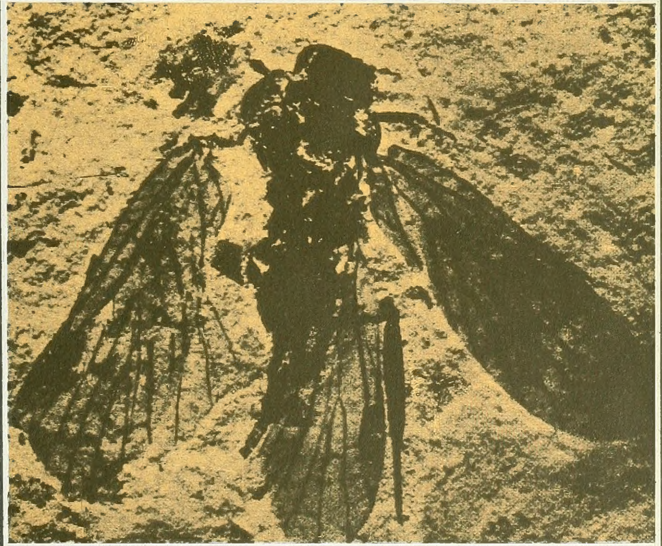
Fundamentals of Paleontology

Volume 9

Arthropoda, Tracheata, Chelicerata

Editor-in-Chief
B.B. ROHDENDORF



The present volume is a continuation of the volume 'Trilobites and Crustaceans' and contains a description of superclasses Tracheata, Chelicerata and Pycnogonides. Besides these, the characteristics of the peculiar phylum Malacopoda, which has almost no known fossil representatives, are also presented.

The first and largest part, forming two-thirds of this volume, includes descriptions of four classes of myriapods and the class Insecta. The second part includes descriptions of the superclasses Chelicerata and Pycnogonides and the third of phylum Malacopoda.

The general plan of presentation and coverage of the material remains more or less uniform throughout this publication. The only exception to this plan is perhaps to be found in the brief survey of the Cenozoic fauna. The characteristics of only the higher taxa, namely families and superfamilies, of Tertiary tracheates and chelicerates are discussed. The genera, particularly of chelicerates from Tertiary deposits, are simply enumerated or the total population indicated without any description. This brief presentation of the taxonomic part was necessitated by the occurrence in the Tertiary beds of an extremely large number of species belonging to genera that also occur in the recent fauna. Further, the Tertiary species have not been studied thoroughly, so the complete characteristics of the genera of Paleogene and Neogene insects and chelicerates are not presented.

On the whole, more than 1,900 descriptions of taxa are given in this volume, including 660 genera.

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Volume 9

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In Fifteen Volumes

FUNDAMENTALS OF PALEONTOLOGY

VOLUME 9

Arthropoda, Tracheata, Chelicerata

Editor-in-Chief

B.B. Rohdendorf

Donald R. Davis
General Editor
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FOREWORD TO THE ENGLISH EDITION

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

Compilations involving extensive review of the world's literature of any branch of science are essential not only to comprehend what has been accomplished but also to assist in directing future research programs. The present volume is the ninth in a series of 15, begun in 1959 under the chief editorship of Yu. A. Orlov, which attempted to review the major animal and plant taxa represented in the fossil record. English translations of at least seven volumes (nos. 1, 2, 5, 6, 7, 11, 13) have been previously published by the Smithsonian Institution Libraries Translation Publishing Program, pursuant to an agreement with the National Science Foundation.

In 1976 I learned that no translation of volume 9 treating the terrestrial Arthropoda had been published. Because I considered such a translation important at the time, a request to the translation program of the Smithsonian Libraries was submitted. Undoubtedly, the availability of an English translation in the late seventies would have been more useful than now. Even then the work was becoming increasingly outdated due to numerous paleontological discoveries since initial publication in 1961. Partially because of inadequate funding, translation of volume 9 was delayed more than a decade. Now with the publication of F. Carpenter's long awaited synthesis (Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, volumes 3 and 4 (Hexopoda), Geological Society of America and the University of Kansas, Boulder and Lawrence), the Russian treatise is more or less relegated to serve as a historical document. In this regard it should always be of some importance to any student of these groups, largely because of the large number of family level taxa proposed (especially in Diptera) and also as a reflection of certain systematic opinions prevalent at the time.

Inconsistency among sections of a multi-authored compilation such as this is not unexpected. Unfortunately, these inconsistencies were exacerbated in volume 9 because of the extreme differences in expertise apparent among the different authors. Some sections were prepared by leading authorities of that taxon, whereas other sections were written by authors unfamiliar with the overall systematics of their assigned group. Thus, it should be of no surprise to discover that the treatment on Diptera to be one of the most revisionary sections, because that order was of special interest to B.B. Rohdendorf, the principal editor of volume 9.

Corrections in the English translation have been limited to editorial inconsistencies or major errors and are indicated by footnotes. No attempt, other than footnotes, was made to revise seriously outdated portions of the text because, as a historical document, the original meaning should be preserved. I am indebted to the following authorities for editorial assistance with the groups specified: C.A. Child (superclass Pycnogonides); O.S. Flint, Jr. (order Ephemeroptera, superorders Megasecopteroidea, Odontoidea, Neuropteroidea, Mecopteroidea); E.E. Grissell and D.R. Smith (superorder Hymenopteroidea); T.J. Henry (order Heteroptera); W.N. Mathis (order Diptera); E.L. Mockford (superorder Psocopteroidea); S. Nakahara (superorder Thysanopteroidea); D.A. Nickle (superorders Blattopteroidea, Orthopteroidea); W.A. Shear (subclass Araneae); M.B. Stoetzel (suborder Sternorrhyncha); P.J. Spangler, Jr. (superorder Coleopteroidea); and S.W. Szczytko (superorder Plecopteroidea).

Smithsonian Institution
1991

Donald R. Davis, Curator
Department of Entomology

FOREWORD

The present volume is a continuation of the volume 'Trilobites and Crustaceans' and contains a description of superclasses Tracheata, Chelicerata and Pycnogonides. Besides these, the characteristics of the peculiar phylum Malacopoda, which has almost no known fossil representatives, are also presented.

The first and largest part, forming two-thirds of this volume, includes descriptions of four classes of myriapods and the class Insecta. This part of Tracheata was written by E.E. Aizenberg, E.E'. Bekker-Migdisova, V.N. Vishnyakova, A.S. Danilevskii, O.M. Martynova, N.I. Novozhilov, A.G. Ponomarenko, Yu.A. Popov, B.B. Rohdendorf, O.A. Chernova and A.G. Sharov. It was edited by B.B. Rohdendorf.

The second part includes descriptions of the superclasses Chelicerata and Pycnogonides and the third, of phylum Malacopoda. These parts were contributed by V.B. Dubinin, N.I. Novozhilov and A.G. Sharov. Editing was done by B.B. Rohdendorf. Later B.B. Rohdendorf edited all these parts, adding supplementary information.

The general plan of presentation and coverage of the material remains more or less uniform throughout this publication. The only exception to this plan is perhaps to be found in the brief survey of the Cenozoic fauna. The characteristics of only the higher taxa, namely families and superfamilies, of Tertiary tracheates and chelicerates are discussed. The genera, particularly of chelicerates from Tertiary deposits, are simply enumerated or the total population indicated without any description. This brief presentation of the taxonomic part was necessitated by the occurrence in the Tertiary beds of an extremely large number of species belonging to genera that also occur in the Recent fauna. Further, the Tertiary species have not been studied thoroughly, so the complete characteristics of the genera of Paleogene and Neogene insects and chelicerates are not presented.

A number of specialists on modern insects offered suggestions and assistance to the authors in devising the classification of particular groups. G.Ya. Bei-Bienko advised us on contemporary Orthoptera, A.N. Kirichenko on

Heteroptera, S.G. Lepneva on Trichoptera, and M.N. Nikolskii, V.V. Popova and A.P. Rasnitsyn on Hymenoptera. The authors express gratitude to them.

On the whole, more than 1,900 descriptions of taxa are given in this volume, including 660 genera.

As regards to illustrations, it was a problem to provide figures for all the taxa whose characteristics are discussed in the text. In the main the illustrations are line drawings. A few illustrations are photographs. The drawings were done by artists of the Graphic Art Center—T.F. Belotsvetova, I.P. Velikanova, V.I. Dorofeev, N.L. Korchazhinskaya, G.M. Lyakhov, K.P. Meshkov, V.N. Popova, A.N. Potapova and T.L. Savranskaya, and the photographs were taken by A.V. Skinder, V.A. Presnyakov, N.P. Finogenov and Yu.A. Popov. Some of the sketches were drawn by the authors themselves: O.M. Martynova, B.B. Rohdendorf, O.A. Chernova, E.E'. Bekker-Migdisova and A.G. Sharov.

The following persons saw this volume through the press and compiled the plates: O.M. Martynova, E.E'. Bekker-Migdisova, V.A. Ivanova, N.L. Grombchevskaya, A.G. Sharov, N.P. Meshkova, I.D. Sukacheva, V.N. Vishnyakova and E.M. Sosnovskaya.

B.B. Rohdendorf, Editor

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* Editor's note: Throughout this volume most superfamily names terminate in -idea. Article 29A of the third edition (1985) of the International Code of Zoological Nomenclature recommends that the suffix should be -oidea.

Major Stratigraphic Subdivisions Adopted in This Publication

The scheme reproduced here is based on the one submitted by the Joint Stratigraphic Committee of the USSR on June 30, 1955

Groups	Systems	Series		Stages (and other subdivisions)
Cenozoic	Quaternary	Holocene	Recent	
		Pleistocene	Upper	
			Middle	
			Lower	
	Tertiary	Neogene	Pliocene	Upper Middle Lower
			Miocene	Upper Middle Lower
		Paleogene	Oligocene	Upper Middle Lower
			Eocene	Upper Middle Lower
			Paleocene	Upper Lower

1	2	3	4		
Mesozoic	Cretaceous	Upper	Danian		
			Senonian	Upper	Maestrichtian
					Campanian
				Lower	Santonian
					Coniacian
			Turonian		
			Cenomanian		
		Lower	Albian		
			Aptian		
			Neocomian		Barremian
					Hauterivian
					Valanginian
	Jurassic	Upper or Malm	Titonian		Upper Volgian
					Lower Volgian
			Kimmeridgian		
			Oxfordian		Lucituian
			Callovian		
		Middle or Dogger	Bathonian		
			Bajocian		
			Aalenian		

1	2	3	4	
Mesozoic	Jurassic	Lower or Lias	Upper	Toarcian
			Middle	Domerian
				Pleinsbachian
			Lower	Lotaringian
				Sinemurian
				Hettangian
	Triassic	Upper		Rhaetian
				Norian
				Carnian
		Middle		Ladinian
				Anisian
		Lower or Scythian		Campellian[1]
				Seissian[1]
Paleozoic	Permian	Upper		Tatarian
				Kazanian
		Lower		Kungurian
				Artinskian
			Sakmarian	Sakmarian
				Asselian

[1] According to the recommendations of the Joint Stratigraphic Committee held on May 10, 1956 the Lower Triassic is divided into Indian and Olenekian stages.

1	2	3	4	
Paleozoic	Carboniferous	Upper	Orenburgian	
			Gigulevian	Gzhelian Kasimovian
		Middle	Moscovian Bashkirian	
		Lower	Namurian Visean Tournaisian	
	Devonian	Upper	Famennian Frasnian	
		Middle	Givetian Eifelian	
		Lower	Coblenzian Gedinnian	
	Silurian	Upper	Ludlovian	
		Lower	Wenlockian Llandoverian	
	Ordovician	Upper	Ashgillian Caradocian	
		Middle	Llandeilian	
		Lower	Arenigian Tremadocian	

1		2	3	4
Paleozoic		Cambrain	Upper	Not defined
			Middle	
			Lower	Lenian Aldanian
Proterozoic	Upper subgroup			
	Lower subgroup			
Archean				

SUBPHYLUM MANDIBULATA

Mandibulate Arthropods

SUBPHYLUM MANDIBULATA

Mandibulate Arthropoda

19 These arthropods are characterized by one or two pairs of anterior appendages (antennules and antennae), transformation of the third pair into mandibles and formation of a complex cephalic region by the fusion of the first head segment (acron) with the next four segments. The anterior end of the body axis preserves its primary straight position and does not bend upward. The walking legs are located on the thorax and are without gnathobases.

Included in this subphylum of Arthropoda are two large superclasses—Crustaceomorpha and Tracheata. The former subclass has already been dealt with in an earlier volume. In the present volume the tracheate arthropods are discussed.

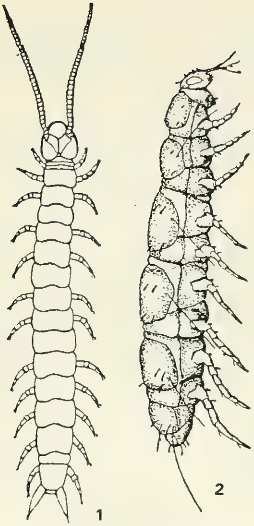
Superclass TRACHEATA

20 Terrestrial arthropods breathing atmospheric air through a system of branching chitinous tubes—the tracheae developed from outer covering of body, opening on surface of segments by openings called spiracles or 'stigmata', usually paired and located in pleural region or (rarely) unpaired and opening on tergum. Rarely tracheae underdeveloped and closed and not in contact with outer atmosphere, as in some aquatic larvae. A single pair of antennae and three pairs of jaws. Very rarely antennae and third pair of jaws absent. Anterior division of body—head—always demarcated, with antennae, jaws and eyes. Body long, consists of many segments. Head and middle part of body—thorax—usually sharply defined, fused only in very exceptional cases, as in some insects of order Heteroptera. Intestines with a few weakly developed blind outgrowths, or diverticulae. Silurian to Recent. Five classes: Pauropoda, Diplopoda, Chilopoda, Symphyla and Insecta.

Not much is known about phylogenetic relationships within the superclass. A distinct link between the last two classes and the great isolation of the first three classes are evident. Due to absence of reliable paleontological evidence, phylogenetic generalizations are based on structure and development of modern forms only.

The first four classes of tracheate arthropods are usually grouped under the general term Myriopoda, but these classes are similar only in the non-demarcation of the posterior division of the body—the abdomen. The real differences within this group of Myriopods are considerable. They justify the high rank of class given to individual groups. The first scientific description of fossil Myriopods of Paleozoic age was given by Scudder (1882). The classic work by Fritsch (1889) on Permian myriopods of Czechoslovakia gave a basic account of the Paleozoic fauna and retains its significance to-date. A description of a large number of Tertiary Myriapods from Baltic amber was given by Bachofen von Echt (1942).

The overwhelming majority of extant myriopods inhabit damp biotopes in soil, under stones, in forest litter, decaying vegetable matter, etc. This probably explains the paucity of these animals preserved as fossils. Some fossil forms of



Figs. 1 and 2. Classes Symphyla and Pauropoda.
1. *Scutigerella immaculata* Newport; × 20. Recent (Snodgrass, 1952). 2. *Pauropus silvaticus* Latzel; × 50. Recent (Tiegs, 1947).

myriopods are found to have had an amphibious existence. They are known for certain from the Carboniferous and have been found in the Silurian, which has also yielded some problematic remains (Peach, 1882, 1898).

21

Class SYMPHYLA

(A.G. Sharov)

Small forms (less than 8 mm). Cuticle thin and non-pigmented. Head prognathous, without eyes. Antennae long and many segmented. Second pair of maxillae partly fused to form a lower lip. Twelve pairs of legs. Trunk in adults with 14 segments, and an anal lobe, fused with the last segment. Usually 13th segment fused with 14th, with unsegmented cerci. On third and following segments legs with styli and bulging saccules present on their basal segment (Fig. 1). Saprophagous and phytophagous. Tertiary to Recent. Three families; Scolopendrellidae, Geophilellidae and Scutigerellidae, last two without fossil representatives.

Family SCOLOPENDRELLIDAE Bagnal, 1913

15 tergites. First pair of legs usually smaller or equal in length to second pair. Styli not clear. Paleogene to Recent. Of the three genera that occur as fossils, one is from the Paleogene of Europe (Baltic amber).

Class PAUROPODA

(A.G. Sharov)

Small (less than 1.5 mm in length), weakly sclerotized myriopods with hypognathous head, without eyes, five-segmented (in adult). Antennae branched at the ends, branches extending as multi-segmented plaits. Second maxillae absent. Trunk in adults 11–12 segmented, anal lobe and first segment (neck) without legs. Adults with usually nine or rarely 10 pairs of legs. Tergites of third, fifth, seventh and ninth segments armed along the sides with trichobothria. Tergites of first, fourth, eighth and tenth segments quite reduced (Fig. 2). Saprophages. Fossil forms of pauropods not known.

22 # Class DIPLOPODA

(A.G. Sharov)

Medium-sized or large (0.7–5 cm) myriapods. Antennae short, eight to 10 segmented. Groups of simple eyes or compound eyes present on the sides of head. Segment of second maxilla reduced and, in post-embryonic period, it disappears completely. Tergites markedly convex. First segment simple, without appendages. Following three segments also simple but with a pair of appendages each. Bases of appendages close together because of reduced sterna. Genital openings double, located on third thoracic segment. Fossil representatives abundant, comprising around 80% of reported myriapods. Carboniferous to Recent.

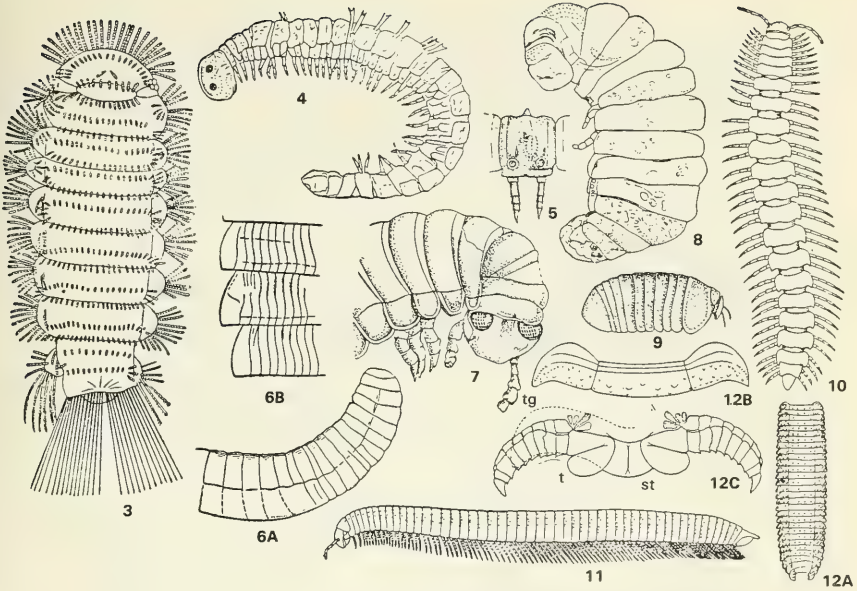
Superorders: Pselaphognatha, Chilognatha.

SUPERORDER PSELAPHOGNATHA

Body wall soft, without calcium carbonate in cuticle. Bristles on body with very complex structure (such as toothed, saw-shaped, scaly, etc.), occur in bundles. Trichobothria present on head. Gonopods and telopods absent. Tertiary to Recent. One order with one family, Polyxenidae.

Family POLYXENIDAE Latreille, 1825

Thorax 10–12 segmented, anal lobes present. Pleurae developed (Fig. 3).



Figs. 3–12. Class Diplopoda.

3. *Polyxenus largus* Linnaeus; × 25. Recent (Attems, 1926). 4. *Acantherpestes vicinus* Fritsch; × 5. L. Permian, W. Europe (Laurentiaux, 1953, after Fritsch, 1900). 5. *Euphoperia llarenai* Melendez; segments of trunk; × 3. L. Permian, W. Europe (Laurentiaux, 1953, after Melendez, 1948). 6. *Tomiulus angulatus* Martynov; A—posterior end, B—lower part of three trunk segments on outside; × 10. Upper Triassic, Kuznetsk Basin (Martynov, 1939). 7. *Pleurojulus levis* Fritsch; × 7. L. Permian, W. Europe (Laurentiaux, 1953, after Fritsch, 1900). 8. *Archiscudderia tapeta* Fritsch; × 2. L. Permian, W. Europe (Laurentiaux, 1953, after Fritsch, 1900). 9. *Glomeris marginata* Villers; × 2. Recent. (Attems, 1926). 10. *Polydesmus* sp.; × 1.5. Recent (Attems, 1926). 11. *Julus lingulifer* Latzel; × 2. Recent (Attems, 1926). 12. *Arthropleura armata* Jordan and Meyer; A—abdomen (× 0.05). B—anterior tergum; C—reconstruction of a pair of appendages; St—sternum; t—ventral lobe, tg—tergum, x—rosettelike organ; Carboniferous. W. Europe and Karaganda basin (Størmer, 1944).

Paleogene to Recent. Ten Recent genera, of which two are from the Paleogene of Europe (Baltic amber).

23 SUPERORDER CHILOGNATHA

Chitinous cover of body impregnated with lime. Bristles, if present, simple, not occurring in bundles. Trichobothria absent. Males with gonopods on sixth segment or telopods at end of body. Carboniferous to Recent. Nine orders: Palaeocoxopleura, Eurysterna, Palaeomorpha, Oniscomorpha, Polydesmodea, Nematophora, Juliformia, Colobognatha and Limacomorpha. The last has no known fossil representatives.

Order PALAEOCOXOPLEURA

Medium- to large-sized (up to 50 cm). Body cylindrical. Long spines of different forms on different segments; do not curl up, either into a ball or into a spiral. Head large and quadrate. Antennae six- to eight-segmented. Eyes made up of a large number of closely-placed simple eyes. Terga form only a half-ring of the segment. Pleura and sterna fused (hence the name of the order). They form lower half of ring of segment. On fused coxosterno-pleura there are slit-like openings which appear to be stigmata or glandular pores and fringed cylindrical openings; the significance of the latter is not clear. In some representatives the stigmata and openings are situated on terga. Appendages most probably five-segmented. Coxae very close (Figs. 4, 5). The links between forms of this order and present-day myriapods not clear. Carboniferous to Permian. One family, Euphoberidae, outside the USSR.

Order EURYSTERNA

Large myriapods with hypognathous head, bearing apparently faceted eyes. Body cylindrical, with large number (60 or more) of segments, without spines, capable of rolling up into a spiral. Glandular pores present or absent. Each tergum subdivided into protergite and metatergite. Pleura fused with the body and sharply demarcated from the terga, fringed by marginal lines of varying widths. Carboniferous to Triassic. One family, Archijulidae.

Family ARCHIJULIDAE Scudder, 1873

(Projulidae Fritsch, 1899)

Tergites finely spotted or striped. Sternites large, wide and at times fused into a single sclerite. Carboniferous to Trias. Seven genera.

Tomiulus Martynov, 1936. Genotype—*T. angulatus* Martynov, 1936; Trias., Kuznetsk basin (Maltsevian series; Babii Kamen). Pleura very narrow, not demarcated, with convex lower borders, angular and protruding outside. Longitudinal stripes on terga clear, extend to protergites. Height of segment about 4.5 mm (Fig. 6A, B). One species from the Triassic of Kuznetsk basin.

Outside the USSR: *Archijulus* Scudder, 1873; *Pylojulus* Fritsch, 1899 (*Xylobius* Dawson, 1859); *Isojulus* Fritsch, 1899; *Pleurojulus* Fritsch, 1899 (Fig. 7); *Anthracojulus* Fritsch, 1899; *Purkynia* Fritsch, 1899.

Order PALAEOMORPHA

Medium sized myriapods with small head, bearing compound eyes, and few terga (16–17). Rolled up like Recent Oniscomorpha, but head not covered by anal shield which is markedly reduced. Tergites fringed by spines or smooth, sometimes divided into pro- and metatergites. Paratergites resemble pleurae (Fig. 8). Carboniferous. Three families: Acroglomeridae, Proglomeridae, Sphaerherpestidae—outside the USSR.

24

Order ONISCOMORPHA

Medium sized myriapods with a small head, reduced eyes and not many tergites (14–16). Legs 17 to 21 pairs. Spines and paratergites absent. Preanal segment large, when the animal rolls up it completely covers the head. Cretaceous to Recent. Four families of extant forms of which only Glomeridae has fossil representatives.

Family GLOMERIDAE Brandt, 1833

Prefemur of the 19th pair of legs in males with an appendix carrying a bristle or only with a bristle. Femur and tibia with inner lobe-like outgrowths. Animal capable of rolling into a ball (Fig. 9). Cretaceous to Recent. A few genera, including one in Paleogene of Europe (Baltic amber).

Order POLYDESMODEA

Body large. Trunk with 19 to 22 segments. Spinning glands on anal segment absent. Animal rolls into a spiral (Fig. 10). Tertiary to Recent. Fossil remains known from Paleogene of Europe (Baltic amber), a questionable identification.

Order NEMATOPHORA

Trunk segments 26 or more. Two or three pairs of spinning glands on anal segment which open on one to three pairs of spinnerets. Tertiary to Recent. About 30 families of Recent forms, of which only one family, Craspedosomatidae, has fossil representatives.

Family CRASPEDOSOMATIDAE Verhoeff, 1889

With a maximum of 30, more often 28, trunk segments. Mentum subdivided into submentum and promentum. Second pair of legs in females well developed. Paleogene to Recent. About 20 extant genera, one represented in Paleogene of Europe (Baltic amber).

Order JULIFORMIA

Myriapods with cylindrical body, well-developed head with eyes consisting of densely packed simple eyes. Number of segments of trunk exceeds 40. Spinning glands absent. Mesozoic to Recent. Nearly 15 families represented in the Recent fauna of which only one, Julidae, has fossil forms.

Family JULIDAE Verhoeff, 1911

Both pairs of gonopods hidden in a depression. Penis wide with two openings and two lateral spines (Fig. 11). Cretaceous to Recent. More than 40 extant genera, of which one is represented in Paleogene of Europe (Baltic amber) and one extinct genus is reported from Cretaceous of Greenland.

Order COLOBOGNATHA

Head small and triangular with massive antennae. Upper lip without teeth. Trunk short and broad or long and narrow. Tertiary to Recent. Five extant families known, of which one, Polyzoniidae, has fossil representatives.

Family POLYZONIIDAE Gervais, 1844

Sterna free. Gnathochilarium consists of one plate. Eyes present. Head free, not covered by terga of following segments. Paleogene to Recent. About 10 extant genera recognized, of which one is represented in Paleogene of Europe (Baltic amber).

