 675. *Holo.*
Ceresopsis BECKER-MIGDISOVA, 1958, p. 66 [**C. costalis*; OD]. Fore wing broader than in *Darniopsis*, with conspicuous sclerotized area between costal margin and R+M basally; 3 apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146, 4. **C. costalis*; fore wing, $\times 10$ (BECKER-MIGDISOVA, 1958).
Darniopsis BECKER-MIGDISOVA, 1958, p. 65. [**D. tragopea*; OD]. Fore wing elongate, with very wide limbus; costal margin only slightly convex; 4 apical cells; M and CUA with common stem; anal area large, triangular. *Trias.*, USSR (Kirghiz).—FIG. 146, 3. **D. tragopea*; fore wing, $\times 10$ (BECKER-MIGDISOVA, 1958).
Maguviopsis BECKER-MIGDISOVA, 1953c, p. 463 [**M. kotchnevi*; OD]. Fore wing with costal-

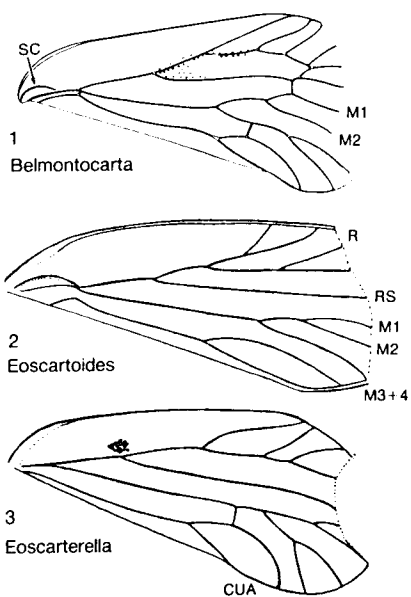


FIG. 147. Eoscarterellidae (p. 228).

distal margin broadly curved; anterior half of wing sclerotized; R and M not coalesced with CUA; M unbranched, straight. *Jur.*, USSR (Asian RSFSR).—FIG. 146.5. **M. kotchnevi*; fore wing, $\times 16$ (Becker-Migdisova, 1953c).

Minuta BECKER-MIGDISOVA, 1958, p. 64 [**M. heteropterata*; OD]. Little-known genus; fore wing short, sclerotized from midwing to front margin; R, M, and CUA merged with CUP basally; CUA long; no apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146.6. **M. heteropterata*; fore wing, $\times 20$ (Becker-Migdisova, 1958).

Sphongophoriella BECKER-MIGDISOVA, 1958, p. 63 [**S. reticulata*; OD]. Fore wing elongate, reticulate; M and CUA not coalesced to form a common stem; venation reduced; cells elongate-oval; anal area narrow, 3 apical cells. *Trias.*, USSR (Kirghiz).—FIG. 146.2. **S. reticulata*; fore wing, $\times 34$ (Becker-Migdisova, 1958).

Family AETALIONIDAE Spinola, 1850

[Aetalionidae SPINOLA, 1850, p. 53]

Similar to Cicadellidae; fore wing with vein RS absent; M1+2 (or M1 and M2) extending to apex of wing; M3+4 usually forked; CUA unbranched. Hind wing with RS absent. *Oligo.-Holo.*

Aetalion LATREILLE, 1810, p. 263. STATZ, 1950a. *Oligo.*, Europe (Germany)—*Holo.*

Family EOSCARTERELLIDAE Evans, 1956

[Eoscarterellidae EVANS, 1956, p. 220]

Fore wing with vein RS arising from R about one-third wing length from base; R with at least 2 branches; CUA separate from M. *Perm.-Trias.*

Eoscarterella EVANS, 1956, p. 220 [**E. media*; OD] [= *Probolopsites* BECKER-MIGDISOVA, 1960, p. 90 (type, *P. tillyardi*)]. Fore wing tegminous and rugose, broadest in distal half; RS and M parallel for most of their lengths; M with 4 branches. EVANS, 1961. *Trias.*, Australia (Queensland).—FIG. 147.3. **E. media*; fore wing, $\times 5.5$ (Evans, 1956).

Belmontocarta EVANS, 1958, p. 112 [**B. perfecta*; OD]. Fore wing with SC very short, curving distally towards R+M; M1 and M2 longer than M3 and M4; CUA curved and joined to base of M by short crossvein. *Perm.*, Australia (New South Wales).—FIG. 147.1. **B. perfecta*; fore wing, $\times 4.5$ (Evans, 1958).

Eoscartoides EVANS, 1956, p. 220 [**E. bryani*; OD]. Fore wing with complete marginal border; R and M arched basally; M1+2 forked. EVANS, 1961. *Trias.*, Australia (Queensland).—FIG. 147.2. **E. bryani*; fore wing, $\times 4.5$ (Evans, 1961).

Family PROCERCOPIDAE Handlirsch, 1906

[Procercopidae HANDLIRSCH, 1906b, p. 500]

Fore wing slender, at least three times as long as wide; vein RS arising in basal third of wing; M and CUA branching in distal third of wing, their branches short. Hind wing very little known. EVANS, 1956. *Trias.-Jur.*

Procercopis HANDLIRSCH, 1906b, p. 500 [**P. alutacea*; SD BECKER-MIGDISOVA, 1962b, p. 180]. Fore wing elongate, about 4 times as long as broad; M with at least 3 branches; several crossveins in distal part of wing. *Trias.*, USSR (Kirghiz); *Jur.*, Europe (Germany).—FIG. 148.3. *P. longipennis* BECKER-MIGDISOVA, *Trias.*; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Procercopina MARTYNOV, 1937a, p. 99 [**P. asiatica*; OD]. Fore wing as in *Procercopis* but relatively broader; only one crossvein between adjacent veins. EVANS, 1956. *Jur.*, USSR (Kirghiz).—FIG. 148.5. **P. asiatica*; fore wing, $\times 4.6$ (Becker-Migdisova, 1962b).

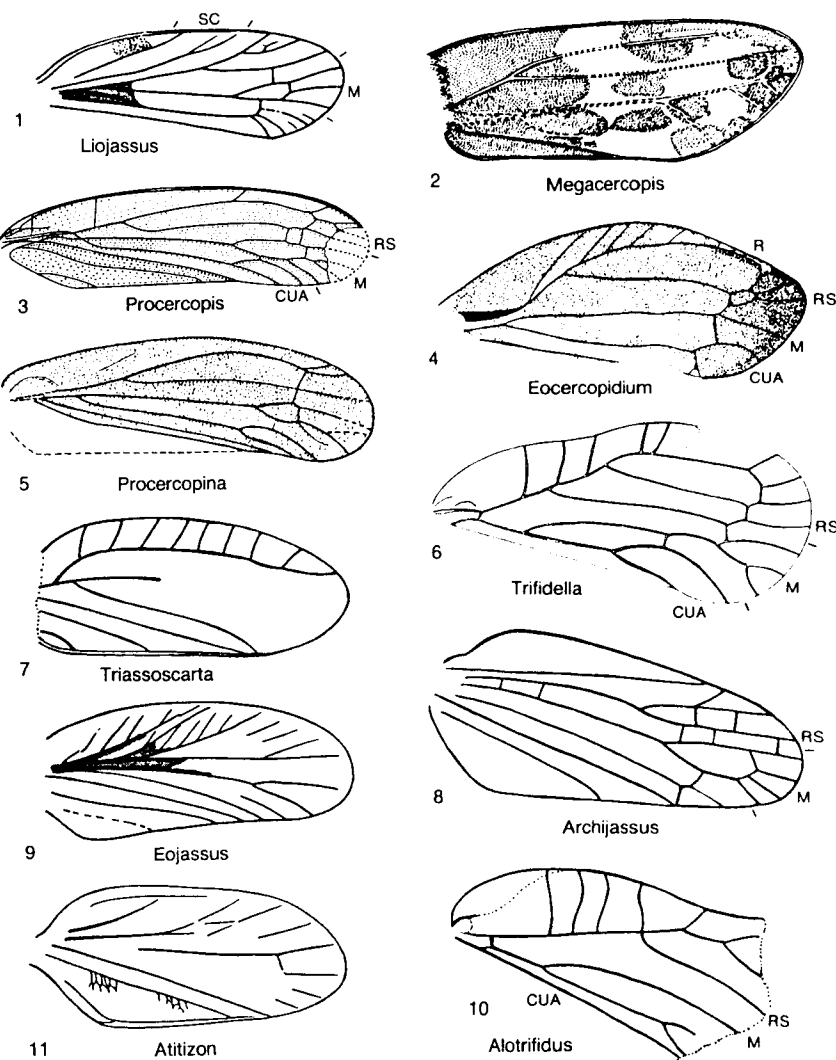


FIG. 148. Procercopidae, Cercopidae, and Archijassidae (p. 228–233).

Family DYSMORPHOPTILIDAE Handlirsch, 1906

[Dysmorphoptilidae HANDLIRSCH, 1906b, p. 492]

Tegmen of irregular form, abruptly narrowed distally, strongly sclerotized; vein SC apparently fused with R; several short

branches from R to costal margin; RS arising before midwing. EVANS, 1956. *Trias.-Jur.*

Dysmorphoptila HANDLIRSCH, 1906b, p. 492 [**Belostoma liasina* GÜBEL, 1856, p. 371; OD]. Broad portion of tegmen extending only to about midwing; M with only one distal fork. EVANS, 1956. *Jur.*, Europe (Germany).

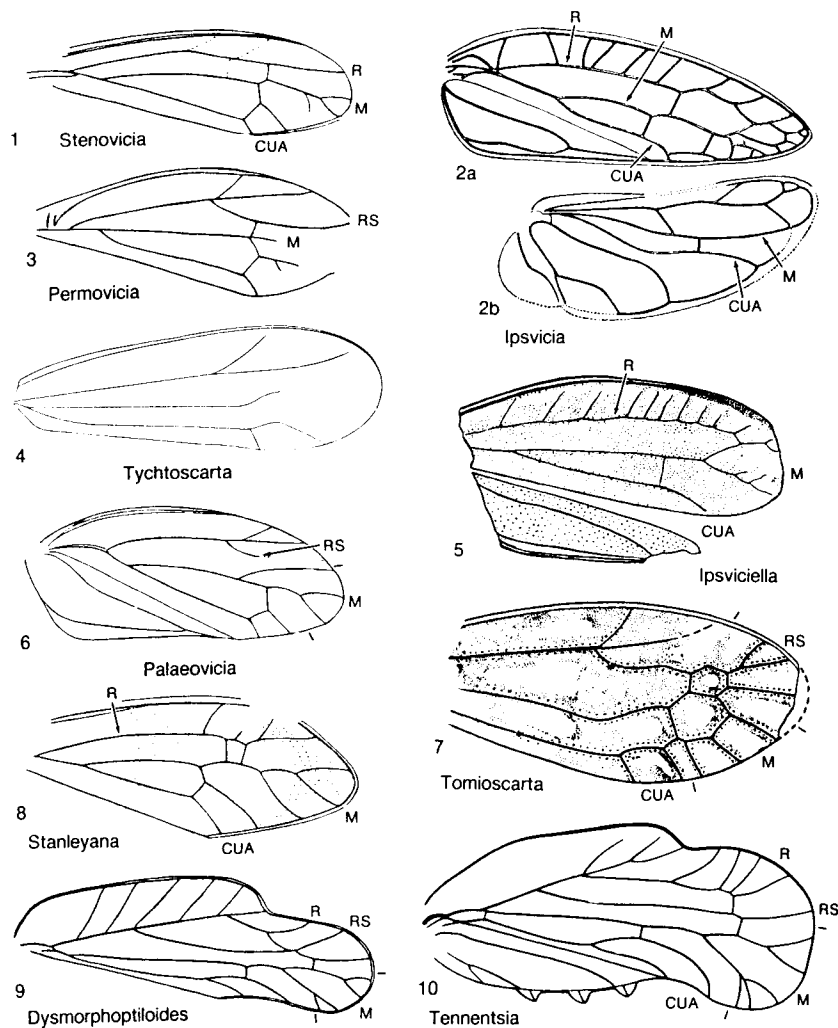


FIG. 149. Dymorphoptilidae and Ipsiviidae (p. 230–233).

Dymorphoptiloides EVANS, 1956, p. 218 [**D. elongata*, OD]. Tegmen as in *Dymorphoptila*, but broad portion extending nearer to apex; M with 2 distal forks. RIEK, 1974b. *Trias.*, Australia (Queensland), South Africa.—FIG. 149, 9. **D. elongata*; tegmen, $\times 3.4$ (Evans, 1956).

Mesoatraxis BECKER-MIGDISOVA, 1949b, p. 40 [**M. reducta*, OD]. Tegmen as in *Dymorphoptiloides* but with shorter distal area; M with 3 terminal

branches. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Tadzhik).

Tennentsia RIEK, 1976b, p. 813 [**Dymorphoptiloides protuberans* RIEK, 1974c, p. 22; OD]. Fore wing similar to that of *Dymorphoptiloides*, but SC with several distal branches and RS unbranched; M and CU apparently connected basally by a crossvein. *Trias.*, South Africa.—FIG. 149, 10. **T. protuberans*; fore wing, $\times 2.3$ (Riek, 1976b).

Family CERCOPIIDAE Westwood, 1838

[Cercopidae WESTWOOD, 1838, p. 39]

Head narrower than pronotum, usually as wide as anterior margin of scutellum; ocelli on disc of crown, each at posterior end of sulcus; length and width of eyes almost equal; antennae originating in cavities below anterior margin of head; postclypeus commonly protuberant. Fore wings usually coriaceous. [The Aphrophoridae are included here, as a subfamily, because of the difficulty of recognizing the distinguishing features in the fossils.] EVANS, 1956. *Trias.*—*Holo.*

Cercopis FABRICIUS, 1775, p. 688. [Numerous extinct species from Tertiary deposits and described before 1900 were placed in the genus, but their assignment to *Cercopis* has not been generally accepted (see HANDLIRSCH, 1907, p. 1072–1074). However, a few, well-preserved specimens appear to justify at least tentative placement in the genus.] SCUDDER, 1890; COCKERELL, 1920a, 1927b; EVANS, 1956. *Eoc.*, Canada (British Columbia), USA (Colorado, Wyoming), USSR (Asian RSFSR)—*Holo.*

Alotrifidus EVANS, 1956, p. 216 [**A. interruptus*, OD]. Fore wing as in *Trifidella*, but costal margin arching basally and RS arising further distally. *Trias.*, Australia (Queensland).—FIG. 148, 10. **A. interruptus*; fore wing, $\times 10$ (Evans, 1956).

Aphrophora GERMAR, 1821, p. 48. COCKERELL, 1922f, 1925g; PONGRÁČ, 1928; PITON, 1936c; THÉOBALD, 1937a; BECKER-MIGDISOVA, 1964. *Eoc.*, Europe (Baltic, France), Canada (British Columbia); *Oligo.*, England, Europe (France); *Mio.*, USSR (Asian RSFSR)—*Holo.*

Cercopites SCUDDER, 1890, p. 316 [**C. calliscens* SCUDDER, 1890, p. 316; SD CARPENTER, herein]. Head relatively small; thorax hexagonal; fore wing more than twice as long as broad. *Eoc.*, USA (Wyoming), Canada (British Columbia).

Clastoptera GERMAR, 1839, p. 187. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*

Dawsonites SCUDDER, 1895b, p. 18 [**D. veter.*, OD]. Similar to *Palecphora*, but RS arising at midwing. *Mio.*, Canada (British Columbia).

Eocercopidium ZEUNER, 1944a, p. 116, *nom. subst. pro Eocercopis* ZEUNER, 1941a, p. 88, *non* HANDLIRSCH, 1939 [**Eocercopis maculata* ZEUNER, 1941a, p. 88; OD]. Fore wing similar to that of *Aphrophora*, but R strongly bent anteriorly near base; preradial part of wing very wide, crossed by pectinate branches from R; radial-median area very broad; M separating from CUA very near to base. *Eoc.*, Scotland.—FIG. 148, 4. **E.*

maculata (ZEUNER); fore wing, $\times 6.4$ (Zeuner, 1944a).

Megacercopis COCKERELL, 1925g, p. 9 [**M. optima*, OD]. Little-known fore wing with venation similar to that of *Stenecphora*, but apex much more pointed. *Mio.*, USSR (Asian RSFSR).—FIG. 148, 2. **M. optima*; fore wing, $\times 2.5$ (Cockerell, 1925g).

Palaeoptysma SCUDDER, 1895b, p. 21 [**P. venosa*, OD]. Little-known fore wing, related to *Aphrophora* but very slender. *Eoc.*, Canada (British Columbia).

Palaphrodes SCUDDER, 1890, p. 333 [**P. irregularis* SCUDDER, 1890, p. 333; SD CARPENTER, herein]. Fore wing as in *Cercopis*, but head very obtuse and rounded in front, narrower distally than thorax. COCKERELL, 1908k. *Oligo.*, USA (Colorado).

Palecphora SCUDDER, 1890, p. 324 [**P. communis* SCUDDER, 1890, p. 324; SD CARPENTER, herein]. Fore wing longer and more slender than that of *Palaphrodes*; costal margin less arched. COCKERELL, 1908k. *Oligo.*, USA (Colorado).

Petrolystra SCUDDER, 1878a, p. 530 [**P. gigantea* SCUDDER, 1878a, p. 530; SD CARPENTER, herein]. Large insects; head large, flat dorsally, twice as broad as long, the front broadly convex; scutellum very small, about half as long as thorax. SCUDDER, 1890. *Oligo.*, USA (Colorado).

Philagra STÅL, 1863, p. 593. COCKERELL, 1925g. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Ptyelus LE PLETIER & SERVILLE, 1828, p. 608. THÉOBALD, 1937a. *Oligo.*, Europe (France)—*Holo.*

Prysmaphora SCUDDER, 1895b, p. 21 [**P. fletcheri*, OD]. Fore wing as in *Palaeoptysma* but with costal margin straighter. *Eoc.*, Canada (British Columbia).

Sinophora MELICHAIR, 1902, p. 113 [**S. maculosa*, OD]. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Stenecphora SCUDDER, 1895b, p. 17 [**S. punctulata*, OD]. Fore wing with very broad apex, slender clavus; RS arising near base. *Eoc.*, Canada (British Columbia).

Stenolocris SCUDDER, 1895b, p. 19 [**S. venosa*, OD]. Little-known fore wing, with very strong costal vein and RS arising at wing base. [Family assignment doubtful.] *Mio.*, Canada (British Columbia).

Triassoscarta TILLYARD, 1919c, p. 874 [**T. subcostalis*, OD]. Little-known genus, based on incomplete tegmen. SC apparently absent; R long, nearly parallel with costal margin and connected to costal margin by about 8 subequal crossveins. [Originally placed in the *Scytinopteridae* but transferred to *Cercopidae* by EVANS (1956).] *Trias.*, Australia (Queensland).—FIG. 148, 7. **T. subcostalis*; fore wing, $\times 6$ (Evans, 1956).

Triecphora AMYOT & SERVILLE, 1843, p. 561. WOODWARD, 1879. *Eoc.*, England—*Holo.*

Trifidella EVANS, 1956, p. 215 [**T. perfecta*; OD]. Fore wing tegminous, coarsely rugose; several long veinlets between wing margin and R; M and CUA fused basally; CUA forked. *Trias.*, Australia (Queensland).—FIG. 148,6. **T. perfecta*; fore wing, $\times 10$ (Evans, 1961).

Family IPSVICIIDAE Tillyard, 1919

[Ipsviciidae TILLYARD, 1919c, p. 878] [=Stenovicidae EVANS, 1956, p. 205]

Fore wing uniformly sclerotized; costal margin thick and flattened; vein R consisting usually of R and less commonly of RS; R joined to M by a prominent crossvein; M and CUA usually arising from a common basal stem; M typically branched; CUA and CUP apparently unbranched. Hind wing (known only in *Ipsvicia*) strongly curved anteriorly in distal area; CUA branched. Body unknown. *Perm.*—*Trias.*

The systematic position of this family is obscure. TILLYARD (1919c) originally assigned it to the Homoptera, close to the extinct family Syntonopteridae, but later (1926d) transferred it to the Fulgoroidea of the Homoptera. Subsequently, it has been placed in the Heteroptera by EVANS (1956), in the Homoptera (Auchenorrhyncha) by BECKER-MIGDISOVA (1962b), in the Homoptera (Peloridioidea) by CHINA (1962), and in the Homoptera (Cercopoidea) by EVANS (1963). Also, eight of the genera discussed below (*Stenovicia*, *Permocentrus*, *Permagra*, *Pernomia*, *Stanleyana*, *Palaeovicia*, *Apheloscyta*, and *Permoscarta*) were placed in a new family, Stenovicidae, by EVANS (1956), although most of these were previously assigned to the Ipsviciidae (EVANS, 1943b). BECKER-MIGDISOVA (1962b) concluded that the new family is unnecessary, and I have followed her treatment in retaining these genera in the Ipsviciidae.