25 Order Incertae sedis

Family ARTHROPLEURIDAE Zittel, 1848

(Nestor Novozhilov)

Large arthropods which attain a length of 1.5 m. Lateral outgrowths of terga broad, separated from the central shield, reminding one of segmentation of pleura in representatives of order Eurysterna. All segments alike except three or four posterior ones, which are somewhat smaller in size. Number of segments nearly 30. Legs attached to base of segments which forms a convex ventral lobe. This is regarded as a gill. Four short radial plates constitute a special organ—the 'rosette'. Each leg consists of nine small segments, last of which being pretarsus. Details of structure of appendages still not clear. Waterlot (1934) believed them to be biramous with closely situated rami. Størmer (1944) believed that the two rami may be dorsal and ventral surfaces of the same ramus. Head and telson not known. Absence of data on structure of head and reliable information on structure of legs preclude determination of affinities between these arthropods and other groups. Schulze (1939) linked Arthropleurids with arachnids. Størmer

(1944) considered defining arthropleurids as a special class. New research by Komarek (Sharov, 1960) point to the closeness of these arthropods to diplopod myriapods called Polydesmodea. Carboniferous. Only one genus.

Arthropleura Jordan and Meyer, 1854. Geno type—*A. armata* Jordan and Meyer, 1854. Found in Carboniferous of Saar basin. Pleura with strong spines of almost equal size and a keel. Keel passes very close to anterior margin of pleura, loops around smoothly, following curvature of anterior margin of pleura, which is markedly convex. Posterior margin of pleura somewhat notched. Tubercles with spines present on terga proper in two rows (Fig. 12A, B). Seven species. Occurrence: Middle and Upper Carboniferous of Western Europe; Carboniferous of Karagandinian basin (other forms not yet described).

Class CHILOPODA. Centipedes

(A.G. Sharov)

Large myriapods. Head sharply separated from trunk. Antennae with a large number (14 or more) of similar segments. Second maxillae well developed, fused at base with sternum. Trunk dorsoventrally flattened. Appendage of first trunk segment transformed into maxilliped. Carboniferous to Recent. Only controversial remains of Chilopoda found in Carboniferous of Europe. Orders: Epimorpha and Anamorpha.

Order EPIMORPHA

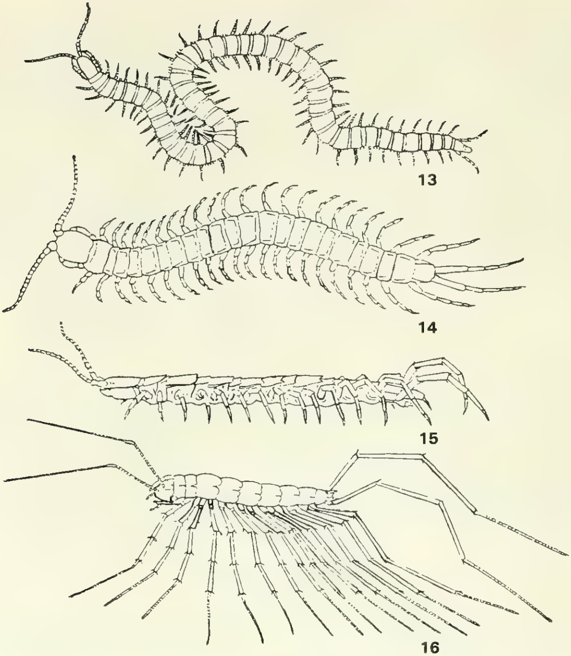
Terga similar, each one bears a pair of appendages. Post-embryonic development epimorphic: adults hatch after all segments and appendages are developed. Tertiary to Recent. Two suborders: Geophilomorpha and Scolopendromorpha.

Suborder Geophilomorpha

Body very long and slender. Number of segments varies from 35 to 177. Fourteen segments on antenna. Eyes absent. Mesozoic to Recent. About 10 families of Recent forms known, of which only Geophilidae has fossil representatives.

Family GEOPHILIDAE Newport, 1844

Upper lip formed of three sclerites. One or two light-colored spots on the clypeus. Paratergites absent. Legs six or seven segmented (Fig. 13). Cretaceous to Recent. More than 60 genera, one occurs in Paleogene of Europe (Baltic amber) and another extinct genus reported from Cretaceous of North America.



26 Figs. 13–16. Class Chilopoda.

13. *Pachymerium ferrugineum* Koch; × 3. Recent (Attems, 1926). 14. *Otocryptops sexspinosus* (Say); × 1.5. Recent (Snodgrass, 1952). 15. *Lithobius* sp.; × 1.5. Recent (Snodgrass, 1952). 16. *Scutigera* sp.; × 1.2. Recent (Koch, 1863).

Suborder Scolopendromorpha. Scolopendrids

Body comparatively short and broad. Segments 25 to 27, legs 21 to 23 pairs. Tertiary to Recent. Two families: Scolopendridae and Cryptopidae.

26 Family SCOLOPENDRIDAE Newport, 1844

Eyes present. Tarsus two segmented (Fig. 14). Paleogene to Recent. More than 20 genera of Recent forms, one of them includes fossil forms found in Paleogene of Europe (Baltic amber).

Family CRYPTOPIDAE Newport, 1844

Eyes absent. Tarsus usually single segmented. Paleogene to Recent. More than 10 genera of Recent forms, one of them represented in Paleogene of Europe (Baltic amber).

Order ANAMORPHA

Tergites dissimilar. Development anamorphic: animal emerges from egg short of some segments and legs, which appear in the post-embryonic period. Trunk 19 segmented with 15 pairs of legs. Paleogene to Recent. Two suborders: Lithobiomorpha and Scutigeromorpha.

Suborder Lithobiomorpha. "Dragging legs" centipedes

Segments with walking legs have 15 alternating large and small tergites. Thirty or more segments in antennae. Eyes simple. Tertiary to Recent. Four families of Recent forms, fossil forms belong to one of these families, namely, family Lithobiidae.

27

Family LITHOBIIDAE Newport, 1844

Eyes on fringe of head shield. Legs from first to fifth pair have coxal glands. Gonopods of male single or two segmented (Fig. 15). Paleogene to Recent. Of the 40 genera of Recent forms only one represented in Paleogene of Europe (Baltic amber).

Suborder Scutigeromorpha. Long-legged centipedes

On leg bearing segments 2–16 only eight clear tergites seen. Up to 400 segments on antennae. Legs unusually long and slender. Tarsus whip-like, subdivided into a large number of small secondary segments. Eyes large and faceted. Tertiary to Recent. Only one family: Scutigeridae.

Family SCUTIGERIDAE Gervais, 1847

Tergites of maxillipeds small. Stigmata not in pairs, located on posterior border of tergites, except last tergum (Fig. 16). Paleogene to Recent. Of about 15 genera of Recent forms one includes fossil forms from Paleogene of Europe (Baltic amber).

28

REFERENCES

Andrée, K. 1909. Neu Funde von *Arthropleura armata* Jordan. *Zbl. Miner. usw.*, p. 753.

Andrée, K. 1910. Zur Kenntnis der Krustaceen-Gattung *Arthropleura* und deren systematische Stellung. *Palaeontographica*, vol. 57, p. 67.

Attems, C. 1926. Myriopoda. In: Kukental "Handbuch der Zoologie", vol. 4, No. 1, pp. 1–402.

Bachofen von Echt, A. 1942. Ueber die Myriapoden des Bernstein. *Palaeontographica*, vol. 7, No. 5–6, pp. 394–406.

Baldwin, W. 1911. Fossil Myriapoda from the middle coal measures of Sparth Bottom Rochdale, Lancashire. *Geol. Mag.*, vol. 8, pp. 74–80.

Bagnal, A.S. 1913. On the classification of the order Symphyla. *Journ. Linn. Soc. London*, vol. 32.

Fritsch, A. 1899. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, vol. 4, No. 1–2, pp. 1–64.

Gervais, P. 1844. Sur la ponte et le développement des Glomerides. Procés verbaux soc. philomat. Paris.

Gervais, P. 1847. Myriapodes in Walkenaer "Histoire naturelle des insectes apteres", vol. 4.

Guthöri, P. 1934. Die Arthropoden aus dem Karbon und Perm des Saar-Nahe-Pfalz-Gebeites. *Abh. Geol. Landesanst.*, N.F., No. 164.

Guthori, P. 1936. *Arthropleura*, der Riesengliderfüssler des Oberkarbons, und seine Verbreitung in den europäischen Steinkohlenbecken, Glückauf. No. 39, pp. 966–975.

Jordan, H. and H. Meyer. 1854. Ueber die Crustacean der Steinkohlenformation von Saarbrücken. *Palaeontographica*, vol. 4, pp. 13–15.

Latreille, P.A. 1825. Familles naturelles du régne animal.

Laurentiaux, D. 1953. Classe des Myriapodes. In: Piveteau *Traité de paléontologie*, vol. III, Paris.

Martynov, A.V. 1936. O Nekotorykh novykh materialakh chelenistonogikh zhivotnykh iz kuznetskogo basseina (Some new materials on Arthropod life in the Kuznetsk basin). *Izv. Akad. Nauk. SSR. Biol. Ser.*, No. 6, pp. 1258–1260.

Melendez, B. 1948. Un Miriapodo fosil en el Estefaniense de Llombera (Léon). Madrid, *Bol. R. Soc. española Hist. Nat.*, vol. XIV.

Newport, G. 1844. A list of the species of Myriapoda, order Chilopoda, contained in the cabinets of the British Museum. *Ann. and Mag. Nat. Hist.*, vol. 13.

Peach, B.N. 1882. On some fossil myriapods from the lower old Red Sandstone of Forfarshire. *Proc. Roy. Phys. Soc., Edinburgh* , vol. 7, pp. 177–188.

Pruvost, P. 1912. Sur la présence du genre *Arthropleura* dans le terrain houiller du Nord et du Pas-de-Calais. *Ann. Soc. Géol. Nord*, vol. 41, p. 59.

Pruvost, P. 1930. La faune continentale du terrain houiller de la Belgique. *Mém. Mus. Roy. Hist. Nat. Belg.*, vol. 44. p. 171.

Schulze, P. 1939. Bemerkenswerte palaeozoische Arthropoden, die wahrscheinlich in die Spinnentierreiche gehoren. *Ztschr. Morph. u. Ökol. d. Tiere*, vol. 35.

Scudder, S.H. 1882. Archipolypoda, a subordinal type of spined myriapods from the Carboniferous formation. *Mem. Bost. Soc. Nat. Hist.*, vol. III.

Sharov, A.G. 1960. Yu. Komarek O sistematicheskom polozhenii *Arthropleura* (Yu. Komarek on the systematic position of *Arthropleura*). *Paleontol. Zhurn.*, No. 3, p. 140.

Snodgrass, R.E. 1952. A textbook of Arthropod anatomy. pp. 1–363, N.Y.

Størmer, L. 1944. On the relationships and phylogeny of fossil and Recent Arachnomorpha. *Skrifter Utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse*, No. 5, pp. 1–152.

Tiegs, O.W. 1947. The development and affinities on the Pauropoda, based on a study of *Pauropus silvaticus. Quart. Journ. Micr. Sci.*, vol. 88, pt. 2, pp. 165–336.

Verhoeff, K.W. 1911. Zur Systematik, Phylogenie und vergleichenden Morphologie der Juliden und über einige andere Diplopoden. *Archiv f. Naturgeschichte,* vol. I.

Verhoeff, K.W. 1911. Zur Kenntnis des Mentum der Juliden und über Protojuliden. *Zool. Anz.*, vol. 38, No. 24.

Waterlot, G. 1934. La faune continentale du terrain houiller Sarro-Lorrain. Études de gîtes minéraux de la France. Lille, pp. 52-110.

Class INSECTA. Insects

General Observations

(B.B. Rohdendorf)

REVIEW OF LITERATURE

29 Insects form the most extensive and varied class of arthropods, exceeding any other group of animals in variety and number. This abundance of insects probably explains the great disparity in studies on different groups of this class. Besides the well-studied orders, there remain large, little-known groups which still are at the primary, cataloging stage of study. Still, on the whole this class of arthropods forms one of the earliest- and best-studied classes in zoology.

Insects of the geological past have been studied far less than recent ones. The main reason is that fossil remains of insects are very difficult to study because of their imperfect preservation, small number and rare occurrence*.

Description of insects of the past started long ago. In the first half of the 18th century Sendelius (1742) drew and described a large number of insects from Baltic amber. But a more systematic description of the fossil remains of insects started only in the 20s of the last century. Initial studies concerned Tertiary and Mesozoic fauna. Such descriptions of European Tertiary insects were given by Thoussaint de Serres (1829) and later by Heer (1847–60), Hagen (1854, 1866), C. Heyden and L. Heyden (1856–70) and finally by Oustalent (1870, 1873, 1874). More or less at the same time the works of the following authors on the European Mesozoic insects appeared: Germar (1837, 1839, 1842), Brodie (1845), Giebel (1856) and later Weyenbergh (1869, 1874) and Oppenheim (1885, 1888).

The first Paleozoic insects came to be studied only in the middle of the 19th century, by Goldenberg (1854, 1873, 1877). More detailed descriptions of primitive insects were given by Scudder (1878, 1884, 1890) from North America

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*Editor's note: Many recent discoveries have shown that insects were abundant in the past. Huge deposits of fossil insects in many parts of the world have revealed their diversity. There has been a tremendous increase in their study as their importance in terrestrial Paleoecology and even their potential for stratigraphy has been realized.

and by Woodward (1887) and particularly Brongniart (1885, 1893) from Western Europe.

The work of the last century was summed up in the very important works of Handlirsch (1904, 1906, 1908, 1919, 1925). His monograph is the most important summary of all the Insecta of the earth's past to this day. It includes drawings and descriptions of Paleozoic and Mesozoic insects. It also contains a complete catalog and a description of Cenozoic species. In fact, Handlirsch's work stimulated the development of paleoentomological research in Western Europe. Bolton (1911, 1925) studied Paleozoic insects and Meunier (1899–1910) Tertiary ones. In North America Sellards (1909) studied Permian insects and Cockerell (1906–15) and other workers studied Tertiary fauna.

30 Further development of paleoentomology goes to the credit of Tillyard (1916–48), who studied the fossil remains of Insecta of various ages from Australia, Europe and distant North America. The ages ranged from Tertiary through Triassic and Mesozoic to Paleozoic, primarily Permian. Tillyard's works undoubtedly reflect the depth and thrust of his paleoentomological research in elaborating the historical development of different groups of insects. This study of faunal complexes became the basic material for later investigation to bring to light the phylogenetic relationships among the various groups.

However, important conclusions and generalizations relating to the insects of the past are to be found in the works of A.V. Martynov (1924–40). Martynov developed the phylogenetic approach to paleoentomology and in every possible way extended the comparative-analytical technique to recent insects to throw more light on the characteristics of fossil insects. He conducted extensive research on the Jurassic, Permian and some other faunal complexes from different localities in Central Asia, the Urals, Arkhangelsk and many other places. Almost all these sites were excavated and studied for the first time. Martynov's works are particularly important in that they inaugurated study of fossil insects from the territories of the USSR. Until his work we had no paleoentomology at all and all the limited finds of fossil remains of insects studied by foreign scientists were only as extensive and varied as the materials obtained from the fossil insects of the Baltic amber. Martynov compiled a survey of all the locations (about 50), wrote up a series of faunal complexes and suggested a well-thought-out phylogenetic scheme of classification for all groups of insects (1938).

At the end of the 1920's the American entomologist, F.M. Carpenter, a specialist in some groups of recent insects of North America, started to work on paleoentomology (1926–29). He conducted these studies in collaboration with his contemporary and senior colleagues, Tillyard and Martynov. In his works Carpenter wrote exhaustively about fossil remains, made a large number of general reconstructions of many Paleozoic insects and critically examined the problems of taxonomy of various groups. Besides descriptions of new forms of insects, Carpenter also wrote comprehensive articles on the insect fauna of the geological past. His method of classification, particularly for the extinct insects, is dealt with in the well-known book by Bruce, Melander and Carpenter (1952). Today Carpenter is one of the most experienced paleoentomologists.

After the publication of the monograph by Handlirsch, an important turning point in the development of paleoentomological knowledge resulted from Martynov's investigations. The specialized study of certain groups of insects, their phylogeny and characteristics of functional morphology lent greater reliability to the conclusions reached. These studies helped to spread the pursuit of paleoentomology in our country along with other investigations. Such studies were undertaken by U.M. Zalessky on the Permian fauna of the Urals (1931–56). Work on Lepidoptera from Baltic amber was carried out by N.Y. Kuznetsov (1941). Other studies include the work of B.B. Rohdendorf (1938, 1946, 1949, 1951) on the historical development of Diptera and the evolution of flight in insects, the research of E.E. Bekker-Migdisova (1940–48, 1949, 1952) on the morphology and evolution of Homoptera and that of O.M. Martynova (1942, 1948, 1949, 1952) on the evolution of Mecoptera and Neuroptera. Study of regional faunal complexes acquired a new character and began to be undertaken collectively by many specialists. Such studies, as for example, the work on the Paleozoic fauna of the Kuznetsk basin, help in estimating the diversity of faunal complexes and arriving at a more accurate determination of the horizons of layered deposits.

GENERAL CHARACTERISTICS AND MORPHOLOGY

Insects are arthropods with the body divided into three well-defined parts, namely, head, thorax and abdomen. This division of body is present in larval stages as well. The body may undergo secondary reduction in adult or larval phases. The head consists of six embryonic segments, always with one pair of antennae on second segment. No appendages on first and third segments. Three pairs of appendages on remaining three, constituting mouth parts, including mandibles. Mouth parts often highly modified. Thorax consists of three segments that normally bear three pairs of legs on sterno-pleural surface and two pairs of wings on dorsal surface. Primitive number of abdominal segments eleven. Appendages usually found only on last three or four of these. Air breathing normally carried out through a system of tracheae. Tracheae commonly in the form of a complex metameric system. Branchial respiration observed in some larvae which probably is a secondary phenomenon. Nervous system a ventral chain: consisting of two complex ganglia in head, three in
31 thorax and up to 11 in abdomen. Abdominal ganglia often fused to form complex ganglionic masses. Alimentary canal consists of three parts: fore-, mid and hind gut; usually a pair of salivary glands. Characteristic organs called Malpighian tubules present. Female genital aperture lies on eighth and male genital aperture on ninth abdominal segment. Sexes separate. Post-embryonic development of insects in an overwhelming majority of cases accompanied by

metamorphosis, often expressed in an extreme form. Among present-day animals insects have the largest number of species and exhibit maximum diversity of all animals on earth. Only a few forms, primarily larval stages, live in fresh water. Insect representatives in the seas and oceans are very few. In salty water of inland seas larvae of insects are often encountered in large numbers.

Among Recent animals class Insecta has the widest distribution and in fact almost exceeds the number of all other known animal species. The number of present-day insects that have been described runs up to a million species. Even now, in the study of the fauna of some regions of the earth, particularly the tropics, the number of newly-discovered species of insects continues to increase.

Class Insecta is of great interest not only because of its biological characteristics but also because of the value or the damage that accrues to man and his economy from their activity. Among insects there are many forms with highly developed instincts, as revealed by the intensive care they take of their progeny, and their social mode of life. The adaptations of insects to the environment are exceptionally varied.

The size of the body of insects is highly variable. It varies from 200 to 250 mm (in various tropical stick insects, Phasmatodea) to 0.25 mm (in beetles of family Ptiliidae) or still smaller (in hymenopterous egg parasites of family Mymaridae).

Different orders of class Insecta differ from each other in their morphology, development and ecology. The organization and biology of Recent insects can be studied easily. The study of fossil remains of insects, which are always fragmentary, is difficult. Even if the insect fossils are in the form of impressions of whole bodies of insects, they are often too incomplete to allow study of main morphological characters, whose structure is important for recognizing taxonomic relationships. Hence the classification and systematics of extinct insects are unavoidably incomplete. They are based on descriptions and studies of just a few well-preserved structures which, in Recent forms, are little used as bases of classification and hence are insufficiently known. In exceptional circumstances the wings of insects, on the basis of which Recent insects are classified, are preserved in sedimentary rocks. The incompleteness of paleoentomological material is thus more than compensated by the perfect preservation of the wings, which are one of the most important structures for systematic classification. Moreover, this is the reason for the peculiarity of the study of fossil remains of insects which is mainly based on the study of wings and detailed description of the different parts of wings. The paleoentomologist must be able to distinguish groups of insects not just by their most typical diagnostic features, like the structure of the mouth parts and their modifications, but also by the venation of the wings, their shape and size.

The structure of the wings of insects is fairly complex. This is particularly useful because it differs widely in different groups of insects. In the vast majority of cases it is easy to distinguish not only the orders of insects but also much lower taxonomic categories by the structure of the wings. This kind of universal significance of the wings for the distinction of taxonomic categories has to be applied with caution when introducing the main insect groups on the basis of structure of wings alone.

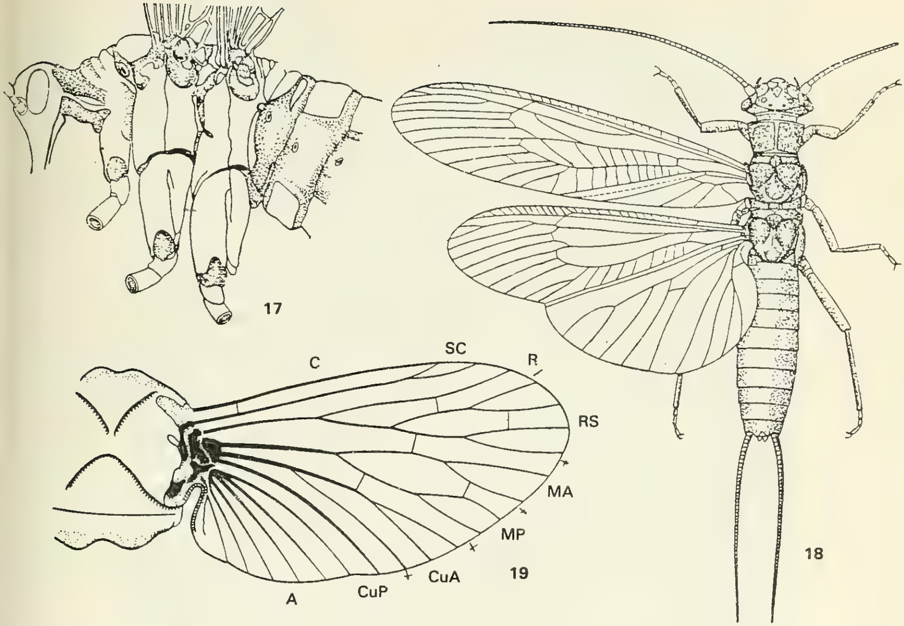
Wings of insects are special plate-like structures evolved from the lateral parts of the dorsal part of thoracic segments. They are connected with the body by a complex articulation, capable of perfect movement or strokes (Figs. 17–19). Wings are located only on two segments of thorax, the mesothorax and the
32 metathorax. Paleozoic insects are well known (Palaeodictyoptera and Paraplecoptera) in which small wing-like appendages are present on the anterior thoracic segment. These appendages were not true wings because they were not articulated with the segment and lacked mobility. Besides performing the basic function of flight, wings also have certain other functions including that of protection. As we will see later, the points outlined above are of great significance in evaluating the role of these organs in systematics: variations in wing venation indicate whether they are meant for flight or protection.

The shape of wings differs in different groups of insects. Sometimes wings are markedly elongated and narrow, for example, in dragonflies and some other primitive winged insects (Megasecoptera), some Neuroptera, scorpion flies and dipterans. The most common shape of wing in most insects is an uneven triangle or a parallelogram.

The shape of the wing is conditioned by the mechanical requirements of aerodynamics during flight and by the necessity of the wing to fold up when the insect is not in flight. Anterior margin of the wing is called costa (see Fig. 19). At the tip this margin bends backward, forming the apex of the wing. Posterior margin of wing usually distinctly more convex than anterior margin and often subdivided into a terminal margin (tegmen) and an anal margin (analis), with a distinct angle or tornus. Modification of wings into protective structures is common, with changes in the shape and thickness to form elytra.

33 The most important part of wings—their supporting structure is the venation, which consists of a system of branching tubes filled with hemolymph in living insects. These tubes or veins are variously distributed on the wing plates. Their distribution depends on the mechanical requirements of different parts of the wing plates in regions of main stress during flight. For our purposes it is necessary to note the marked asymmetry in distribution of veins on the wing. The veins on the anterior half of the wing, near the anterior margin run quite differently from those on the posterior half. At the anterior margin of the wing the veins are often close together and evenly thickened, making the anterior margin quite hard in comparison with the anal margin. This process is called costalization, and its extent reflects the degree of adaptation of the wing to strong, fast flight. The nature of costalization differs in different insects.

Individual veins give rise to certain systems of veins bearing special names (Fig. 19). On anterior margin of wing is the vein called costa or costal vein



32 Figs. 17–19. Structure of body of insect.

17. *Panorpa* sp.: structure of thoracic segments, lateral view. From left to right: head, prothorax with bases of prothoracic legs; mesothorax with bases of mesothoracic legs and forewings; metathorax with bases of metathoracic legs and hindwings; base of abdomen (Shvanvich, 1940). 18. *Perla* sp.: divisions of body. Head, prothorax with prothoracic legs; mesothorax with mesothoracic legs and forewings; metathorax with metathoracic legs and hind wings; segmented abdomen with cerci (Handlirsch, 1925). 19. Structure of winged segment of thorax of insect (schematic diagram) (Shvanvich, 1949).

(C). In the vast majority of cases costa is a single vein. It often runs around the whole wing along the margin up to the wing base. Sometimes in the basal part of the anterior part of the wing, in front of the costal vein there is a special area of the wing called the precostal area. This area bears one or more precostal veins (PC). Precostal veins are developed only in a very small group of insects—the primitive dragonflies and some orthopterans. Posterior to costal vein runs subcostal vein or subcosta (SC), which is branched in primitive insects like cockroaches, various orthopterans, scorpion flies, etc. It usually does not branch in most other groups. The next group of veins is the radius (R). These veins form an extensive system of very short branching stems that occupy much of the anterior half of the whole wing. The part of radial veins lying behind the anterior branch of R and forming the main part of the vein and sometimes sharply demarcated is called radial sector (RS). The next systems of veins are medial veins, sometimes called media (M). Usually the medial vein is subdivided into two stems—anterior and posterior, correspondingly called media anterior (MA) and media posterior (MP). These veins are located approximately in the middle of the wing and may divide into many branches. Posterior systems of veins are termed cubital (Cu) and anal (A) veins. These veins in turn give rise to many more branches which are correspondingly marked CuA, CuP, A_1 , A_2, A_3 etc. Posterior to all these systems of veins, on the wings of neopterous insects, is another system of peculiar jugal veins (Ju).