Ipsvicia TILLYARD, 1919c, p. 878 [**I. jonesi*; OD]. R with several anterior branches to costa near middle of tegmen. TILLYARD, 1923b. *Trias.*, Australia (Queensland).—FIG. 149,2. **I. jonesi*; a, tegmen; b, hind wing, $\times 4$ (Evans, 1956).

Apheloscyta TILLYARD, 1922b, p. 458 [**A. meso-campa*; OD]. Branches of all veins of tegmen very short. [Family assignment doubtful.] EVANS,

1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Ipsviciella BECKER-MIGDISOVA, 1962a, p. 100 [**I. asiatica*; OD]. Tegmen with rounded apex; R nearly straight, with several parallel branches to costal margin; CUA unbranched, merging with M basally. *Trias.*, USSR (Kirghiz).—FIG. 149,5. **I. asiatica*; tegmen, $\times 6.5$ (Becker-Migdisova, 1962b).

Ipsviciopsis TILLYARD, 1922b, p. 464 [**I. elegans*; OD]. RS separating from R near base of tegmen. EVANS, 1963. *Trias.*, Australia (Queensland).

Palaeovicia EVANS, 1943b, p. 189 [**P. incerta*; OD]. Tegmen: RS short; M with 3 branches. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).—FIG. 149,6. **P. incerta*; tegmen, $\times 8$ (Evans, 1943b).

Permagra EVANS, 1943a, p. 7 [**P. distincta*; OD]. Tegmen as in *Tomioscarta* but lacking closed cells. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Permocentrus EVANS, 1956, p. 207 [**Permoscarta trivenulata* TILLYARD, 1926a, p. 19; OD]. Tegmen with M and CUA independent basally. BECKER-MIGDISOVA, 1962b. *Perm.*, Australia (New South Wales).

Permoscarta TILLYARD, 1918b, p. 726 [**P. mitchelli*; OD]. Little-known genus. Tegmen as in *Permocentrus* but with 2 crossveins between M and CUA. EVANS, 1943a, 1956; BECKER-MIGDISOVA, 1962b. *Trias.*, Australia (Queensland).

Permovicia EVANS, 1943b, p. 189 [**P. obscura*; OD]. Tegmen with RS broadly curved. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 149,3. **P. obscura*; $\times 10$ (Evans, 1943b).

Stanleyana EVANS, 1943b, p. 188 [**S. pulchra*; OD]. Tegmen with RS apparently absent; M and CUA coalesced basally; M with 3 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 149,8. **S. pulchra*; tegmen, $\times 6.5$ (Evans, 1943b).

Stenovicia EVANS, 1943b, p. 188 [**S. angustata*; OD]. Tegmen as in *Ipsvicia* but much more slender; R long, arising at about midwing; M with 2 very short branches; CUA and M coalesced basally. [Type of family Stenovicidae EVANS, 1956.] *Perm.*, Australia (New South Wales).—FIG. 149,1. **S. angustata*; fore wing, $\times 8$ (Evans, 1943b).

Tomioscarta BECKER-MIGDISOVA, 1961c, p. 350 [**T. surijokovensis*; OD]. Tegmen with R branched at point of origin of RS; several closed cells between M, CUA, and RS. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 149,7. **T. surijokovensis*; fore wing, $\times 6.5$ (Becker-Migdisova, 1961c).

Tychoscarta BECKER-MIGDISOVA, 1961c, p. 350 [**T. sokolovensis*; OD]. Little-known genus.

Tegmen long and narrow; RS unbranched and continuing in a straight line from stem of R; M unbranched; CUA forked distally. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 149,4. **T. sokolovensis*; fore wing, $\times 8$ (Becker-Migdisova, 1961c).

Family ARCHIJASSIDAE Becker-Migdisova, 1962

[Archijassidae BECKER-MIGDISOVA, 1962a, p. 95]

Fore wing very wide, in some species with triangular costal area traversed by vein SC; SC usually divided into 2 long branches; RS present; numerous crossveins between branches of R and M; anal area wide, triangular. *Jur.*

Archijassus HANDLIRSCH, 1906b, p. 501 [**Cercopidium heeri* GEINITZ, 1880, p. 529; SD CARPENTER, herein]. Fore wing with costal margin strongly angular; RS arising beyond midwing; M with 4 branches. EVANS, 1956. *Jur.*, Europe (Germany).—FIG. 148,8. **A. heeri* (GEINITZ); fore wing, $\times 8$ (Evans, 1956).

Atitizon HANDLIRSCH, 1939, p. 144 [**A. jassoides*; OD]. Fore wing very broad; costal margin strongly curved but not angular basally; RS arising at midwing. *Jur.*, Europe (Germany).—FIG. 148,11. **A. jassoides*; fore wing, $\times 8$ (Handlirsch, 1939).

Eojassus HANDLIRSCH, 1939, p. 145 [**E. indistinctus*; OD]. Little-known genus, based on fore wing; costal margin smoothly curved. *Jur.*, Europe (Germany).—FIG. 148,9. **E. indistinctus*; fore wing, $\times 6.5$ (Handlirsch, 1939).

Liojassus HANDLIRSCH, 1939, p. 146 [**L. affinis*; OD]. Fore wing: SC with 2 long branches; RS arising at midwing; costal margin smoothly curved; M with 3 branches. [Family assignment doubtful.] *Jur.*, Europe (Germany).—FIG. 148,1. **L. affinis*; fore wing, $\times 6.5$ (Handlirsch, 1939).

Family HYLICELIDAE Evans, 1956

[Hylcellidae EVANS, 1956, p. 195]

Fore wing as in Hylcellidae (recent), with M coalesced basally with CUA, but CUA1 present and coalesced with part of M3+4 distally. *Trias.*

Hylcella EVANS, 1956, p. 195 [**H. colorata*; OD] [=Hylcellites BECKER-MIGDISOVA, 1962a, p. 95, (type, *Hylcella reducta* EVANS)]. CUA with abrupt basal bend; 2 crossveins between RS and M1+2; 1 crossvein between M1+2 and M3+4. *Trias.*, Australia (Queensland).—FIG. 150,6. **H. colorata*; fore wing, $\times 5$ (Evans, 1956).

Family MUNDIDAE Becker-Migdisova, 1960

[Mundidae BECKER-MIGDISOVA, 1960, p. 31]

Fore wing weakly tegminous, without pits; veins thick; RS, M, and CUA with prominent projections; costal area and anal area broad. *Perm.*

Mundus BECKER-MIGDISOVA, 1960, p. 31 [**M. nodosus*; OD]. Fore wing relatively broad, with asymmetrical, blunt apex; R diverging abruptly at midwing toward costal margin, forking; R2 parallel to RS. *Perm.*, USSR (European RSFSR).—FIG. 150,5. **M. nodosus*; fore wing, $\times 8$ (Becker-Migdisova, 1960).

Family PEREBORIIDAE Zalesky, 1930

[nom. correct. BRUES, MELANDER, & CARPENTER, 1954, p. 813 (pro Pereboridae ZALESKY, 1930, p. 1026)] [=Permoglyphidae EVANS, 1943b, p. 183]

Fore wing membranous; veins R, RS, and CUA with extensive branching. BECKER-MIGDISOVA, 1962b. *Perm.*—*Trias.*

Pereboria ZALESKY, 1930, p. 1021 [**P. bella*; OD]. Little-known genus, based on fore wing. R with close pectinate branching; crossveins numerous, irregular; wing large, about 40 mm long. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).—FIG. 150,9. **P. bella*; fore wing, $\times 1.5$ (Becker-Migdisova, 1962b).

Crosbella EVANS, 1956, p. 192 [**C. elongata*; OD]. Fore wing as in *Permobrachus*, but M more extensively branched. *Trias.*, Australia (Queensland).—FIG. 150,1. **C. elongata*; fore wing, $\times 4.5$ (Evans, 1956).

Kaltanopibrocha BECKER-MIGDISOVA, 1961c, p. 357 [**K. boreoscytinoides*; OD]. Little-known genus, based on hind wing fragment. Costal margin almost straight; R directed posteriorly in apical region, pectinately branched; M forking before RS. [Family assignment doubtful.] *Perm.*, USSR (Asian RSFSR).—FIG. 150,10. **K. boreoscytinoides*; hind wing, $\times 4.5$ (Becker-Migdisova, 1961c).

Neuropibrocha BECKER-MIGDISOVA, 1961c, p. 356 [**N. ramisubcostalis*; OD]. Fore wing as in *Pereboria*, but R with fewer pectinate branches and less dense reticulation of branches of RS, M, and CUA; area between stems R and M with few crossveins. *Perm.*, USSR (Asian RSFSR).—FIG. 150,7. **N. ramisubcostalis*; fore wing, $\times 2.0$ (Becker-Migdisova, 1961c).

Permobrachus EVANS, 1943b, p. 183 [**Permodiptera dubia* TILLYARD, 1926a, p. 24; OD]. Fore wing shaped as in *Scytophura*, but R1 curv-

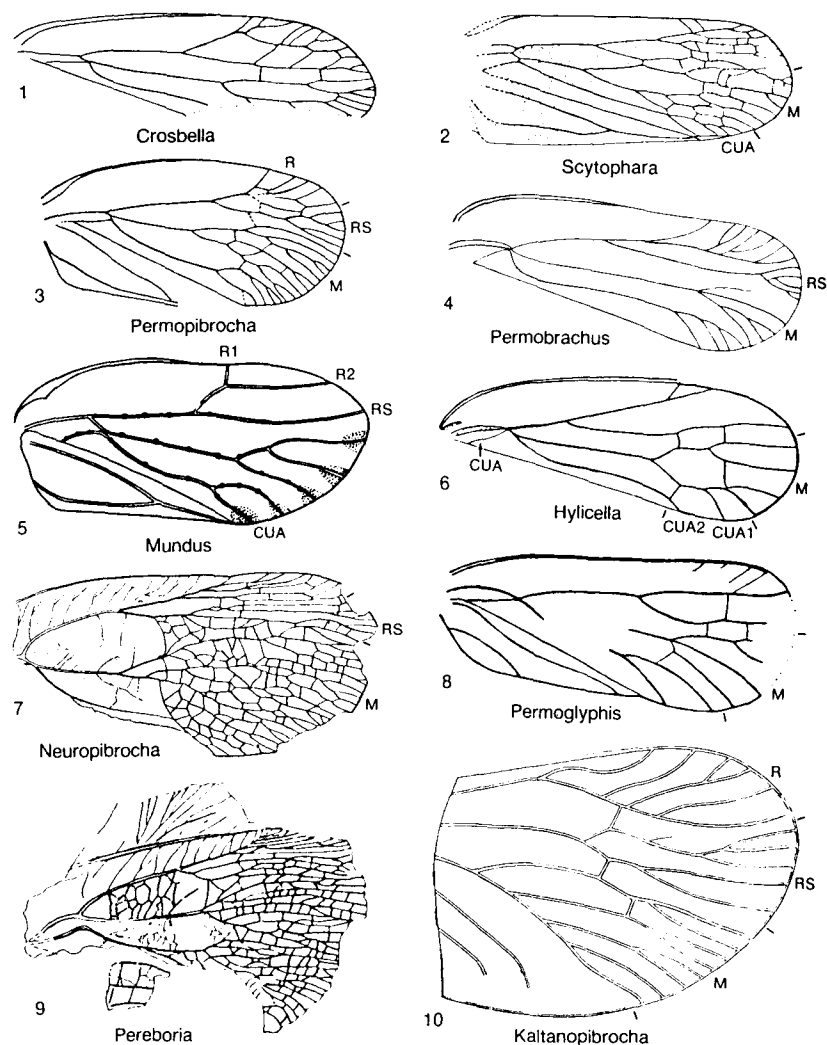


FIG. 150. Hylcellidae, Mundidae, and Pereboriidae (p. 233–235).

ing abruptly to anterior margin; branching of R2 pectinate; M branching well beyond midwing. *Perm.*, Australia (New South Wales).—FIG. 150.4. *P. magnus* EVANS; fore wing, $\times 3.5$ (EVANS, 1943b).

Permoglyphis TILLYARD, 1926a, p. 22 [**P. belmontensis*; OD]. Little-known genus, based on fore wing; similar to *Permopibrocha* but apparently with less branching of R, RS, and M; costal margin nearly straight. *Trias.*, Australia (New

South Wales).—FIG. 150.8. **P. belmontensis*; fore wing, $\times 4.5$ (EVANS, 1956).

Permopibrocha MARTYNOV, 1935c, p. 18 [**P. ramosa*; OD]. Fore wing as in *Pereboria*, but R with fewer branches; M more deeply forked than CUA; fore wing small. *Perm.*, USSR (European RSFSR).—FIG. 150.3. **P. ramosa*; fore wing, $\times 3.5$ (MARTYNOV, 1935c).

Scytophara MARTYNOV, 1937b, p. 36 [**S. extensa*; OD]. Fore wing more slender than in *Permopi-*

brocha; costal margin straight beyond base; M forking at about level of origin of RS. *Perm.*, USSR (European RSFSR).—FIG. 150.2. **S. extensa*; fore wing, $\times 6.5$ (MARTYNOV, 1937b).

Family FULGORIDIIDAE Handlirsch, 1939

[*nom. transl.* BECKER-MIGDISOVA, 1962b, p. 184, ex Fulgoridiidae HANDLIRSCH, 1939, p. 122]

Fore wing tegminous; costal margin only slightly arched; vein SC long, without branches; RS arising at about midwing; CUA forking well before origin of RS; crossveins few. Hind wing a little shorter than fore wing; anal area very broad; RS simple or with short fork; 1A arched away from CUP. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*

Fulgoridium HANDLIRSCH, 1906b, p. 496 [**Phryganidium balticum* GEINITZ, 1880, p. 527; OD] [= *Fulgoridulum* HANDLIRSCH, 1939, p. 140 (type, *F. agens*)]. Fore wing slender; usually with maculations; SC close to margin; R with a series of short branches distally; CUA with several long branches. BODE, 1953; EVANS, 1956. *Jur.*, Europe (Germany).—FIG. 151.2a. *F. punctatum* HANDLIRSCH; fore wing, $\times 10$ (HANDLIRSCH, 1939).—FIG. 151.2b. *F. reductum* HANDLIRSCH; hind wing, $\times 10$ (HANDLIRSCH, 1939).

Metafulgoridium CARPENTER, herein [**M. spilotum* HANDLIRSCH, 1939, p. 139; OD]. Fore wing as in *Fulgoridium*, but CUA2 unbranched. [The original generic name, *Metafulgoridium*, was a *nomen nudum* (HANDLIRSCH, 1939).] *Jur.*, Europe (Germany).—FIG. 151.1. **M. spilotum*; fore wing, $\times 6.5$ (HANDLIRSCH, 1939).

Family LOPHOPIDAE Stål, 1866

[Lophopidae Stål, 1866, p. 130]

Head markedly narrower than pronotum; vertex usually narrow; pronotum short and broad, tricarinate. Fore wing coriaceous, with conspicuous venation and supernumerary longitudinal veins and crossveins; wing usually elongate; apical margin broadly rounded; claval veins united before apex. Fore and middle tibiae usually compressed. *Jur.*—*Holo.*

Lophops SPINOLA, 1838, p. 205. *Holo.*

Eofulgoridium MARTYNOV, 1937a, p. 164 [**E. kityliense*; OD]. Fore wing with SC about midway between C and R; M dividing at midwing; M with 3 branches. Hind wing little known; costal margin concave; RS arising beyond midwing; M and CUA dividing beyond midwing. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*, USSR

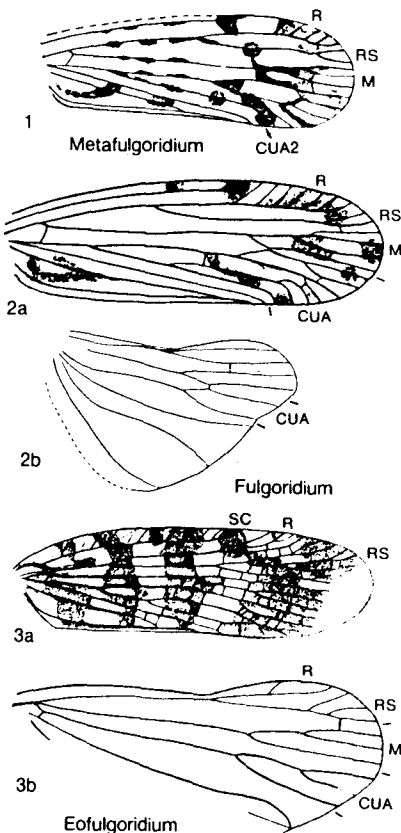


FIG. 151. Fulgoridiidae and Lophopidae (p. 235).

(Kirghiz).—FIG. 151.3a. **E. kityliense*; fore wing, $\times 4.2$.—FIG. 151.3b. *E. proximum* MARTYNOV; hind wing, $\times 5$ (MARTYNOV, 1937a). *Scoparidea* COCKERELL, 1920c, p. 243 [**S. nebulosa*; OD]. Fore wing with RS parallel to R; apical region with numerous, parallel veins; no regular gradate series of veins. [Family assignment doubtful.] *Eoc.*, USA (Colorado).

Family CIXIIDAE Spinola, 1838

[Cixiidae SPINOLA, 1838, p. 204]

Head not elongate; antennae with 2 segments, bearing flagella; wings unusually well developed. In fore wing, veins SC, R, and M with common stem; claval suture distinct; claval veins united into a claval stem. *Perm.*—*Holo.*

Cixius LATREILLE, 1804, p. 168. [The assignment of a Jurassic species from England to this genus is very doubtful (FENNAH, 1961), as is that of the several species in Baltic amber (GERMAR & BERENDT, 1856).] SCUDDER, 1890. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado)—*Holo.*

Asiocixius BECKER-MIGDISOVA, 1962a, p. 97 [**A. fulgoroides*; OD]. Fore wing membranous, except at base; costal margin smoothly rounded; R2 curved toward RS and giving rise to several veins; RS forked distally; M forking beyond midwing and with extensive pectinate branching; CUA with a long fork. *Trias.*, USSR (Kirghiz). — FIG. 152.6. **A. fulgoroides*; fore wing, $\times 5$ (Becker-Migdisova, 1962b).

Boreocixius BECKER-MIGDISOVA, 1955, p. 1100 [**B. sibiricus*; OD]. Fore wing with costal margin strongly thickened; RS arising very near wing base; R and RS with very short branches; fork of CUA long and curved. *Trias.*, USSR (Asian RSFSR). — FIG. 152.12. **B. sibiricus*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).

Cixiella BECKER-MIGDISOVA, 1962a, p. 98 [**C. reducta*; OD]. Fore wing weakly tegminous, distal portion membranous; RS arising near midwing; M forking beyond level of origin of RS, with 3 terminal branches, and forming a large, closed cell; CUA curved basally. *Trias.*, USSR (Kirghiz). — FIG. 152.8. **C. reducta*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).

Cycloscyrtina MARTYNOV, 1926b, p. 1349 [**C. delutinervis*; OD]. Fore wing tegminous, elongate; costal margin only slightly curved; R with a series of branches as in *Mesocixiella* but shorter; Hind wing little known; M with 2 long branches, arising before midwing. EVANS, 1956. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Kazakh, Tadzhik). — FIG. 152.3. **C. delutinervis*, *Jur.*, Kazakh; fore wing, $\times 6$ (Becker-Migdisova, 1962b).

Diaplegma SCUDDER, 1890, p. 288 [**D. abductum* SCUDDER, 1890, p. 290; SD CARPENTER, herein]. Similar to *Cixius*, but RS arising near midwing, each of its forks dividing into 2 or 3 distal, curved branches. *Oligo.*, USA (Colorado).

Eofulgorella COCKERELL, 1909, p. 172 [**E. bradburyi*; OD]. Fore wing resembling that in *Oliarius* but elongate and with costal margin concave; crossveins forming a very regular series. [Family assignment doubtful.] *Eoc.*, USA (Colorado).

Eoliarius COCKERELL, 1925a, p. 10 [**E. quadrivittatus*; OD]. Similar to *Oliarius*, but RS arising well before the pterostigmal area and giving rise to 4 very oblique branches anteriorly. *Eoc.*, USA (Colorado).

Hyalesthes SIGNORET, 1865, p. 128 [**H. obsoletus*; OD]. STATZ, 1950a. *Oligo.*, Europe (Germany)—*Holo.*

Mesocixiella BECKER-MIGDISOVA, 1949b, p. 38 [**M.*

asiatica; OD]. Fore wing with costal margin only slightly curved; R with a series of parallel branches leading to margin; RS arising before midwing with 3 or 4 terminal branches; M forked beyond midwing. EVANS, 1956. *Trias.*, USSR (Kirghiz); *Jur.*, USSR (Kazakh). — FIG. 152.7. **M. asiatica*; fore wing, $\times 6.5$ (Becker-Migdisova, 1962b).

Mesocixius TILLYARD, 1919c, p. 876 [**M. triarsicus*; OD]. Fore wing with RS forking about halfway between origin of RS and wing apex; fork of M less distal. EVANS, 1956. *Trias.*, Australia (Queensland). — FIG. 152.10. **M. triarsicus*; fore wing, $\times 5.4$ (Tillyard, 1919c).

Mundopoides COCKERELL, 1925g, p. 11 [**M. cisibhenaria*; OD]. Similar to *Mundopa* (recent), having nearly straight costal and outer margins, the apex being obliquely truncate; SC terminating at midwing. *Mio.*, USSR (Asian RSFSR).

Myndus STÅL, 1862, p. 307. COCKERELL, 1926b. *Oligo.*, England—*Holo.*

Oeclixius FENNAH, 1963, p. 43 [**O. amphion*; OD]. Similar to *Oeclis* (recent) but with long, slender tibiae; pterostigma only moderately developed; tegminal veins distinctly granulate. *Mio.*, Mexico (Chiapas). — FIG. 152.5. **O. amphion*; fore wing, $\times 13$ (Fennah, 1963).

Oliarites SCUDDER, 1890, p. 293 [**Mnemosyne terrentula* SCUDDER, 1878b, p. 773; OD]. Little-known genus, with head less than half as broad as thorax; veins forming a weak reticulation distally. [Family assignment doubtful.] *Eoc.*, USA (Wyoming).

Oliarius STÅL, 1862, p. 306. COCKERELL, 1910b. *Oligo.*, Europe (Baltic)—*Holo.*

Oligonila CARPENTER, herein [**O. defectuosa* THÉOBALD, 1937a, p. 258; OD]. Fore wing as in *Anila* (recent) but lacking the oblique vein in the costal area. [The original generic name, *Oligonila*, was a *nomen nudum* (THÉOBALD, 1937a).] *Oligo.*, Europe (France).

Permocixiella BECKER-MIGDISOVA, 1961c, p. 361 [**P. venosa*; OD]. Fore wing elongate, costal margin nearly straight; R2 straight; branches of CUA nearly straight. *Perm.*, USSR (Asian RSFSR). — FIG. 152.4. **P. venosa*; fore wing, $\times 5.4$ (Becker-Migdisova, 1961c).

Protoliarius COCKERELL, 1920c, p. 243 [**P. hamatus*; OD]. Similar to *Oliarius* but without a stigmatic spot on wings. COCKERELL, 1924a; COCKERELL & LEVEQUE, 1931. *Eoc.*, USA (Colorado).

Scytocixius MARTYNOV, 1937b, p. 34 [**S. mendax*; OD]. Fore wing broader distally than basally; costal margin smoothly curved; R2 strongly arched away from margin; RS similarly arched but less strongly; M with 3 distal branches; CUA forking at the level of origin of RS. *Perm.*, USSR (Asian RSFSR). — FIG. 152.1. **S. mendax*; fore wing, $\times 10$ (Becker-Migdisova, 1962b).

Surijokocixius BECKER-MIGDISOVA, 1961c, p. 359

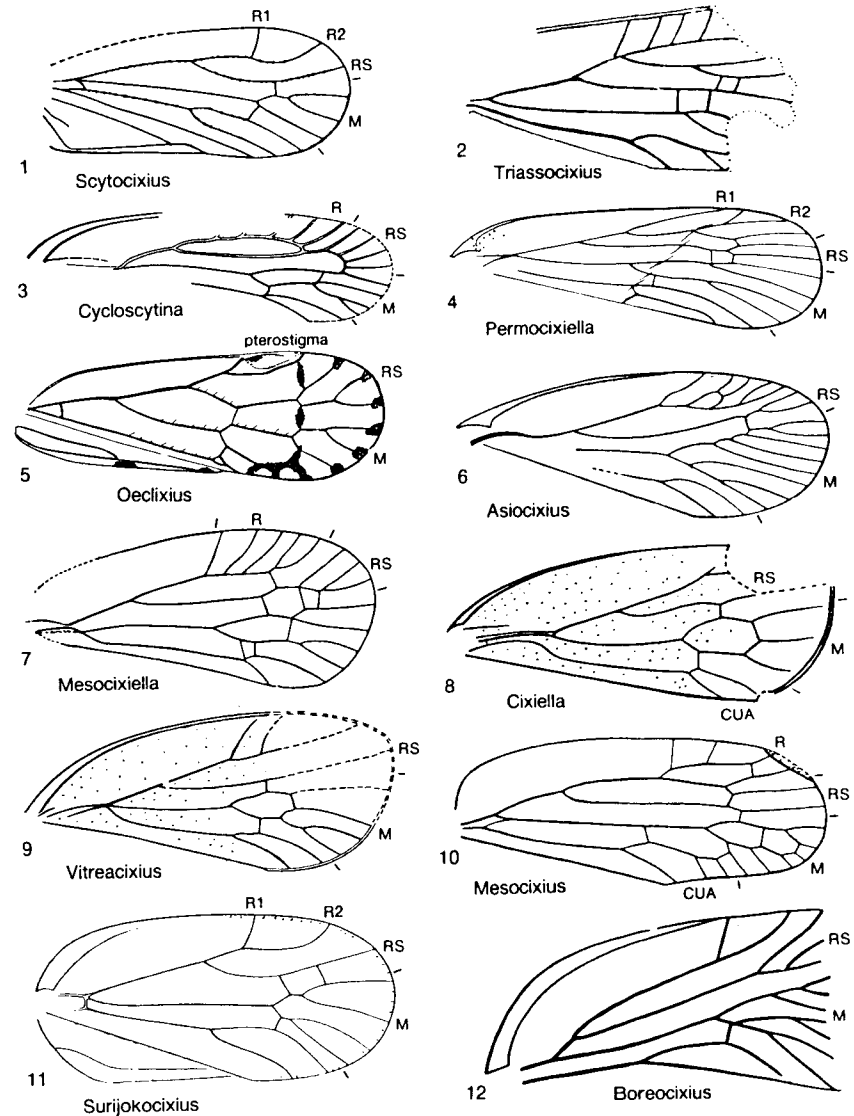


FIG. 152. Cixiidae (p. 236-238).

[**S. tomiensis*; OD]. Fore wing broad, with broadly rounded apex; costal margin thickened; R2 strongly curved; RS unbranched; branches of CUA long and curved. EVANS, 1956. *Perm.*, USSR (Asian RSFSR). — FIG. 152.11. **S. tomiensis*; fore wing, $\times 15$ (Becker-Migdisova, 1961c).

Triassicixius TILLYARD, 1919c, p. 878 [**T. au-*

tralicus; OD]. Little-known genus, based on fragment of fore wing; R forked close to the origin of RS; oblique crossveins from R to costal margin. [Family position uncertain.] *Trias.*, Australia (Queensland). — FIG. 152.2. **T. australicus*; fore wing, $\times 5.5$ (Evans, 1956).

Vitreacixius BECKER-MIGDISOVA, 1962a, p. 99 [**V.*

ellipticus; OD]. Fore wing weakly tegminous; similar to *Cixiella*, but RS arising slightly more basally; M with 4 branches, closed cell smaller than in *Cixiella*. *Trias.*, USSR (Kirghiz).—FIG. 152,9. **V. ellipticus*; fore wing, X6 (Becker-Migdisova, 1962b).

Family ACHILIDAE Stål, 1866

[Achilidae STÅL, 1866, p. 130]

Head usually small; frons and clypeus large. Hind tibiae elongate; second segment of hind tarsus large. Fore wing well developed, basal two-thirds thickened; veins SC and R united for a short interval basally; SC with 2 or more short branches leading to costal margin, forming stigmatic area; R branched only apically, connected to M by 2 or more crossveins; M with at least 3 branches; clavus short, claval veins united to form claval stem. Hind wing moderately large. *Oligo.*—*Holo.*

Achilus KIRBY, 1819, p. 474. *Holo.*
Elidiptera SPINOLA, 1839, p. 304. SCUDDER, 1890. *Oligo.*, USA (Colorado)—*Holo.*
Proptera USINGER, 1939, p. 66 [**P. kaweckii*; OD]. Similar to *Epiptera* (recent) but with vertex distinctly in front of eyes; posterior margin of vertex concavely arcuate. *Oligo.*, Europe (Baltic).

Family RICANIIDAE Amyot & Serville, 1843

[Ricaniidae AMYOT & SERVILLE, 1843, p. 527]

Head usually as wide as the pronotum; vertex short and broad; clypeus much narrower than frons. Fore wing large, broadly triangular; costal margin usually nearly straight; costal area broad with numerous crossveins; basal area of clavus without pustules; venation diverse; veins R, M, and CU typically with numerous branches, with 1 or 2 subapical lines of gradate crossveins. Hind wing smaller than fore wing and with reduced venation. Basal segment of hind tarsus very small, without lateral spines. *Trias.*—*Holo.*

Ricania GERMAR, 1818, p. 221. DALMAN, 1826; GIEBEL, 1862; SCUDDER, 1890. *Eoc.*, Canada (British Columbia); *Oligo.*, Europe (Baltic)—*Holo.*
Cotradachites FENNAH, 1968, p. 144 [**C. lithinus*; OD]. Similar to *Cotrades* (recent), but tegmen twice as long as broad; costal area broad, with dense venation. *Paleoc.*, USA (North Dakota).

Dilaropsis COCKERELL, 1920c, p. 244 [**D. ornatus*; OD]. Fore wing broad, triangular; costal margin slightly convex; SC ending about two-thirds wing length from base; M diverging abruptly from R near origin of RS. *Eoc.*, USA (Colorado).

Eobladina HAUPT, 1956, p. 13 [**E. antiqua*; OD]. Little-known genus, based on fore wing; costal area wide distally; SC joined to R at base by curved crossvein, forming a very short basal cell; RS arising well before midwing. *Eoc.*, Europe (Germany).—FIG. 153,2. **E. antiqua*; fore wing, X6 (Haupt, 1956).

Eoricania HENRIKSEN, 1922b, p. 24 [**E. danica*; OD]. Fore wing as in *Ricania* (recent), but 1A and 2A joined proximally beyond wing base. *Eoc.*, Europe (Denmark).—FIG. 153,4. **E. danica*; fore wing, X2.5 (Henriksen, 1922b).

Hammapteryx SCUDDER, 1890, p. 298 [**H. reticulata*; OD]. Fore wing subtriangular; costal margin arched at base; numerous crossveins from SC to margin; R with at least 2 arcuate branches distally; RS arising well before midwing. COCKERELL, 1920a, 1920b; COCKERELL & SANDHOUSE, 1921; HENRIKSEN, 1922b; PITON, 1940a. *Eoc.*, USA (Colorado, Wyoming), Europe (Denmark, France), England.—FIG. 153,3. *H. paucistriata* HENRIKSEN, Denmark; fore wing, X4 (Henriksen, 1922b).

Ludibrium BECKER-MIGDISOVA, 1962a, p. 100 [**L. ludus*; OD]. Hind wing little known; RS apparently arising distally as a continuation of stem R; M forked to about midwing. *Trias.*, USSR (Kirghiz).—FIG. 153,5. **L. ludus*; hind wing, X6 (Becker-Migdisova, 1962a).

Neoricania CARPENTER, 1990, p. 131, *nom. subst. pro Eoricania* HAUPT, 1956, p. 12, *non* HENRIKSEN, 1922b [**Eoricania reticulata* HAUPT; OD]. Fore wing with costal space much narrower than in *Eoricania*; SC much closer to C. *Eoc.*, Europe (Germany).

Scolypopites TILLYARD, 1923a, p. 17 [**S. bryani*; OD]. Fore wing as in *Scolypopa* (recent), but SC shorter, reaching only to a little beyond midwing; only one series of gradate veins. *Mio.*, Australia (Queensland).—FIG. 153,6. **S. bryani*; fore wing, X3.5 (Tillyard, 1923a).

Family NOGODINIDAE Melichar, 1898

[Nogodinidae MELICHAR, 1898, p. 204]

Head about as wide as pronotum; frons longer than wide. Fore wing large, usually broadest towards apex, coriaceous or hyaline, with numerous veins and crossveins; costal area with several crossveins; basal cell usually large; clavus not punctulate; claval stem reaching apex of fore wing. Hind tibiae with

lateral spines; second segment of hind tarsus small, with a pair of spines distally. *Eoc.*—*Holo.*

Nogodina STÅL, 1859, p. 326. *Holo.*
Detyopsis COCKERELL, 1920c, p. 242 [**D. scuderi*; OD]. Fore wing much as in *Detya* (recent); veinlets from SC to costal margin numerous; RS forking well before midwing. *Eoc.*, USA (Colorado).

Tritophania JACOBI, 1937, p. 188 [**T. patruelis*; OD]. Similar to *Gaetulia* (recent), but frons without a keel; pterostigma absent. *Oligo.*, Europe (Baltic).—FIG. 153,1. **T. patruelis*; whole insect, X3.4 (Jacobi, 1937).

Family FULGORIDAE Latreille, 1807

[Fulgoridae LATREILLE, 1807, p. 163]

Head usually large and simple, but often with prominent, cephalic process; postclypeus large, triangular; compound eyes large. Fore wing well developed, with numerous supernumerary veins and crossveins; hind wing with the anal and jugal areas reticulate. *Eoc.*—*Holo.*

Fulgora LINNÉ, 1767, p. 703. *Holo.*
Callosiploperon COCKERELL, 1920c, p. 245 [**C. ocellatum*; OD]. Fore wing broad, with obtuse apex; costal area much reduced; SC short; anterior veinlets from SC and R very oblique; ocelliform spots near outer margin. [Family assignment doubtful.] *Eoc.*, USA (Wyoming).
Eucophora SPINOLA, 1839, p. 200. SCUDDER, 1895b. *Eoc.*, Canada (British Columbia)—*Holo.*
Lystra FABRICIUS, 1803, p. 56. SCUDDER, 1890. [Generic assignment of fossil doubtful.] *Eoc.*, USA (Wyoming)—*Holo.*
Nyktalos METCALF, 1952, p. 230, *nom. subst. pro Nyctophylax* SCUDDER, 1890, p. 279, *non* FITZINGER, 1860 [**Nyctophylax ubleri* SCUDDER; OD]. Large species of uncertain affinities; head with a stout, recurved process; legs stout; femora and tibiae carinate. *Oligo.*, USA (Colorado).
Poiocera LAPORTE, 1832, p. 221. GERMAR & BERENDT, 1856. *Oligo.*, Europe (Baltic)—*Holo.*

Family FLATIDAE Spinola, 1838

[Flatidae SPINOLA, 1838, p. 205]

Head narrower than thorax; lateral edges of face not angular. Fore wing with costal area having crossveins; basal area of clavus granulate; clavus often open, claval veins separate or joined apically. Hind tibiae without a movable spur; first hind tarsomere short,

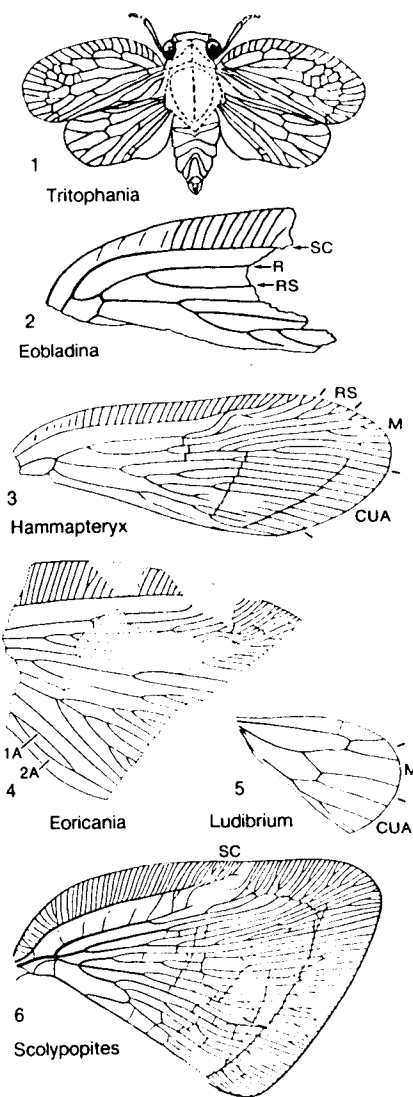


FIG. 153. Ricaniidae and Nogodinidae (p. 238–239).

second one small with a spine on each side. *Eoc.*—*Holo.*

Flata FABRICIUS, 1798, p. 511. *Holo.*
Aphaena GUÉRIN & MÉNEVILLE, 1833, p. 452. SCUDDER, 1890; COCKERELL, 1920c. *Eoc.*, USA (Wyoming); *Oligo.*, USA (Colorado)—*Holo.*

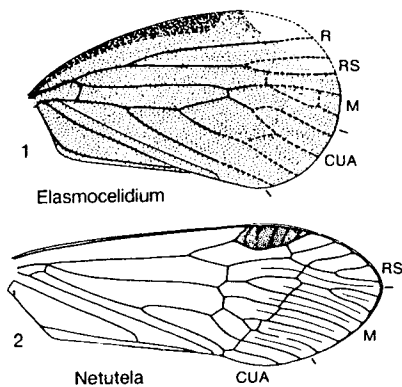


FIG. 154. Issidae and Dictyopharidae (p. 240–241).

Ficarasites SCUDDER, 1890, p. 301 [**F. stigmaticum*; OD]. Little-known genus; costal area narrow, with oblique veinlets; few crossveins. *Eoc.*, USA (Wyoming).

Giselia HAUPT, 1956, p. 14 [**G. multifurcata*; OD]. Fore wing as in *Uxantis* (recent); SC curved away from margin as it approaches midwing; R and M fused basally, separating early, with RS arising about one-sixth wing length from base; CUA apparently with a deep fork. *Eoc.*, Europe (Germany).

Lechaea STÅL, 1866, p. 236. HENRIKSEN, 1922b. *Eoc.*, Europe (Denmark)—*Holo.*

Ormenis STÅL, 1862, p. 68. COCKERELL, 1926a. *Tert.* (*epoch unknown*), Argentina. *Holo.*

Poekilloptera LATREILLE, 1796, p. 90. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Thaumastocladus COCKERELL & SANDHOUSE, 1921, p. 456 [**T. simplex*; OD]. Fore wing as in *Gaga* (recent); costal area broad, with numerous oblique veinlets; R branching apically; M and CUA coalesced to about midwing; CUP distinctly forked. [Family position doubtful.] COCKERELL, 1924a. *Eoc.*, USA (Wyoming).

Family ARAEOPIDAE Metcalf, 1938

[*Araeopidae* METCALF, 1938, p. 281]

Head usually small; antennae short, usually not longer than head and thorax combined. Fore wing diverse, ranging from brachypterous, with reduced venation, to fully developed, with normal venation; vein SC typically with 2 branches; R coalesced with SC for about half its length, then coalesced with part of M; M usually with 3 branches; CU with 3 branches. Hind wing usually present, sometimes reduced; SC and R coalesced for more than half their lengths; M

unbranched. Hind femora and tibiae elongate; spur well developed at apex of tibia, either spinelike or much enlarged and complex. *Eoc.*—*Holo.*

Araeopus SPINOLA, 1839, p. 336. COCKERELL, 1924a; STATZ, 1950a. *Eoc.*, USA (Colorado); *Oligo.*, Europe (Germany)—*Holo.*

Amagua COCKERELL, 1924a, p. 3 [**A. fortis*; OD]. Fore wing as in *Stenocranus* (recent); wing of uniform width, narrow; crossveins m-cu long. *Mio.*, USSR (Asian RSFSR).

Chloriona FIEBER, 1866, p. 519. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Liburnia STÅL, 1866, p. 179. COCKERELL, 1917h. *Mio.*, Burma—*Holo.*

Family ISSIDAE Spinola, 1838

[*Issidae* SPINOLA, 1838, p. 158]

Head usually at least as wide as thorax; lateral margins of thorax not keeled; anterior margin of pronotum rounded and extended. Fore wing usually with reduced venation and often small; costal area small, without crossveins, or absent; base of costal margin not strongly curved; clavus not granulate. Hind tibiae with 2 to 4 spines; second hind tarsomere with a spine on each side. *Jur.*—*Holo.*

Issus FABRICIUS, 1803, p. 99. BERVOETS, 1910. *Oligo.*, Europe (Baltic)—*Holo.*

Elasmocelidium MARTYNOV, 1926b, p. 1355 [**E. rotundatum*; OD]. Fore wing short, much broadened distally; SC nearly parallel to costal margin; costal margin thickened; RS arising well before midwing; RS and M forked distally; anal area extending only to about midwing. BODE, 1953; EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh); Europe (Germany).—FIG. 154, 1. **E. rotundatum*, Kazakh; fore wing, $\times 6.3$ (Becker-Migdisova, 1962b).