Areas of wing membrane surrounded by veins are called cells, usually named after the vein in front and rarely by its location. Between the systems of veins described above there is yet another system of veins, called cross veins, of completely different origin. They originate from a peculiar, reticulate venation of the primary wings of primitive insects known as Archedictyon (Fig. 41).

Archedictyon in its primitive version can be seen in wings of primitive Carboniferous Paleodictryoptera, Orthoptera and cockroaches. During evolution, the archedictyon is modified into cross veins.

The way the wings are folded when the insect is at rest is very significant. This feature of insects allows them to fly and also to fold the wing and to shelter in confined space. The flight mechanism was perfected very early in the history of development of primitive winged insects. The wings increased in size and the ability to beat them easily was made possible by a stable mechanical arrangement of the wings for movement. In the first neopteran insects, particularly in cockroaches, a different feature is observed. In them the adaptation to life under cover and in restricted habitats developed very early. Their wings acquired the facility to fold over the body. Complex links between the wings and the thoracic segments developed with corresponding skeletal and muscular apparatus. The insects thus acquired the capacity to live in any kind of restricted habitat such as cracks in the soil, under stones and among plants.

While concluding these observations on wings of insects we should take into account their size and position in relation to the body. In the primitive
34 Orthoptera of the Carboniferous, in cockroaches and in some primitive Palaeoptera, the length of the wing is about equal to the length of the body while in the majority of Palaeoptera, some Orthoptera and others, developed long wings where the wings were longer than the body. Another line of evolution of the wings saw a reduction in size eventually with reduction, producing wingless species. In this case one has to distinguish shortening of wings in relation to reduction of the flight function leading to winglessness, from shortening of the wings because of strengthening by costalization, in the interest of strength and speed of wing of beats. The latter is observed in the most specialized,

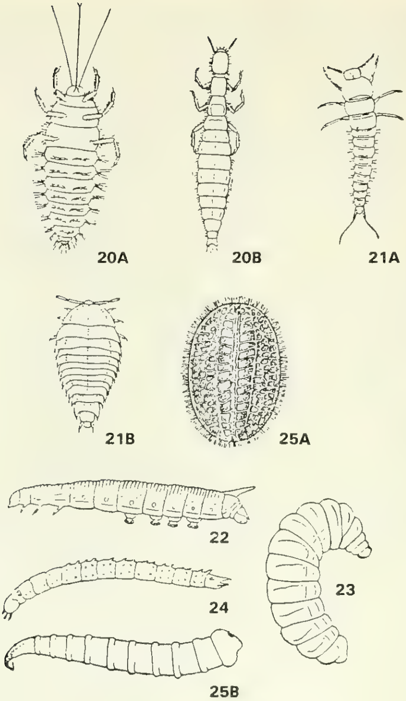
geologically recent groups like Diptera and, particularly, Hymenoptera.

An examination of fossil remains of insects that are perfectly preserved would almost always include study of characteristics of flight organs, particularly the position of the wings, which allows us to determine their affinities. The structure of most organs of the body (Figs. 17–19) of insects is less important for paleoentomological research.

The shape of the head of insects is highly variable, but in general it approaches that of an incomplete sphere or hemisphere. Antennae, eyes and mouth parts also exhibit wide variations, which differ in different orders and groups.

Besides wings, the thorax also bears legs, which consist of a massive, usually short basal segment, coxa, by means of which the leg is joined to the pleura of the thoracic segment. To the coxa is attached a short pivotal segment, called trochanter, which sometimes is made up of two segments. Trochanter forms a vital mechanical part, certain muscles, which generally facilitate movement of all the legs, are attached to it. Next comes the compact and often the longest segment of leg, femur, which bears main muscles responsible for movement of distal sections of legs—tibia and tarsus. The tibia is nearly equal in size to femur, but is often thinner and it can fold up very close to femur. All these parts are involved in walking. The tarsi in most insects are multi-segmented. The number of segments varies from one to five in different groups. The distal segment of the tarsus has various very short appendages located on a special sclerite, called pretarsus. Each segment of thorax has a tergum or scutum, a sternum and pleura. Tergum is occasionally divided into separate dorsal sclerites (notum, postnotum) and shields (prescutum, scutum, scutellum). Well developed, individual segments of thorax (mesothorax in Diptera or Hymenoptera, metathorax in Coleoptera), have very complex structures and consist of many separate sclerites. Pleura of thoracic segments are divided into two major sclerites: an anterior episternum and a posterior epimeron, which are further subdivided. Thoracic sterna are similarly divided into sclerites. Abdomen consists of segments built on a general plan. Abdominal sclerites differ in size and position. Large tergites sometimes extend to ventral region, as in certain Hymenoptera and Diptera. In other cases sternites grow to a large size, as in Coleoptera. Various sexual appendages are located at the end of the abdomen. These structures are often useful in distinguishing the taxonomic relationships of species, and occasionally of genera, of many insects. Last segment of abdomen bears a pair of cerci. In primitive groups of insects cerci are multisegmented and often very long, as in the majority of Palaeoptera and many orthopteroids. In certain other insects cerci are short and not segmented. At times they are hardly distinguishable.

Postembryonic development of insects is very peculiar and differs in different groups. The vast majority of insects, in general, exhibit metamorphosis, so that the insect emerging from the egg differs distinctly from



34 Figs. 20–25. Larvae of insects.

20. Larvae of Neuroptera: A—*Sisyra* sp.; B—*Raphidia* sp. (Handlirsch, 1925). 21. Larvae of Coleoptera: A—*Catops* sp.; B—*Silpha* ph. (Handlirsch, 1925). 22. Larvae of Lepidoptera: caterpillar of Sphingidae (Handlirsch, 1925). 23. Larva of stinging Hymenoptera [Apidae](Handlirsch, 1925). 24. Larva of Diptera, Nematocera, Bibionidae (Handlirsch, 1925). 25. Larva of Diptera, Brachycera: A—Larva of hover fly *Microdon*, living in anthills; B—larva of Muscidae (Handlirsch, 1925).

the adult or sub-adult stage in its organizational features (Figs. 20–25). Only certain insects of Apterygota emerge from the egg, resembling adults, but differing in their small size and undeveloped gonads. In all winged insects the young hatching from eggs always differ from adults in some way.

Two main forms of postembryonic deveopment of insects are distinguished: incomplete metamorphosis or hemimetaboly, and complete metamorphosis or holometaboly. In hemimetaboly, even in the early stages of development most of the adult characters, such as compound eyes and three pairs of legs appear. Development in Hemimetabola includes an increase in size and appearance and development of rudiments of wings and genitalia. The last molt of the larva, called the nymph, transforms the insect into a full-grown insect with wings of adult type. A resting phase (pupa) is not found in this kind of metamorphosis. Specialized organs and adaptations of larvae are also rare. Food and ecology of postembryonic stages of insects with incomplete metamorphosis do not differ from those of adults. Hemimetaboly is exhibited by orthopterans and cockroaches.

In complete metamorphosis larvae emerging from eggs are quite different from adult insects in their characteristics. Such larvae have simple eyes and often bear additional appendages on the abdomen or are completely bereft of them. The ecological factors differ for the larvae and the imago of insects with complete metamorphosis. The larvae become suitably adapted to live under different ecological conditions. Eventually they enter a peculiar non-feeding pupal stage, where they develop adult characteristics. After this period of rest the adult insects emerge. This complete metamorphoses or holometaboly is observed in Coleoptera, Diptera, Hymenoptera, Neuroptera for example.

These two major kinds of metamorphoses are subdivided into many secondary types which do not concern us in this manual, but it is to be noted that the complexity of postembryonic development of insects and the highly different larval stages, depart not only from the adult form but also from the general plan of structure of insects in general. For example, the larvae of beetles, Hymenoptera and Diptera are legless, and those of higher Diptera are without strong cephalization.

PRINCIPLES OF TAXONOMY

The extensive subdivision of the class Insecta into subclasses, infraclasses, cohorts, superorders and orders take into account the characteristic features of ontogeny, morphology and ecology of larval and adult stages. For a broad classification, the general nature of metamorphosis and ecology of the larval stages and characteristics of mouth parts and flight mechanisms in adults are taken into account. The subclass of winged insects, Pterygota, includes two infraclasses, Palaeoptera and Neoptera. The latter is further divided into four cohorts: Archaeoneoptera, Polyneoptera, Paraneoptera and Holometabola or Oligoneoptera. This division, based on the structure of the wings, also stresses the modes and characteristics of larval development. The infraclasses and cohorts of winged insects mentioned above include variable numbers of superorders and orders. The characteristics of these groups are to a large measure supplemented by structural features of mouth parts. As for characteristics of the still lower taxa of Insecta (superfamily, family and genus), it is not really possible to generalize the differences in their characteristics. In 36 different orders these taxonomic units are very different and their diagnostics are based on the behavior of highly varied organ systems. On the basis of taxonomy of different orders and groups, as discussed in essays on the subject, we also emphasize the importance of structure of wings as one of the major features for the formation of taxonomic units of almost any rank.

ORIGIN AND EVOLUTION

The phylogenetic relationships of insects with other arthropods cannot yet be considered to have been finally elucidated. Apparently there is a true similarity between insects and the group of myriopods called Symphyla. Other approaches, such as the search for the ancestors of insects amid trilobites and crustaceans, do not deserve serious consideration: these views rest on flimsy grounds. Above all, the rise of insects was accompanied by a striking expression of the process of tagmatization, which demarcated the middle division of the body, the thorax. The thorax performed the function of locomotion. Only three segments of the thorax were provided with locomotory appendages—the walking legs. This determined the typical subdivision of the body of the insect into three tagmata—head, thorax and abdomen.

The next stage in the evolution of insects, namely the rise of present-day insects with free mouth parts, tracheal system, abdomen with 11 segments, long antennae and cerci, embryonic development with extensive blastokinesis and formation of embryonic envelopes, is still very little understood. Similarly very little has been found out about the origin of Pterygota and their divergence from the group of Thysanura by the appearance of wings. To date these processes have been studied and explained only on the basis of purely comparative anatomical data and hypotheses, but there are fairly reliable suggestions as to the 37 conditions determining phylogenetic direction. There are no true paleontological records so far to throw light on these important landmarks in evolution.

Much more reliable is the information on the origin of two infraclasses of Pterygota–Neoptera and Palaeoptera. Representatives of infra-class Neoptera, order Archaeoptera, very recently discovered from the Devonian strata* had the simplest structure, close to the ancestral forms of Pterygota. The cohort Archaeneoptera was created for these peculiar forms. The stout wings of these insects reveal the characteristics of primitive wings. It can be seen that they are outgrowths of dorsal part of thoracic segment called the paranota. Venation of wings had only weakly developed although the form of the wing had already attained aero-dynamic adaptations. These Devonian insects were already 'neopterans' because they could fold the wings back over the body. Hence it is suggested that the ancestral Palaeoptera arose exactly along similar lines of early

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* Editor's note: Corrected later as these are parts of Crustacea, not Insecta.

development of large membranous wings so as to enable them to inhabit open spaces and quickly attain perfection in terms of adaptation to flight.

Another line of development relating to perfection of wing organization of insects living in sheltered places, includes development of venation and conversion of forewings into wing covers, leading to development of dissimilar wings. Only the hind wings remained light, stretched out organs of flight with the capacity to fold back as well as move rapidly. Such wings are seen in cohort Polyneoptera, particularly in order Blattodea.

Further evolution of these infra-classes is very different. In the Paleozoic itself, Palaeoptera quickly differentiated into a series of secondary groups which comprise not fewer than three superorders and many orders and suborders. A still more complex development continued in the infra-class of Neoptera, which
38 is divided into four extensive cohorts with many superorders and orders.

Phylogenetic relationships of the major groups of Pterygota are shown in schematic diagrams (Figs. 26 and 27). Characteristics of history of infra classes and cohorts are examined in the articles cited. The diagrams show the time of divergence of major groups. These divergences originated during the course of Devonian and, partly, Carboniferous periods. It is important to notice that actual paleontological proofs of early history of Pterygota are still lacking and we can only guess about them on the basis of indirect (comparative morphological and other) data.

The most primitive paleontological record on the history of Pterygota dates back to Upper Devonian. Such a find from the northern Urals is the peculiar winged insect *Eopterum devonicum* Rohdendorf (p.101)*, belonging to a special order, Archaeoptera, which is closest to the cockroaches (Rohdendorf, 1961). This form had reduced fore wings with a few longitudinal veins. In spite of its primitive character it already bore some specialized features.

Various remains of Pterygota first appeared in paleontological history in the top layers of Lower Carboniferous—from the Namurian. Such remains of some Palaeoptera, Homoptera, Orthoptera and primitive Mecoptera occur in Europe and North America. In the Westphalian stage of Middle Carboniferous of Western Europe and in the corresponding deposits of North America, rich faunal complexes comprising representatives of various orders have been discovered. In short, the appearance of the remains of Pterygota in Carboniferous deposits is quite sudden, and this confirms the unreliability of the paleontological data. All the forms discovered belong to orders distributed in a still later geological period. Hence they do not throw much light on the time of origin and divergence of the major groups of the class.

Particularly important in these primitive faunal complexes of representatives of orders of insects are finds pertaining to groups that flourished only in distinctly later times. Such finds include, for example, primitive scorpion

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* Editor's note: Actually a crustacean.

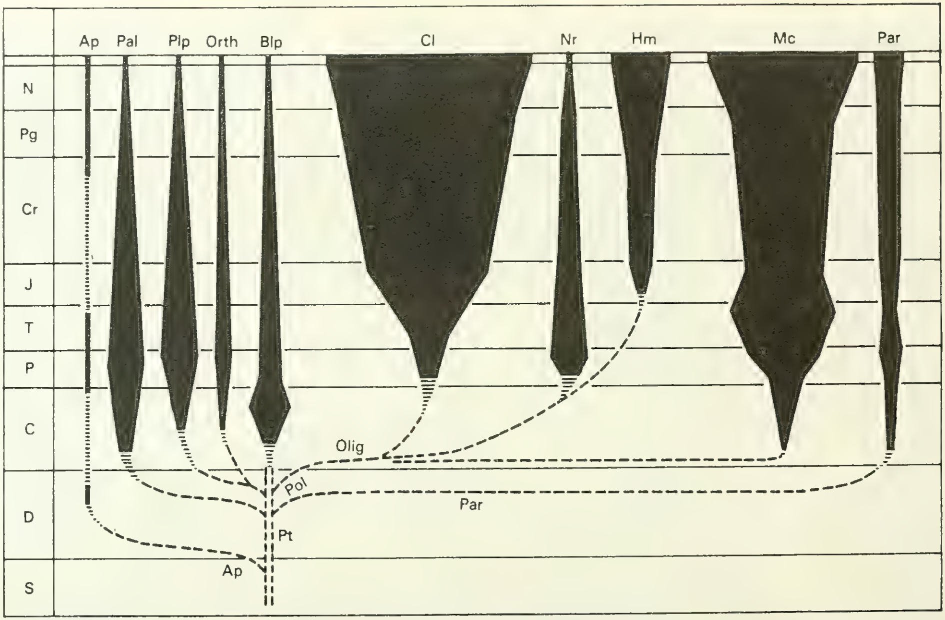

Fig. 26. Schematic diagram of phylogenetic relationships of subclasses, infra classes, cohorts and some superorders of class Insecta.

C—Carboniferous, Cr—Cretaceous, D—Devonian, J—Jurassic, N—Neogene, P—Permian, Pg—Paleogene, S—Silurian, T—Trias., Ap—Apterygota, Blp—Blattopteroidea, Cl—Coleopteroidea, Hm—Hymenopteroidea, Mc—Mecopteroidea, Nr—Neuropteroidea, Olig—Oligoneoptera, Orth—Orthopteroidea, Pal—Palaeoptera, Par—Paraneoptera, Plp—Plecopteroidea, Pol—Polyneoptera, Pt—Pterygota. The schematic diagram was compiled in 1958, cohort Archaeoneoptera is not shown (Rohdendorf, Bekker-Migdisova, Martynova, Sharov, 1961).

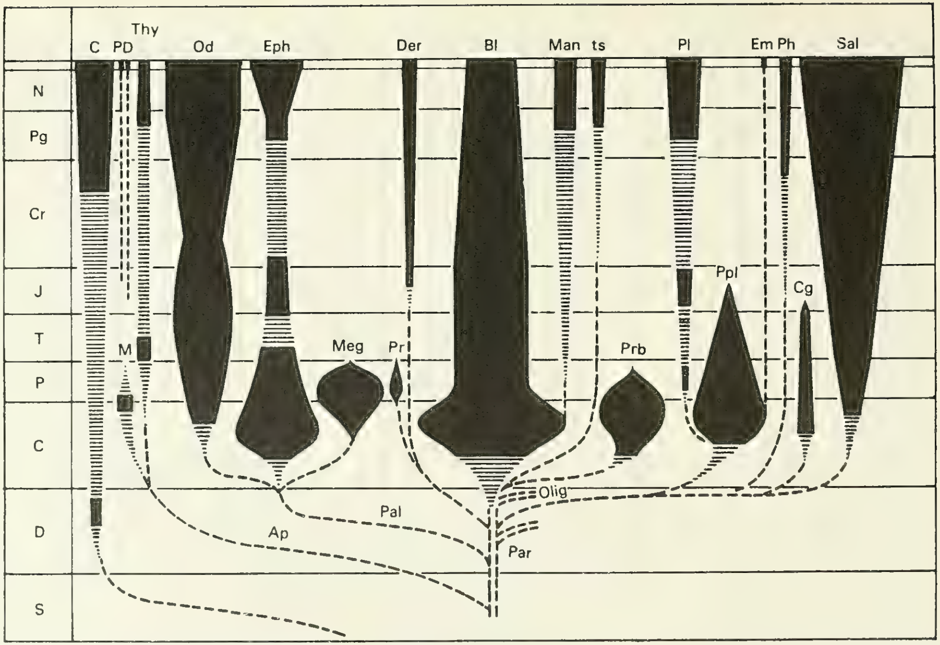

Fig. 27. Schematic diagram of phylogenetic relationships of subclasses of Apterygota, infraclasses of Palaeoptera and cohorts of Polyneoptera.

Ap—Apterygota, Bl—Blattodea, C—Collembola, CG—Caloneurodea and Glosselytrodea, D—Diplura, Der—Dermaptera, E—Embioptera, Eph—Ephemeroptera, Is—Isoptera, M—Monura, Man—Manteodea, Meg—Megasecoptera, Od—Odonata, Olig—Oligoneoptera, P—Protura, Pal—Palaeoptera, Par—Paraneoptera, Ph—Phasmatodea, Pl—Plecoptera, Ppl—Paraplecoptera, Pr—Protelytroptera, Prb—Protoblattodea, Sal—Saltatoria, Thy—Thysanura (Rohdendorf et al., 1961).

flies (*Metropator pusillus* Handlirsch) in the top layers of Lower Carboniferous (Potsville) of North America, primitive Homoptera (*Protoprosbole straeleni* Laurentiaux) from the Namurian of Western Europe and from the Alykaevian series of Carboniferous of Southern Siberia (*Blattoprosbole tomiensis* Bekker Migdisova).These facts compel us to set back in time the origin of infraclasses and cohorts of winged insects, particularly of the most progressive groups Paraneoptera and Holometabola.

The lack of paleoentomological data means that solution of the problems of the phylogeny of large groups of subclass Pterygota must be primarily based on comparative morphological research, studies in ontogeny and ecology. Paleontological data are inadequate for elucidating a specific line of phylogenetic development.

MODE OF LIFE, ECOLOGY AND TAPHONOMY

The distribution of insects around the world in general coincides with the distribution of the ground flora. Only the extreme polar zones and high mountains with perpetual snows are without insects. Insects are also alien to the sea, which only a few special forms inhabit. Such are the peculiar swimming bugs living on the surface of tropical seas and the larvae of some Diptera inhabiting coastal waters and the tide-line. Relatively numerous larvae of insects, particularly Diptera and Trichoptera, inhabit tidal pools low in salinity.

The vast majority of insects are inhabitants of dry land and freshwater bodies, such as rivers and freshwater lakes.

In considering the general distribution of insects it is necessary to bear in mind their extraordinary diversity and abundance as compared to other classes and types of organism. The main reasons for this are the small size and the high degree of organization of insects. In the process of evolution these have become perfectly adapted to varied living conditions. Insects have been able to take over and populate literally any area on earth where organic life is possible.

Insects of different climatic belts defining different zoogeographical provinces are very different. The insect fauna provides convincing evidence for
39 zoogeographical zonation anywhere. Particularly striking, of course, are the differences between the tropical and temperate belts. Besides this, the various tropical and temperate fauna are quite distinct from region to region, for example, the insects of South America, Africa and South Asia and the fauna of North America and Eurasia.

All insects can be broadly divided into two unequal ecological groups. The smaller group includes either insects, which spend their whole lives in water bodies (certain beetles and bugs), or aquatic larvae, whose adult forms are terrestrial. Most of the insects found in water belong to the latter category (dragonflies, mayflies, stone-flies, caddis flies, some lacewings, flies, etc.). The second group of insects—the most numerous land insects—includes forms that show a gradual transition from aquatic forms through insects living on aquatic vegetation, damp meadows or moist soil to habitats such as forests, fields and steppes. Finally, the deserts of all countries are populated by numerous, very peculiar, specialized insects. The special ecological characteristics of the habitat are reflected in the morphology of these animals. As with aquatic insects, these insects also show adaptation to their special mode of life. These and other ecological conditions are reflected in the structure of the body of the organism. Hence we are able to determine the mode of life of an insect from its structure.

Feeding, reproduction and development of insect species are extraordinarily varied. It may be said that insects in general are truly omnivorous animals. Perhaps there is no single natural complex organic substance, except some decaying nitrogenous substance which does not serve as food for some species of insects. The majority of insects eat plant matter (phytophages), while a minority are predators, attacking other insects or other creatures. Finally, many groups are parasites on a variety of animals: many vertebrates, mollusks, arthropods (including other insects, arachnids, myriopods, and also some crustaceans) and annelids. A biologically peculiar group of insects includes those that feed on decaying vegetable and animal matter, carcasses and excreta of animals (scatophages). The versatility of insects is remarkable. There are insects that can live in crude oil. Such are the well-known petroleum fly, whose larvae live in pools of crude oil and feed on microorganisms (insects—Ed.) trapped in the petroleum. Various kinds of termites (tropical insects, often highly destructive) live on almost pure cellulose, devouring dry timber. The food preference of insects is much complicated due to metamorphosis. Usually larvae consume different food than adults. Sometimes the mouthparts of the adult insects are reduced and they do not feed. These forms live off the fat stored during their larval development. Examples of such insects are many Diptera (gadflies, midges, etc.), Lepidoptera (many silk worm adults), Ephemeroptera and males of Strepsiptera and coccids. This widely distributed phenomenon among insects, reveals a unique evolutionary trend, called pedomorphosis, in which the adult stage is very brief. The adult survives for a distinctly shorter time than the larval stage. Such pedomorphic insects perform only the function of reproduction (+ distribution—Ed.) in the adult stage. All other life functions are much curtailed.

The biology of reproduction is also very diverse. In insects sexes are separate. In the vast majority of cases females lay eggs. Rarely, they give birth to live larvae, which sometimes mature fully after feeding and developing in the body of the female. The fecundity of insects varies from group to group within very wide limits. There are species that lay fewer than 10 eggs throughout their life, and there are species known for their extraordinary fecundity, laying a fantastic number (20,000) of eggs.

Some insects are capable of rapid multiplication producing large swarms. For example, the swarm of locusts—orthopteran insects of subtropical and tropical countries—various harmful species of Lepidoptera, Coleoptera, and other insects, and mass flights of Ephimeroptera and the appearance in large numbers of some Odonata, Lepidoptera and many other insects of no direct economic importance. The occurrence of rapid multiplication is influenced by complex ecological conditions of the habitat of the different species of insects, such as favorable climate, abundance of food and reduction in the number of natural enemies.

40 In all these cases it is observed that great complexity and extreme specificity exist, which lead to rapid multiplication of the different species. A deeper examination of these phenomena is of no direct interest for paleontology, but the wide occurrence of mass flights of some insects in the past, which had a direct bearing on the formation and accumulation of fossil remains is an important fact. Because of mass flights of these insects there is an accumulation of their dead bodies or isolated skeletal parts, often in very large quantities, under conditions conducive to their preservation: in basins where sediments also accumulate and provide the right condition for fossilization. Such basins are in lakes, lagoons, estuaries, creeks of rivers and deltas. This explanation of the sites of fossil remains of insects as the result of mass flights of different species undoubtedly has an important role. We get sites of fossil insects containing numerous remains of one particular or, often, a few species. To this category presumably belong, for example, the Upper Permian insect fossils in Arkhangelsk province along the River Soyana, Mesozoic insect fossils in East Siberia—Turgin and Ust-Bailey fauna—and, finally, Tertiary insect fossils in the Miocene deposits of Stavropol in the North Caucasus, and probably many others. In all these faunal complexes of the past the remains of numerous specimens of some species are preserved, testifying beyond doubt to their mass character.

Along with series of remains of certain insect species in innumerable sites there are also solitary entire specimens of some other insect species. We also get whole faunal complexes of fossil insects, along with unique specimens of numerous other insect species. In all these cases there is no evidence to suggest the occurrence of mass flights of insects. Evidently, the sources and conditions of formation of rich fossil localities of such type are not due only to the swarming of insects. They only reflect the accidental, selective character of the conditions that befell the insects at the time of their burial. This explanation of the site of insects is the key to their wide distribution. The accidental burial of insects calls for a thorough knowledge of the composition of the actually existing fauna. Examples of such selective, species rich faunal complexes are the sites of Permian insect fossils in the Urals (for example, Chekarda) and many Tertiary sites (for example, those of Oligocene insects from Rotta, Germany). The particularly well-known sites of Jurassic insect fossils in Kazakhstan (Karatau) contain a very large number of individuals of certain species (hundreds), besides the isolated remains of certain other representatives.