Issites HAUPT, 1956, p. 16 [**I. glaber*; OD]. Fore wing as in *Issus* (recent) but without the dense reticulation. *Eoc.*, Europe (Germany).

Mesotubulistrum BECKER-MIGDISOVA, 1949b, p. 35 [**M. asiaticum*; OD]. Similar to *Elasmocelidium*, but RS arising near midwing. *Jur.*, USSR (Kazakh).

Tetragonidium BODE, 1953, p. 194 [**T. paralelogramma*; OD]. Fore wing as in *Elasmocelidium*, but M with more branches. *Jur.*, Europe (Germany).

Family DICTYOPHARIDAE Spinola, 1838

[*Dictyopharidae* SPINOLA, 1838, p. 202]

Head relatively large; structural details of vertex and frons diverse. Legs usually slender

and elongate; hind tibiae commonly with 3 to 5 stout spines; second hind tarsal segment large, with a row of small spines at apex. Fore wing either normal or reduced; vein SC and R coalesced beyond basal area of wing; R branching irregularly distally; an irregular transverse line commonly formed by series of crossveins in apical third of wing. Hind wing usually large, with irregular venation. EMELJANOV, 1983. *Cret.*—*Holo.*

Dictyophara GERMAR, 1833, p. 175. [The family assignment of “*Dictyophara*” *scudderii* PITON (1940a), from the Eocene of France, is uncertain.] SCUDDER, 1890; BECKER-MIGDISOVA, 1964; EMELJANOV, 1983. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Chanithus AMYOT, 1847, p. 160. BECKER-MIGDISOVA, 1964; EMELJANOV, 1983. *Mio.*, USSR (Asian RSFSR)—*Holo.*

Florissantia SCUDDER, 1890, p. 293 [**F. elegans*; OD]. Little-known genus, apparently related to *Dictyophara*. [Originally placed in Cixiidae by SCUDDER (1890); transferred to Dictyopharidae by EMELJANOV (1983).] COCKERELL, 1909a. *Oligo.*, USA (Colorado).

Netutela EMELJANOV, 1983, p. 84 [**N. annunciator*; OD]. Similar to *Cladodiptera* (recent), but clavus of fore wing without crossveins; M forking distally of origin of RS. *Cret.*, USSR (Asian RSFSR).—FIG. 154, 2. **N. annunciator*; fore wing, $\times 6.5$ (Emeljanov, 1983).

Family ARCHESCYTINIDAE Tillyard, 1926

[*Archescytinidae* TILLYARD, 1926g, p. 385] [= *Permosyllidae* TILLYARD, 1926g, p. 390; *Lithoscytinidae* CARPENTER, 1933a, p. 436; *Mauertidae* ZALESSKY, 1937e, p. 54; *Permoscytinopsidae* ZALESSKY, 1939, p. 36; *Uraloscytinidae* ZALESSKY, 1939, p. 40; *Maripsocidae* ZALESSKY, 1939, p. 44; *Kaltanaphididae* SZELEGIEWICZ, 1971, p. 63]

Fore and hind wings membranous, similar in size and almost alike in venation. Fore wing with vein SC very close and parallel to R + M, R, and R1; R forming a pterostigma; RS originating at about midwing; M usually with at least 3 branches; CUA arising from stem CU, then directed towards R + M, which it touches at the point of separation of M; CUA forked; anal area small. Hind wing similar to fore wing except that CUA arises as an independent vein from the wing base and is not directed towards R + M. Head hypognathous; beak long; antennae long, multisegmented; ovipositor prominent in some genera at least. SZELEGIEWICZ & POPOV, 1978. *Perm.*

Archescytina TILLYARD, 1926g, p. 385 [**A. permiana*; OD] [= *Maueria* ZALESSKY, 1937e, p. 54 (type, *M. sylvensis*); *Permoscytinops* ZALESSKY, 1939, p. 36 (type, *P. maueriaeformis*)]. Fore wing with costal margin nearly straight except near base; SC close and parallel to R; R + M arched anteriorly; R2 parallel to RS; M usually with 3 branches. Antennae long and slender, with about 25 segments; beak long; forelegs with thickened femora; female with long, retractible ovipositor. CARPENTER, 1931b, 1939; ZALESSKY, 1937e, 1939; BECKER-MIGDISOVA, 1961c, 1961d, 1962b. *Perm.*, USA (Kansas), USSR (European and Asian RSFSR).—FIG. 155, 1a. *Archescytina* sp., USSR; lateral view of body, $\times 6$ (Becker-Migdisova, 1961d).—FIG. 155, 1b, c. **A. permiana*, Kansas; b, fore wing; c, hind wing, $\times 6.5$ (Carpenter, 1939).

Bekkerscytina EVANS, 1958, p. 111 [**B. primitiva*; OD]. Similar to *Eoscytina*, but RS arising nearer to origin of M. *Perm.*, Australia (New South Wales).—FIG. 155, 10. **B. primitiva*; fore wing, $\times 6.3$ (Evans, 1958).

Eoscytina EVANS, 1958, p. 109 [**E. migdisovae*; OD]. Similar to *Archescytina*, but fork of CUA very deep and broad and stem of CUA, as it leaves CUP, sigmoidally curved. *Perm.*, Australia (New South Wales).—FIG. 155, 9. **E. migdisovae*; fore wing, $\times 6$ (Evans, 1958).

Kaltanaphis BECKER-MIGDISOVA, 1959a, p. 107 [**K. permianis*; OD]. Little-known genus, based on fragment of hind wing. [Originally assigned to Permaphidopseidae; placed in new family, Kaltanaphididae, by SZELEGIEWICZ, 1971; transferred to Archescytinidae by SZELEGIEWICZ & POPOV, 1978.] *Perm.*, USSR (Asian RSFSR).

Kaltanoscytina BECKER-MIGDISOVA, 1959a, p. 105 [**K. nigra*; OD]. Wings as in *Archescytina*, but R longer and straighter in both pairs. BECKER-MIGDISOVA, 1961c; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (Asian RSFSR).—FIG. 155, 8. **K. nigra*; fore wing, $\times 7$ (Becker-Migdisova, 1961c).

Maripsocus ZALESSKY, 1939, p. 44 [**M. ambiguus*; OD]. Little-known fore wing; venation as in *Archescytina*, but M apparently with 2 branches. EVANS, 1956. *Perm.*, USSR (European RSFSR).

Paleoscytina CARPENTER, 1931b, p. 118 [**P. brevistigma*; OD]. Similar to *Archescytina*, but CUA of fore wing unbranched. BECKER-MIGDISOVA, 1961c. *Perm.*, USA (Kansas), USSR (Asian RSFSR).—FIG. 155, 3. **P. brevistigma*; fore wing, $\times 18$ (Carpenter, 1933a).

Permosylla TILLYARD, 1926g, p. 390 [**P. americana*; OD] [= *Lithoscytina* CARPENTER, 1933a, p. 436 (type, *L. cubitalis*)]. Fore wing as in *Archescytina* but relatively broader; costal margin slightly concave at level of origin of M. BECKER-MIGDISOVA, 1960, 1961c, 1962b. *Perm.*, USA (Kansas), USSR (European and Asian RSFSR).—FIG. 155, 7. **P. americana*; fore wing, $\times 16$ (Carpenter, 1931b).

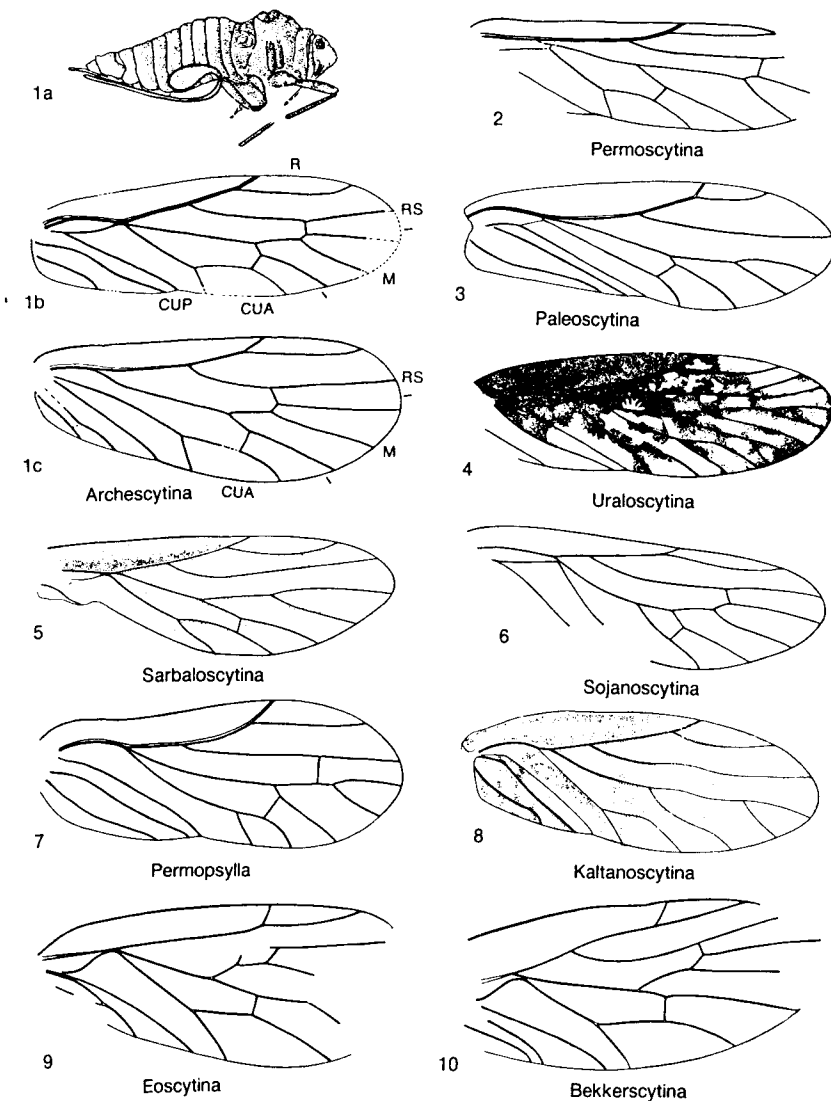


FIG. 155. Archescytinidae (p. 241-243).

Permopsyllopsis ZALESSKY, 1939, p. 38 [**P. rosica*; OD]. Little-known fore wing; venation as in *Archescytina*, but RS straight. BECKER-MIGDISOVA, 1960. *Perm.*, USSR (Asian RSFSR). *Permoscytina* TILLYARD, 1926g, p. 387 [**P. kansanensis*; OD]. Similar to *Archescytina*, but SC and R nearly straight basally; proximal branch

of M arising at about level of origin of RS. CARPENTER, 1939. *Perm.*, USA (Kansas). — FIG. 155.2. **P. kansanensis*; fore wing, $\times 4.2$ (Carpenter, 1939). *Sarbaloscytina* BECKER-MIGDISOVA, 1959a, p. 104 [**S. angustipennis*; OD]. Similar to *Archescytina*, but stem R+M short and nearly straight.

BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR). — FIG. 155.5. **S. angustipennis*; fore wing, $\times 4.5$ (Becker-Migdisova, 1961c). *Sojanoscytina* MARTYNOV, 1933c, p. 885 [**S. grandis*; OD] [= *Ivascytina* MARTYNOV, 1933c, p. 888 (type, *I. difficilis*)]. Fore wing similar to that of *Archescytina*, but M with 4 or more branches. *Perm.*, USSR (European RSFSR). — FIG. 155.6. **S. grandis*; fore wing, $\times 3.4$ (Becker-Migdisova, 1961c). *Tshekardaella* BECKER-MIGDISOVA, 1960, p. 59 [**T. tshekardaensis*; OD; = *Tshekardaella tshekardaensis* BECKER-MIGDISOVA, 1948a, p. 130, *nom. nud.*]. Little-known genus, based on wing and body fragments. Fore wing as in *Archescytina* but shorter and more nearly oval. BECKER-MIGDISOVA, 1962b; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (Asian RSFSR). *Uraloscytina* ZALESSKY, 1939, p. 40 [**U. prosbolioides*; OD]. Fore wing as in *Archescytina*, but M more extensively branched and with proximal branch arising about the level of origin of RS. [Type of family Uraloscytinidae ZALESSKY, 1939.] *Perm.*, USSR (Asian RSFSR). — FIG. 155.4. *U. multinervosa* BECKER-MIGDISOVA; fore wing, $\times 4$ (Becker-Migdisova, 1962b).

Family BOREOSCYTIDAE Becker-Migdisova, 1949

[Boreoscytidae BECKER-MIGDISOVA, 1949a, p. 171]

Little-known family. Fore wing much broader distally than basally; vein M with at least 3 branches. Hind wing and body unknown. *Perm.*

Boreoscyta BECKER-MIGDISOVA, 1949a, p. 172 [**B. nefasta*; OD]. Fore wing triangular; RS with pectinate branches directed to costal margin. ROHDENDORF, 1957. *Perm.*, USSR (European RSFSR). — FIG. 156.4. *B. mirabilis* BECKER-MIGDISOVA; fore wing, $\times 6.5$ (Becker-Migdisova, 1949a).

Archescytinopsis BECKER-MIGDISOVA, 1949a, p. 175 [**Sojanoscytina latipennis* MARTYNOV, 1933c, p. 887; OD]. Fore wing not so markedly triangular as in *Boreoscyta*; RS without pectinate branches. *Perm.*, USSR (European RSFSR). — FIG. 156.3. **A. latipennis* (MARTYNOV); fore wing, $\times 6.5$ (Becker-Migdisova, 1949a).

Family PINCOMBEIDAE Tillyard, 1922

[Pincombeidae TILLYARD, 1922a, p. 282]

Little-known family of uncertain affinities. Fore(?) wing triangular; veins M and CUA originating at same point on R; anal area apparently very narrow. Hind wing appar-

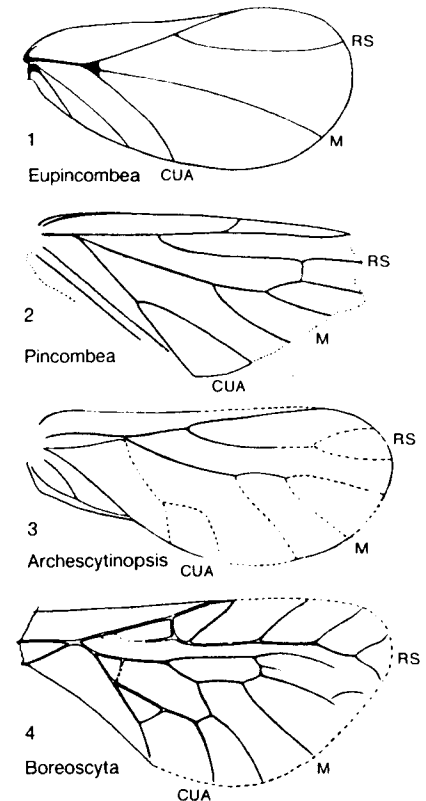


FIG. 156. Boreoscytidae and Pincombeidae (p. 243).

ently smaller than fore; R, M, and CUA diverging from same place. Body unknown. *Perm.*

Pincombea TILLYARD, 1922a, p. 282 [**P. mirabilis*; OD]. Fore(?) wing: M with 3 branches; CUA forked to half its length; one crossvein between M and RS, none between CUA and M. EVANS, 1956. *Perm.*, Australia (New South Wales). — FIG. 156.2. **P. mirabilis*; fore(?) wing, $\times 16$ (Tillyard, 1922a).

Eupincombea DAVIS, 1942, p. 114 [**E. postica*; OD]. Hind wing: RS, M, and CUA unbranched; costal area triangular. EVANS, 1956. *Perm.*, Australia (New South Wales). — FIG. 156.1. **E. postica*; hind wing, $\times 20$ (Davis, 1942).

Protopincombea EVANS, 1943b, p. 193 [**P. obscura*; OD]. Fore wing as in *Pincombea*, but 2 crossveins between RS and M and one between

M and CUA. EVANS, 1956. *Perm.*, Australia (New South Wales).

Family PROTOPSYLLIDIIDAE Carpenter, 1931

(Protopsyllidiidae CARPENTER, 1931b, p. 119) [=Pernaphidiopseidae BECKER-MIGDISOVA, 1960, p. 57]

Fore wing variable in shape; vein SC not a distinct vein; RS typically unbranched; stem of M fused with CUA; anal area small but distinct and coriaceous; CUP straight. Hind wing smaller than fore wing. Body structure little known; legs slender. *Perm.*-*Jur.*

Protopsyllidium TILLYARD, 1926a, p. 26 [**P. australe*; OD]. Fore wing with RS arising well before midwing; M with 2 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157.9. **P. australe*; fore wing, $\times 16$ (Tillyard, 1926a).

Asiopsyllidium BECKER-MIGDISOVA, 1959a, p. 113 [**A. unicum*; OD]. Fore wing much wider distally than basally; RS arising well before midwing; M with 2 branches; CUA with a narrow fork. *Trias.*, USSR (Kirghiz).—FIG. 157.6. **A. unicum*; fore wing, $\times 10$ (Becker-Migdisova, 1959a).

Belipsylla EVANS, 1943b, p. 192 [**B. reticulata*; OD]. Fore wing broad distally; M with 3 straight branches; one crossvein between RS and M1+2 and another between RS and M1; CUA with small fork; anal area with Y-shaped vein. *Perm.*, Australia (New South Wales).—FIG. 157.10. **B. reticulata*; fore wing, $\times 12$ (Evans, 1943b).

Cicadellopsis MARTYNOV, 1937a, p. 107 [**C. incerta*; OD]. Fore wing with costal margin strongly convex; RS arising near wing base; M forked; CUA with small distal fork. EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Trias.-Jur.*, USSR (Kirghiz).—FIG. 157.8. **C. incerta*, *Jur.*; fore wing, $\times 13$ (Martynov, 1937a).

Cicadopsyllidium BECKER-MIGDISOVA, 1959a, p. 112 [**C. elongatum*; OD]. Little-known genus. Fore wing narrow; pterostigma apparently absent; RS arising well before midwing; M and CUA apparently fused basally. [Family assignment doubtful.] *Trias.*, USSR (Kirghiz).

Clavopsyllidium DAVIS, 1942, p. 117 [**C. minutum*; OD]. Fore wing as in *Protopsyllidium*, but M with 3 branches; CUA1 arched. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).—FIG. 157.7. **C. minutum*; fore wing, $\times 18$ (Davis, 1942).

Pernaphidopsis BECKER-MIGDISOVA, 1960, p. 58 [**P. sojanensis*; OD]. Little-known genus, based on hind wing. Wing broad distally; M coalesced

basally with CUA; CUA forked distally with strongly curved CUA1. SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (European RSFSR).

Permopsyllidium TILLYARD, 1926a, p. 27 [**P. mitchelli*; OD]. RS arising near midwing; M with 3 branches. CARPENTER, 1931b. *Perm.*, Australia (New South Wales).—FIG. 157.5. **P. mitchelli*; fore wing, $\times 14$ (Tillyard, 1926a).

Permopsyllidops DAVIS, 1942, p. 116 [**P. stanleyi*; OD]. Fore wing similar to *Protopsyllidium*, but CUP absent or poorly developed; M with 3 branches. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157.1. **P. stanleyi*; fore wing, $\times 15$ (Davis, 1942).

Permopsylloides EVANS, 1943b, p. 193 [**P. insolita*; OD]. Fore wing of uniform width; costal area wide; RS arising before midwing, curved; M apparently with 2 branches; CUA sinuate; anal area with Y-shaped vein. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 157.4. **P. insolita*; fore wing, $\times 12$ (Evans, 1943b).

Permothea TILLYARD, 1926a, p. 28 [**P. latipennis*; OD]. Fore wing much as in *Protopsyllidium*, but M with 3 branches. CARPENTER, 1931b; EVANS, 1956. *Perm.*, Australia (New South Wales).

Permotheella DAVIS, 1942, p. 116 [**P. scytinopteroides*; OD]. RS strongly curved; M with 3 branches; anal veins forming Y-shaped vein. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).—FIG. 157.3. **P. scytinopteroides*; fore wing, $\times 14$ (Davis, 1942).

Propatrix BECKER-MIGDISOVA, 1960, p. 55 [**P. psylloides*; OD]; =*P. psylloides* BECKER-MIGDISOVA, 1948a, p. 130, *nom. nud.*. Fore wing with long pterostigmal area. RS arising at midwing; M with 3 branches; CUA with wide fork. BECKER-MIGDISOVA, 1962b; SZELEGIEWICZ & POPOV, 1978. *Perm.*, USSR (European RSFSR).—FIG. 157.2. **P. psylloides*; fore wing and body, $\times 8$ (Becker-Migdisova, 1960).

Psocopsyllidium DAVIS, 1942, p. 115 [**P. media*; OD]. Fore wing as in *Protopsyllidium* but more slender. EVANS, 1943b, 1956. *Perm.*, Australia (New South Wales).

Psocoscytina DAVIS, 1942, p. 112 [**P. bifida*; OD]. Similar to *Protopsyllidium*, but M with 3 branches; RS arising at midwing with distal fork. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 158.2. **P. bifida*; fore wing, $\times 12$ (Davis, 1942).

Psyllidella EVANS, 1943b, p. 192 [**P. magna*; OD]. Fore wing with RS arising beyond midwing; M with 3 long branches; costal margin sinuate. *Perm.*, Australia (New South Wales).—FIG. 158.5. **P. magna*; fore wing, $\times 10$ (Evans, 1943b).

Psyllidiana EVANS, 1943b, p. 192 [**P. davisia*; OD] [= *Protopsyllidops* EVANS, 1943b, p. 192 (type, *P. minuta*)]. Fore wing as in *Protopsyllid-*

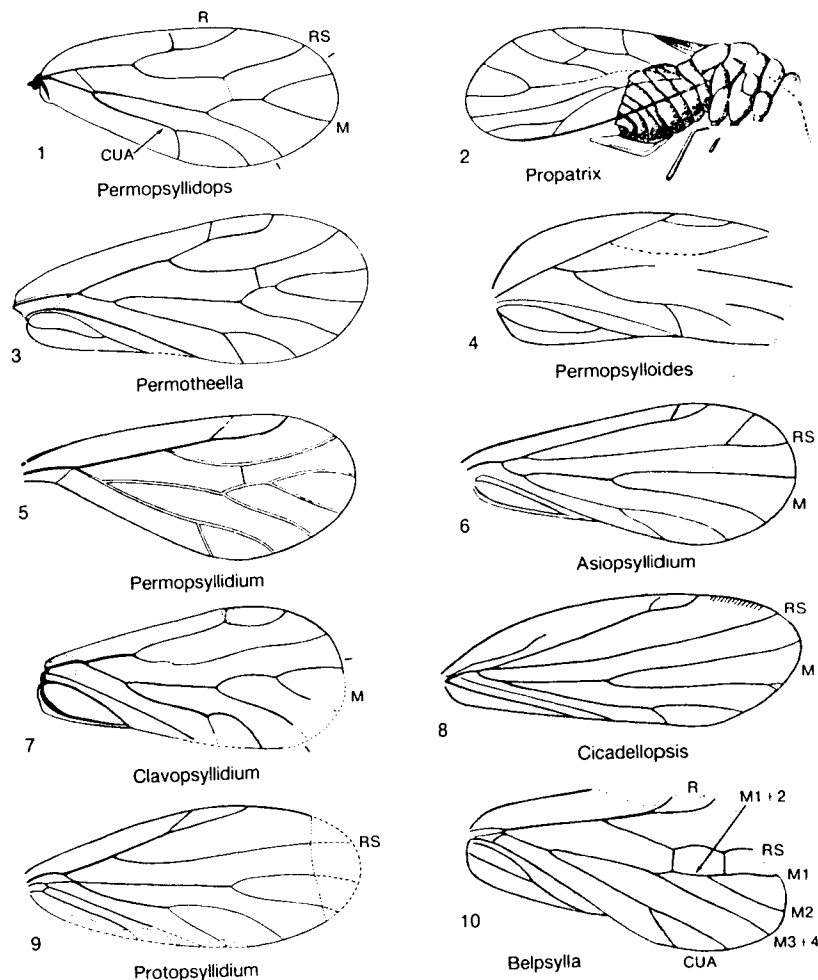


FIG. 157. Protopsyllidiidae (p. 244).

lidium, but RS arising near midwing and very straight; CUA deeply forked. EVANS, 1956. *Perm.*, Australia (New South Wales).—FIG. 158.1. **P. davisia*; fore wing, $\times 22$ (Evans, 1943b).

Tomiopsyllidium BECKER-MIGDISOVA, 1959a, p. 112 [**T. iljinskiense*; OD]. Fore wing slender, triangular; RS arising just before midwing, curving away from R distally. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).—FIG. 158.4.

**T. iljinskiense*; fore wing, $\times 22$ (Becker-Migdisova, 1960).

Triassopsylla TILLYARD, 1918b, p. 753 [**T. plecioides*; OD]. Little-known genus, based on wing fragment; RS curved; M with 3 branches. EVANS, 1956. *Trias.*, Australia (New South Wales).

Triassothea EVANS, 1956, p. 236 [**T. analis*; OD]. Fore wing as in *Protopsyllidium*, but RS arising near wing base; M+CUA very short; M with distal fork. *Trias.*, Australia (Queensland).

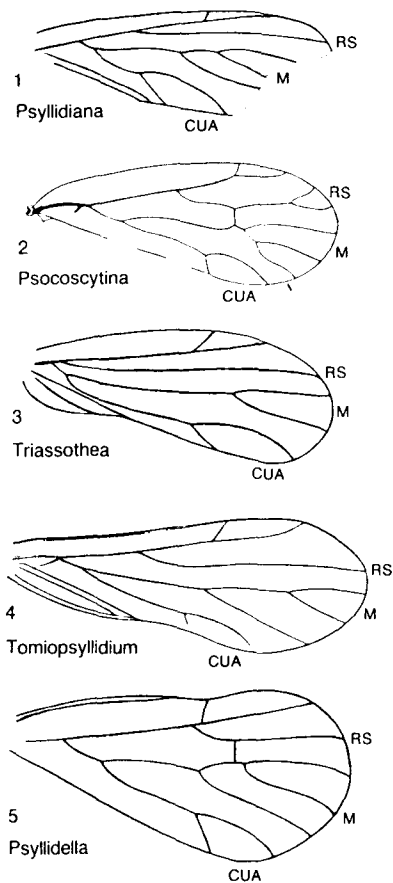


FIG. 158. Protopsyllidiidae (p. 244-246).

— FIG. 158,3. **T. analis*; fore wing, $\times 14$ (Evans, 1956).

Family GENAPHIDIDAE Handlirsch, 1907

[Genaphididae Handlirsch, 1907, p. 643]

Little-known family. Antennae with 7 segments, bearing annular, secondary sense organs (rhinaria). Fore wing with all veins of nearly same thickness; M arising at level of base of pterostigma, with 3 terminal branches; CUA with short base, arising from stem R+M. HEIE, 1967, 1985; SHAPOSHNIKOV, 1979b, 1980. *Jur.*

Genaphis HANDLIRSCH, 1907, p. 643 [**Abbis valdensis*; OD]. Little-known genus. RS arising near middle of pterostigma. HEIE, 1967. *Jur.*, England. — FIG. 159,1. **G. valdensis*; fore wing, $\times 18$ (Heie, 1967).

Juraphis SHAPOSHNIKOV, 1979b, p. 66 [**J. crassipes*; OD]. Fore wing with RS arising slightly distally of middle of pterostigma. Antennae and legs stout. HEIE, 1985. *Jur.*, USSR (Kazakh). — FIG. 159,4. **J. crassipes*; fore and hind wings, $\times 18$ (Shaposhnikov, 1979b).

Family CANADAPHIDIDAE Richards, 1966

[*nom. transl.* KONONOVA, 1976, p. 119, ex Canadaphidinae RICHARDS, 1966, p. 757]

Head dorsoventrally flattened, prolonged anteriorly; antennal bases ventral, in front of compound eyes; antennae with 5 to 6 segments; rostrum apparently very short; tarsi long; ovipositor well developed; siphuncles and cauda apparently not present. Fore wing with vein M with two forks. Hind wing relatively large. *Cret.*

Canadaphis ESSIG in CARPENTER & others, 1937, p. 19 [**C. carpenteri*; OD]. M of fore wing arising near origin of CUA1; CUA1 slightly sinuate; tarsi with 2 segments. HEIE, 1967, 1981; KONONOVA, 1976. [A record of this genus (*C. mordvilkei* KONONOVA, 1976, p. 120) from the Cretaceous of USSR (Asian RSFSR) is very questionable. See KONONOVA, 1976, and HEIE, 1985.] *Cret.*, Canada (Manitoba). — FIG. 159,2. **C. carpenteri*; dorsal view, $\times 35$ (Essig in Carpenter & others, 1937).

Alloambria RICHARDS, 1966, p. 756 [**A. caudata*; OD]. Antennae with at least 5 segments. Fore wing with CUA1 and CUA2 arising independently from stem SC+R+M; CUA1 sinuate. Tarsi with 2 segments. *Cret.*, Canada (Manitoba). — FIG. 159,3. **A. caudata*; dorsal view, $\times 50$ (Richards, 1966).

Pseudambria RICHARDS, 1966, p. 758 [**P. longirostris*; OD]. Antennae with 6 segments. Fore wing with CUA1 sinuate; CUA2 very weakly developed. HEIE, 1981, 1985. *Cret.*, Canada (Manitoba).

Family PALAEOAPHIDIDAE Richards, 1966

[*nom. transl.* KONONOVA, 1976, p. 121, ex Palaeoaphidinae RICHARDS, 1966, p. 750]

Similar to Canadaphididae, but antennae with 7 segments; ovipositor well developed. Fore wing with vein RS arising from proxi-

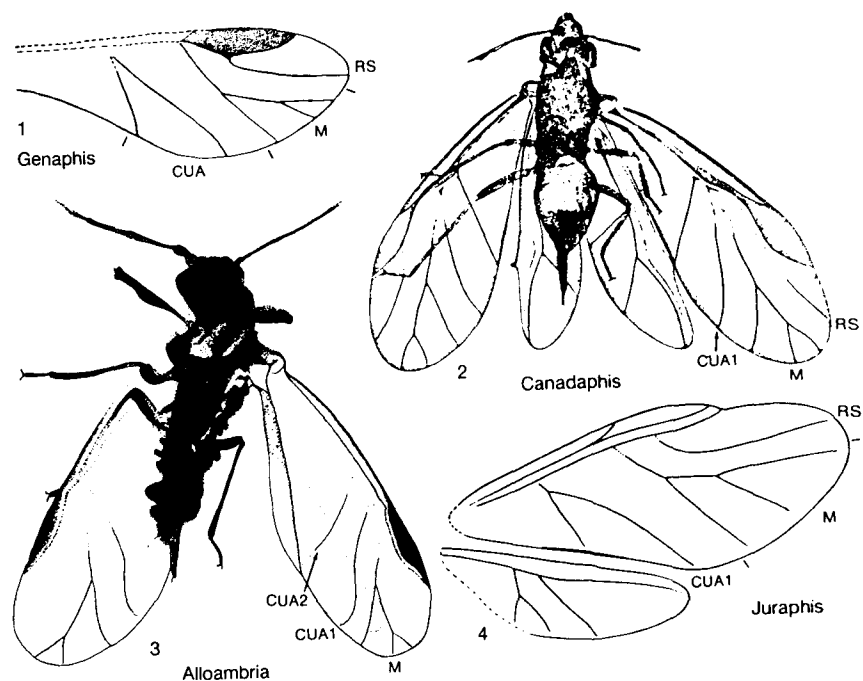


FIG. 159. Genaphididae and Canadaphididae (p. 246).

mal third of pterostigma; hind wing relatively shorter than in Canadaphididae. HEIE, 1985. *Cret.*

Palaeoaphis RICHARDS, 1966, p. 750 [**P. archimedia*; OD]. Little-known genus. Media of fore wing incomplete basally; legs with short hairs. [The assignment of *P. incognata* KONONOVA, 1976, p. 121 (Cretaceous of USSR) to the family Palaeoaphididae is very uncertain.] HEIE, 1985. *Cret.*, Canada (Manitoba). — FIG. 160,1. **P. archimedia*; fore wing, $\times 45$ (Richards, 1966).

Ambaraphis RICHARDS, 1966, p. 752 [**A. costalis*; OD]. Similar to *Palaeoaphis*, but apical tarsal segments with long, conspicuous preapical setae. HEIE, 1985. *Cret.*, Canada (Manitoba).

Family SHAPOSHNIKOVIIDAE Kononova, 1976

[Shaposhnikovidae KONONOVA, 1976, p. 122]

Little-known family. Antennae with 7 segments, its total length only half that of fore wing. Fore wing: vein M with 3 terminal

branches; CUA1 and CUA2 widely separated basally. HEIE, 1981, 1985. *Cret.*

Shaposhnikovia KONONOVA, 1976, p. 122 [**S. electri*; OD]. Fore wing with M arising from base of pterostigma. Second segment of fore tarsus about one-fourth as long as tibia. HEIE, 1981. *Cret.*, USSR (Asian RSFSR).

Family OVIPARASIPHIDAE Shaposhnikov, 1979

[Oviparasiphidae SHAPOSHNIKOV, 1979b, p. 75]

Antennae with annular, secondary sense organs (rhinaria). Fore wing with vein RS arising from middle of pterostigma; M with 3 branches; CUA1 and CUA2 originating separately from a common stem (SC+R+M). Ovipositor large. *Cret.*

Oviparasiphum SHAPOSHNIKOV, 1979b, p. 75 [**O. jakovlevi*; OD]. Rhinaria on antennae forming convex rings. Femora stout. *Cret.*, Mongolia.

Family TAJMYRAPHIDIDAE Kononova, 1975

[Tajmyraphididae KONONOVA, 1975, p. 795]

Antennae with 4 to 6 segments. Fore wing broadly rounded distally; pterostigma short, vein RS not connected to it; M with one fork; CUA1 about three times as long as CUA2. HEIE, 1985. *Cret.*

Tajmyrphis KONONOVA, 1975, p. 796 [**T. zherichini*; OD]. Antennae with 5 or 6 segments. *Cret.*, USSR (Asian RSFSR).

Jantardakhia KONONOVA, 1975, p. 804 [**J. electri*; OD]. Antennae with 5 segments. Fore wing with bases of CUA1 and CUA2 widely separated. *Cret.*, USSR (Asian RSFSR).

Khatangaphis KONONOVA, 1975, p. 803 [**K. sibirica*; OD]. Similar to *Tajmyrphis*, but antennae with 4 or 5 segments; pterostigma of fore wing very short. *Cret.*, USSR (Asian RSFSR).

Retinaphis KONONOVA, 1975, p. 801 [**R. glandulosa*; OD]. Similar to *Tajmyrphis*, but antennae longer, with 6 segments. *Cret.*, USSR (Asian RSFSR).

Family MINDARIDAE Tullgren, 1909

[Mindaridae TULLGREN, 1909, p. 58]

Cauda subtriangular. Fore wing with pterostigma narrow, pointed, extending to apex of wing; vein RS arising from the proximal part of pterostigma. *Cret.—Holo.*

Mindarus KOCH, 1857, p. 277 [= *Pterostigma* BUCKTON, 1883, p. 178 (type, *P. recurvus*); *Schizoneuroides* BUCKTON, 1883, p. 178 (type, *S. scudderi*); *Sychnobrochus* SCUDDER, 1890, p. 268 (type, *S. reviviscens*)]. BAKER, 1922; HEIE, 1967, 1969b, 1985. *Oligo.*, Europe (Baltic), USA (Colorado)—*Holo.*

Nordaphis KONONOVA, 1977, p. 593 [**N. sukatchevae*; OD]. Little-known genus. Antennae with 6 segments. Fore wing with pterostigma very elongate; RS straight; M with one fork. Legs long. [Placed in Drepanosiphidae by KONONOVA but transferred to Mindaridae by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).

Family HORMAPHIDIDAE Mordvilko, 1908

[Hormaphididae MORDVILKO, 1908, p. 364]

Antennae with 3 to 5 segments, much shorter than body; antennae of alate form with narrow, ringlike, secondary rhinaria. Fore wing with veins CUA1 and CUA2 arising from same point on SC+R+M. *Oligo.—Holo.*

Hormaphis OSTEN-SACKEN, 1861, p. 422. *Holo.* *Electrocornia* HEIE, 1972, p. 249 [**E. antiqua*; OD]. Little-known genus, based on nymph. Antennae with 5 segments; head and pronotum fused; frons with 2 hornlike processes. [Originally placed in Thelaxidae but later transferred to Hormaphididae (HEIE, 1985).] *Oligo.*, Europe (Baltic).

Family ELEKTRAPHIDIDAE Steffan, 1968

[Elektraphididae STEFFAN, 1968, p. 11]

Antennae with 5 segments. Fore wing with vein RS greatly reduced; M typically without branches; CUA1 and CUA2 arising from stem CUA or originating independently from stem SC+R+M. KONONOVA, 1976. *Cret.—Oligo.*

Schizoneurites COCKERELL, 1915, p. 487 [**S. brevirostris*; OD] [= *Antiquaphis* HEIE, 1967, p. 88 (type, *A. robustus*); *Elektraphis* STEFFAN, 1968, p. 11 (type, *E. polykrypta*)]. Fore wing with CUA1 and CUA2 arising from common stem CUA. Antennae with transverse folds. HEIE, 1967, 1976, 1980, 1985; STEFFAN, 1968. *Oligo.*, Europe (Baltic), England.—FIG. 160.5. *S. robustus* (HEIE), Baltic; fore wing, $\times 34$ (Heie, 1967).

Antonaphis KONONOVA, 1977, p. 589 [**A. brachycera*; OD]. Antennae short, with 5 segments. Fore wing with RS long, slightly curved; M branched once. [Originally placed in Pemphigidae but transferred to *Elektraphididae* by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).

Tajmyrella KONONOVA, 1976, p. 118 [**T. cretacea*; OD]. Similar to *Schizoneurites*, but CUA1 and CUA2 arising independently from stem SC+R+M. HEIE, 1981. *Cret.*, USSR (Asian RSFSR).

Family THELAXIDAE Baker, 1920

[Thelaxidae BAKER, 1920, p. 21]

Antennae with 5 segments. Media of fore wing with 2 terminal branches. Hind wing with two oblique veins. *Oligo.—Holo.*

Thelaxes WESTWOOD, 1840, p. 118. *Holo.* *Palaeothelaxes* HEIE, 1967, p. 42 [**P. setosa*; OD]. Little-known genus. All body segments of apterous form with very thick, large setae; frons of alate form with similar large setae. *Oligo.*, Europe (Baltic).

Family ANOECIIDAE Tullgren, 1909

[Anoeciidae TULLGREN, 1909, p. 186]

Antennae commonly with 6 segments, and in alate forms with oval or subcircular sec-

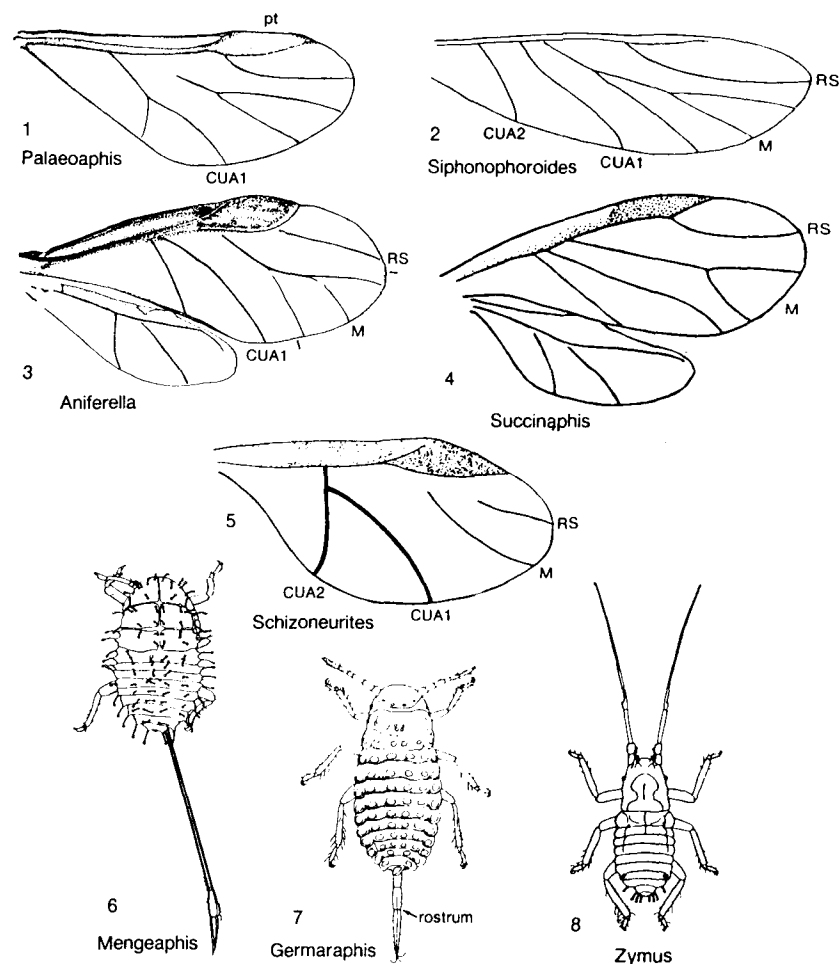


FIG. 160. Palaeoaphididae, Elektraphididae, Pemphigidae, and Drepanosiphidae (p. 247–251).

ondary rhinaria; marginal tubercles present on prothorax and some abdominal segments. Pterostigma of fore wing not more than four times longer than its width. *Oligo.—Holo.*

Anoecia KOCH, 1857, p. 275. *Holo.* *Berendtaphis* HEIE, 1971, p. 262 [**Lachnus cimicoides* GERMAR & BERENDT, 1856, p. 5; OD]. Little-known genus, based on apterous form. Antennae with 6 segments, distal segments conspicuously thickened; head and pronotum not fused. *Oligo.*, Europe (Baltic).