It is possible to study the relative measurements of well preserved remains and their density, i.e. of fragments of various sizes. The majority of fossil insects are fragmentary. In better cases whole wings are preserved. Usually the paleoentomologist does his work with scraps of wings, some parts of the body, and disjointed legs or sclerites (for example, thoracic sterna of beetles). Extremely rarely the insects are wholly or nearly wholly preserved. There are faunal complexes of insects composed solely of insects of small sizes. The occurrences of Upper Permian insect fossils in Kuznetsk basin (Sokolova II) and Triassic insect fossils in Central Asia are such examples. In these cases preservation of the remains took place certainly after their transfer by currents and mechanical sorting, along with associated fine-grained sediments. On the other hand, preservation of complete bodies of insects, as observed in the Karatau type, must have taken place *in situ*, where the insects died before the process of fossilization. Thus, from the nature of the preservation of the insects one can infer that if they are perfectly preserved it can be presumed that they had not been transferred by water currents.

Accidental burial of insects sometimes leads to finds of fragments among totally unexpected and uncommon faunal complexes. For example, the remains of hind legs of saltatorial Orthoptera occur amidst the remains of Tertiary deep-sea fishes in fine-grained rocks of obviously marine, non-continental character (Sarmatian deposits of North Caucasus). Finds of elytra of Coleoptera occur amidst marine organisms. In such cases the very great mechanical strength and small weight of the skeletal parts of the insects allowed them to be transported for long distances by wind and water currents to the unusual environments where they were buried.

The peculiarities of dead bodies of insects—small size, compactness of
41 skeleton and certain mechanical features—account for the occurrence of fossil remains of insects alongside remains of Conchostraca and certain ostracod crustaceans, lamellibranch mollusks and, occasionally, Lingulidae. This throws light on the size of the crustaceans, mollusks and Lingulidae and their habitats in the lagoons and pools where burial of the remains of insects took place. Among the remains of other organisms the remains of fishes, in particular certain Clupeidae, are encountered. Remains of fishes, primarily scales, which are very common in sites of Neogene insect fossils, are almost always confined to certain horizons, for example, Karagan zone of Miocene of Stavropol. Sometimes well-preserved, almost complete skeletons of fishes are found alongside insects. The Jurassic 'fishy' or 'papery' shales of Karatau and many Mesozoic sites in Mongolia and Baikal are examples of this. The origin of these occurrences is different. It is probably connected with processes of periodic desiccation and sequential deposition of fine-grained sediments in basins of a special kind. The fish perished by asphyxiation as the basin dried up. The insects were carried far out, into the basin by wind and were quickly buried, almost without any further transportation by currents.

Besides remains of animals, fossil insects have always been associated with remains of plants too. Most of the finds comprise pieces of wood, bits of leaves and whole small fruits or seeds. Preservation of vegetative remains depends on their mechanical properties and on the possibility of transportation along with remains of the insects. This explains the absence or paucity of insects in layers rich in bulky vegetative remains: leaves, branches, stems and trunks of plants. Here insects are rarely trapped. Only the large, heavy forms or those with large wings are likely to be entangled. But the presence of numerous seeds of plants in sedimentary rocks is always accompanied by finds of insect remains.

Finally, let us remember the peculiar mode of preservation of fossil insects in hardened resin of coniferous plants—amber or copal. The resin of some conifers does not recrystallize when it dries and preserves a glasslike transparent structure during its concentration. This allows us to examine with ease all inclusions that got trapped in the resin during its secretion. As a result of natural hardening, which transforms it into a thick hard body—amber or copal—so-called natural 'permanent preparations' were created in resins of primitive plants. The transparency of amber or copal is so high that many inclusions are visible with exceptional clarity. Considering the great antiquity of [some] amber, whose age of formation is Upper Cretaceous, the study of amber inclusions is obviously very valuable for information on past fauna. But the data and value of the materials on amber fauna are limited: they throw light only on the composition of forest faunal complexes, including primarily small insects living on tree-trunks and bark and, rarely those that lived in the soil or on the leaves. Large insects and those living in open terrain are not preserved in amber. The insects in amber are associated with varied remains of plants (even with well-preserved flowers!) and some animals—spiders and myriopods. Occurrences of fossil resins—amber and copal—are fairly rare. Our knowledge of the insects of these faunal complexes has been mainly gained from study of the well-known Baltic amber.

IMPORTANCE OF INSECTS

The importance of insects is due to their abundance, variety and very broad distribution. They are diverse and very important to man. The destructive action of insects is partly compensated by their usefulness. Examples of this are sericulture, bee-keeping, pollination of flowers by insects, insect parasites of harmful insects, and lastly, production of lac, wax and some dyes.

Insects have an importance, which is altogether special in paleontology. Besides being land dwellers, insects have extraordinarily broad distributions in all ecological and geographical regions. They allow easy and accurate characterization of various districts and places where they live. Their abundance and diversity and the small absolute size of their bodies afford important and useful materials on the ecological and geographical characteristics of any part of the land. This determines their significance for geological bio-stratigraphy. The

42 rarity of remains of other organisms in continental deposits enhances the potential value of fossil remains of insects.

Although the significance of fossil remains of insects for stratigraphy cannot be denied, the actual application of the results of paleoentomological research and in general the use of fossil remains of insects in geological work may not be quite clear. One reason is the insufficiency of existing data on the insects of faunal complexes of the past. To-date the fossil sites of insects are justifiably considered rare and the finds of insects are few or isolated and exclusive. In fact, until the 1920's the sites of fossil insects in the territory of the Soviet Union were few and the remains of insects were not numerous (a few dozen). Today the number of known sites where fossil insects have been found is nearly 300. The number of insect remains collected and studied has reached tens of thousands. These extensive materials allow us to describe fairly completely the fauna of our territory in different periods of geological time, beginning with the Carboniferous. During the period of their historical development insects changed radically. The faunal complexes differ sharply, not only from one epoch to another but also, evidently, according to the geographic and climatic peculiarities of different regions.

CHARACTERISTICS OF STUDIES OF TAXONOMIC COMPOSITION OF INSECTS OF DIFFERENT FAUNAL COMPLEXES

Carboniferous faunas are the most primitive, if the few finds from the Devonian are not considered. They have been studied best in Western Europe and North America. In the territories of the USSR they are still not sufficiently known. Only in recent years have the sites in Siberia, which had been opened long ago, containing deposits of Lower Balakhonian series of the Kuznetsk basin, been fairly thoroughly studied. On the whole, Carboniferous faunas are characterized by palaeodictyopteroids, blattoids and protoblattoids. To these may be added certain groups of orthoptera-like insects, primitive suborders of dragonflies (Meganisoptera) and Megasecoptera. Against this main background appear relatively less numerous representatives of many other groups, which reached the acme of their development later (e.g., primitive Homoptera, Mecoptera and Ephemeroptera). The question of a division into climatic districts of Carboniferous fauna remains open to this day. The answer must wait till study of the corresponding complexes of Angarida and Gondwana.

Permian faunas have been studied much more completely than the Carboniferous faunas. They were known from a series of sites in the European part of the USSR (Urals and Urals-Arkhangelsk province) and in Southern Siberia (Kuznetsk basin). Permian locations are known in North America, Australia and Western Europe, but the most complete materials on Permian fauna have been collected from our territory. The chief feature of Permian fauna is the rapid rise of Mecoptera (if the Carboniferous find of Metropatridae, which otherwise first appeared in the Permian, is excluded) and Homoptera, and also the first appearance of Coleoptera.

Abundance of various Palaeoptera from the superorder Megasecopteroidea, particularly part of the suborder Protohymenoptera and the odonate suborders Protanisoptera and Permanisoptera, is very characteristic of the Permian. The order Protelytroptera also belongs to the Permian.

Triassic faunas have been studied very little. There are extremely few sites, limited to Central Asia, the Kuznetsk basin and a few spots in Western Europe and Australia. It is difficult to characterize the Triassic fauna: it is possible to give only a general outline. The main events are the great development of Coleoptera, appearance of the first Diptera and Heteroptera, the survival of a few relicts of some Orthoptera-like orders of the Permian (Gloselytrodea), and the complete disappearance of Palaeodictyoptera.

Jurassic faunas are the best studied among Mesozoic faunas. A lot of data have been obtained during the study of Lower Jurassic insects in Central Asia (occurrences at Shurab, Kizil-Kiya and others) and Upper Jurassic in Kazakhstan (well known in the Karatau Hills). Outside the USSR Jurassic insects are known only from a few sites in Western Europe (Germany and England), China, Mongolia and Australia. The principal and richest sites of Jurassic fauna are confined to the territory of the USSR. Besides the above major examples, finds of insects of this age in Western Siberia (Kuznetsk basin and Cheliabinsk province), Eastern Siberia (Ust-Bailey and others), Kazakhstan
43 (Turgai valley), the Caucasus and certain other districts can also be cited. A rich development of Coleoptera and Diptera characterizes the Jurassic fauna. Amid these orders families which have survived upto the Recent epoch start appearing. Still the general composition of all the faunas is peculiar. Most of the Jurassic families are extinct. Hymenoptera first appeared in the Jurassic. Highly characteristic of Jurassic fauna is the development of the peculiar, large similar winged Palaeontinidae, which at one time were erroneously regarded as butterflies. These huge cicada-like insects are the obvious "index" fossils for all Jurassic faunal complexes. Among the primitive-winged insects one notices the appearance of Jurassic mayflies characterized by unequal wings, the rich development of suborder Anisozygoptera of dragonflies (of these only one relict genus is still found in Asia) and the appearance of the new, now widely distributed, suborder Anisoptera.

The Cretaceous fauna studied are considerably fewer than the Jurassic or Triassic ones. On the whole, some 10 sites are known in Western Siberia, Povolzh and Western Kazakhstan (Emba River), where isolated remains of Cretaceous fauna have been discovered. Occurrences of Cretaceous insects in other countries include Western Europe, North America and China. They have been very little studied so far and hence do not give reliable or complete information on faunal characteristics. One of the sites of insects of this age discovered in the last decades holds possibilities of interesting information. This is the Canadian site of Cretaceous amber at Cedar Lake. The age of this amber corresponds to Uppermost Cretaceous, bordering Paleocene. The strata of the whole system have been little studied. Cretaceous faunas of insects differ from the Jurassic: they contain more new groups that have survived into the Recent epoch. Such are some families of Diptera (Ceratopogonidae, Chironomidae), Neuroptera (Psychopseidae) and probably many Coleoptera. Apparently the purely Jurassic groups of Homoptera are already absent in the Cretaceous.

Tertiary insects are the best represented in collections of insect remains in museums throughout the world. Numerous sites of Tertiary insects have been found on all the continents, including the territories of the USSR. The finds in the USSR include the sites of Baltic amber known along the shores of the Baltic Sea in the Lithuanian SSR and the Kaliningrad region. Sites richer in Miocene insects are found in North Caucasus (Stavropol), Tien-Shan (Cho-Tuz) and in the Moldavian SSR, Western Ukraine, etc. The sites of Tertiary insects in Western Europe are innumerable, for example the Oligocene insects of Germany (Rott), France, Switzerland and Italy. Very rich sites of Miocene insects are encountered in North America (Florissant) and many other places*.

Despite the variety and wide distribution of sites of Tertiary insects they are not particularly well studied. The reason is their contiguity with Recent fauna. This situation calls for a complete knowledge of Recent living faunas, and that would require narrow specialization of the paleontologist engaged in Tertiary insect study. So far this requirement has not been fulfilled and specialists have not studied or written about them. Therefore most of the works on Tertiary insects are not accurate. They need to be critically reexamined. It can be said that this division of paleontology is the most laborious and has been worked out very little. To characterize Tertiary insects completely would be very difficult: they are so close to Recent ones. It is possible to point out generally that almost all Recent families of all orders are present in Tertiary fauna. There are very few extinct families and for many groups, none. Comparing Paleogene faunas with Recent, one finds that extinct Paleogene genera of insects are common. The finding is different for Neogene faunas. Extinct genera are entirely absent from the best-known Miocene. The peculiarities of these faunas in comparison with Recent ones are limited to the different species composition. Recent species are not rare in Miocene fauna. This general account of Tertiary insects is, of course, very sketchy and needs to be improved on the basis of examination of specific faunal complexes.

Quaternary complexes of insects have been studied still less. In essence their study is inseparably linked with the work of insect taxonomists engaged in elucidating the history and composition of Recent insects. Quaternary insects are very important for zoogeographical studies which reflect the not too distant history of and changes in the geographical distribution of certain species

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* Editor's note: The Miocene amber deposits of the Dominican Republic are now known to be rich in arthropod remains.

44 complexes. Specialization of studies in the case of Quaternary insects is similar to that of Recent insects.

In conclusion a few words must be said on the prevailing opinion as to the extreme rarity of fossil remains of insects, the difficulty of collecting them, and the occasional impossibility of systematic studies. Such opinions, based on insufficient and inadvertent data, were quickly dispelled by paleontologists. In the past finds of fossil remains of insects were always in passing and accidental during geological surveys, and made in collections of 'archi-stratigraphic' items, primarily plant remains. Now this kind of opinion is true only to the least extent. As the course of development of paleoentomological knowledge in the USSR, particularly through the works of A.V. Martynov, has shown, sites of remains of insects are by no means exceptionally rare and difficult to discover. By the organization of specialized exploration the remains of insects are always discovered by careful and attentive study of associated sedimentary rocks.

The basic condition for finds of insect remains is the presence of fine-grained sedimentary rocks, usually of continental origin. Careful examination of the cracks in the different layers of rock using a lens with a magnification of 10 times will often reveal fossil remains that might otherwise escape detection. Often many hours of fruitless search are rewarded by the discovery of an insect-bearing stratum which later yields rich and varied material.

Study of the material—the fossil remains of insects—is the most taxing part in every paleoentomological investigation. The extraordinary variety of insects in any faunal complex beginning from the top of the Lower Carboniferous, makes accurate determination of the systematic affiliations of the ancient insects discovered, difficult. Any accurate determination of the entire taxonomic composition of any one faunal complex of insects cannot be carried out by one investigator. Therefore paleoentomologists have to specialize in the taxonomy of various groups of Recent insects and be up-to-date in them. In most cases of study of whole faunas, inaccurate or unreliable identifications can be avoided by the inclusion of a paleoentomologist in the team. (See: Rohdendorf, 1957; Rohdendorf, Bekker-Migdisova, Martynova and Sharov, 1961.)

Classification

Subclass APTERYGOTA.[1] Primitive wingless insects

(O.M. Martynova)

45 Small insects, 0.2–15 mm in length, rarely 40 mm. Wings always absent. Tarsal segments three or less. On first segment of abdomen paired or unpaired (fused) appendages in the form of sacs, rods or rudimentary legs.

Metamorphosis incomplete or absent. Live among plants (grass, moss, etc.), in soil, under stones or crust of melting ground frost; some forms live in damp places in houses, anthills or on cliffs. Consume vegetative matter such as mold, fungal mycellium, lichen and sometimes vascular plant tissues and decayed plant remains.

Very rare as fossils. Best known from Baltic amber, from which a small number of forms of the orders Protura, Collembola and Diplura, which are close to myriopods have been described. Only Thysanura and Monura are related to winged insects. There is no doubt that Thysanura-like forms gave rise to all winged insects with complete as well as incomplete metamorphosis. Except Protura, all other orders of apterygote insects have fossil representatives. Devonian to Recent. Five orders: Collembola, Protura, Diplura, Thysanura, Monura.

Order COLLEMBOLA. Springtails

Mouth parts entognathous. Antennae four or five segmented. Eyes simple. Tarsus unisegmented, with one claw. Abdomen six segmented, first segment

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[1] Many Soviet and other entomologists have now suggested that Protura, Collembola and Diplura should be considered as independent classes. The author agrees with this suggestion. Still, for the sake of convenience of presentation and discussion of the problem, the old classification of Apterygota is retained in the present work.

with a paired or fused, retractile sac. Fifth segment with springing organ or furcula. Cerci absent. Length of body varies from 0.2 to 10 mm. Devonian to Recent. Two suborders: Arthropleona, Symphypleona.

Suborder Arthropleona. Segmented-abdomens

Body elongated and cylindrical. Thoracic and abdominal segments free, not fused. Devonian to Recent. Three superfamilies: Poduromorpha, Protentomobryomorpha and Entomobryomorpha.

46

SUPERFAMILY PODUROMORPHA

Body with a granulated surface. Antennae shorter than head. Postantennal organ with one central tubercle, with sessile peripheral tubercles on it. Mesonotum and metanotum equal in length. Pronotum a little shorter, not covered by anterior margin of mesonotum. Paleogene to Recent. Three families: Hypogastruridae, Poduridae and Onychiuridae. Fossil representatives of the last two yet to be found.

Family HYPOGASTRURIDAE Börner, 1906

[nom. transl. Börner, 1913 (ex Hypogastrurinae Börner, 1906)]

Furcula clearly visible, short, but protruding beyond ventral tube. Length of body varies from 0.8 to 1 mm (Fig. 28). Paleogene to Recent. Six genera in Recent fauna, out of which one is represented in Paleogene of Europe (Baltic amber) and the remaining five lack fossil representatives.

SUPERFAMILY PROTENTOMOBRYOMORPHA

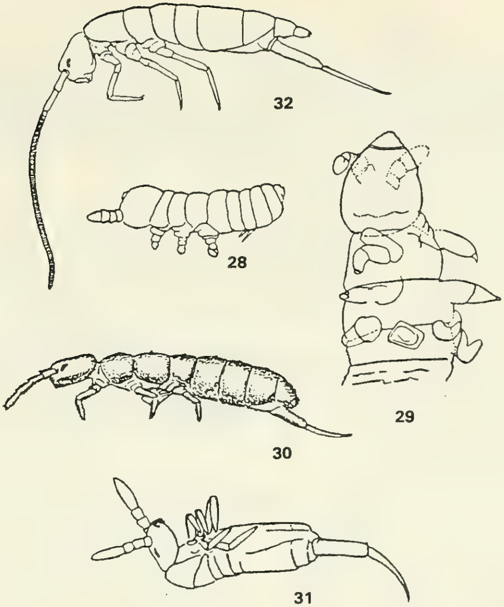
Antennae shorter or of same length as head. Pronotum reduced completely covered by anterior margin of mesonotum. Mesonotum equal in length to metanotum. Devonian to Cretaceous. Family: Protentomobryidae.

Family PROTENTOMOBRYIDAE Folsom, 1938

Eyes with six to seven individual facets. First segment of abdomen a little shorter than the others. Furcula with two simple branches. Length of body 0.65–5 mm (Fig. 29). Devonian to Cretaceous. Three genera. Outside the USSR: *Rhyniella* Hirst and Maulik, 1926; *Rhyniognatha* Tillyard, 1928; *Protentomobrya* Folsom, 1937.

SUPERFAMILY ENTOMOBRYOMORPHA

Integument almost always smooth, without granulation. Sometimes with scales. Antennae longer than head. Postantennal organ absent or consists of a single tubercle. Pronotum small and almost undeveloped, completely covered by the



Figs. 28–32. Suborder Arthropleona.

28. *Hypogastrura protoviatica* Handschin; lateral view, × 23.5. Paleogene, Europe (Baltic amber) (Handschin, 1926). 29. *Rhyniella praecursor* Hirst and Maulik; anterior part of body, × 57. Devonian, Scotland (Scourfield, 1940). 30. *Laotoma saltans* Nicolet; lateral view, × 16. Recent, Europe (Handschin, 1929). 31. *Lepidocyrtus ambricus* Handschin; general view, × 45. Paleogene, Europe (Baltic amber) (Handschin, 1926). 32. *Tomocerus longicornis* Lubbock; lateral view, × 12. Recent, Europe (Handschin, 1929).

anterior margin of the mesonotum. Includes nearly 600 Recent species, of which most are Palearctic. Paleogene to Recent. Families: Isotomidae, Entomobyidae, Tomoceridae, Astaletidae and Cyphoderidae. The last two not represented as fossils.

Family ISOTOMIDAE Carl, 1899

[nom. transl. Börner, 1913 (ex Isotominae Carl, 1899)]

Antennae short, with four almost identical segments. Trochanter on posterior pair of legs absent. Fourth abdominal segment longer than third. Length of body ranges from 0.6 to 3 mm (Fig. 30). Paleogene to Recent. Five genera in Recent fauna, one of which also present in the Paleogene of Europe (Baltic amber).

Family ENTOMOBRYIDAE Börner, 1913

Antennae of varying length, four to six segmented, fourth segment longest. Trochanter of posterior leg provided with a group of projecting spines. Fourth abdominal segment considerably longer than the third. Length of body 1.5–3.5 mm (Fig. 31). Paleogene to Recent. Five genera in Recent fauna, three in Paleogene of Europe (Baltic amber).

47

Family TOMOCERIDAE Schaffer, 1896

[nom. transl. Börner, 1913 (ex Tomocerinae Schaffer, 1896)]

Antennae long, four segmented; third segment longest, annulated. Fourth segment of abdomen shorter than the third. Length of body 1.5–6 mm (Fig. 32). Paleogene to Recent. One genus. Paleogene of Europe (Baltic amber).

Suborder Symphypleona. Non-segmented-abdomens

Body very short. First four segments of abdomen fused with thoracic segments and fifth and sixth segments free. Paleogene to Recent. Families: Sminthuridae, Neelidae and Dicyrtomidae.

Family SMINTHURIDAE Nicolet, 1841

[nom. transl. Lubbock, 1870 (ex Sminthurelles Nicolet, 1841)]

Antennae located on posterior half of head. Fourth segment of antenna longer than the third. Boundaries of fused segments of abdomen indistinct. Anal and genital segments sharply differentiated. Length of body 0.2–1 mm (Fig. 33). Paleogene to Recent. About 200 Recent species. Most of them Palearctic. Belonging to five genera: two genera from Paleogene of Europe (Baltic amber).

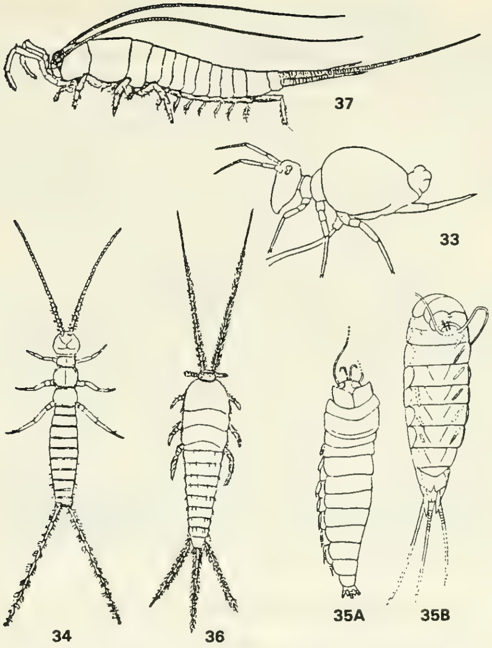
Order DIPLURA. Two-pronged bristletails

Mouth parts entognathous. Eyes absent. Antennae long, multisegmented, hairy. Tarsus one or two segmented with claws. Abdomen 10 segmented. Small pencil-like appendages on sterna. Last abdominal segment with long, segmented or forceps-like cerci. Live in soil, under stones or under bark of decaying trees. Herbivores. Development without metamorphosis. Length of body usually 2–5 mm, rarely 40 mm. Paleogene to Recent. Three families: Campodeidae, Japygidae, Projapygidae, last one not represented as fossils.

Family CAMPODEIDAE Lubbock, 1873

[nom. transl. Handlirsch, 1906 (ex Campodeidae Lubbock, 1873)]

Antennae usually longer than head and thorax combined. Cerci filamentous, segmented, of same length as abdomen (Fig. 34). Paleogene to Recent. About 20



Figs. 33–37. Suborder Symphypleona, orders Diplura and Thysanura.

33. *Sminthurus minnesotensis* Guthrie; lateral view, × 27. Recent, America (Guthrie, 1903). 34. *Campodea* sp.; dorsal view, × 4.5. Recent, Europe (Handlirsch, 1925). 35. *Triassomachilis uralensis* Sharov; × 6. A—dorsal view; B—ventral view. Trias, Pre-Urals (Sharov, 1948). 36. *Lepisma sacharinum* Linnaeus; dorsal view, × 3.2. Recent, Europe (Handlirsch, 1925). 37. *Machilis* sp.; lateral view, × 4.5. Recent, Europe (Snodgrass, 1952).

Recent genera: one from Paleogene of Europe (Baltic amber) and another from Miocene of North America.

Family JAPYGIDAE Lubbock, 1873

Antennae somewhat shorter than head and thorax combined. Cerci short, unisegmented and spinelike. Neogene to Recent. Six Recent genera, of which two represented from Paleogene of North America.

48

Order THYSANURA. Silverfish and bristletails

Body elongated. Mouth parts ectognathous. Maxillary palpi five to six segmented. Antennae long and segmented. Eyes compound. Tarsal segments variable. Abdomen 11 segmented. Sterna with Styli and protruding vesicles. Long segmented cerci and a central unpaired cerciform process present. Body with scales. Active, live in sheltered places (soil, cracks in rock, etc.). Triassic to Recent. Five families: Triassomachilidae, Lepismatidae, Machilidae, Meinertellidae, Nicoletidae, last two have no fossil representatives.

Family TRIASSOMACHILIDAE Sharov, 1948

Eyes with a small number of facets isolated from each other. Pleural surface of abdomen exposed. Styli on sides of first 10 sterna. Triassic. Only one genus.

Triassomachilis Sharov, 1948. Genotype—*T. uralensis* Sharov, 1948. Occurs in Triassic of Bashkirian ASSR (Nakyz river). Styli segmented. Length of body 6 mm (Fig. 35). Only one species. Occurrence: Triassic of Urals.

Family LEPISMATIDAE Leach, 1815

[nom. transl. Escherich, 1904 (ex Lepismida Leach, 1815)]

Compound eyes small, often absent; no ocelli. Styli only on last two segments of abdomen. Length of body 1–12 mm (Fig. 36). Paleogene to Recent. About 50 Recent genera, one genus represented in Paleogene of Europe (Baltic amber) and another in Miocene of North America.

Family MACHILIDAE Grassi, 1888

Compound eyes large and close to each other, three ocelli present. Styli on all abdominal segments. Length of body 7–17 mm (Fig. 37). Paleogene to Recent. About 30 Recent genera, two genera from Paleogene of Europe (Baltic amber); one genus from Miocene of North America.

Order MONURA. One-pronged bristletails

Body elongated. Mouth parts ectognathous, Maxillary palpi six segmented, well developed. Antennae short and segmented. Eyes compound. Rudiments of terga seen on head capsule. Mandibular, maxillary and labial segments more developed than in Thysanura. Tarsus not segmented, with a unique, large pretarsus. Body uniformly segmented, without clearly distinguishable regions of thorax and abdomen, made up of 14 segments, terminating in an unpaired, segmented filament, nearly equal in length to the body. Cerci absent. No scales on body. Upper Carboniferous to Lower Permian. Family Dasyleptidae.

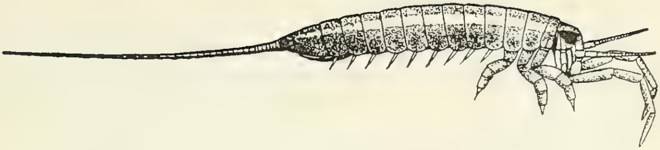


Fig. 38. Order Monura.
Dasyleptus brongniarti Sharov; reconstruction, × 5, Lower Permian, Kuznetsk basin (Sharov, 1957).

Family DASYLEPTIDAE Sharov, 1951

Antennae short and not many-segmented, with two large basal segments. Ovipositor short, not segmented. Tergum of 13th segment larger than that of 12th segment. Upper Carboniferous to Lower Permian. One genus.

Dasyleptus Brongniart, 1885. Genotype—*D. lucasi* Brongniart, 1885, occurs in Stephanian stage, France. Eyes crescent-shaped with convex lower and straight or slightly concave upper margin. Length of first thoracic tergum half of second thoracic tergum. On the venter of the overhanging lateral margin of the first segment of thorax, close to its anterior margin and parallel to it, there is a notch, resembling a suture. Length of tergum of 13th segment twice the length of 14th segment (Fig. 38). Two species. Upper Carboniferous of France and Lower Permian of Kuznetsk basin.

Subclass PTERYGOTA. Winged insects

(B.B. Rohdendorf)

49 Mesothoracic and metathoracic segments with pairs of wings. Wings absent in larval stages and some adult forms, having been lost secondarily. Mouth parts not entognathous, but ectognathous, in some cases completely reduced due to aphagy. Development always involves metamorphosis. Devonian to Recent. Two infraclasses: Palaeoptera and Neoptera. Separation and formation of the infraclasses probably took place in the Devonian period. Existing paleontological evidence supports a still later period for wing development. Representatives of both infraclasses found among fauna of Lower Carboniferous (Namurian).

Infraclass PALAEOPTERA. Primitive-winged insects

Wings elongated, devoid of jugal lobes. Normally wings cannot be flexed backward and folded over the body to cover the abdomen. Wings spread out in the rest position. Only one specialized order of the superorder Megasecopteroidea (Diaphanopterodea) have become adapted to fold the wings over the body. Mouth parts of the biting type or in the form of a long proboscis, which is formed from all the mouth parts. Development known only for two Recent orders. It takes place in aquatic medium, with incomplete metamorphosis, without pupal stage. Lower Carboniferous to Recent. Most varied in the Palaeozoic. Three superorders: Palaeodictyopteroidea, Megasecopteroidea and Odonatoidea. The phylogenetic relations of these superorders have been little studied. Palaeodictyopteroidea is the most primitive and ancestral to the other two. The rise of the other two superorders reflects flight specialization and unexplained changes in the mode of life. This is especially clear in the relationship of Odonatoidea, which are characterized by their sharply elongated wings that have developed strong traction and an increase in flight velocity. This is reflected in the structure of the thoracic parts, in which there is marked development of the pleural muscles which control movement of the wings directly, and not indirectly as in other insects. The rise of the large and specialized superorder Megasecopteroidea and its complete extinction by Recent period are unexplained, though the peculiar morphological adaptations of its representatives were highly specialized.

50 SUPERORDER PALAEODICTYOPTEROIDEA

Wings have straight or moderately convex anterior and convex anal borders (never stalked). Costal and subcostal areas always narrow. Cross veins differ distinctly from the firm longitudinal veins, being often irregular, forming a network, sometimes absent or forming archedictyon of Recent forms. Cross veins never arranged in clear transverse rows. Long cerci always present, sometimes, unpaired paracerci present. Carboniferous to Recent. Four orders known from the Palaeozoic: Palaeodictyoptera, Eubleptodea, Archodonata and Ephemeroptera. The last represented in Mesozoic and Cenozoic also.

Order PALAEODICTYOPTERA

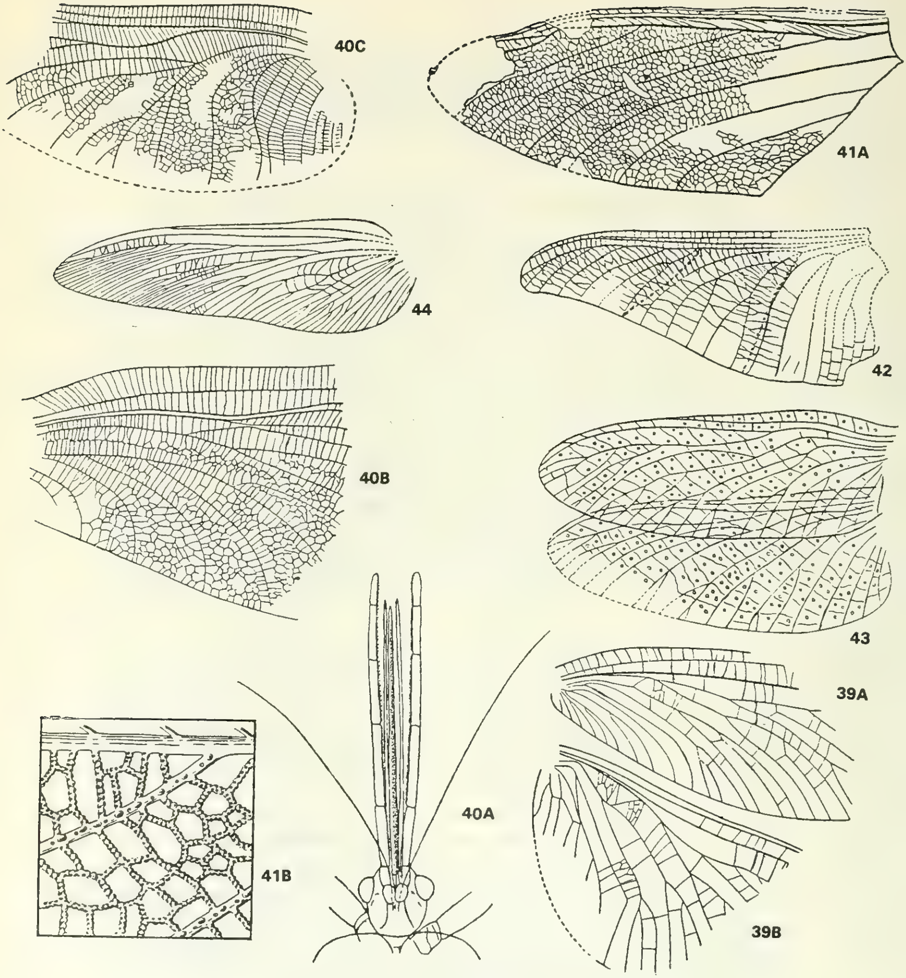
Head not large, with piercing mouth parts. Often winglike appendages present on pronotum. Usually with a dense network of cross veins or archedictyon. Sometimes veins very thin and numerous, rarely entirely absent. Unpaired paracercus absent. Carboniferous to Permian. Three suborders: Eupalaeodictyoptera, Parapalaeodictyoptera and Metapalaeodictyoptera.

Suborder Eupalaeodictyoptera

Anal margin of wing often considerably more convex than anterior. RS usually pectinate. SC almost reaches wing apex, which is moderately acute and usually obtuse. Often archedictyon well expressed. Carboniferous to Permian. Five superfamilies: Lithomanteidea, Dictyoneuridea, Breyeriidea, Homoiopteridea and Polycreagridea.

SUPERFAMILY LITHOMANTEIDEA

Wings almost similar. Hindwing weakly expanded. Basal parts of major veins fused. A large number of faint, irregular cross veins form a network. Sometimes archedictyon present at places. Carboniferous to Permian. Six families: three from the Carboniferous of Western Europe (Lithomanteidae, Lycocercidae and Lusiellidae), two from the Carboniferous of North America [Syntonopteridae (Fig. 39) and Thesoneuridae] and one from the Permian of Western Europe (Eugereonidae).



Figs. 39–44. Suborder Eupalaeodictyoptera.

39. *Lithoneura lameeri* Carpenter; A—forewing, × 1.7; B—hindwing, × 1.7. Carboniferous of North America (Carpenter, 1933). 40. *Eugereon boeckingi* Dohrn; A—head, × 1; B—forewing, × 1.1; C—hindwing, × 1. Permian, Germany (Handlirsch, 1906). 41. *Asiodictya rossica* Rohdendorf; A—wing × 1.9; B—Part of wing, × 12. Carboniferous, Kuznetsk basin (Rohdendorf, 1961). 42. *Breyeria borinensis* Borre; wing, × 0.9. Carboniferous, Western Europe (Handlirsch, 1906). 43. *Homoioptera woodwardi* Brongniart; wing, × 0.8. Carboniferous, Western Europe (Handlirsch, 1906). 44. *Polycreagra elegans* Handlirsch, wing × 0.9. Carboniferous, North America (Handlirsch, 1906).

Family EUGEREONIDAE Handlirsch, 1906

Both fore- and hindwings wide, with archedictyon present in posterior part of the wing. Cross veins present in front (Fig. 40 A, B). Head not large. Antennae fine, threadlike. Eyes convex. Segmented, piercing proboscis several times longer than the head. Legs thin. Tarsus short. Permian. One genus from Permian of Germany.

SUPERFAMILY DICTYONEURIDEA

Wings similar, or hind ones slightly expanded at the base. Archedictyon well expressed. Rarely numerous, usually branching fine cross veins present. Carboniferous. Six families: one from the Middle and Upper Carboniferous of Western Europe, Asia and North America (Dictyoneuridae), four from the Upper Carboniferous of Western Europe (Peromapteridae, Cockerelliellidae, Mecynopteridae and Protagriidae) and one from the Upper Carboniferous of North America (Hypermegethidae).

Family DICTYONEURIDAE Handlirsch, 1906

(Stenodictyopteridae Brongniart, 1893, nom. invalid., Megaptilidae Handlirsch, 1906; Fouqueidae Handlirsch, 1906; Pteronidiidae Bolton, 1912; Saarlandiidae Guthorl, 1930; Rochlingiidae Guthorl, 1934, syn. nov.)

Wings of equal length, moderately wide at the base. Typical archedictyon consisting of small cells. At places numerous delicate cross veins formed. Carboniferous. About 50 genera in Western Europe and North America and one genus from the USSR.

Asiodictya Rohdendorf, 1961. Genotype— *A. rossica*Rohdendorf, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Zariyalovo). SC and R very close to C. Radial area with oblique branches of RS. Other cells of wing with typical archedictyon. Length of wing around 65 mm and width, 18 mm (Fig. 41 A, B). One species from the Middle Carboniferous of Kuznetsk basin.

SUPERFAMILY BREYERIIDEA

Hindwing with markedly wide basal part; many fine, curved cross veins with
52 large-meshed reticulation in some places. Archedictyon absent. Carboniferous.
Two families from the Middle and Upper Carboniferous of Western Europe: Breyeriidae (Fig. 42) and Cryptoveniidae.

SUPERFAMILY HOMOIOPTERIDEA

Wings similar, moderately elongated with numerous spots all over, with many fine cross veins. No archedictyon. Carboniferous. Two families from Upper

Carboniferous of Western Europe; Homoiopteridae (Fig. 43) and Rhabdoptilidae.

SUPERFAMILY POLYCREAGRIDEA

Wing markedly wide at base, with pointed apex. RS and M with many parallel additional branches (up to 30); SC not reaching wing apex. Archedictyon not developed. Many fine irregular cross veins not forming a network (Fig. 44). Only one family—Polycreagridae—with one genus from the Middle Carboniferous of North America.

Suborder Parapalaeodictyoptera

Wing moderately elongated with uniformly convex anterior and anal margins; wing apex acute or sharply rounded; with a few cross veins which are irregular and often form a network or large cells. Archedictyon absent, RS usually branches dichotomously or sometimes irregularly pectinate, SC not reaching wing apex and sometimes not distinct. Carboniferous to Permian. Eight families, of which four are from the Lower and Middle Carboniferous of Western Europe (Macropteridae, Synarmogidae, Jongmansiidae, Orthocostidae), one from the Upper Carboniferous of North America (Heolidae) and the remaining three from the Permian of the USSR and North America (Eohymenidae, Bardapteridae, Calvertiellidae). Most probably not primitively winged!

Family EOHYMENIDAE Martynov, 1937

Wing narrow, SC not clear, M and Cu with only two simple branches each. Cross veins fine and in certain areas form two rows of cells. Permian. One genus.

Eohymen Martynov, 1937. Genotype—*E. maculipennis* Martynov, 1937. Permian, Orenburg region (Kargala). Costal area with straight cross veins. Two areas have two rows of cells—between the branches of RS and between M and Cu. Length of wing 38.8 mm and width 11.8 mm (Fig. 45). One species. Permian of southern Urals.

53 Family BARDAPTEIDAE G. Zalessky, 1944

Wing moderately wide. SC faint but perceptible, M with three and Cu with two branches. Posterior branches of M and all branches of Cu exhibit secondary branching at wing margin. Cross veins irregular and almost always form two rows of cells. Permian. One genus.

Bardapteron G. Zalessky, 1944. Genotype— *B. ovale* G. Zalessky, 1944; Lower Permian, Perm province (Kungurian stage, Barda). Costal area with numerous oblique cross veins. RS with five branches. Length of wing more than 50 mm and width 18 mm (Fig. 46). One species from the Lower Permian of the Urals.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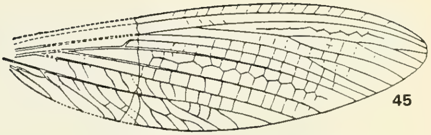
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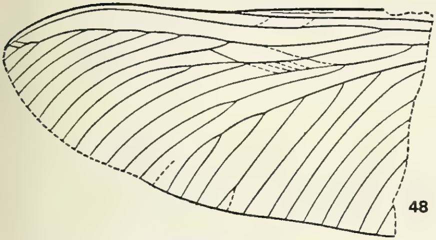
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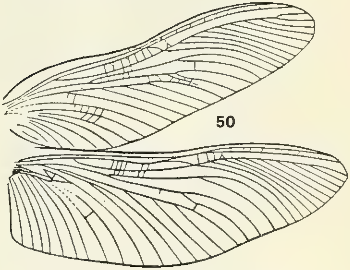
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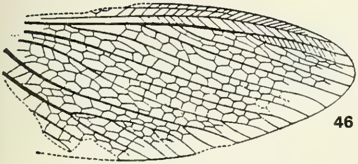
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52 Figs. 45–50. Suborders Parapalaeodictyoptera and Metapalaeodictyoptera.

45. *Eohymen maculipennis* Martynov; wing, × 1.9. Permian, Urals (Martynov, 1937). 46. *Bardapteron ovale* G. Zalessky; wing, × 1.2. Permian, Urals (Yu. Zalessky, 1944). 47. *Neuburgia altaica* Martynov; wing, × 2. Carboniferous, Kuznetsk basin (Martynov, 1931). 48. *Abaptilon sibiricum* G. Zalessky; wing, × 1.4. Carboniferous, Kuznetsk basin (Yu. Zalessky, 1946). 49. *Permiakovia quinquefasciata* Martynov; wing, × 1.6. Permian, Urals (Martynov, 1941). 50. *Doropteron mirum* G. Zalessky, × 1.5. Permian, Urals (Yu. Zalessky, 1946).

Suborder Metapalaeodictyoptera

Wing elongated, with anterior margin straight or slightly concave in middle and markedly convex anal margin. Wing apex fairly acute. Costal and subcostal areas narrow and, usually without cross veins. Archedictyon or network of cross veins absent. Cross veins straight, relatively distinct and far apart. Sometimes cross veins almost totally absent. SC reaches up to wing apex. Carboniferous to Permian. Four families, of which one is from the Middle Carboniferous of North America (Homothetidae), one from the Upper Carboniferous of Western Europe (Lamproptilidae), one from the Carboniferous of Kuznetsk basin (Neuburgiidae) and one from the Carboniferous of Europe and America, and the Permian of southern Urals (Spilapteridae).

Family NEUBURGIIDAE Rohdendorf, 1961

Wing elongated. Anal margin moderately convex. RS branching from R almost at base of wing, not pectinate, dichotomously branched. Carboniferous. One genus.

Neuburgia Martynov, 1931. Genotype— *N. altaica* Martynov, 1931; Mid Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Verkhotomskoe). Radial area very wide, with a few cross veins in middle of wing. Nine branches of RS and eight of M on the edge of the wing. SC and R very close. Length of wing about 30 mm (Fig. 47). One genus. Carboniferous of Kuznetsk basin.

Family SPILAPTERIDAE Brongniart, 1893

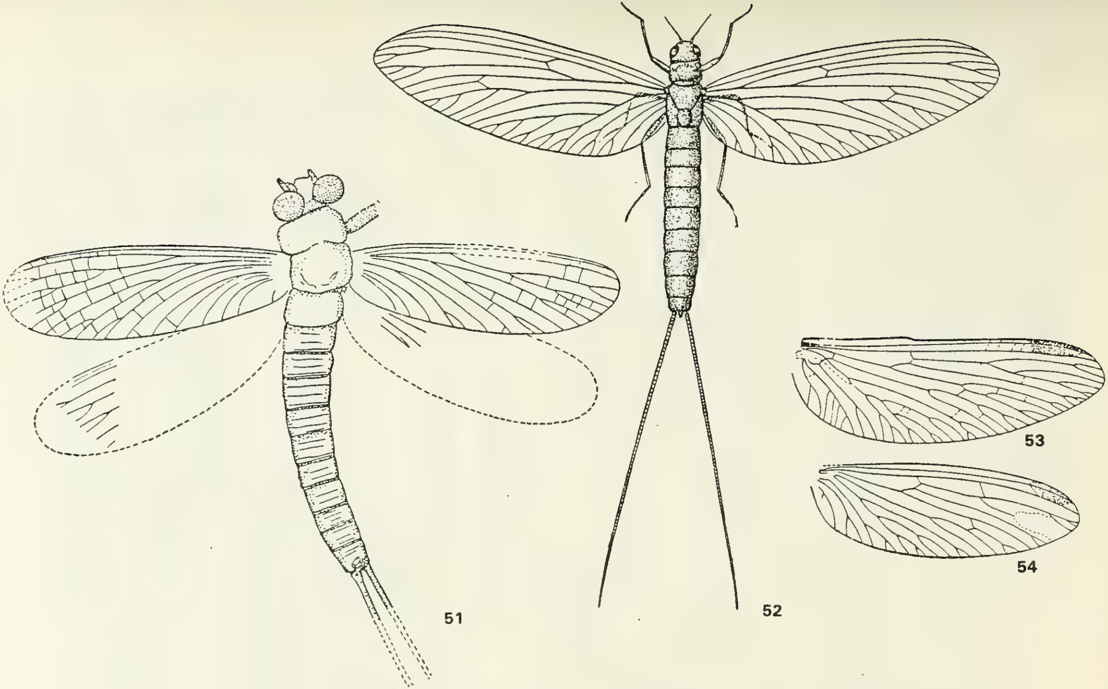
Wing moderately elongated with sharply convex anal and clearly concave anterior margins. RS usually branching from R away from base of wing, always pectinate. Cross veins numerous. Sometimes delicate and indistinct. Carboniferous to Permian. Fifteen genera reported.

Abaptilon G. Zalessky, 1946. Genotype— *A. sibiricum* G. Zalessky, 1946; Upper Carboniferous,Kuznetsk basin(Upper Balachonian series, Prokopevsk). RS branches off near middle of wing and bears seven branches. M and CuA with six branches each. Radial area without cross veins. Length of wing around 40 mm, width 15 mm (Fig. 48). One species, Carboniferous of Kuznetsk basin.

Permiakovia Martynov, 1941. Genotype— *P. quinquefasciata* Martynov, 1941; Lower Permian, Perm province (Kungurian stage, Chekarda). RS branches from R in basal part of wing. It bears a crown of seven branches, two of which are forked. M with five branches and CuA with 6 branches. Radial area narrow with clear cross veins. Length of wing 34 mm and width 12.5 mm (Fig. 49). One species. Lower Permian of Urals.

Doropteron G. Zalessky, 1946. Genotype— *D. mirum* G. Zalessky, 1946; Lower Permian. Perm province (Kungurian stage, Chekarda). RS branches at the basal quarter of wing. It bears a ten-branched crown in normal forms. Four branched M. CuA with five branches on the forewing and six on the hindwing. Radial area moderately large with numerous cross veins. Length of wings varies from 36 to 37 mm. Width of forewing 10 mm and of hindwing 13 mm (Fig. 50). One species from Lower Permian of Urals.

Outside the USSR: Middle Carboniferous of Europe—*Severinula* Pruvost, 1930; *Severinopsis* Kukalova, 1958; *Bojoptera* Kukalova, 1958; Middle Carboniferous of North America—*McLuckiepteron* Richardson, 1956; Upper Carboniferous of Europe—*Palaeoptillus* Brongniart, 1893; *Spilaptera* Brongniart, 1885; *Epitethe* Handlirsch, 1906; *Compsoneura* Brongniart, 1885; *Becquerelia* Brongniart, 1893; *Homaloneurina* Handlirsch, 1906; *Homaloneurites* Handlirsch, 1906; *Homaloneura* Brongniart, 1885.



Figs. 51–54. Orders Eubleptodea and Archodonata.

51. *Eubleptus danielsi* Handlirsch; general view, × 4. Carboniferous, North America (Handlirsch, 1906). 52. *Permothemidia caudata* Rohdendorf; dorsal view, × 6 (Reconstruction). Permian, Urals (Rohdendorf, 1949). 53. *Permothemis libelluloides* (Martynov), wing, × 3.6. Permian, Arkhangelsk province (Martynov, 1932). 54. *Ideliella decora* G. Zalessky; wing, × 3.2. Permian, Urals (Yu. Zalesskii, 1937).

54 Order EUBLEPTODEA

Wings similar and moderately elongate. Anterior margin of wing gently convex. C, SC and R close to each other. RS and M dichotomously branched, without "intercalary" veins. Cu and A simple and arched. Archedictyon absent. Cross veins straight and few. Head with short mouth parts. Eyes very large, project markedly. Antennae apparently short. Thoracic segments almost of equal length. Prothorax devoid of paranotal expansions. Abdomen ten-segmented. A pair of long threadlike cerci present. Length of wing about 14 mm (Fig. 51). Carboniferous. Family: Eubleptidae, with one genus from the Middle Carboniferous of North America.

55 Order ARCHODONATA

One pair of forewings. Hindwings and paranotal outgrowths absent on prothorax. Anterior margin of wing straight or slightly convex; anal margin strongly convex. All longitudinal veins equally thick, triads not formed. RS usually pectinate, M and Cu weakly developed, several anal veins. Abdomen 9-segmented. Paranotal outgrowths absent. One pair of long cerci. Length of wing 10–17 mm (Fig. 52). Carboniferous to Permian. Four families: Permothemistidae, Rectineuridae, Doteridae and Permoneuridae, of which the last two are from the Lower Permian of North America and the first two from the Upper Carboniferous of Europe.

Family PERMOTHEMISTIDAE Martynov, 1934

Branches of RS not clearly pectinate or dichotomous. Almost all veins with terminal forks. Pterostigma well developed. Cross veins few but distinct. Permian. Four genera.

Permothemidia Rohdendorf, 1940 (*Uralothemis* G. Zalessky, 1951, syn. nov.). Genotype—*P. caudata* Rohdendorf, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Anterior margin of wing straight. RS with more or less pectinate branches. Posterior stem of M with two to four branches. Length of wing 10.5–12 mm and width 3.5–4 mm. Two species. Lower Permian. Southern Urals.

Permothemis Martynov, 1934. (*Palaeothemis* Martynov, 1932). Genotype—*Palaeothemis libelluloides* Martynov, 1932; Upper Permian. Arkhangelsk province (Kazanian stage, Soyana). Anterior margin of wing straight. RS dichotomously branched. Posterior stem of M with five branches. Length of wing 17 mm, width 5.75 mm (Fig. 53). One species. Upper Permian. Arkhangelsk province.

Ideliella G. Zalessky, 1937. Genotype—*I. decora* G. Zalessky, 1937; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Anterior margin of wing weakly, but noticeably convex. RS dichotomously branched. Posterior stem of

M with three branches. Length of wing 12.3 mm, width 4.5 mm (Fig. 54). One species. Upper Permian of Urals.

Outside the USSR: *Kansasia* Tillyard, 1937 (Lower Permian of North America).

Order EPHEMEROPTERA. Mayflies

(O.A. Chernova)

Head not large. Recent forms with reduced mouth parts and short antennae. Prothorax devoid of paranotal outgrowths. Wing often with straight anterior margin along which lie the long, straight SC and R. Longitudinal veins with peculiar ''intercalary'' veins between them on the wing margin at least in the region of RS; branches of RS with asymmetric dichotomous branching. RS not pectinate. Archedictyon absent. Cross veins numerous, thin and straight, rarely, almost absent. Long cerci and paracercus present, latter sometimes almost reduced to a rudiment. Nymphs live in water. Upper Carboniferous to Recent. Suborders: Protephemeroptera, Plectoptera.

Suborder Protephemeroptera

Wings almost similar with weak development of ''intercalary'' veins in the region of RS. RS branches out from R at a considerable distance from base of
56 wing. They are not joined with M. Costal arculus absent at base of wing. Costal area long with cross veins. Length of body 24 mm, length of wing 21 mm (Fig. 55). Upper Carboniferous of France. Family: Triplosobidae.

Suborder Plectoptera

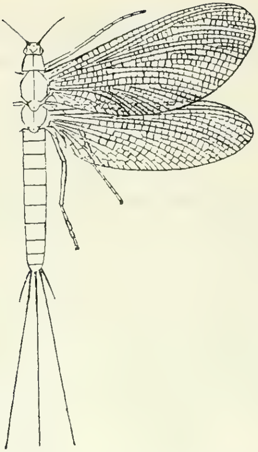
RS branches out from R at base of wing. With costal arculus at base of wing. Permian to Recent. Infraorders: Permoplecoptera, Euplecoptera.

Infraorder Permoplectoptera

Metathorax large and sharply demarcated from mesothorax. Wings almost similar. At the very base of the wing the costal arculus separates from the anterior margin of costal vein and forming a loop joins R. Permian to Jurassic. Superfamilies: Protereismatidea, Mesephemeridea.

SUPERFAMILY PROTEREISMATIDEA

Main longitudinal veins equidistant to one another, not converging in pairs. Permian. Three families: Protereismatidae, Misthodotidae, Eudoteridae.



55 Fig. 55. Suborder Protephemeroptera.
Triplosoba pulchella (Brongniart) (Reconstruction) × 1.2. Upper Carboniferous, Western Europe (Demoulin, 1956).