Family PEMPHIGIDAE Koch, 1857

[Pemphigidae KOCH, 1857, p. viii]

Antennae short, usually with 6 segments and with one very short terminal process. Fore wing with vein M unbranched or with one fork. Hind wing with 1 or 2 oblique veins. *Oligo.—Holo.*

Pemphigus HARTIG, 1839, p. 645. *Holo.* *Eriosoma* LEACH, 1818, p. 60. HEIE, 1968a, 1969a,

1969c, 1985. *Mio./Plio.*, Europe (Germany)—*Holo.*
Geramaraphis HEIE, 1967, p. 47 [**Lachnus dryoides* GERMAR & BERENDT, 1856, p. 29; OD]. Little-known genus, based mainly on apterous specimens. Antennae with 5 or 6 segments, the second one at least as long as the fourth. [Originally placed in Phloeomyzidae by HEIE (1967) and BECKER-MIGDISOVA (1973) but transferred to Pemphigidae by HILLE RIS LAMBERS (1980) and HEIE (1985).] HEIE, 1969b, 1972, 1985; BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic). — FIG. 160.7. **G. dryoides*; apterous specimen, reconstruction, X30 (Heie, 1967).
Succinaphis HEIE, 1967, p. 173 [**S. flauensgaardii*; OD]. Apparently similar to *Pemphigus* (recent). Media of fore wing branched; wing membrane with fine reticulation. HEIE, 1985. *Oligo.*, Europe (Baltic). — FIG. 160.4. **S. flauensgaardii*; fore and hind wings, X45 (Heie, 1967).

Family DREPANOSIPHIDAE Koch, 1857

[Drepanosiphidae KOCH, 1857, p. vii]

Closely allied to the Aphididae. Secondary transverse or circular rhinaria usually present on third antennal segment of alate females. Fore wing: vein M with 2 or 3 terminal branches. Hind wing with 2 or 3 oblique veins. HEIE, 1980, 1982. *Cret.—Holo.*

Drepanosiphum KOCH, 1855, p. 201. *Holo.*
Aixaphis HEIE, 1970b, p. 115 [**Tetraneura oligocnica* THÉOBALD, 1937a, p. 16; OD]. Antennae about half body length, with 6 segments. Fore wing: M with 3 terminal branches; CUA1 and CUA2 arising independently from stem SC+R+M, their bases relatively remote. [Family assignment doubtful.] HEIE, 1985. *Oligo.*, Europe (France).
Aniferella RICHARDS, 1966, p. 759 [**A. bostoni*; OD]. Antennae with 5 segments. Fore wing with well developed pterostigma; RS nearly straight; M with 2 forks; CUA1 and CUA2 arising separately from stem SC+R+M. HEIE, 1981, 1985. *Cret.*, Canada (Alberta). — FIG. 160.3. **A. bostoni*; fore and hind wings, X35 (Richards, 1966).
Balticaphis HEIE, 1967, p. 160 [**B. exsiccata*; OD]. Little-known genus, based on apterous form. Antennae with 5 or 6 segments. Fore femora thickened. HEIE, 1985. *Oligo.*, Europe (Baltic).
Balticomaraphis HEIE, 1967, p. 167 [**B. latens*; OD]. Little-known genus, based on cast cuticle of nymph. Antennae with 6 segments; ocular

tubercles well developed. *Oligo.*, Europe (Baltic).
Conicaudus HEIE, 1972, p. 255 [**C. longipes*; OD]. Little-known genus, based on alate form. Antennae about as long as body. M of fore wing with 3 or 4 terminal branches. Tarsi very long. *Oligo.*, Europe (Baltic).
Cretacallis SHAPOSHNIKOV, 1979a, p. 730, footnote [**C. polysensoria*; OD]. Antennae with 6 segments. Fore wing: M with 3 terminal branches; CUA1 and CUA2 arising independently from stem SC+R+M. [Family position doubtful.] *Cret.*, Mongolia.
Electrocallis HEIE, 1967, p. 147 [**E. bakeri*; OD] [= *Dimeraphis* BECKER-MIGDISOVA, 1973, p. 87 (type, *D. arnoldii*)]. Antennae of alate form much longer than body and composed of 6 segments. Fore wing with pterostigma short; M with 3 terminal branches; CUA1 and CUA2 arising separately from stem SC+R+M. Fore femora thicker than the others. *Oligo.*, Europe (Baltic).
Megantennaphis HEIE, 1967, p. 142 [**M. hanniensis*; OD]. Antennae with 6 segments and much longer than body. Fore wing with pterostigma long, pointed; RS almost straight; M with 3 terminal branches. Fore and hind femora large and strong. BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic).
Megapodaphis HEIE, 1967, p. 155 [**M. monstrabilis*; OD]. Antennae with 6 segments and at least as long as body. Fore wing: M with 2 terminal branches. Fore femora strongly thickened. HEIE, 1972, 1985. *Oligo.*, Europe (Baltic).
Mengeaphis HEIE, 1967, p. 113 [**Lachnus glandulosus*; OD]. Little-known genus, based on immature nymphs. Antennae with 4 segments; rostrum at least twice the length of body. BECKER-MIGDISOVA, 1973. *Oligo.*, Europe (Baltic). — FIG. 160.6. **M. glandulosus*; dorsal view, X85 (Becker-Migdisova, 1973).
Oligocallis HEIE, 1967, p. 133 [**O. larisoni*; OD]. Little-known genus, based on alate form. Similar to *Pterasthenica* (recent), but venation of fore wing less reduced in *Oligocallis*. HEIE, 1972. *Oligo.*, Europe (Baltic).
Oryctaphis SCUDDER, 1890, p. 266 [**O. lesueurii*; OD]. Little-known genus, possibly a synonym of *Siphonophoroides*. HEIE, 1985. *Oligo.*, USA (Colorado).
Palaeophyllaphis HEIE, 1967, p. 97 [**P. longirostris*; OD]. Antennae with 6 segments. Fore wing: M with 2 or 3 terminal branches; pterostigma slightly pointed but short. GERMAR & BERENDT, 1856; HEIE, 1972, 1985. *Oligo.*, Europe (Baltic).
Palaeosiphon HEIE, 1967, p. 119 [**Aphis hirsuta* GERMAR & BERENDT, 1856, p. 6; OD]. Little-known genus. Antennae of apterous form with 5 segments. Fore wing: M with 3 terminal branches. Hind wing with only one oblique vein.

Head and first two thoracic segments of alate form with long, curved, hornlike projections. HEIE, 1971. *Oligo.*, Europe (Baltic).
Siphonophoroides BUCKTON, 1883, p. 176 [**S. antiqua*; OD] [= *Archilachnus* BUCKTON, 1883, p. 177 (type, *A. pennata*); *Aphantaphis* SCUDDER, 1890, p. 253 (type, *S. exsua*); *Cataneura* SCUDDER, 1890, p. 245 (type, *C. absens*); *Amalancon* SCUDDER, 1890, p. 270 (type, *A. lutosus*)]. Antennae slender, longer than body. Fore wing with RS very long, relatively straight, arising from proximal half of pterostigma; M with 3 terminal branches. COCKERELL, 1908u, 1909b; HEIE 1967, 1985. *Eoc.*, Europe (Denmark); *Oligo.*, USA (Colorado). — FIG. 160.2. **S. antiqua*; fore wing, X14 (Heie, 1967).
Sternaphis HEIE, 1972, p. 257 [**S. electricola*; OD]. Fore wing with RS short and straight; M with 2 terminal branches. *Oligo.*, Europe (Baltic).
Succaphis HEIE, 1967, p. 110 [**S. holgeri*; OD]. Little-known genus, based on apterous form. Head and pronotum separated; antennae with 4 segments; rostrum longer than body. [Family assignment doubtful.] HEIE, 1985. *Oligo.*, Europe (Baltic).
Tertiaphis HEIE, 1969b, p. 144 [**T. baentzscheli*; OD]. Antennae with 6 segments and shorter than body. Fore wing: M with 2 terminal branches; CUA1 and CUA2 arising separately from stem SC+R+M. HEIE, 1985. *Oligo.*, Europe (Baltic).
Zymus HEIE, 1972, p. 254 [**Z. succinicola*; OD]. Little-known genus, based on nymph. Antennae with 4 segments and with long, filamentous terminal segment; head and pronotum fused; strong bristles on head and posterior part of abdomen. *Oligo.*, Europe (Baltic). — FIG. 160.8. **Z. succinicola*; dorsal view of nymph, X24 (Heie, 1972).

Family APHIDIDAE Latreille, 1802

[Aphididae LATREILLE, 1802a, p. 263]

Compound eyes large in all instars; antennae commonly with 6 segments (rarely with 5), at least half length of body. Fore wing: vein RS with 2 or 3 terminal branches; CUA and CUP arising independently from stem R+M+CU. Hind wing commonly with 2 oblique veins, rarely only one. Wings slanted at rest. *Cret.—Holo.*

Aphis LINNÉ, 1758, p. 451. *Holo.*
Aphidocallis KONONOVA, 1977, p. 595 [**A. caudatus*; OD]. Antennae with 5 segments. Fore wing with pterostigma short, extending only to about level of midwing; M with 3 terminal branches. *Cret.*, USSR (Asian RSFSR).

Baltichaitophorus HEIE, 1967, p. 180 [**B. jurandicus*; OD]. Little-known genus, based on apterous forms. Antennae with 6 segments, about as long as body. HEIE, 1980. *Oligo.*, Europe (Baltic).
Diatomyzus HEIE, 1970a, p. 163 [**D. eocaenicus*; OD]. Little-known genus, based on alate specimens. Similar to several existing genera, but RS of fore wing unusually long. *Eoc.*, Europe (Denmark).
Pseudamphorophora HEIE, 1967, p. 175 [**P. succini*; OD]. Little-known genus, based on apterous forms. [Family assignment doubtful.] HEIE, 1971, 1980. *Oligo.*, Europe (Baltic).

Family LACHNIDAE Koch, 1857

[Lachnidae KOCH, 1857, p. vii]

Similar to Anoeciidae, but prothorax and abdominal segments lacking marginal tubercles. Pterostigma of fore wing commonly much longer than 4 times its width. *Mio./Plio.—Holo.*

Lachnus BURMEISTER, 1835, p. 92. *Holo.*
Longistigma WILSON, 1909, p. 385. HILL & FRIEDRICH, 1971; HEIE, 1985. *Mio./Plio.*, Iceland—*Holo.*

Family ALEYRODIDAE Westwood, 1840

[Aleyrodidae WESTWOOD, 1840, p. 442]

Wings slightly thickened, commonly covered with a powdery wax. Fore wing venation weakly formed, only veins R and M extending to distal part of wing. Antennae with 7 segments; terminal abdominal segment with a large, dorsal opening, associated with storage of honey dew. *Oligo.—Holo.*

Aleyrodes LATREILLE, 1796, p. 93. [Generic assignment of fossil doubtful.] MENGE, 1856; SCHLEE, 1970. *Oligo.*, Europe (Baltic)—*Holo.*
Aleurodicus DOUGLAS, 1892, p. 32. [Generic assignment of fossil doubtful.] COCKERELL, 1919c; SCHLEE, 1970. *Mio.*, Burma—*Holo.*

Family COLEOSCYTIDAE Martynov, 1935

[Coleoscytidae MARTYNOV, 1935c, p. 24]

Fore wing oval, weakly coriaceous, membranous distally; subcostal area abruptly widened at base; costal margin at right angles to wing axis at this point; vein SC marginal;

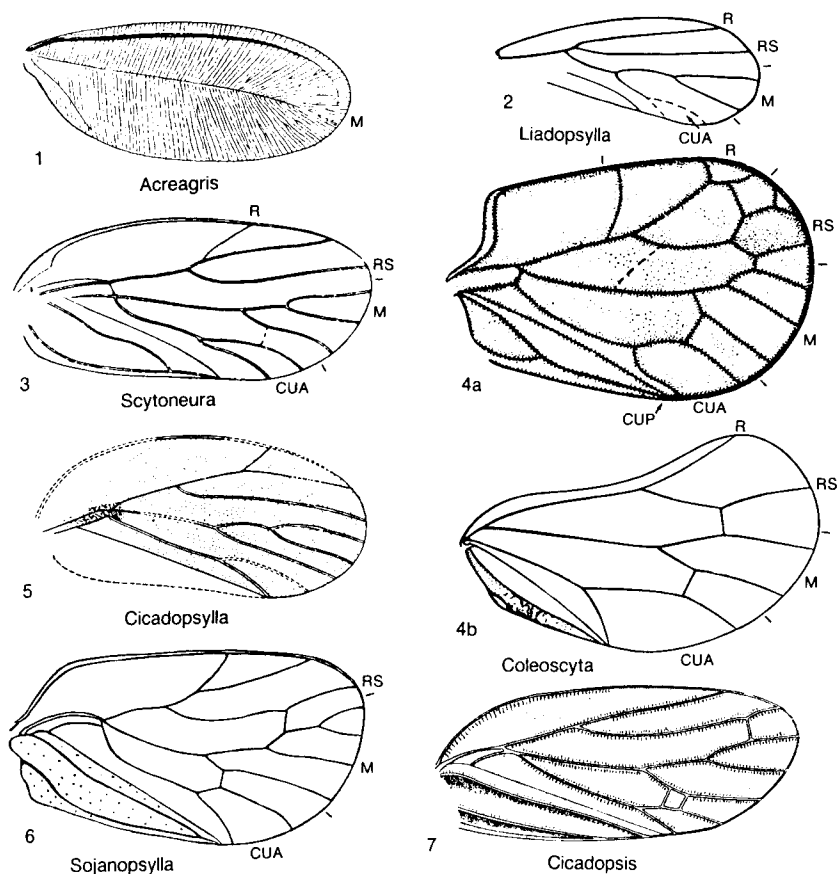


FIG. 161. Coleoscytidae, Cicadopsyllidae, Psyllidae, and Margarodidae (p. 252-254).

R long, with a branch to costal margin near midwing; M and CUA distally branched; CUP straight, unbranched; 1A and 2A with a common stem. Hind wing membranous, widened distally, more slender than fore wing, with concave anterior margin; subcostal area very narrow; M forked, CUA with a very wide fork; anal area narrow. Head hypognathous; eyes not divided. Hind coxae large. *Perm.*

Coleoscyta CARPENTER, herein [**C. rotundata* MARTYNOV, 1935c, p. 24; OD] [= *Coleoscytodes* CARPENTER, herein (type, *C. venosa* MARTYNOV,

1935c, p. 24; OD)]. Fore wing very broad, costal margin thickened; RS with distal fork. [The original generic names, *Coleoscyta* and *Coleoscytodes*, were *nomen nudum* (MARTYNOV, 1935c).] BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (European RSFSR).—FIG. 161.4a. **C. rotundata*; fore wing, X8. — FIG. 161.4b. *C. venosa* (MARTYNOV); hind wing, X8 (Becker-Migdisova, 1960).

Sojanopsylla BECKER-MIGDISOVA, 1960, p. 45 [**S. brevipennis*; OD]. Fore wing as in *Coleoscyta*, but subcostal area gradually widened basally and R and RS longer; M with 3 or 4 branches. *Perm.*, USSR (European and Asian RSFSR).—FIG. 161.6. **S. brevipennis*; fore wing, X4.5 (Becker-Migdisova, 1960).

Family CICADOPSYLLIDAE

Martynov, 1931

[*nom. transl.* MARTYNOV, 1935c, p. 16, ex Cicadopsyllinae MARTYNOV 1931c, p. 172]

Fore wing elongate oval, commonly membranous; subcosta apparently close to costal margin; RS long, ending near wing apex. Hind wing with M apparently arising from stem of R; CUA originating independently of R+M. Head hypognathous, with protuberances on vertex. Hind coxae conical, elongate. BECKER-MIGDISOVA, 1962b. *Perm.*

Cicadopsylla MARTYNOV, 1931c, p. 173 [**C. permiana*; OD]. Fore wing with M forking near level of midwing. *Perm.*, USSR (European RSFSR). — FIG. 161.5. **C. permiana*; fore wing, X4 (Becker-Migdisova, 1962b).

Cicadopsis BECKER-MIGDISOVA, 1959a, p. 110 [**C. rugosipenna*; OD]. Similar to *Cicadopsylla*, but R without distal, anterior branch. *Perm.*, USSR (Asian RSFSR). — FIG. 161.7. **C. rugosipenna*; fore wing, X8 (Becker-Migdisova, 1962b).

Scytoneura MARTYNOV, 1935c, p. 16 [**S. elliptica*; OD]. Fore wing similar to *Cicadopsylla*, but M dividing more distally. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR). — FIG. 161.3. **S. elliptica*; fore wing, X3 (Becker-Migdisova, 1962b).

Scytoneurella ZALESSKY, 1939, p. 39 [**S. major*; OD]. Fore wing membranous, costal margin slightly convex; M dividing distally of fork of CUA, with 3 short branches. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).

Family PSYLLIDAE Latreille, 1807

[Psyllidae LATREILLE, 1807, p. 168]

Fore wing usually coriaceous; costal area broad; veins M and CUA united to form a basal stem; RS arising from R independently; M and CU usually arising as a common stem; RS unbranched; M and CUA forked. Hind wing smaller and more slender, with R and M unbranched. Antennae with 9 to 10 segments. *Jur.*—*Holo.*

Psylla GEOFFREY, 1762, p. 482. BECKER-MIGDISOVA, 1964. *Oligo.*, England; *Mio.*, USSR (European RSFSR)—*Holo.*

Agonoscaena ENDERLEIN, 1914, p. 234. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Catopsylla SCUDDER, 1890, p. 277 [**C. prima*; OD].

Little-known genus. Fore wing as in *Psylla*, but cell of CU much longer. *Oligo.*, USA (Colorado). *Liadopsylla* HANDLIRSCH, 1920, p. 213 [**L. geinitzi*; OD]. Fore wing oval, membranous; R and RS long, parallel; stem of R short; fork of M long. MARTYNOV, 1926b; BECKER-MIGDISOVA, 1949b. *Jur.*, Europe (Germany), USSR (Asian RSFSR). — FIG. 161.2. *L. tenuicornis* MARTYNOV, USSR; fore wing, X20 (Martynov, 1926b).

Livilla CURTIS, 1836, p. 625. COCKERELL, 1921d. *Oligo.*, England—*Holo.*

Necropsylla SCUDDER, 1890, p. 276 [**N. rigida*; OD]. Little-known genus; fore wing as in *Psyllis* (recent) but subtriangular. COCKERELL, 1911b, 1915. *Oligo.*, USA (Colorado), England.

Psyllites COCKERELL, 1914f, p. 636 [**P. crawfordi*; OD]. Little-known genus, probably a synonym of *Catopsylla*. *Oligo.*, USA (Colorado).