Family PROTEREISMATIDAE Sellards, 1907
[nom. corr. Tillyard, 1932 (ex Protereismephemeridae Sellards, 1907)]

CuA with distinct ''intercalary'' vein; bifurcates approximately at its middle. In the regions of M and Cu wing margin with many auxiliary veins. Innumerable cross veins arranged densely. Permian. One genus.

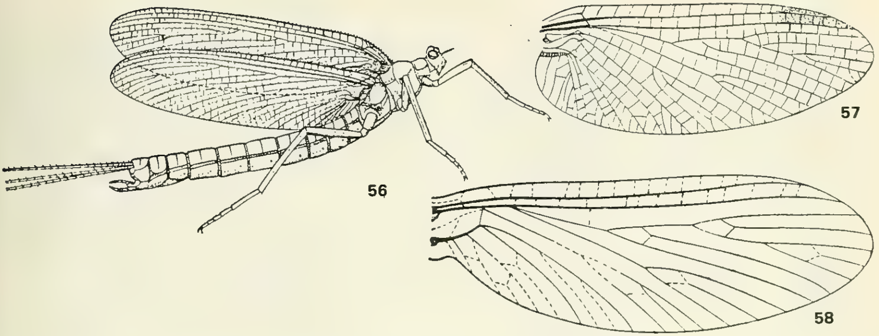
Protereisma Sellards, 1907 (*Loxophlebia* Martynov, 1928). Genotype—*P. permian* Sellards, 1907; Lower Permian, North America (Kansas). Costal arculus well developed on forewing, thicker than on hindwing (Fig. 56). Length of wing 15–30 mm, width 4.5–9.5 mm. A few species in North America, three from the Lower Permian of the Urals and the Upper Permian of the Pre-Ural region.

Family MISTHODOTIDAE Tillyard, 1932

CuA without three long branches, with only short terminal forks. Auxiliary veins present along wing margin. Cross veins not very dense (Fig. 57). Length of wing 9–15 mm, width 3.5–5 mm. One genus. Lower Permian of North America.

Family EUDOTERIDAE Demoulin, 1954

Cross veins weakly developed. CuA simple, with blurred branches. Auxiliary



Figs. 56–58. Families Protereismatidae, Misthodotidae and Eudoteridae.

56. *Protereisma permiana* Sellards (Reconstruction), × 2.5. Lower Permian, North America (Tillyard, 1932). 57. *Misthodotes obtusus* (Sellards); hindwing, × 5.5. Lower Permian, North America (Tillyard, 1932). 58. *Eudoter delicatulus* Tillyard; hindwing, × 12.5. Lower Permian, North America (Tillyard, 1932).

veins along wing margin absent. Small size, length of wing 6 mm (Fig. 58). Lower Permian of North America. One genus.

SUPERFAMILY MESEPHEMERIDEA

Longitudinal veins (RS_3 and RS_4; RS_5 and MA_1, etc.) approach the wing margin
57 in pairs. Cross veins few and not noticed in all areas. Many auxiliary veins with
free basal ends. Permian to Jurassic. Family Mesephemeridae.

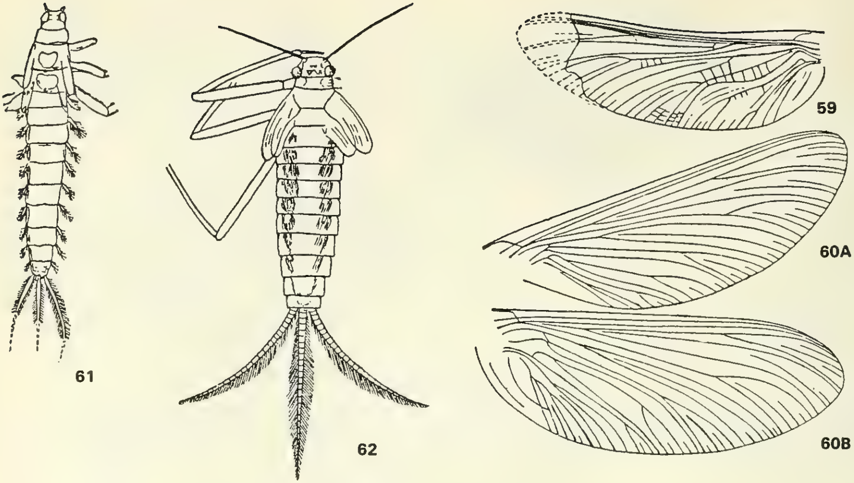
Family MESEPHEMERIDAE Carpenter, 1932

(Palingeniopsidae Martynov, 1938, syn. nov.)

Cross veins weakly developed and indistinct. CuA and A_1 with forks. Costal area not large. Permian to Jurassic. Two genera.

Palingeniopsis Martynov, 1932. Genotype—*P. praecox* Martynov, 1932; in Upper Permian of Arkhangelsk province (Kazanian stage, Soyana). Anterior margin of wing slightly concave. CuP strongly curved. Length of wing about 32 mm, width 11.5 mm (Fig. 59). One species. Upper Permian of Arkhangelsk province.

Outside the USSR: *Mesephemera* Handlirsch, 1906. Upper Jurassic of Western Europe (Fig. 60).



Figs. 59–62. Family Mesephemeridae; Permoplectoptera incertae sedis.

59. *Palingeniopsis praecox* Martynov; hindwing, × 1.7. Upper Permian, Arkhangelsk province (Martynov, 1934). 60. *Mesephemera prisca* (Germar): A—forewing, B—hindwing, × 3. Upper Jurassic, Western Europe (Demoulin, 1955). 61. *Phthartus rossicus* Handlirsch; general view, × 1.5. Permian, Pre-Urals (Handlirsch, 1906). 62. *Mesoplectopteron longipes* Handlirsch; general view, × 3.5. Triassic, Western Europe (Handlirsch, 1918).

Permoplectoptera Incertae sedis

Phthartus Handlirsch, 1904. Genotype—*P. rossicus* Handlirsch, 1904; Permian, Orenburg province (Kungurian stage, Kargala). Nymph: rudiments of wings similar. Legs short. Nine pairs of rodlike gills. Edges of thoracic segments straight. Caudal filaments covered with hairlike setae. Paracercus a little shorter than cerci (Fig. 61). Two species. Permian of Pre-Urals.

Mesoptectopteron Handlirsch, 1948. Genotype—*M. longipes* Handlirsch, 1948. Triassic. Western Europe (Bogezy). Nymph: rudiments of wings nearly similar. Legs thin, very long. Eight pairs of gills located on dorsal surface of abdomen. Abdominal segments with straight edges. Caudal filaments covered with hairlike setae. Paracercus of same length as cerci (Fig. 62). One species. Triassic of Western Europe.

Infraorder Euplectoptera

Metathorax smaller than mesothorax, but intimately fused with it. Wings markedly dissimilar, hindwings always shorter than forewings. Sometimes there are no wings. C located at the base at the very edge of the wing. Jurassic to Recent. Six superfamilies: Paedephemeridea, Ephemeridea, Siphlonuridea, Heptageniidea, Neoephemeridea, Caenidea. Last two found only in Recent fauna.

58 SUPERFAMILY PAEDEPHEMERIDEA

Longitudinal veins numerous, sometimes converge in pairs: MP_1 and CuA_1 parallel at base of wing. Hind wing considerably larger than one-half of forewing. Upper Jurassic. Two families: Paedephemeridae, Hexagenitidae.

Family PAEDEPHEMERIDAE Lameere, 1917

(Stenodicranidae Demoulin, 1954, syn. nov.)

Anal margin of forewing rounded, its anal angle not expressed. Veins not convergent. CuA_1 of forewing without clear bifurcation. Nymphs not known (Fig. 63). One genus. Upper Jurassic of Western Europe.

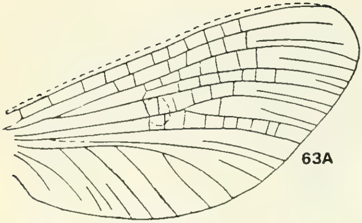
59 Family HEXAGENITIDAE Lameere, 1917

[nom. transl. Demoulin, 1954 (ex Hexagenitinae Lameere, 1917)] (Ephemeropsidae Cockerell, 1924, syn. nov.)

Forewing triangular with well expressed anal angle; convergence of veins clear; CuA on forewing bifurcates, and between the forks, branches forming a series of regular looplike forks are given out. Nymph with seven pairs of distinct leaflike gills. Caudal filaments densely covered with hairlike setae. Jurassic. Two genera.

Ephemeropsis Eichwald, 1864 (*Phacelobranchus* Handlrisch, 1906). Genotype—*E. trisetalis* Eichwald, 1864; Upper Jurassic, Transbaikal (Turino-Vitimian suite, Tovega). Very large mayflies. Anal margin of forewing a little longer than its apical margin; CuA_1 sharply bent with numerous cross veins; in many instances longitudinal veins are clearly seen to converge in pairs. Length of body of adult insect 50 mm (without caudal filaments). Length of forewing 35–42 mm, hindwing 17–24 mm. Nymph with large eyes and projecting posterior corners on its abdominal segments; length of body 45–55 mm, caudal filaments 15–25 mm (Figs. 64–66; Pl. I, Figs. 1–3). Two species. Upper Jurassic of Transbaikal, Mongolia and North China.

Hexagenites Scudder, 1880. Genotype—*H. weyenberghi* Scudder, 1880; Upper Jurassic, Western Europe (Malm, Solenhofen). Insects of medium size. Apical margin of forewing longer than anal margin; CuA_1 nearly straight; cross veins few; the only longitudinal veins to exhibit distinct convergence in pairs are



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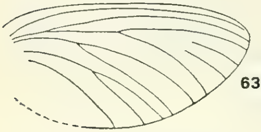

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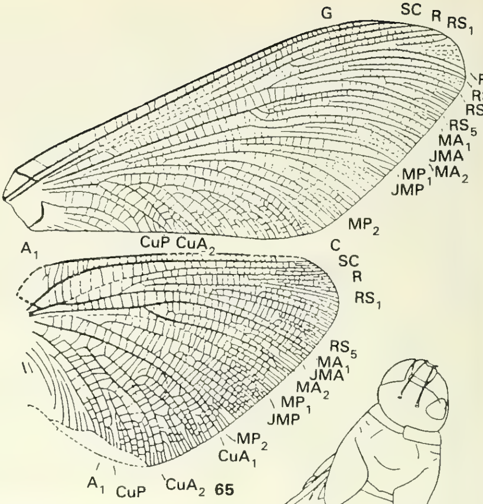

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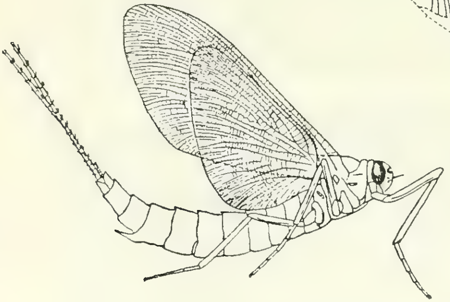

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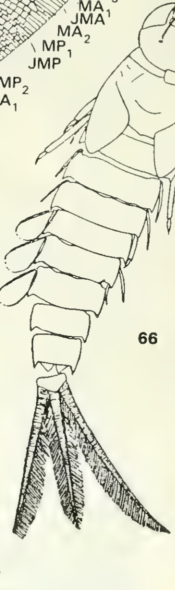

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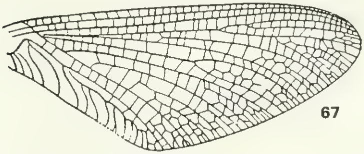

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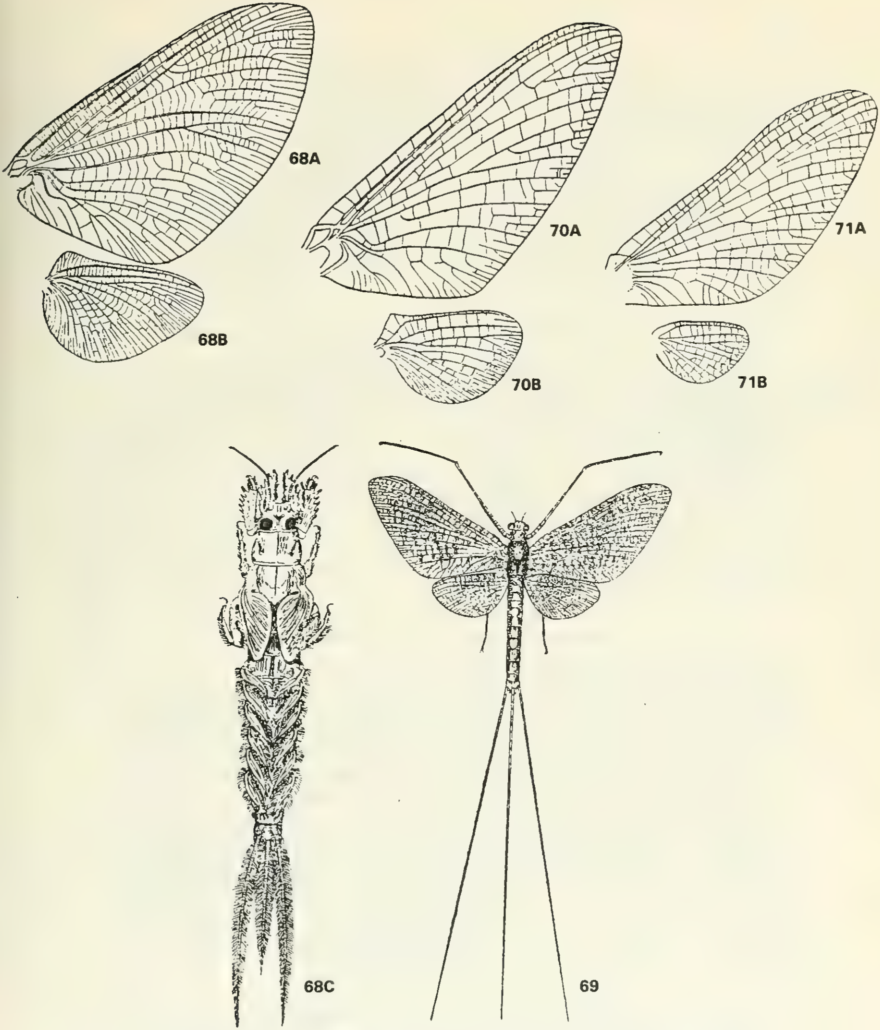
Figs. 63–67. Families Paedephemeridae and Hexagenitidae.

63. *Paedephemera multinervosa* (Oppenheim): A—forewing, B—hindwing, × 2.9. Upper Jurassic, Western Europe (Handlirsch, 1906). 64. *Ephemeropsis trisetalis* Eichwald (reconstruction), × 1.4. Upper Jurassic, Transbaikal (Chernova, 1961). 65. *E. martynovae* Tshernova; wings, × 2.4. Upper Jurassic, Transbaikal (Chernova, 1961). 66. *E. trisetalis* Eichwald; nymph, × 3. Upper Jurassic, Transbaikal (N.P. Meshkova, 1961). 67. *Hexagenites weyenberghi* Scudder; forewing, × 3.2. Upper Jurassic, Western Europe (Carpenter, 1932).



Figs. 68–71. Families Palingeniidae, Ephemeridae, Potamanthidae and Polymitarcidae.

68. *Palingenia longicauda* (Olivier): A—forewing, B—hindwing, × 1.7, C—nymph, × 1.3. Recent (Schoenemund, 1930). 69. *Ephemera vulgata* Linnaeus; dorsal view, × 1.5. Recent (original figure). 70. *Potamanthus luteus* Linnaeus: A—forewing, × 5.5, B—hindwing, × 4.5. Recent (Schoenemund, 1930). 71. *Ephoron virgo* Olivier: A—forewing, B—hindwing, × 3. Recent (Ulmer, 1929).

branches of RS. Length of forewing 15–19 mm (Fig. 67). Two species. Upper Jurassic, Western Europe.

SUPERFAMILY EPHEMERIDEA

Longitudinal veins of forewing often converge in pairs; MP_1 and CuA_1 distinctly divergent at base. Hindwings large and somewhat shorter than one-half of length of forewings. Paleogene to Recent. Families: Palingeniidae, Ephemeridae, Potamanthidae, Behningiidae, Polymitarcidae. Last two found only in Recent fauna.

Family PALINGENIIDAE Klapalek, 1909

Longitudinal veins always converge in pairs; CuA forked; auxiliary veins in cubital area straight. Nymphs bury themselves with their wide fore tibiae and flattened maxillae* bearing teeth along their outer margin. Large insects. Paleogene to Recent. Six genera in Recent fauna, of which one is represented in Paleogene of Europe (Baltic amber).

Palingenia Burmeister, 1839. Genotype—*Ephemera longicauda* Olivier, 1791; Recent, Western Europe. Numerous longitudinal and cross veins in fore- and hindwings. MA of forewing branches beyond middle of wing (Fig. 68). Paleogene to Recent. In Recent fauna three species, one of which is represented in Paleogene of Europe (Baltic amber).

Family EPHEMERIDAE Klapalek, 1909

Longitudinal veins of forewing do not converge in pairs; CuA without fork; auxiliary veins in cubital area branch out from CuA and run obliquely toward posterior margin of wing; CuP weakly bent; between A_1 and wing margin series of cross veins seen. Nymphs bury themselves with slender, smooth, long projections of maxillae* with outwardly bent tips. They also possess biramous feathery gills, reflexed upon the dorsal part of abdomen. Large insects (Fig. 69). Paleogene to Recent. Six genera in Recent fauna, of which *Hexagenia* Walsh, 1863 is also represented from Neogene of North America. Also described from the Paleogene of Western Europe is the insufficiently known genus *Parabetis* Haupt, 1956 whose taxonomic relationships are not clear (Demoulin, 1957) and also a series of incorrectly determined remains of ?*Ephemera* Linnaeus, 1746 from the Paleogene of Europe (two species of which are from Baltic amber), Neogene of Western Europe, North America and Australia.

Family POTAMANTHIDAE Klapalek, 1909

CuP markedly bent in forewing; series of cross veins absent between A_1 and

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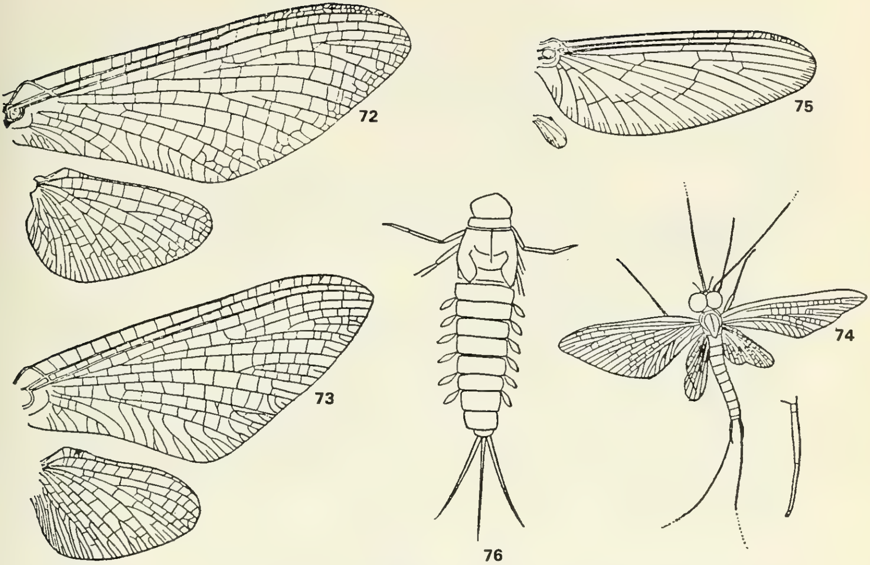
* An obvious error in the original; should read 'mandibles'—General Editor.



61 Figs. 72–76. Families Siphlonuridae and Baetidae.

72. *Siphlonurus aestivalis* Eaton; forewing and hindwing, 3.5. Recent (Schoenemund, 1930). 73. *Isonychia ignota* Walker; forewing and hindwing, × 4.2. Recent (Schoenemund, 1930). 74. *Cronicus anomalus* (Pictet); general view, × 3 and forceps, × 1.5. Paleogene, Europe (Baltic amber) (Demoulin, 1955). 75. *Baetis pumilus* (Burmeister); forewing and hindwing, × 10. Recent (Schoenemund, 1930). 76. *Mesobaetis sibirica* Brauer, Redtenbacher and Ganglbauer; general view, × 3.8. Lower Jurassic, Siberia (Brauer, Redtenbacher and Ganglbauer, 1889).

wing margin. Nymphs live amid vegetation. Biramous, feathery gills located in abdominal region. Insects of medium size (Fig. 70). Neogene to Recent. Eight genera in Recent fauna, of which genus *Potamanthus* Pictet, 1845 is also represented in Miocene of North America.

Family POLYMITARCIDAE Klapalek, 1909

Longitudinal veins of forewing not converging in pairs; CuA forked, in its fork auxiliary veins are located. Nymphs bury themselves with long projections of maxillae*, with inwardly bent tips. Large or moderately sized insects (Fig. 71). Paleogene to Recent. 12 genera in Recent fauna, of which *Ephoron* Williamson, 1802 was also found in Paleogene of Europe (Baltic amber).

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* An obvious error in the original; should read 'mandibles'—General Editor.

60 SUPERFAMILY SIPHLONURIDEA

MP$_1$ and CuA$_1$ either parallel or weakly divergent at base; longitudinal and cross veins reduced in some groups. Hindwings sometimes very small or absent. Upper Jurassic to Recent. Seven families: Siphlonuridae, Oligoneuridae, Baetidae, Leptophlebiidae, Ephemerellidae, Baetiscidae, Tricorythidae; the last two found only in Recent fauna.

61 Family SIPHLONURIDAE Klapalek, 1909

Forewing with numerous, bent auxiliary veins running from CuA$_1$ toward anal margin, some of which branch. Hindwings well developed. Paleogene to Recent. Subfamilies: Siphlonurinae, Isonychiinae.

Subfamily Siphlonurinae Klapalek, 1909

[nom. transl. Edmunds and Traver., 1954 (ex Siphlonuridae Klapalek, 1909)]

CuA$_1$ terminates at anal angle of wing; auxiliary veins run from CuA toward anal margin of wing, and are bent. Nymphs with cylindrical abdomen and seven pairs of gills on lateral sides of segments. Terga of abdomen with pointed lateral outgrowths, directed backward. Caudal filaments fringed with dense long hairs (cerci fringed only on inner surface) (Fig. 72). Large or moderately sized insects. Neogene to Recent. 19 genera in Recent fauna. One extinct genus *Siphlurites* Cockerell, 1923 is from Neogene of North America.

Subfamily Isonychinae Edmunds and Traver, 1954

Hindwings large: CuA$_1$ terminates considerably anterior to anal angle; auxiliary veins run from CuA$_1$ and branch (Fig. 73). Nymphs possess oral and sternothoracic gills besides seven pairs of gills located on sides of abdomen. Insects of medium size. Paleogene to Recent. Six genera in Recent fauna. One extinct genus from Paleogene of Europe (Baltic amber).

Cronicus Eatoh, 1871. Genotype—*Baetis anomalus* Pictet, 1854; Paleogene, Europe (Baltic amber). Differs from Recent genera, in that third segment of forceps is long, almost equal to second (Fig. 74). One species. Paleogene of Europe (Baltic amber).

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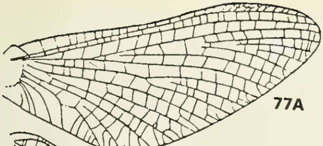
63 Figs. 77–83. Families Leptophlebiidae, Ephemerellidae, Siphlonuridae incertae sedis and Heptageniidae.

77. *Leptophlebia marginata* (Linnaeus): A—forewing, B—hindwing, × 5.7. Recent (Ulmer, 1929). 78. *Ephemerella ignita* Poda: A—forewing, B—hindwing, × 5.2. Recent (Schoenemund, 1930). 79. *Mesoneta antiqua* Brauer, Redtenbacher and Ganglbauer; dorsal view, × 5. Lower Jurassic. 80. *Turfanella tingi* (Ping); abdomen of nymph, × 9. Upper Jurassic, Central Asia (Demoulin, 1954). 81. *Heptagenia flava* Rostock: A—forewing, B—hindwing, × 4.6. Recent (Schoenemund, 1930). 82. *Electrogenia dewalschei* Demoulin: A—general view, × 6; B—terminal part of abdomen, × 40. Paleogene of Europe (Baltic amber). 83. *Miocenogenia gorbunovi* Tschernova; general view, × 5.1. Neogene, West Siberia (Chernova, 1962).



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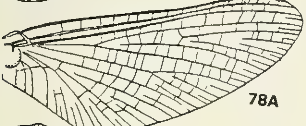

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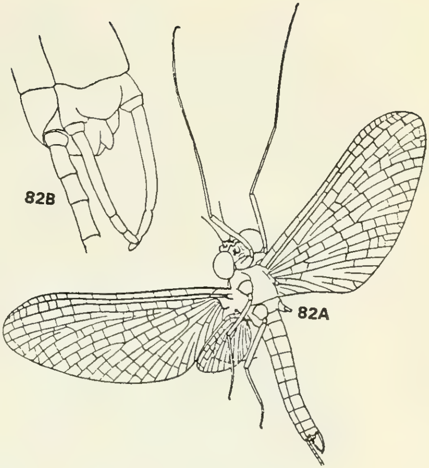

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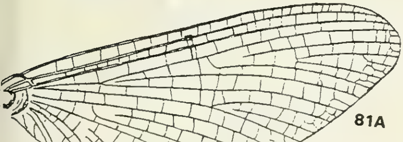

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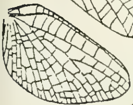

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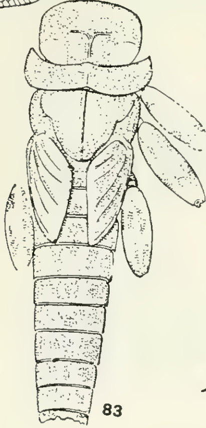

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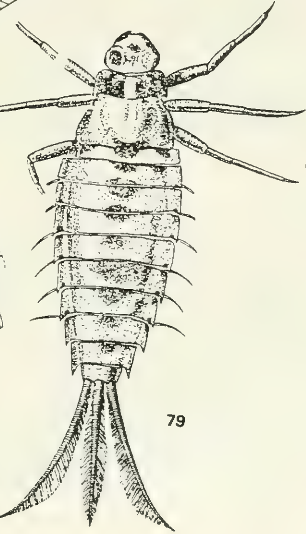

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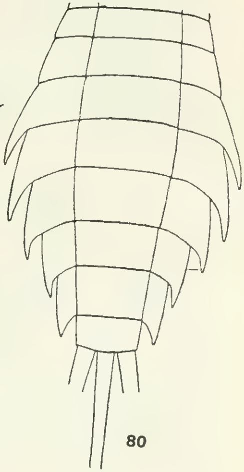

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Family OLIGONEURIIDAE Ulmer, 1920

Longitudinal veins of forewing converge in pairs throughout: MA_2 converges towards MP_1; MP_2 converges towards CuA_1; cross veins few. Nymphs devoid 62 of mandibular projections. Seven pairs of gills in the form of small plates covered with tufts of filaments. Insects of medium size. Neogene to Recent. 11 genera in Recent fauna. One extinct genus *Protoligoneuria* Demoulin, 1955 is from the Neogene of Brazil.

Family BAETIDAE Klapalek, 1909

Forewings oval in shape; MA does not branch. Cross veins few. Hindwings very small with two or three longitudinal veins and a few cross veins; at times hindwings absent. Upper section of compound eyes in males very big, mushroom-shaped or turbanlike and light colored. Nymphs swim; with cylindrical abdomen, without any outgrowths but with seven pairs of platelike gills on lateral sides of abdomen and caudal filaments fringed by dense hair-like setae (cerci fringed only on their inner side). Small sized insects. Paleogene to Recent. 16 genera in Recent fauna, of which two are found in the fossil state.

Baetis Leach, 1815. Genotype—*Ephemera bioculata* Linnaeus, 1746; Recent, Europe. Basal half of costal area of forewing and costal area of hindwing devoid of cross veins. Hindwing egg shaped with two or three longitudinal veins (Fig. 75). Nymph with seven pairs of separate gills. About 150 species in Recent fauna, three species in Paleogene (Baltic amber) and one species in Lower Miocene of North America.

Cloeon Leach, 1815. Genotype—*Ephemera diptera* Linnaeus, 1746; Recent, Europe. Hindwings absent. First cross vein between R and RS located nearer to base of wing than cross vein of following area. First six pairs of gills in nymph biramous. 70 species in Recent fauna. One species known from Upper Miocene of Australia.

Family LEPTOPHLEBIIDAE Westwood, 1840

Wings with many cross veins. Rarely, hindwings absent. Auxiliary veins in forewing absent between MP_1 and MP_2, and between MP_2 and CuA_1. Forceps of males with two or three short terminal segments. Nymphs possess seven pairs of biramous leaflike or filamentous, similar gills which are located in abdominal region. Insects of medium or small size. Lower Jurassic to Recent. In Recent fauna there are 45 genera, of which two are also represented as fossils. One of the extinct, little-studied genera is from the Lower Jurassic.

Mesobaetis Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*M. sibirica* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk region (Cheremkhovian suite, Ust-Bailey). Nymph with a slender abdomen, three caudal filaments and thin, indistinct gills (Fig. 76). Jurassic through Neogene. Two species from Siberia and North America.

Leptophlebia Westwood, 1840. Genotype—*Ephemera vespertina* Linnaeus, 1746; Recent, Europe. Pterostigmal part of costal area of forewing has branching cross veins; auxiliary veins in cubital area almost parallel, their basal ends connected to cross veins. Anterior margin of hindwing with a weak but noticeable notch (Fig. 77). Paleogene to Recent. Recent fauna include about 20 species. One species from Paleogene of Europe (Baltic amber).

Atalophlebia Eaton, 1881. Genotype—*Ephemera australis* Walker, 1850; Recent, Australia. Whole costal area including the pterostigma has simple nonbranching cross veins; auxiliary veins in cubital area fuse and converge at their basal ends. Anterior edge of hindwing with no trace of a notch. Neogene to Recent. About 40 species of Recent fauna in Australia, South Asia, Africa and South America. One species from the Miocene of Australia.

Family EPHEMERELLIDAE Klapalek, 1909

Wings with many cross veins. Hindwings present. Two short auxiliary veins occur in forewing between MP_1 and MP_2 and between MP_2 and CuA_1 (Fig. 78). Forceps in males with only one terminal segment. Nymph with five pairs of gills located on the dorsal side of third through seventh segments of abdomen. Upper part of each gill, in the form of a cover plate. Insects small- or medium-sized. Jurassic to Recent. Eight genera in Recent fauna, of which one represented also in Neogene. Two extinct genera from the Mesozoic.

Mesoneta Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*M. antiqua* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk
64 region (Cheremkhovian suite, Ust-Bailey. Nymph with large eyes, broad abdomen, acute projections on lateral sides of segments, uniramous gills located on sides of segments and three caudal filaments (Fig. 79). One species from Lower Jurassic of East Siberia.

Turfanella Demoulin, 1954. Genotype—*Ephemeropsis tingi* Ping, 1935; Upper Jurassic, China Sintszyan (Turfan). Nymph with broad abdomen, with acute, drawn out outgrowths on sides of segments and three stout caudal filaments (Fig. 80). Upper Jurassic. One species.

Outside the USSR the genus *Ephemerella* Walsh, 1862 is reported from the Miocene of North America from insufficiently-studied material.

SUPERFAMILY HEPTAGENIIDEA

Longitudinal veins of forewing do not converge in pairs. MP_1 and CuA_1 almost parallel at base. One or two straight auxiliary veins present in cubital area. Hindwings well developed, but less than one-half of length of forewings. Paleogene to Recent. Two families: Heptageniidae, Ametropodidae. Latter occurs only in fossil fauna.

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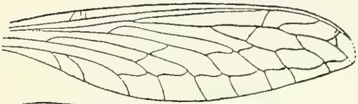

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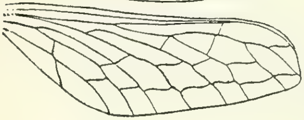

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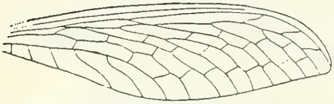

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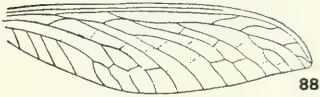

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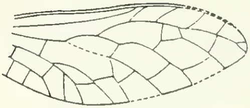

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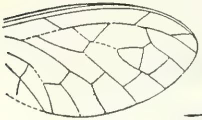

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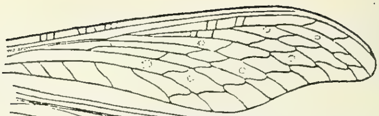

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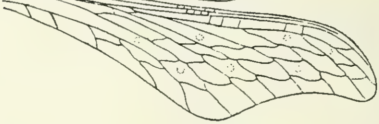

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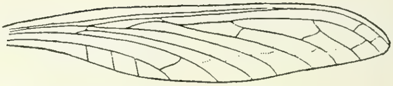

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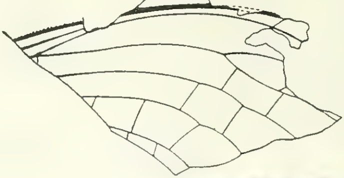

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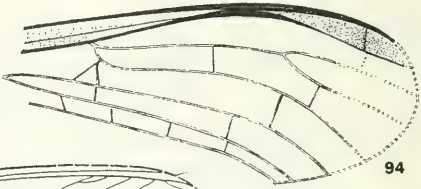

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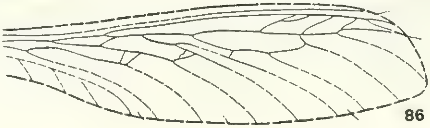

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Family HEPTAGENIIDAE Ulmer, 1920

Two pairs of auxiliary veins in cubital area of which the longer one lies close to CuA_2. Nymphs inhabit quick-flowing streams or rapids, live on stones. They are flat with seven pairs of gills located on sides of abdomen. Upper part of gill leaflike and lower part in the form of tuft of threads (Fig. 81). Insects of medium size. Paleogene to Recent. 25 genera in Recent fauna. Besides these, two extinct genera from the Paleogene and Neogene.

Electrogenia Demoulin, 1955. Genotype—*E. dewalschei* Demoulin, 1955; Paleogene, Europe (Baltic amber). Cross veins simple and nonbranching (Fig. 82) in pterostigmal part of costal as well as subcostal areas of fore and hindwings. One species. Paleogene of Europe (Baltic amber).

Miocoenogenia Tshernova, 1961. Genotype—*M. gorbunovi* Tschernova, 1961; Neogene of West Siberia (Middle Miocene, Tym river). Nymph with broad head; pronotum with projections directed forward; wing rudiments large; legs with broad femora; both abdomen and legs with patchy markings; three caudal filaments; length of body 13.5 mm (Fig. 83). One species. Neogene of West Siberia.

SUPERORDER MEGASECOPTEROIDEA

(B.B. Rohdendorf)

Wings usually narrow at base, sometimes petiolate like extant forms; costal and subcostal areas usually very narrow or absent because of sharp costalization of wing; cross veins firm and few, arranged in rows; network or archedictyon never present. Long cerci present at end of abdomen. Paracercus always absent. Carboniferous to Permian. Three orders: Megasecoptera, Diaphanopterodea, Campylopterodea.

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65 Figs. 84–94. Suborder Eumegasecoptera.

84. *Brodia priscocincta* Scudder; wing, × 1.2. Middle Carboniferous, Western Europe (Handlirsch, 1906). 85. *Parabrodia* sp., × 1.9. Middle Carboniferous, North America (Carpenter, 1933). 86. *Carbonoptera furcaradii* Guthorl; forewing, × 2.5. Upper Carboniferous, Western Europe (Guthorl, 1940). 87. *Foriria maculata* Meunier: A—forewing, B—hindwing, × 1.7. Upper Carboniferous, Western Europe (Carpenter, 1951). 88. *Corydaloides scudderi* Brogniart: A—forewing, B—hindwing, × 1.3. Upper Carboniferous, Western Europe (Carpenter, 1951). 89. *Rhaphidiopsis diversipenna* Scudder: A—forewing, B—hindwing, × 1.4. Middle Carboniferous, North America (Handlirsch, 1906). 90. *Mischoptera nigra* Brongniart: A—forewing, B—hindwing, × 0.9. Upper Carboniferous, Western Europe (Carpenter, 1951). 91. *Sphecoptera gracilis* Brongniart: A—forewing, B—hindwing, × 1.2. Upper Carboniferous, Western Europe (Carpenter, 1951). 92. *Ischnoptilus elegans* Brongniart; wing, × 3.1. Upper Carboniferous, Western Europe (Carpenter, 1951). 93. *Sibirichymen asiaticus* Rohdendorf; part of wing, × 5.4. Carboniferous, Kuznetsk basin (Rohdendorf, 1961). 94. *Vorkutia tschernovi* Rohdendorf; part of wing, × 3.7. Upper Permian, Vorkuta basin (Rohdendorf, 1947).

Order MEGASECOPTERA

Wings always spread, do not fold back; anterior margin of wing always even, without projections; petiole well developed on narrow basal part of wing; SC always long, never short, rarely indistinct in distal half; sometimes this vein is fused with R because of costalization; all cross veins arranged in regular rows. Carboniferous to Permian. Two suborders: Eumegasecoptera, Protohymenoptera.

Suborder Eumegasecoptera

Costal area narrow, often with cross veins; SC prominent; radial veins consist of R and isolated RS. Carboniferous. Eight families: Brodiidae, Parabrodiidae, Carbonopteridae; Foriridae, Corydaloididae, Raphidiopseidae, Mischopteridae, Vorkutiidae.

66 **Family BRODIIDAE Handlirsch, 1906**

Wing apex blunt; petiole of wing long; SC not distinct in distal half of costal area; cross veins randomly distributed, do not form transverse rows (Fig. 84). Length of wing 50–60 mm. Middle Carboniferous. Single genus from Westphalian stage of Western Europe.

Family PARABRODIIDAE Carpenter, 1933

Structure of base of wing not known. SC placed far from C, traverses 2/3 of wing, without reaching its apex; R placed a little away from the anterior margin of wing; basal part of MA and RS fused; both with two branches. Length of wing fragment 24 mm, width 7 mm (Fig. 85). Carboniferous. One species from Middle Carboniferous of North America.

Family CARBONOPTERIDAE Guthorl, 1940

Wing apex not blunt; SC almost reaches apex of wing and joins C; anterior branches of RS ascend toward R, which at its extremity has a small narrow bifurcation; RS with three parallel branches; M fused with RS at base, bears three parallel branches; a few short cross veins present in middle of wing between CuA and MP, MP and MA, MA and RS. Length of wing nearly 33 mm (Fig. 86). Middle Carboniferous. One genus from Westphalian stage of Germany.

Family FORIRIIDAE Handlirsch, 1919

Hindwings somewhat shorter than forewings, rather blunt; MA + MP and CuA + CuP in the form of isolated, simple forks that are not joined with one another or with RS; base of wing moderately narrow; SC fuses with R at a point which is one-fourth from apex; cross veins located in form of two definite rows that are distinctly apart. Length of wing 30–35 mm (Fig. 87). Upper Carboniferous. One genus from Stephanian stage of France.

Family CORYDALOIDIDAE Handlirsch, 1906

Wings similar, moderately narrowed at base; MA partly fused with RS, and CuA with the main trunk of M; SC traverses top three-fourths of wing and is free at its end; RS and MP with three of four branches; cross veins straight, lie in three indistinct rows. Pronotum and segments of abdomen with numerous pointed paranotal outgrowths. Length of wing 48 mm (Fig. 88). Upper Carboniferous. One genus from Stephanian stage of France.

Family RHAPHIDIOPSEIDAE Handlirsch, 1906

Hindwings shorter and broader than forewings, with narrower subcostal margin; M fused to RS. Length of wings about 25–30 mm (Fig. 89). Carboniferous. One genus from Middle Carboniferous of North America.

Family MISCHOPTERIDAE Handlirsch, 1906

Wings similar and markedly narrow at basal part, in form of petiole; length of SC equal to two-thirds of wing; MA always fused with trunk of RS at base; CuA free or, sometimes, fused with MP; cross veins firm and wavy and form one to three transverse rows. Length of wing ranges from 30 to 75 mm. Carboniferous. Six genera from Upper Carboniferous Stephanian stage of Western Europe distributed among four subfamilies: Mischopterinae (Fig. 90), Sphecopterinae (Fig. 91), Cyclocelidinae, Ischnoptilinae (Fig. 92).

Family VORKUTIIDAE Rohdendorf, 1947

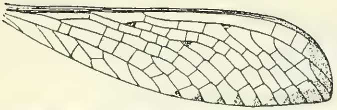
SC slender, free and distinct in basal half of wing; after branching from RS sharply drawn toward C, converging toward top of costal area; radial area devoid of cross veins; between longitudinal veins one or two rows of cross veins; cross veins located in posterior half of wing, near margin. Length of wing 17–30 mm. Carboniferous through Permian. Two genera.

Sibiriohymen Rohdendorf, 1961. Genotype—*S. asiaticus* Rohdendorf, 1961; Middle Carboniferous (Lower Balachonian suite, Alykaevian subsuite, Verkhotomskoe). One series of cross veins between RS and M; a cross vein between stalk of RS and MA. Length of wing about 17 mm (Fig. 93). One species. Carboniferous of Kuznetsk basin.

Vorkutia Rohdendorf, 1947. Genotype—*V. tshernovi* Rohdendorf, 1947; Lower Permian, Vorkutsk basin. Two series of cross veins between RS and Cu; cross veins absent between stalk of RS and MA. Length of wing about 30 mm (Fig. 94). One species. Lower Permian. Vorkutsk basin.

Suborder Protohymenoptera

Costal area absent because of contiguity of C, SC and R; RS sometimes partly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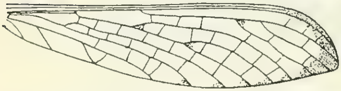
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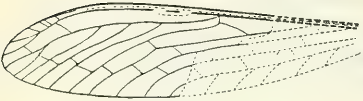
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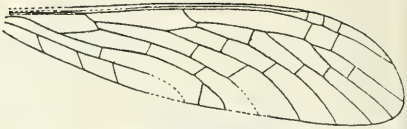
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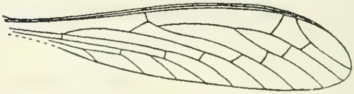
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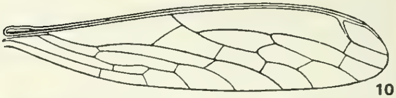
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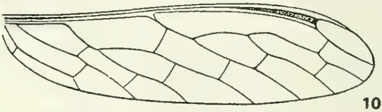
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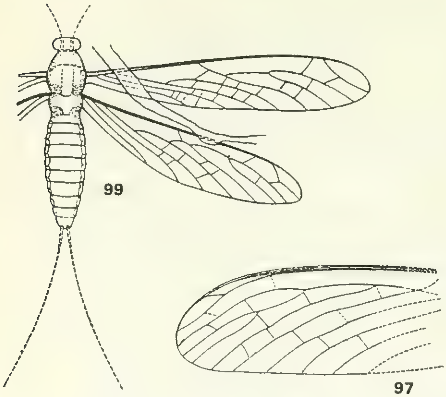
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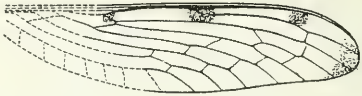
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Figs. 95–105. Suborder Protohymenoptera.

95. *Aspidothorax triangularis* Brongniart: A—forewing, B—hindwing, × 2. Upper Carboniferous, Western Europe (Carpenter, 1951). 96. *Bardohymen magnipennifer* G. Zalessky; wing, × 1.5. Lower Permian, Urals (Yu. Zalessky, 1937). 97. *Sylvohymen robustus* Martynov; wing, × 2.1. Lower Permian, Urals (Martynov, 1941). 98. *Calohymen permianus* Carpenter; wing, × 2.8. Lower Permian, North America (Carpenter, 1947). 99. *Pseudohymen angustipennis* Martynov; (reconstruction), × 1.8. Lower Permian, Urals (Martynov, 1931). 100. *Ivahymen constrictus* Martynov; wing, × 3.3. Upper Permian, Arkhangelsk province (Martynov, 1931). 101. *Protohymen permianus* Tillyard; wing, × 6. Lower Permian, North America (Carpenter, 1930). 102. *Permohymen schucherti* Tillyard; wing, × 5. Lower Permian, North America (Carpenter, 1930). 103. *Tshekardohymen martynovi* Rohdendorf; wing, × 1.3. Lower Permian, Urals (Rohdendorf, 1940). 104. *Scytohymen extremus* Martynov; wing, × 1.5. Lower Permian, Urals (Martynov, 1937). 105. *Aspidohymen extensus* Martynov; wing, × 1.8. Upper Permian, Urals (Martynov, 1930).

67 fused with R. Carboniferous to Permian. Five families: Aspidothoracidae, Bardohymenidae, Protohymenidae, Scytohymenidae, Aspidohymenidae.

Family ASPIDOTHORACIDAE Handlirsch, 1919

MA distinctly separate from RS, latter bears four branches in the form of a comb; R hugs anterior margin throughout its length; cross veins numerous. Length of wing 30–40 mm (Fig. 95). Carboniferous. One genus in Stephanian stage of France.

Family BARDOHYMENIDAE G. Zalessky, 1937

MA distinct or convergent with RS for a short distance; RS bears three to five branches in the form of a comb; R leaves margin at apex of wing and bears branches or cross veins; cross veins in one or two rows. Length of wing 25–45 mm. Permian. Three genera.

Bardohymen G. Zalessky, 1937. Genotype—*B. magnipennifer* G. Zalessky,
68 1937; Lower Permian, Perm province (Kungurian stage, Barda). Four cross veins between end of R and wing margin; R with a bifurcation at its end; RS with five branches; MA distinct from basal cross vein of RS. Length of wing about 43 mm (Fig. 96). One species. Lower Permian, Urals.

Sylvohymen Martynov, 1940. Genotype—*S. robustus* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). End of R with one to three apical cross veins; RS with four branches; MA convergent with RS at base. Length of wing about 40 mm (Fig. 97). Two species. Lower Permian of Urals and North America.

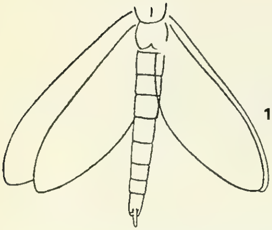
Calohymen Carpenter, 1947. Genotype—*C. permianus* Carpenter, 1947; Lower Permian, North America. End of R simple, connected with wing margin by three straight cross veins; RS with three branches. Length of wing 25 mm (Fig. 98). One species. Lower Permian, North America.

Family PROTOHYMENIDAE Tillyard, 1924

MA fused with basal part of RS for some distance; RS with two branches in the form of a fork. R leaves wing margin at apex of wing, forming an oval cell; cross veins always present between MP and CuA and CuP. Permian. Four genera.

Pseudohymen Martynov, 1931. Genotype—*P. angustipennis* Martynov, 1931; Lower Permian, Perm province (Kungurian stage, Chekarda). Two cross veins between R and anterior branch of RS; wing narrow, its anal margin nearly five times its width. Length of forewing 19–27.5 mm and width, 3.5–5.2 mm. Length of hindwing 24.5 mm (Fig. 99). Two species. Lower Permian of Urals and North America.

Ivahymen Martynov, 1931. Genotype—*I. constrictus* Martynov, 1931; Upper Permian, Arkhangelsk Province (Kazanian stage, Soyana). Two cross veins between R and anterior branch of RS. Anal margin of wing convex. Base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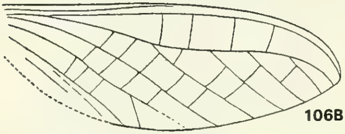
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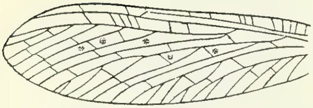
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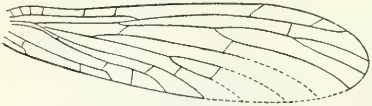
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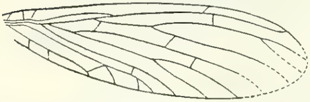
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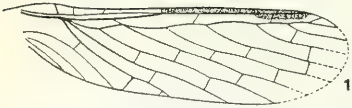
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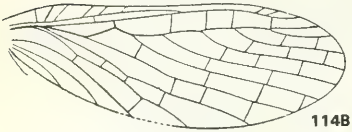
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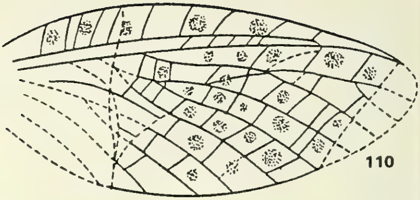
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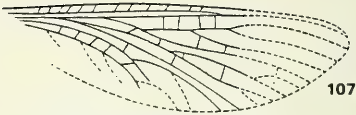
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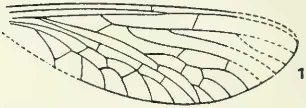
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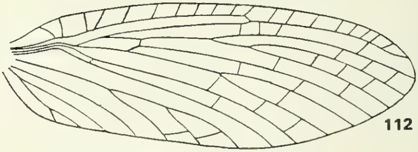
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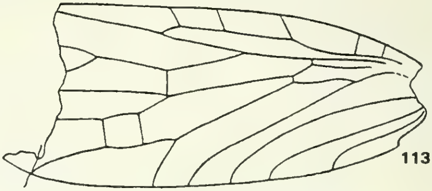
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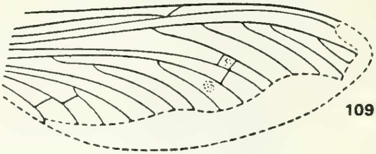
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of wing narrowed sharply and stalklike. Length of wing exceeds its width by not more than four times. Length of wing 18 mm (Fig. 100). Single species. Upper Permian of Arkhangelsk Province.

Protohymen Tillyard, 1924. Genotype—*P. permianus* Tillyard, 1924; Lower Permian, North America. One cross vein lies between last segment of R and anterior branch of RS; two cross veins between MA and MP (not counting base of MA); anal margin of wing sharply convex. Length of wing, 3.2 to 4.4 times its width, i.e. 10–20 mm (Fig. 101). Five species. Lower Permian of North America.

Permohymen Tillyard, 1924. Genotype—*P. schucherti* Tillyard, 1924; Lower Permian, North America. One cross vein between R and anterior branch of RS; one cross vein between MA and MP (not counting base of MA); anal margin of wing sharply convex. Length of wing, 3 to 3.5 times its width, i.e. 12–13 mm (Fig. 102). One species. Lower Permian of North America.

Family SCYTOHYMENIDAE Martynov, 1937

MA comes into contact, at about one point with base of RS, which consists of two branches in the form of a fork; R diverges gradually from wing margin at apex of wing and does not form oval cell; cross veins between MP, CuA and CuP absent. Permian. Two genera.

Tshekardohymen Rohdendorf, 1940. Genotype—*T. martynovi* Rohdendorf, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Series of cross veins between C, R, RS_1, RS_2, MA and MP, the five cross veins placed so that each region has one cross vein. Length of wing 35 mm (Fig. 103). One species. Lower Permian of Urals.

Scytohymen Martynov, 1937. Genotype—*S. extremus* Martynov, 1937; Upper Permian, Urals (Savinov ravine). In radial area only two cross veins

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70 Figs. 106–114. Suborders Protodiaphanopterodea and Eudiaphanopterodea.

106. *Sypharoptera pneuma* Handlirsch: A—general view of fossil, × 2.8; B—wing, × 4.7. Carboniferous, North America (Handlirsch, 1911). 107. *Prochoroptera calopteryx* Handlirsch: A—forewing, B—hindwing, × 3.1. Middle Carboniferous, North America (Handlirsch, 1911). 108. *Diaphanoptera munieri* Brongniart; wing, × 1.4. Upper Carboniferous, Western Europe (Handlirsch, 1906). 109. *Philiasptilon maculosum* M. Zalessky; wing, × 1.2. Carboniferous, Kuznetsk basin (M. Zalessky, 1931). 110. *Tchirkovaea guttata* M. Zalessky; wing, × 0.94. Carboniferous, Kuznetsk basin (M. Zalessky, 1931). 111. *Elmoa trisecta* Tillyard: A—forewing, B—hindwing, × 5.6. Upper Permian, North America (Carpenter, 1943). 112. *Parelmoa revelata* Carpenter; wing, × 4.7. Lower Permian, North America (Carpenter, 1947). 113. *Kaltanelmoa sibirica* Rohdendorf; wing, × 5.7. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 114. *Martynovia insignia* Tillyard: A—forewing, B—hindwing, × 3.75. Lower Permian, North America (Carpenter, 1943).

observed between R and anterior branch of RS. Length of wing 41 mm (Fig. 104). One species. Upper Permian of Pre-Urals.