Retroacizzia HESLOP-HARRISON, 1961, p. 504. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Strophingia ENDERLEIN, 1914, p. 233. *Oligo.*, Europe (Baltic)—*Holo.*

Trioza FÖRSTER, 1848, p. 67. BECKER-MIGDISOVA, 1964. *Mio.*, USSR (European RSFSR)—*Holo.*

Family COCCIDAE Fallén, 1814

[Coccidae FALLÉN, 1814, p. 23]

Adults with marked sexual dimorphism. Males with fore wings normally developed; hind wings reduced or halterlike. Females apterous; antennae diverse, commonly much reduced; abdominal spiracles absent. *Oligo.*—*Holo.*

Coccus LINNÉ, 1758, p. 455. MENGE, 1856; COCKERELL, 1906b; BECKER-MIGDISOVA, 1962b. *Oligo.*, Europe (Baltic)—*Holo.*

Family ORTHEZIIDAE

Amyot & Serville, 1843

[Ortheziidae AMYOT & SERVILLE, 1843, p. 619]

Similar to Coccidae. Females with body clearly segmented; antennae with distinct segmentation; abdominal spiracles present. *Oligo.*—*Holo.*

Orthezia BOSCH, 1784, p. 173. *Holo.*

Ochyrocoris MENGE, 1856, p. 17 [**O. electrina*; OD]. Little-known genus, probably a synonym of *Orthezia* (recent). COCKERELL, 1906a; BECKER-MIGDISOVA, 1962b. *Oligo.*, Europe (Baltic).

Family MARGARODIDAE Cockerell, 1899

[Margarodidae COCKERELL, 1899, p. 390]

Males commonly winged, with few unbranched veins. Females with convex body, strongly sclerotized, with clear segmentation; abdomen with an anal tube or a sclerotized ring, lacking setae. *Cret.*—*Holo.*

Margarodes GUILDING, 1829, p. 118. *Holo.*

Acreagris KOCH in KOCH & BERENDT, 1854, p. 123 [**A. crenata*; OD]. Female adult: antennae with 9 segments; body entirely or nearly devoid of setae; tarsi two-segmented. Male adult: compound eyes; wings with a single vein paralleling the costal margin to wing apex; M delicate, bisecting the wing diagonally; hind wing reduced to slender halteres; antennae with at least 8 segments; tarsi one-segmented; abdomen with long threads of wax arising from clusters of dorsal ducts. FERRIS, 1941. *Oligo.*, Europe (Baltic).—FIG. 161, 1. **A. crenata*; fore wing of male, X6 (Ferris, 1941).

Electrococcus BEARDSLEY, 1969, p. 271 [**E. canadensis*; OD]. Male small; antennae with 10 segments, pedicel conspicuously enlarged; legs long and slender; compound eye reduced to a single row of ommatidia. Fore wing well developed, with R and M distinct. *Cret.*, Canada (Manitoba).

Family PSEUDOCOCCIDAE Cockerell, 1905

[Pseudococcidae COCKERELL, 1905, p. 193]

Similar to the Coccidae. Females typically covered with a mealy or filamentous, waxy secretion, commonly protruding as short lateral and long anal filaments; legs well developed. Males apterous or winged, typically with two long caudal wax filaments. *Oligo.*—*Holo.*

Pseudococcus WESTWOOD, 1840, p. 118. *Holo.*
Puto SIGNORET, 1875, p. 394. COCKERELL, 1908g. *Oligo.*, Europe (Baltic)—*Holo.*

Family UNCERTAIN

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

Anconatus BUCKTON, 1883, p. 177 [**A. dorsuosus*; OD]. Little-known aphidoid of uncertain affinities. HEIE, 1967, 1985. *Oligo.*, USA (Colorado).
Annulaphis SHAPOSHNIKOV, 1979b, p. 73 [**A. rar-*

nitsyni; OD]. Little-known genus, based on incomplete specimens; apparently related to *Ellinaphis*. [Originally placed in Palaeoaphididae, but transferred by HEIE (1985) to family uncertain.] *Cret.*, USSR (Asian RSFSR).

Aphidioides MOTSCHULSKY, 1856, p. 29 [**A. sacrificera*; OD]. Little-known aphidoid genus, based on apterous form. HEIE, 1967, 1985. *Oligo.*, Europe (Baltic).

Aphidulum HANDLIRSCH, 1939, p. 163 [**A. pusillum*; OD]. Little-known genus. HEIE, 1967. *Jur.*, England.

Archeglyphis MARTYNOV, 1931a, p. 89 [**A. crassinervis*; OD]. Little-known wing fragment. BECKER-MIGDISOVA, 1961c; ROHDENDORF & RASNITSYN, 1980. *Perm.*, USSR (Asian RSFSR).

Archipsyche HANDLIRSCH, 1906b, p. 624 [**A. eichstattenis*; OD]. Little-known genus, apparently similar to *Limacodites*. *Jur.*, Europe (Germany).

Austroscytina EVANS, 1943b, p. 181 [**A. imperfecta*; OD]. Little-known wing, possibly related to *Archescytinidae*. *Perm.*, Australia (New South Wales).

Beaconiella EVANS, 1963, p. 21 [**B. fennabi*; OD]. All principal veins of fore and hind wings multibranching; possibly a fulgoroid. RIEK, 1973. *Trias.*, Australia (New South Wales).

Beloptesis HANDLIRSCH, 1906b, p. 625 [**B. oppenheimi*; OD]. Fore wing markedly triangular, nearly as broad as long; venation apparently as in *Limacodites*. Hind wing small, oval. EVANS, 1956. *Jur.*, Europe (Germany).

Bernaia SCHLEE, 1970, p. 18 [**B. neocomica*; OD]. Female with head wider than pronotum; median ocellus present; antennae with 7 segments, the third segment much longer than distal segments. Veins absent on hind wing, represented by lines of pigment. [Placed by SCHLEE in "Aleyrodina *sensu lato*," without family assignment.] *Cret.*, Lebanon.

Borisorhdendorfia BECKER-MIGDISOVA, 1959b, p. 138 [**B. picturata*; OD]. Based on distal fragment of wing. BECKER-MIGDISOVA, 1961c. *Perm.*, USSR (Asian RSFSR).

Cercopidium WESTWOOD, 1854, p. 394 [**C. habni* WESTWOOD, 1854, p. 394; SD CARPENTER, herein]. Little-known genus, based on wing fragment. HEER, 1870a; HENRICKSEN, 1922b. *Jur.*, England; *Eoc.*, Greenland.

Chiliocyclus TILLYARD, 1919c, p. 868 [**C. scolopoides*; OD]. Fore wing with strongly thickened costal border; RS present, arising before midwing; closed cell between M1+2 and M3+4; CUA connected to base of M by crossvein. [Type of family Chiliocyclidae EVANS, 1956, p. 209.] EVANS, 1956, 1961. *Trias.*, Australia (Queensland).—FIG. 162, 1. **C. scolopoides*; fore wing, X4.5 (Evans, 1956).

Cicadellites HEER, 1853a, p. 119 [**C. pallidus* HEER, 1853a, p. 119; SD CARPENTER, herein]. Little-

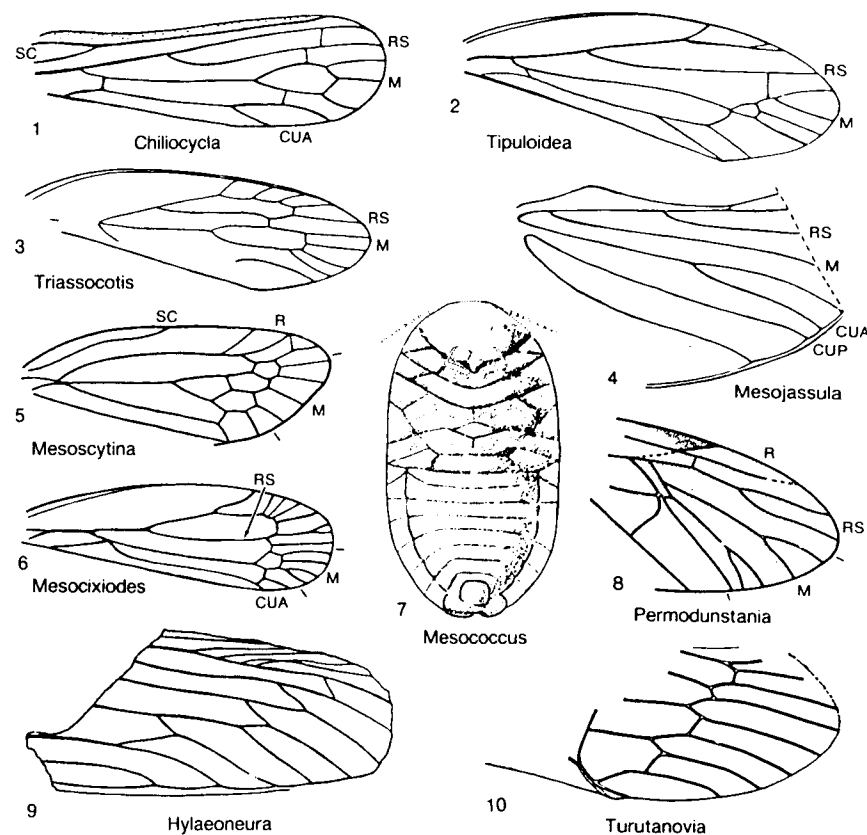


FIG. 162. Uncertain (p. 254-259).

known homopteron, possibly belonging to the Cercopidae. PITON & THÉOBALD, 1935. *Oligo.*, Europe (France); *Mio.*, Europe (Croatia).

Cicadellium WESTWOOD, 1854, p. 394 [**C. dipsas*; SD HANDLIRSCH, 1907, p. 641] [= *Pseudodelphax* HANDLIRSCH, 1907, p. 641 (type, *Delphax pulcher* BRODIE, 1845, p. 33)]. Little-known genus, based on fore wing. EVANS, 1956. *Jur.*, England.

Cixioides HANDLIRSCH, 1906b, p. 498 [**C. liasinus*; OD]. Little-known wing, possibly related to Fulgoridiidae. BECKER-MIGDISOVA, 1962b. *Jur.*, Europe (Germany).

Cixioides HANDLIRSCH, 1906b, p. 640 [**Cixioides maculatus* BRODIE, 1845, p. 33; OD]. Little-known fore wing, possibly related to Cixiidae. *Jur.*, England.

Diphtheropsis MARTYNOV, 1937a, p. 110 [**D. incerta*; OD]. Little-known genus, based on incomplete fore wing with nearly straight costal

margin and long R+M. EVANS, 1956. *Jur.*, USSR (Kirghiz).

Dysmorphoscartella RIEK, 1973, p. 527 [**D. lobata*; OD]. Little-known genus, based on distal fragment of wing. RIEK, 1976a. [Originally placed in Eoscartarellidae.] *Perm.*, South Africa.

Echinaphis COCKERELL, 1913f, p. 229 [**E. rohweri*; OD]. Little-known genus, based on hind wing and body fragments; apparently related to Greenideidae (recent) and Drepanosiphidae. HEIE, 1967, 1970b, 1985. *Oligo.*, USA (Colorado).

Electromyzus HEIE, 1972, p. 250 [**E. acutirostris*; OD]. Fore wing with RS very slightly curved; M with 2 terminal branches, arising close to point of origin of CUA1 and CUA2. HEIE, 1985. *Oligo.*, Europe (Baltic).

Ellinaphis SHAPOSHNIKOV, 1979b, p. 71 [**E. incognita*; OD]. Little-known genus, originally placed

- in Palaeophoridae but transferred by HEIE (1985) to category of family uncertain. *Cret.*, USSR (Asian RSFSR).
- Eochilocyclus* DAVIS, 1942, p. 114 [**E. angusta*; OD]. Little-known genus, based on fore wing; possibly fulgoroid. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Eocicada* OPPENHEIM, 1888, p. 229 [**E. microcephala*; OD]. Little-known genus, based on wing fragment. EVANS, 1956. *Jur.*, Europe (Germany).
- Eopsyllidium* DAVIS, 1942, p. 114 [**E. delicatulum*; OD]. Little-known hind wing, with CUA free from M basally. Possibly related to the Protopsyllidiidae. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Fulgoridiella* BECKER-MIGDISOVA, 1962a, p. 96 [**F. raetica*; OD]. Little-known wing fragment, possibly related to Fulgoridiidae. *Trias.*, USSR (Kirghiz).
- Fulgoropsis* MARTYNOV, 1937a, p. 165 [**F. dubiosa*; OD]. Little-known genus, based on wing fragment, possibly related to Fulgoridiidae. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kirghiz).
- Geranichon* SCUDDER, 1890, p. 248 [**Lachnus petrorum* SCUDDER, 1877b, p. 279; OD]. Little-known genus, possibly belonging to Aphidoidea. HEIE, 1967, 1985. *Eoc.*, Canada (British Columbia).
- Gryllites* GERMAR, 1842, p. 82 [**G. dubius*; OD]. Little-known genus, originally placed in Orthoptera. HAGEN, 1862; ASSMANN, 1877; POPOV, 1971. *Jur.*, Europe (Germany).
- Hastites* COCKERELL, 1922f, p. 161 [**H. muiri*; OD]. Little-known genus. Fore wing elongate; R apparently with a short distal branch; M dividing distally, with 3 terminal branches; CUA with 3 terminal branches. *Oligo.*, England.
- Heidea* SCHLEE, 1970, p. 9 [**H. cretatica*; OD]. Male with head about same width as pronotum; median ocellus present; third antennal segment about as long as distal segments. Vein present in hind wing. [Considered by SCHLEE to be related to the existing and Tertiary Aleurodidae but differing markedly in several traits.] *Cret.*, Lebanon.
- Hooleyia* COCKERELL, 1922f, p. 160 [**H. indecisa*; OD]. Little-known fore wing; costal margin broad; SC apparently separating from R before midwing, and giving rise to a series of short, oblique veinlets to costal margin. *Oligo.*, England.
- Homopterites* HANDLIRSCH, 1906b, p. 499 [**H. anglicus*; OD]. Little-known fore wing. *Jur.*, England.
- Hylaeoneura* LAMEERE & SEVERIN, 1897, p. 37 [**H. lignei*; OD]. Little-known genus, based on distal fragment of fore wing. R with several long, pectinate branches to costal margin; M with 3 branches. *Cret.*, Europe (Belgium). — FIG. 162.9. **H. lignei*; fore wing, $\times 2.5$ (Handlirsch, 1907).
- Hypocixius* COCKERELL, 1926a, p. 501 [**H. obtusescens*; OD]. Little-known genus, based on incomplete fore wing. Possibly related to Cixiidae. *Tert. (epoch unknown)*, Argentina (Jujuy).
- Jurocallis* SHAPOSHNIKOV, 1979b, p. 68 [**J. longipes*; OD]. Antennae tapering from base to apex; RS arising from distal part of pterostigma area; M arising from base of pterostigma and with 3 terminal branches. [Originally placed in Drepanosiphidae.] HEIE, 1985. *Cret.*, USSR (Asian RSFSR).
- Kaltanocicada* BECKER-MIGDISOVA, 1961c, p. 291 [**K. dunstanoides*; OD]. Little-known hind wing, with broadly rounded apex and wide concavity of front wing margin; CUA with long fork. BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (Asian RSFSR).
- Kaltanoscyta* BECKER-MIGDISOVA, 1959a, p. 110 [**K. reticulata*; OD]. Little-known fragment of fore wing, strongly coriaceous and with dense reticulation over wing. Possibly related to Coleoscytidae. *Perm.*, USSR (Asian RSFSR).
- Karabasia* MARTYNOV, 1926b, p. 1356 [**K. paucinervis*; OD]. Little-known insect, possibly related to Jassidae. *Jur.*, USSR (Kazakh).
- Karajassus* MARTYNOV, 1926b, p. 1352 [**K. crassinervis*; OD]. Little-known insect, possibly close to Cicadellidae. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh).
- Kisylia* MARTYNOV, 1937a, p. 109 [**K. psylloides*; OD]. Little-known genus, based on fore wing. Nodus and nodal line absent; stem of R slightly shorter than R + M; CUA not coalesced with M. *Jur.*, USSR (Kirghiz). — FIG. 163.4. **K. psylloides*; fore wing, $\times 3$ (Becker-Migdisova, 1962b).
- Larssonaphis* HEIE, 1967, p. 168 [**L. obnubila*; OD]. Little-known aphidoid genus. HEIE, 1985. *Oligo.*, Europe (Baltic).
- Liassocicada* BODE, 1953, p. 201 [**L. antecessens*; OD]. Little-known genus, based mainly on body structure. Rostrum elongate, extending at least to middle of abdomen. [Liassocicada was redefined by WHALLEY (1983) and provisionally placed in the Cicadidae. However, I doubt that our very slight knowledge of the body structures of these Jurassic and Triassic specimens justifies the extension of the range of the Cicadidae to another 150 million years before the Paleocene. Accordingly, the genus *Liassocicada* is herein provisionally placed in the Homoptera, family uncertain.] WHALLEY, 1983. *Trias.*, England; *Jur.*, Europe (Germany).
- Limacodites* HANDLIRSCH, 1906b, p. 622 [**L. mesozoicus*; OD]. Little-known genus, based on wing fragments. Probably related to *Eocicada*. *Jur.*, Europe (Germany).
- Lithecphora* SCUDDER, 1890, p. 329 [**L. unicolor* SCUDDER, 1890, p. 329; SD CARPENTER, herein]. Little-known insect, with slender fore wing. *Oligo.*, USA (Colorado).

- Lithopsis* SCUDDER, 1878b, p. 773 [**L. fimbriata*; OD]. Body stout; head not produced between the eyes. Tegmina extending well beyond abdomen. SCUDDER, 1890; COCKERELL, 1921b; PONGRÁČ, 1935; PITON, 1940a. *Eoc.*, USA (Wyoming), Europe (France, Germany).
- Locrites* SCUDDER, 1890, p. 323 [**L. capei* SCUDDER, 1890, p. 323; SD CARPENTER, herein]. Little-known homopteron; head large, protuberant; scutellum equiangular. HEER, 1853a. *Oligo.*, USA (Colorado); *Mio.*, Europe (Croatia).
- Margaroptilon* HANDLIRSCH, 1906b, p. 499 [**M. woodwardi* HANDLIRSCH, 1906b, p. 499; SD CARPENTER, herein]. Little-known wings, with numerous small maculations; possibly a fulgoroid. BODE, 1953; EVANS, 1956. *Jur.*, England, Europe (Germany).
- Mesaleuropsis* MARTYNOV, 1937a, p. 108 [**M. venosa*; OD]. Little-known wings. Fore wing rounded distally; pterostigma absent; M with 2 branches; CUA apparently unbranched. Hind wing about half as long as fore wing, with unbranched RS and M. *Jur.*, USSR (Tadzhik).
- Meshemipteron* COCKERELL, 1915, p. 476 [**M. incertum*; OD]. Little-known genus, based on small fragment of wing. *Jur.*, England.
- Mesocicadella* EVANS, 1956, p. 193 [**M. venosa*; OD]. Little-known genus, based on fragment of fore wing. Several parallel, oblique veins between R and wing margin; M with numerous branches. [Originally placed in the Scytinopteridae but moved to family uncertain by EVANS in 1961.] *Trias.*, Australia (Queensland). — FIG. 163.2. **M. venosa*; fore wing, $\times 3.5$ (Evans, 1956).
- Mesocixiodes* TILLYARD, 1922b, p. 462 [**M. termioneura*; OD]. Fore wing with SC very close to costal margin; RS present; M forking in distal part of wing, with a small, closed cell between forks. EVANS, 1956. *Trias.*, Australia (Queensland). — FIG. 162.6. **M. termioneura*; fore wing, $\times 5.2$ (Evans, 1956).
- Mesococcus* BECKER-MIGDISOVA, 1959a, p. 110 [**M. asiaticus*; OD]. Based on wingless form (female?); body oval; legs greatly reduced; abdomen with 9 visible segments. BECKER-MIGDISOVA, 1962b. *Trias.*, USSR (Kirghiz). — FIG. 162.7. **M. asiaticus*; whole insect, $\times 24$ (Becker-Migdisova, 1959a).
- Mesodiphthera* TILLYARD, 1919c, p. 873 [**M. grandis*; OD]. Little-known genus, based on small fragment of fore wing. CUA anastomosed with M basally. [Placed in Tropiduchidae by TILLYARD (1922b) and in Homoptera, family uncertain, by EVANS (1956).] *Trias.*, Australia (Queensland). — FIG. 163.3. **M. grandis*; fore wing, $\times 3.5$ (Tillyard, 1919c).
- Mesojassula* EVANS, 1956, p. 203 [**M. marginata*; OD]. Hind wing with costal margin with marked medial depression; M unbranched; CUA with 2 equal branches; marginal vein present. *Trias.*,

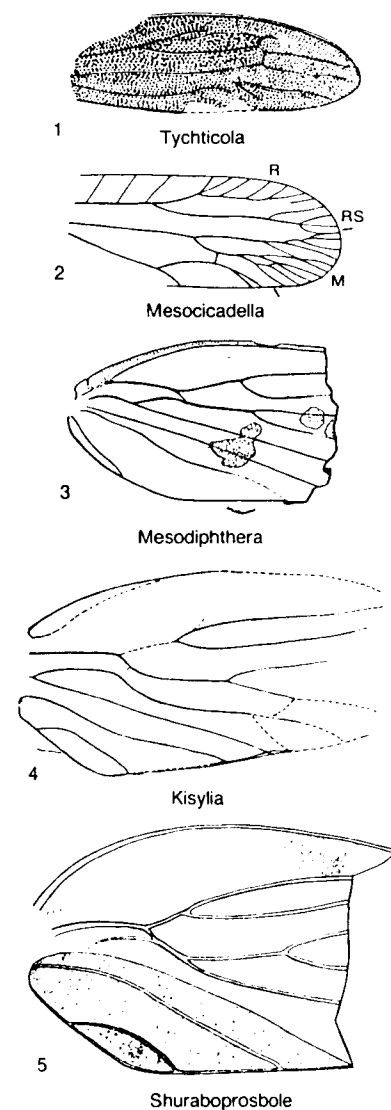


FIG. 163. Uncertain (p. 256–259).

- Australia (Queensland). — FIG. 162.4. **M. marginata*; hind wing, $\times 4.5$ (Evans, 1956).
- Mesoledra* EVANS, 1956, p. 211, *nom. subst. pro Mesojassus* HANDLIRSCH, 1939, p. 145, *non* TILLYARD, 1916 [**Mesojassus pachyneurus* HANDLIRSCH, 1939, p. 145; OD]. Little-known

- genus, based on incomplete wing; possibly related to Cicadellidae. *Jur.*, Europe (Germany).
- Mesoscytina** TILLYARD, 1919c, p. 871 [**M. australis*; OD]. Fore wing with SC distinct, long; RS apparently arising in very distal part of wing; M dividing at midwing and forming a closed cell at fork. Possibly related to Scytinopteridae. EVANS, 1956. *Trias.*, Australia (Queensland).—FIG. 162.5. **M. australis*; fore wing, X5.2 (Evans, 1956).
- Meuniera** PITON, 1936c, p. 1 [**M. haupti*; OD]. Little-known genus, based on fragment of fore wing. RS arising well before midwing; basal stem of M free from R. COOPER, 1941. *Eoc.*, Europe (France).
- Pachypsyche** HANDLIRSCH, 1906b, p. 623 [**Palaeontina vidale* MEUNIER, 1902e, p. 9; OD]. Little-known genus. Fore wing rectangular; anterior margin straight, without nodal break; venation as in *Limacodites*. *Jur.*, Europe (Spain).
- Palaeoforda** KONONOVA, 1977, p. 588 [**P. tajmyrensis*; OD]. Little-known genus. Antennae with 6 segments. Fore wing with RS arising from distal part of pterostigma; M unbranched. Legs short. [Placed in Pemphigidae by KONONOVA but transferred to family uncertain by HEIE (1985).] *Cret.*, USSR (Asian RSFSR).
- Parafulguridium** HANDLIRSCH, 1939, p. 138 [**Fulguridium simplex* GEINITZ, 1880, p. 528; OD]. Little-known genus, based on poorly preserved fore wing. *Jur.*, Europe (Germany).
- Parajassus** BODE, 1953, p. 200 [**P. hattorfensis*; OD]. Little-known wing. BECKER-MIGDISOVA, 1962b. *Jur.*, Europe (Germany).
- Perissovena** RIEK, 1976a, p. 775 [**P. heidia*; OD]. Little-known genus, based on hind wing. *Perm.*, South Africa.
- Permocapitus** EVANS, 1943b, p. 195 [**P. globulus*; OD]. Little-known genus, based on head. Head oval, eyes globular; transverse ridge between eyes. *Perm.*, Australia (New South Wales).
- Permocephalus** EVANS, 1943a, p. 8 [**P. knightii*; OD]. Little-known insects, known only by fragments of head. *Perm.*, Australia (New South Wales).
- Permodontania** BECKER-MIGDISOVA, 1961c, p. 290 [**P. proboloides*; OD]. Distal fragment of fore wing; RS forked; M4 free from M3 distally. *Perm.*, USSR (Asian RSFSR).—FIG. 162.8. **P. proboloides*; fore wing, X2.7 (Becker-Migdisova, 1961c).
- Petropterion** COCKERELL, 1912b, p. 94 [**P. mirandum*; OD]. Little-known genus, based on wing fragment; possibly a fulgoroid. *Cret.*, USA (Colorado).
- Phragmatococcossus** BECKER-MIGDISOVA, 1949b, p. 11 [**P. shurabensis*; OD]. Little-known genus, based on fragment of fore wing. Probably related to Paleontinidae. *Jur.*, USSR (Asian RSFSR).
- Plecophlebus** COCKERELL, 1917h, p. 327 [**P. nebulosus*; OD]. Little-known genus, based on wing and fragments of body. [Originally placed in Trichoptera, but transferred to Homoptera, family uncertain, by BOTOSANEANU, 1981.] *Mio.*, Burma.
- Prolystra** OPPENHEIM, 1888, p. 228 [**P. lithographica*; OD]. Little-known genus, probably close to *Limacodites*. EVANS, 1956. *Jur.*, Europe (Germany).
- Prosbolopsis** MARTYNOV, 1935c, p. 19 [**P. ovalis*; OD]. Little-known insect, with reduced venation in tegmen. [Type of family Prosbolopseidae BECKER-MIGDISOVA, 1946.] EVANS, 1956; BECKER-MIGDISOVA, 1962b. *Perm.*, USSR (European RSFSR).
- Protopsyche** HANDLIRSCH, 1906b, p. 623 [**P. braueri*; OD]. Little-known genus, similar to *Limacodites*. *Jur.*, Europe (Germany).
- Reticulocicada** BECKER-MIGDISOVA, 1961c, p. 362 [**R. brachyptera*; OD]. Little-known tegmen, with coarse reticulation; possibly a fulgoroid. *Perm.*, USSR (Asian RSFSR).
- Sbenaphis** SCUDDER, 1890, p. 250 [**S. quesneli*; OD]. Little-known aphidoid genus. HEIE, 1967, 1985. *Eoc.*, Canada (British Columbia).
- Shuraboprosbole** BECKER-MIGDISOVA, 1949b, p. 23 [**S. plachutai*; OD]. Little-known genus, based on wing fragment. Basal stem of R only about half as long as R+M; RS arising well before midwing; CUA anastomosed with M for a short distance. *Jur.*, USSR (Tadzhik).—FIG. 163.5. **S. plachutai*; fore wing as preserved, X2.5 (Becker-Migdisova, 1949b).
- Stenoglyphis** EVANS, 1947b, p. 432 [**S. kimblensis*; OD]. Little-known genus, possibly related to Scytinopteridae. EVANS, 1956. *Perm.*, Australia (New South Wales).
- Tingiopsis** BECKER-MIGDISOVA, 1953c, p. 461 [**T. reticulata*; OD]. Little-known genus, based on incomplete fore wing with fine reticulation. [Originally placed in Tingidae (Heteroptera) but transferred to Homoptera, probably Cercopidae, by EVANS (1957).] *Trias.*, USSR (Tadzhik).
- Tipuloidea** WIELAND, 1925, p. 23 [**T. rhaetica*; OD]. Little-known genus, based on fore wing. Costal margin arched; SC apparently absent; RS arising before midwing; closed median cell very small. [Originally placed in order Diptera.] EVANS, 1956. *Trias.*, Argentina.—FIG. 162.2. **T. rhaetica*; fore wing, X2 (Evans, 1956).
- Triassoaphis** EVANS, 1956, p. 238 [**T. cubitus*; OD]. Little-known genus, based on wing fragment. [Originally placed in Aphididae but transferred to Aphidoidea, family uncertain, by BECKER-MIGDISOVA & AIZENBERG (1962).] RICHARDS, 1966; HEIE, 1967, 1981; SHAPOSHNIKOV, 1979a. *Trias.*, Australia (Queensland).
- Triassocotis** EVANS, 1956, p. 194 [**T. australis*; OD]. Little-known genus, based on distal half of tegmen. Tegmen narrow; R with 4 branches;

- RS unbranched; M with 4 branches and a cell included between M1+2 and M3+4. [Originally placed in Scytinopteridae but transferred to family uncertain by EVANS (1961).] *Trias.*, Australia (Queensland).—FIG. 162.3. **T. australis*; fore wing, X4.5 (Evans, 1956).
- Triassojassus** TILLYARD, 1919c, p. 887 [**T. proavittus*; OD]. Little-known genus, based on incomplete tegmen. Costal margin unusually convex; RS unbranched; M with 5 branches. [Originally placed in the Jassidae, but EVANS transferred first (1956) to the Chilocyclidae and later (1961) to family uncertain.] *Trias.*, Australia (New South Wales).
- Turutanovia** BECKER-MIGDISOVA, 1949b, p. 21 [**T. karatavia*; OD]. Little-known genus, based on distal fragment of fore wing. BECKER-MIGDISOVA, 1962b. *Jur.*, USSR (Kazakh).—FIG. 162.10. **T. karatavia*; fore wing as preserved, X2 (Becker-Migdisova, 1962b).
- Tychticola** BECKER-MIGDISOVA, 1952, p. 181 [**T. longipenna*; OD]. Little-known genus, based on incomplete fore wing. Wing apparently long and narrow; RS long and parallel to R2. *Perm.*, USSR (Asian RSFSR).—FIG. 163.1. **T. longipenna*; fore wing, X5 (Becker-Migdisova, 1962b).

Suborder HETEROPTERA Latreille, 1810

[Heteroptera LATREILLE, 1810, p. 433]

Fore wing typically with the proximal part strongly coriaceous and the distal part membranous, forming a hemelytron; wings usually held flat over abdomen at rest. *Perm.—Holo.*

Family PROGONOCIMICIDAE Handlirsch, 1906

[Progonocimicidae HANDLIRSCH, 1906b, p. 493] [=Eocimicidae HANDLIRSCH, 1906b, p. 494; Actinocymidae EVANS, 1956, p. 244; Cicadocoridae BECKER-MIGDISOVA, 1958, p. 60]

Small species, dorsoventrally flattened; pronotum distinctly broader than long; fore wing apparently of uniform texture; veins RS and M coalesced basally; SC apparently coalesced with stem of R basally, diverging toward costal margin near midwing; M with 2 to 4 branches; CUA with 2 to 3 branches. [Placed by Popov (1980a) in suborder Peloridiina, along with the Peloridiidae (recent).] *Perm.—Jur.*

Progonocimex HANDLIRSCH, 1906b, p. 494 [**P. jurassicus*; OD] [=Eocimex HANDLIRSCH, 1906b,

- p. 494 (type, *E. liasinus*). Fore wing with rounded apex; clavus broad, nearly triangular; M with 3 branches. BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).—FIG. 164.8. *Progonocimex*; a, **P. jurassicus*, dorsal view; b, *P. liasinus* (HANDLIRSCH), fore wing, both X9 (Popov & Wootton, 1977).
- Actinoscytina** TILLYARD, 1926a, p. 18 [**A. belmontensis*; OD] [=Pseudipsivicia HANDLIRSCH, 1939, p. 17 (type, *P. ala*)]. Little-known genus. Tegmen similar to that of *Progonocimex*, but more slender, anterior margin less curved; SC curving directly toward anterior margin of wing. EVANS, 1956; POPOV & WOOTTON, 1977. *Perm.*, Australia (New South Wales).—FIG. 164.5. **A. belmontensis*; tegmen, X8 (Evans, 1956).
- Archicercopis** HANDLIRSCH, 1939, p. 142 [**A. falcata*; OD]. Anterior margin of fore wing strongly convex basally; precostal area broad; wing apex pointed and directed anteriorly. EVANS, 1956; BECKER-MIGDISOVA, 1962b; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).—FIG. 164.6. **A. falcata*; fore wing, X13 (Popov & Wootton, 1977).
- Cicadocoris** BECKER-MIGDISOVA, 1958, p. 62 [**C. kuliki*; OD]. Tegmen with smoothly curved anterior margin; M with 3 branches; M3+4 unbranched. EVANS, 1961; POPOV, 1982. *Trias.*, USSR (Kirghiz).—FIG. 164.9. **C. kuliki*; restoration, X10 (Becker-Migdisova, 1958).
- Eocercopis** HANDLIRSCH, 1939, p. 142 [**E. ancyloptera*; OD] [=Cercoprisca HANDLIRSCH, 1939, p. 143 (type, *C. similis*); *Cercopinus* HANDLIRSCH, 1939, p. 143 (type, *C. ovalis*)]. Fore wing with very convex and thickened costal margin; apex pointed; clavus broad and nearly triangular. EVANS, 1956; BECKER-MIGDISOVA, 1958; POPOV & WOOTTON, 1977. *Jur.*, Europe (Germany).—FIG. 164.7. **E. ancyloptera*; fore wing, X13 (Popov & Wootton, 1977).
- Heterojassus** EVANS, 1961, p. 23 [**H. membranaceus*; OD]. Tegmen oval; SC and R terminating on costal margin near level of midwing. *Trias.*, Australia (Queensland).—FIG. 164.4. **H. membranaceus*; fore wing, X19 (Evans, 1961).
- Heteroscytina** EVANS, 1956, p. 245 [**H. tillyardi*; OD]. Fore wing narrowed apically, much as in *Actinoscytina*, but costal area narrower and crossveins forming a more nearly complete transverse series. WOOTTON, 1963. *Trias.*, Australia (Queensland).
- Hexascytina** WOOTTON, 1963, p. 250 [**H. transecta*; OD]. Little-known genus, apparently similar to *Progonocimex*, based on incomplete tegmen. SC diverging from stem R near midwing at almost a 90° angle; anterior margin of tegmen distinctly convex. *Trias.*, Australia (Queensland).
- Microscytinella** WOOTTON, 1963, p. 251 [**M. radians*; OD]. Little-known genus, based on small

THE SUPERCLASS HEXAPODA

OUTLINE OF CLASSIFICATION

The following outline of the superclass Hexapoda summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera of fossils in each supra-familial group.

Superclass Hexapoda, 5188, *Dev.-Holo.*
 Class and Order Collembola, 14, *Dev.-Holo.*
 Class and Order Protura, 0, *Holo.*
 Class and Order Diplura, 4, *Paleoc.-Holo.*
 Class Insecta, 5169, *U. Carb.-Holo.*
 Subclass Apterygota, 8, *U. Carb.-Holo.*
 Order Archaeognatha, 5, *U. Carb.-Holo.*
 Order Zygentoma, 3, *Oligo.-Holo.*
 Subclass Prerygota, 5160, *U. Carb.-Holo.*
 Infraclass Palaeoptera, 502, *U. Carb.-Holo.*
 Order Ephemeroptera, 59, *U. Carb.-Holo.*
 Order Palaeodictyoptera, 125, *U. Carb.-Perm.*
 Order Megasecoptera, 34, *U. Carb.-Perm.*
 Order Diaphanopterodea, 20, *U. Carb.-Perm.*
 Order Protodonata, 13, *U. Carb.-Perm.*
 Order Odonata, 204, *Perm.-Holo.*
 Infraclass Palaeoptera, Order Uncertain, 47
 Infraclass Neoptera, 4656, *U. Carb.-Holo.*
 Division Exopterygota, 1393, *U. Carb.-Holo.*
 Order Perlaria, 28, *Perm.-Holo.*
 Order Protorthoptera, 236, *U. Carb.-Trias.*
 Order Blattaria, see p. 134, *U. Carb.-Holo.*
 Order Isoptera, 33, *Cret.-Holo.*
 Order Manteodea, 4, *Oligo.-Holo.*
 Order Protelytroptera, 29, *Perm.-Cret.*
 Order Dermaptera, 16, *Jur.-Holo.*
 Order Orthoptera, 166, *U. Carb.-Holo.*
 Order Grylloblattodea, 0, *Holo.*
 Order Titanoptera, 8, *Trias.*

Order Phasmatodea, 13, *Trias.-Holo.*
 Order Embioptera, 5, *Oligo.-Holo.*
 Order Psocoptera, 58, *Perm.-Holo.*
 Order Zoraptera, 0, *Holo.*
 Order Mallophaga, 0, *Holo.*
 Order Anoplura, 0, *Holo.*
 Order Caloneurodea, 16, *U. Carb.-Perm.*
 Order Miomoptera, 10, *U. Carb.-Perm.*
 Order Thysanoptera, 43, *Perm.-Holo.*
 Order Hemiptera, 728, *Perm.-Holo.*
 Division Endopterygota, 3203, *Perm.-Holo.*
 Order Coleoptera, 1397, *Perm.-Holo.*
 Order Strepsiptera, 4, *Oligo.-Holo.*
 Order Neuroptera, 125, *Perm.-Holo.*
 Order Glosselytrodea, 11, *Perm.-Jur.*
 Order Trichoptera, 112, *Perm.-Holo.*
 Order Lepidoptera, 111, *Cret.-Holo.*
 Order Mecoptera, 82, *Perm.-Holo.*
 Order Siphonaptera, 1, *Oligo.-Holo.*
 Order Diptera, 708, *Trias.-Holo.*
 Order Hymenoptera, 652, *Trias.-Holo.*
 Infraclass Neoptera, Order Uncertain, 60
 Subclass Pterygota, Order Uncertain, 2
 Class Insecta, Subclass Uncertain, 1
 Superclass Hexapoda, Class Uncertain, 1

RANGES OF TAXA

The stratigraphic distribution of classes, orders, and families of Hexapoda recognized in this volume of the *Treatise* is shown graphically in Table 2, which follows (compiled by JACK D. KEIM, computer software by KENNETH C. HOOD and DAVID W. FOSTER).

TABLE 2. Stratigraphic Distribution of the Hexapoda.

	Devonian	Lower Carboniferous	Upper Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
HEXAPODA	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████
COLLEMBOLA	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████
COLLEMBOLA	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Entomobryidae														
Protentomobryidae														
Hypogastruridae														
Isotomidae														
Sminthuridae														
Tomoceridae														
Uncertain														
INSECTA														
APTERYGOTA														
ARCHAEOGNATHA														
MONURA														
Dasyleptidae														
MACHILOIDEA														
Machilidae														
ZYGENTOMA														
Lepidotrichidae														
Lepismatidae														
PTERYGOTA														
NEOPTERA														
EXOPTERYGOTA														
CALONEURODEA														
Amboneuridae														
Caloneuridae														
Apsidoneuridae														
Permobiellidae														
Anomalogrammatidae														
Euthygrammatidae														
Paleothygrammatidae														
Pleisiogrammatidae														
Synomaloptilidae														
Uncertain														
MIOMOPTERA														
Metropatoridae														
Archaeomiopleridae														
Palaeomanteidae														
PROTORTHOPTERA														
Adeloneuridae														
Aenigmatodidae														
Anthracoptilidae														
Anthracothemmidae														
Apithanidae														

EXPLANATION OF TABLE 2

SUPERCLASS ██████████
 CLASS ██████████
 SUBCLASS ██████████
 INFRACLASS ██████████
 DIVISION ██████████
 ORDER ██████████
 SUBORDER ██████████
 Family ██████████

- . 1950. Yurskie Paleontinidae novogo mestorozhdeniya na reke ii [Jurassic Paleontinidae from a new locality on the Ii River]. Doklady akademii nauk SSSR 71:1105-1108, text-fig. 1-3.
- . 1951. Svoeobraznye novye iskopaemye nasekomye iz gruppy paraneopter [New fossil insects of Paraneoptera]. Doklady akademii nauk SSSR 78:1207-1210, text-fig. 1-4.
- . 1952. Novye ravnokrylye iz permi Kuzbassa i nekotorye zamechaniya ob ipsvichiidakh [New Homoptera from the Permian of the Kuznetsk basin and some notes on Ipsviciidae]. Trudy paleontologicheskogo instituta akademii nauk SSSR 40:77-186.
- . 1953a. Obzor faun ravnokrylykh i senoedov erunakovskoy i kuznetskoj svit kuzbassa [Survey of Homoptera and Psocoptera faunas of Erunakovsk and Kuznetsk formation of the Kuznetsk basin]. Doklady akademii nauk SSSR 90:97-100.
- . 1953b. Pervaya nakhodka senoeda (Psocoptera) iz Kuznetskogo bassejna [First record of Psocoptera in the Kuznetsk basin]. Doklady akademii nauk SSSR 90:279-282, text-fig. 1.
- . 1953c. Dva predstavitelja poluzhestkokrylykh nasekomykh iz urochishcha madygen [Two representatives of Hemiptera from the Madygen border]. Doklady akademii nauk SSSR 90:461-464, text-fig. 1-2.
- . 1954. Nakhodka yuzhnoj tsikadky v miotsene zapadnoj sibirii [The discovery of a southern cicada in the Miocene of western Siberia]. Voprosy geologii Azii 1:799-805, text-fig. 1-3.
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