Family ASPIDOHYMENIDAE Martynov, 1930

R fused with SC for some distance, for example, at a distance of one-third from apex, R leaves wing margin and runs parallel to SC and RS; MA isolated from RS, connected only by its cross veins; RS with two long branches; cross veins lie between all longitudinal veins. Permian. One genus.

Aspidohymen Martynov, 1930. Genotype—*A. extensus* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Between R and wing margin lies a cross vein, which like the segment of R at the base of RS is markedly dark. Length of wing approximately 27–35 mm (Fig. 105). Two species. Upper Permian of Pre-Urals.

59 Order DIAPHANOPTERODEA

At rest wings drawn back and folded over at a slight angle to longitudinal axis of body. Wing never petiolate, often fairly wide, rarely narrow; SC shorter than two-thirds of anterior margin of wing, sometimes quite indistinct, rarely long; anterior margin convex, occasionally with projections, rarely straight and costalized. Carboniferous to Permian. Three suborders: Protodiaphanopterodea, Eudiaphanopterodea and Metadiaphanopterodea.

Suborder Protodiaphanopterodea

Wings similar, moderately acute; radial area very wide with strong cross veins; RS comb-like, bears up to five branches spreading to anal margin. Length of wing 12 mm (Fig. 106A, B). Carboniferous. One family, Sypharopteridae, with one genus from the Middle Carboniferous of North America.

Suborder Eudiaphanopterodea

Wings usually blunt; costa weak; anterior margin convex with isolated SC; radial area not expanded, notably lacking in strong cross veins; cross veins numerous, sometimes quite small, but always present in costal area in the form of branches of SC and R (in extreme cases only one strong vein). Carboniferous to Permian. Seven families: Prochoropteridae, Diaphanopteritidae, Diaphanopteridae, Elmoidae, Kaltanelmoidae, Parelmoidae, Martynoviidae.

Family PROCHOROPTERIDAE Handlirsch, 1911

SC considerably longer than half of anterior margin of wing; circular spots on wings absent; venation rich, with innumerable cross veins. Length of wing 20–32 mm (Fig. 107). Carboniferous. Two genera, from Middle and Upper Carboniferous of North America.

Family DIAPHANOPTERITIDAE Handlirsch, 1911

SC very long, circular dark spots on wings between veins of RS and M. Little-known group from the Upper Carboniferous of Western Europe. One genus.

Family DIAPHANOPTERIDAE Handlirsch, 1906

SC nearly two-thirds of anterior margin of wing; prominent dark circular spots on different areas of wing; anal veins in the form of numerous branches starting from one stalk. Carboniferous. Three genera.

Diaphanoptera Brongniart, 1893. Genotype—*D. munieri* Brongniart, 1893; Upper Carboniferous of France (Stephanian stage, Komantri). Costal area with numerous cross veins, moderately convex, terminates a little distal to center of anterior margin. Wing narrow, length, more than three times its width, 35–37 mm (Fig. 108). Two species. Upper Carboniferous of France.

Philiasptilon M. Zalessky, 1931. Genotype—*Ph. maculosum* M. Zalessky, 1931. Genotype—*Ph. maculosum* M. Zalessky, 1931; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Cheremichkino). Anterior margin of wing moderately convex, costal area of distal end of SC with only one cross vein, which descends toward R, over most of area cross veins not distinct; RS with six branches in the form of a comb; spots observed only in middle of wing. Length of wing, more than three times its width, is around 45 mm (Fig. 109). One species. Carboniferous of Kuznetsk basin.

Tchirkovaea M. Zalessky, 1931. Genotype—*T. guttata* M. Zalessky, 1931; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Cheremichkino). Costal area very wide, with many cross veins; SC extends over more than two-thirds of length of wing, whose anterior margin is highly convex; RS with three branches; spots developed over almost all the wing. Wing short and wide. Its length, 2 to 2.5 times its width, is 56 mm (Fig. 110). One species. Carboniferous of Kuznetsk basin.

Family ELMOIDAE Tillyard, 1937

Wings gradually narrowing toward base; SC descends to R; length of R almost equal to that of anterior margin of wing, which is moderately convex; cross veins far apart; MA simple; MP with long bifurcation; CuA and CuP simple; anal veins one or two. Length of wing 12 mm, width more than 3 mm (Fig. 111). One genus from Lower Permian of North America.

71 ### Family PARELMOIDAE Rohdendorf, fam. nov.

SC joins C and R; SC considerably longer than one-half of anterior margin of wing, which is usually convex; MP with bifurcation; CuA simple, without bifurcation; three anal veins; base of wing wide. Length of wing 15–22 mm (Fig. 112). Permian. Two genera: *Pseudelmoa* Carpenter, 1947 and *Parelmoa* Carpenter, 1947 from Lower Permian of North America.

Family KALTANELMOIDAE Rohdendorf, 1961

SC joins C and R, its length is almost equal to one-half of the moderately convex anterior margin; MP with long bifurcation; CuA with a marked bifurcation at its end; it is isolated from M at its base, but connected to it with cross veins; three separate anal veins; base of wing moderately narrow. Permian. One genus.

Kaltanelmoa Rohdendorf, 1957. Genotype—*K. sibirica* Rohdendorf, 1957; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Between C and SC four cross veins; R with a slight bend at the base and straight thereafter, converge gradually toward C; general trunk of M markedly longer than general stem of RS. Length of wing about 12 mm, width 4.2. mm (Fig. 113). One species. Lower Permian of Kuznetsk basin.

Family MARTYNOVIIDAE Tillyard, 1932

SC short, not longer than one-half of anterior margin, latter sharply convex in basal one-third of wing; termination of SC clear, joins either C or R; between SC and C the number of cross veins varies; MA, MP, CuA and CuP simple, without branches. Length of wing 7–22 mm (Fig. 114). Permian. Three genera from Lower Permian of North America.

Suborder Metadiaphanopterodea

Apex of wing blunt; wing sharply costalized, without cross veins in costal area;
72 SC short; often because of extreme costalization, venation absent in costal area; cross veins few, sometimes, absent. Permian. Four families: Biarmohymenidae, Asthenohymenidae, Aenigmatidiidae and Kulojidae.

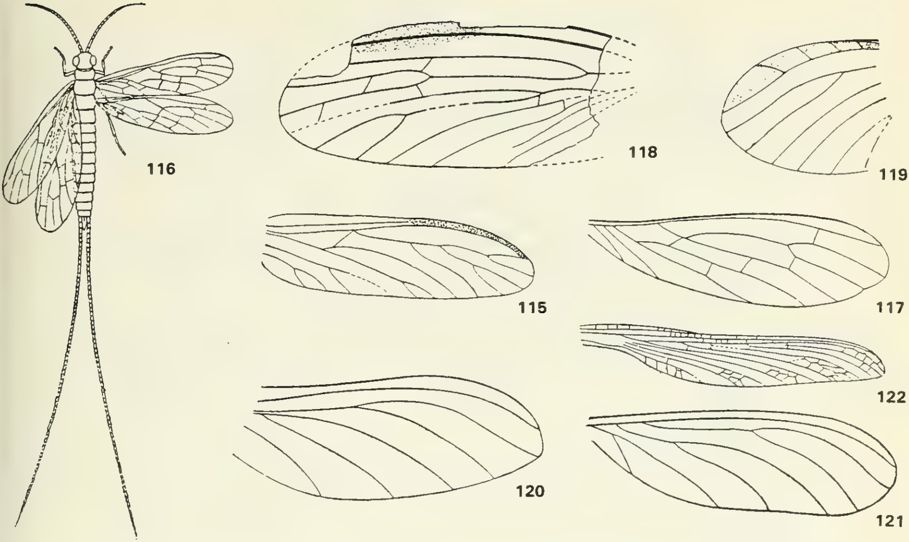
Family BIARMOHYMENIDAE G. Zalessky, 1937

Base of wing very wide; SC reaches middle of wing, joins with C and R and forms part of a long pterostigma; MA and MP simple, without branches; MA fused with RS along some of its length; CuA, CuP and A with bifurcations at their ends. Permian. One genus.

Biarmohymen G. Zalessky, 1937. Genotype—*B. bardense* G. Zalessky, 1937; Lower Permian, Perm province (Barda). Pterostigma somewhat shorter than one-half of anterior margin. RS branches dichotomously, yielding four branches; cross veins absent; main segment of MA looks like an oblique cross vein. Length of wing 24 mm, width 7 mm (Fig. 115). One species. Lower Permian of Urals.

Family ASTHENOHYMENIDAE Tillyard, 1924

Base of wing narrow; wing costalized with poorly differentiated SC in basal half; RS two-branched; MA and MP without branches, former coalesces with RS; CuA and CuP simple; a few cross veins between all longitudinal veins; anal vein single, short and simple. Permian. One genus.



71 Figs. 115–122. Suborder Metadiaphanopterodea and order Campylopterodea.

115. *Biarmohymen bardense* G. Zalessky; wing, × 2. Lower Permian, Urals (Yu. Zalessky, 1937). 116. *Asthenohymen dunbari* Tillyard; (reconstruction); × 3.2. Lower Permian, North America (Laurentiaux, 1953). 117. *A. uralicus* G. Zalessky; wing, × 6.6. Lower Permian, Urals (Yu. Zalessky, 1939). 118. *Aenigmatidia kaltanica* Rohdendorf; wing, × 15. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 119. *Kuloja expansa* Martynov; wing, × 2. Upper Permian, Arkhangelsk province (Martynov, 1928). 120. *Parakuloja paurovenosa* Martynov; wing, × 2.5. Upper Permian, Arkhangelsk province (Martynov, 1931). 121. *Eukuloja cubitalis* (Martynov); wing, × 1.9. Upper Permian, Arkhangelsk province (Martynov, 1931). 122. *Campyloptera eatoni* Brongniart; wing, × 0.8. Upper Carboniferous, Western Europe (Carpenter, 1943).

Asthenohymen Tillyard, 1924. Genotype—*A. dunbari* Tillyard, 1924; Lower Permian, North America (Kansas). Wing apex at end of anterior branch of RS, perceptible, but slightly pointed; one prominent cross vein between R and RS; top of cross vein diverges somewhat from wing margin. Length of wing varies from 4.3 to 10 mm, and width from 1.5 to 3 mm (Figs. 116, 117). Two species from Urals and seven from North America are known.

Family AENIGMATIDIIDAE Rohdendorf, 1961

SC indistinct and reduced; R distant from wing margin and strong; RS with three branches; MA separate from RS, but with a common stem with the forked MP; CuA, CuP and A simple. Permian. One genus.

Aenigmatidia Rohdendorf, 1961. Genotype—*A. kaltanica* Rohdendorf; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Pterostigma large; cross veins between branches of RS, RS and MA and between bases of M and Cu. Length of wing 3.75 mm, width 1.3 mm (Fig. 118). One species. Lower Permian of Kuznetsk basin.

Family KULOJIDAE Martynov, 1928

SC fused with C; R uniformly away from wing margin and stiff; RS with two simple branches. M with independent, fairly long, simple forks (MA + MP); Cu simple or forked; A short and simple. Permian. Three genera.

Kuloja Martynov, 1928. Genotype—*K. expansa* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Ends of R, anterior branch of RS and branches of M parallel, they do not diverge; end of R markedly diverges from wing margin; traces of thin cross veins noticeable. Length of wing around 40 mm, width 11 mm (Fig. 119). One species. Upper Permian of Arkhangelsk province.

Parakuloja Rohdendorf gen. nov. Genotype—*Kuloja paurovenosa* Martynov, 1931; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Ends of R, anterior branch of RS, and branches of RS and M markedly diverge; R approaches C for a while; Cu simple, without branches; cross veins absent. Length of wing about 25 mm, width 8.4 mm (Fig. 120). One species. Upper Permian of Arkhangelsk province.

Eukuloja Rohdendorf, gen. nov. Genotype—*Kuloja cubitalis* Martynov, 1931; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forks of RS and M sharply diverge; R markedly away from wing margin; Cu with two prominent branches—CuA and CuP; cross veins absent. Length of wing 23–28 mm, width 7.5–9 mm (Fig. 121). One species. Upper Permian of Arkhangelsk province.

Order CAMPYLOPTERODEA

Wing with well defined petiole, costalization, straight anterior margin and convex posterior margin, very narrow, length at least six times the width; venation profuse; SC short, not more than one-third of wing, joins C to form a nodus; RS with five branches, most of which are connected with intercalary veins; MA, MP, CuA and CuP simple; cross veins many, distributed all over in no particular order. Length of wing 64 mm, width 11 mm (Fig. 122). Carboniferous. One family, Campylopteridae with one genus from the Upper Carboniferous of France.

73 SUPERORDER ODONATOIDEA.
Dragonfly-like insects

Wings always elongate, several times longer than broad; anterior margin straight or concave; MP and CuA very weakly developed or absent; cross veins strong; archedictyon always absent. Body elongated. Cerci long. Paracercus absent. Carboniferous to Recent. One order: Odonata.

Order ODONATA. Dragonflies and allies

Carboniferous to Recent. Six suborders: Eomeganisoptera, Meganisoptera, Protanisoptera, Zygoptera, Anisozygoptera, Anisoptera.

Suborder Eomeganisoptera

CuP simple and wavy; R isolated from common stalk of MA + RS; MA with a few short branches; nodus and subnodular veins apparently not developed; cross veins few and long. Length of wing around 60 mm (Fig. 123). Lower Carboniferous. One family, Erasipteridae with one genus from Namurian of Czechoslovakia.

Suborder Meganisoptera. Giant dragonflies

Anterior margin of wing straight and without convexity or fracture; nodus not developed; CuP simple and wavy; cross veins numerous; the peculiar cells—triangular and quadrangular—at the base of the wing absent. Wings large. Carboniferous through Mesozoic. Four families: Paralogidae, Meganeuridae, Triadotypidae, Liadotypidae.

74 Family PARALOGIDAE Handlirsch, 1906

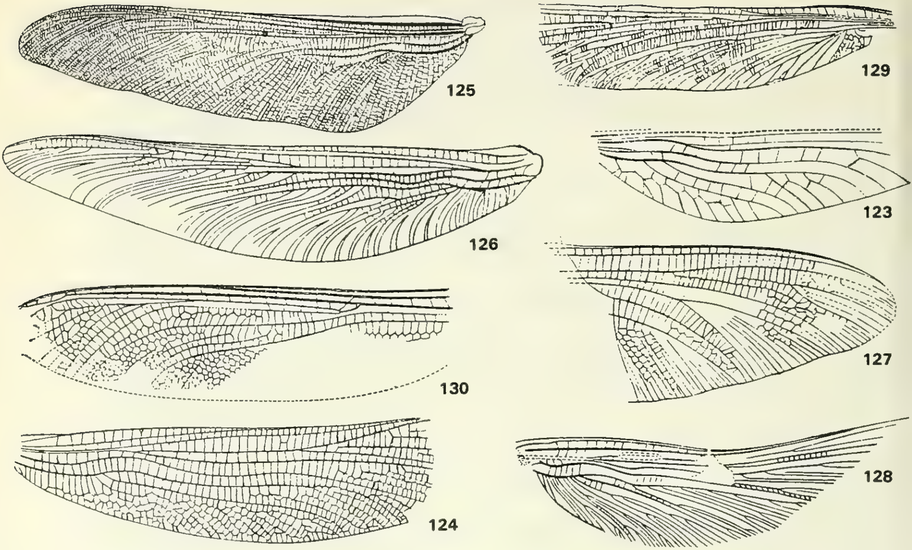
SC short, does not exceed one-half of anterior margin of wing; $RS_1 + RS_2$ and $RS_3 + RS_4$ rarely diverge; rudiment of CuA absent. Length of wing 40–60 mm (Fig. 124). Carboniferous to Permian. Two genera from North America.

Family MEGANEURIDAE Handlirsch, 1907

SC long and never shorter than one-half of anterior margin; all branches of RS diverge at small angles. Carboniferous to Permian. Two subfamilies: Meganeurinae, Typinae.

Subfamily Meganeurinae Handlirsch, 1919

Precostal area long, almost reaches middle of anterior margin of wing; posterior branch of RS branches from main trunk of RS at basal half of wing, not far from branching of MA. Wing large. Length of wing 260–310 mm (Fig. 125).



73 Figs. 123–130. Suborders Eomeganisoptera and Meganisoptera.

123. *Erasipteron tarischi* Pruvost; wing, × 1. Lower Carboniferous, Czechoslovakia (Laurentiaux, 1953). 124. *Oligotypus tillyardi* Carpenter; wing, × 1.9. Lower Permian, North America (Carpenter, 1947). 125. *Maganeura monyi* Brongniart; wing, × 0.25. Upper Carboniferous, Western Europe (Handlirsch, 1906). 126. *Arctotypus sinuatus* Martynov; wing, × 0.75. Upper Permian, Arkhangelsk province (Martynov, 1931). 127. *Kargalotypus kargalensis* (Martynov); wing, × 1.1. Permian, Southern Urals (Martynov, 1931). 128. *Petrotypus multivenosus* G. Zalessky; wing, × 0.75. Upper Permian, Urals (Yu. Zalessky, 1950). 129. *Triadotypus guillaumei* Laurentiaux and Grauvogel; wing, × 0.75. Lower Trias, Western Europe (Laurentiaux, 1953). 130. *Liadotypus relictus* Martynov; wing, × 1.1. Upper Jurassic, Central Asia (Martynov, 1937).

Carboniferous to Permian. Two genera from the Upper Carboniferous of Western Europe and Lower Permian of North America.

Subfamily Typinae Handlirsch, 1919

Precostal area short—considerably less than one-third of anterior margin; posterior branch of RS branches from basal trunk of RS_1, as a rule considerably further than branching of MA. Length of wing not more than 250 mm. Carboniferous to Permian. Six genera.

Arctotypus Martynov, 1931. Genotype—*A. sinuatus* Martynov, 1931;

Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Precostal area very small; SC considerably longer than one-half of anterior margin; branches of MA number seven or eight including the thinnest veins; between main parts of CuP and A there is a short, oblique cross vein markedly thicker than other veins. Length of wing 90–125 mm (Fig. 126). Permian. Two species from Urals and one species from Arkhangelsk province. Another, little-known species from the Kungurian stage of the Urals.

Kargalotypus Rohdendorf, gen. nov. Genotype—*Megatypus kargalensis* Martynov, 1932; Permian, Orenburg province (Kargala). Structure of precostal area and of basal part of wing not known; SC not longer than one-half of length of anterior margin; M branches considerably further than branching of RS, forms a short, wide fan of 14 slender veins; between ends of M and CuP, CuP and A, and MA and RS, two rows of alternating cells produce zigzag longitudinal veins. Length of wing about 135 mm (Fig. 127). One species. Permian of southern Urals.

Petrotypus G. Zalessky, 1950. Genotype—*P. multivenosus* G. Zalessky, 1950; Upper Permian, Urals (Kazanian stage, Vishera); precostal area well developed; SC considerably longer than one-half of anterior margin; MA branches at the same level as RS and forms numerous, densely packed branches (more than nine); CuP, at base of wing, very close to main trunk of R + M; CuP and A distinctly arched. Double row of cells absent. Length of wing around 120 mm (Fig. 128). One species. Upper Permian of Urals.

Outside the USSR: *Meganeurula* Handlirsch, 1906; *Typus* Sellards, 1907; and *Megatypus* Tillyard, 1925.

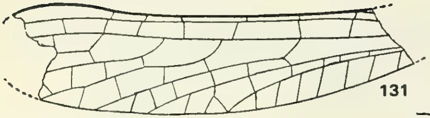
Family TRIADOTYPIDAE Granvogel and Laurentiaux, 1952

Anterior margin straight; SC less than one-third of anterior margin; MA and CuP simple, terminating close to each other on wing margin; CuP moderately wavy; CuA short, joins with CuP, is located almost at base of wing; anals numerous, with countless branches; cross veins numerous, irregularly disposed (Fig. 129). Length of wing about 125 mm. Mesozoic. One species from Triassic of France.

Family LIADOTYPIDAE Martynov, 1937

Anterior margin of wing almost straight, very slightly convex; SC firm, reaches apex of wing, lies very close to C; MA fused with RS at base. CuP leaves A at distal part. Mesozoic. One genus from Lower Jurassic of Central Asia.

Liadotypus Martynov, 1937. Genotype—*L. relictus* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). From point of divergence of RS and M toward the anterior wing margin, two oblique veins lie in one line, and terminate at level of basal part of RS; between CuP and A many rows of cells are located in distal part forming indistinct longitudinal branches.



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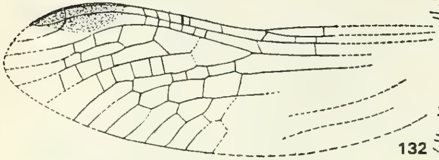

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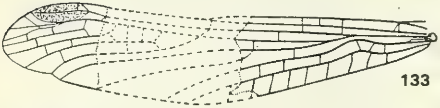

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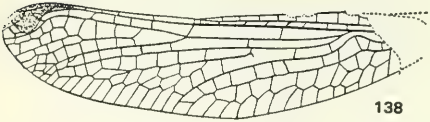

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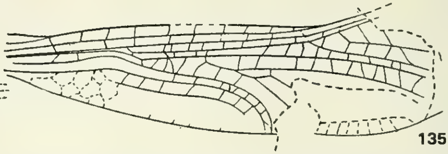

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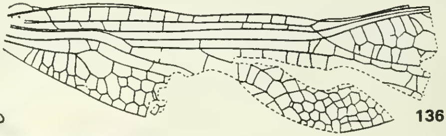

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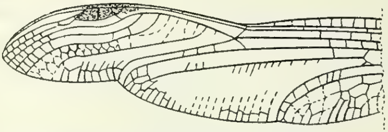

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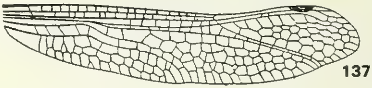

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75 Fig. 131–139. Suborder Protanisoptera.

131. *Kaltanoneura bartenevi* Rohdendorf; wing, × 5.6. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 132. *Ditaxineurella stigmalis* Martynov; wing, × 2.6. Lower Permian, Urals (Martynov, 1941). 133. *D. uralensis* (G. Zalessky); wing, × 2. Lower Permian, Urals (Yu. Zalessky). 134. *Ditaxineura anomalostigma* Tillyard; wing, × 3.3. Lower Permian, North America (Carpenter, 1931). 135. *Pholidoptilon* sp.; wing, × 1.7. Upper Permian, Arkhangelsk province (Yu. Zalessky, 1931). 136. *P. kamense* G. Zalessky; wing, × 1.7. Upper Permian, Pre-Urals (Yu. Zalessky, 1931). 137. *Polytaxineura stanleyi* Tillyard; wing. × 1.2 Upper Permian, Australia (Tillyard, 1935). 138. *Callimokaltania martynovi* G. Zalessky; wing, × 2.4. Lower Permian, Kuznetsk basin (Yu. Zalessky, 1955). 139. *Permaeschna dolloi*Martynov; wing, × 1.3. Upper Permian, Arkhangelsk province (Martynov, 1931).

Length of wing about 67 mm (Fig. 130). One species from Lower Jurassic of Central Asia.

Suborder Protanisoptera

Anterior margin of wing distinctly concave; RS branches at same level or at distal end of SC; CuP simple and wavy; base of wing moderately wide or somewhat narrow, not like a petiole; triangles and quadrangles absent. Permian. Five families: Kaltanoneuridae, Ditaxineuridae, Polytaxineuridae, Callimokaltaniidae, Permaeschnidae.

Family KALTANONEURIDAE Rohdendorf, 1961

Anterior margin gently arched and concave; costal area with many cross veins; pterostigma long and convex; M simple; RS with two branches. Permian. One genus.

Kaltanoneura Rohdendorf, 1961. Genotype—*K. bartenevi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Pterostigma elongate and markedly convex; radial area considerably wider than costal; postnodal cross veins number six; between RS_5 and MA five, and between MA and CuP six cross veins; cubital area with more than seven cross veins. Length of wing about 20 mm (Fig. 131). One species. Lower Permian of Kuznetsk basin.

Family DITAXINEURIDAE Tillyard, 1925

Anterior margin of wing distinctly concave; costal area with a few cross veins; pterostigma very large. Five branches of RS and five or six branches of M; medial area with more than six veins. Permian. Two genera.

Ditaxineurella Martynov, 1940 (*Hemtzygopteron* G. Zalessky, 1955, syn. nov.). Genotype—*D. stigmalis* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area beyond end of SC with six cross veins; pterostigma extremely big. No fewer than four cross veins between every two consecutive branches of RS. Length of wing about 37 mm (Figs. 132, 133). Two species. Lower Permian of Urals.

Ditaxineura Tillyard, 1925. Genotype—*D. anomalostigma* Tillyard, 1925;
76 Lower Permian, North America (Kansas). Costal area beyond end of SC with one cross vein or no cross vein at all; pterostigma of moderate size; between every two consecutive branches of RS, two or three cross veins. Length of wing 25 mm (Fig. 134). Two species. Lower Permian of North America.

Family POLYTAXINEURIDAE Tillyard, 1935

Anterior margin distinctly concave. Costal area with numerous cross veins; pterostigma of moderate size; medial area with 10 to 13 veins extending to margin of wing. Permian. Two genera.

Pholidoptilon G. Zalessky, 1931. Genotype—*P. kamense* G. Zalessky, 1931; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Anterior margin of wing with three notches; pterostigma narrow; radial area devoid of cross veins. Length of wing about 60 mm (Figs. 135, 136). One species. Upper Permian of Pre-Urals.

Polytaxineura Tillyard, 1935. Genotype—*P. stanleyi* Tillyard, 1935; Upper Permian, Australia. Anterior margin of wing has single nodus at level of end of SC; pterostigma is short and broad; radial area with many cross veins. Length of wing 50 mm (Fig. 137). One species. Upper Permian of Australia.

Family CALLIMOKALTANIIDAE G. Zalessky, 1955

Anterior margin slightly concave; costal area with many cross veins; pterostigma very large and rounded; medial area with eight veins reaching margin of wing. Permian. One species.

Callimokaltania G. Zalessky, 1955. Genotype—*C. martynovi* G. Zalessky, 1955; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Nodular and subnodular cross veins somewhat isolated; posterior branch of MA long. Anal area with two rows of cells. Length of wing 28 mm (Fig. 138). One species. Lower Permian of Kuznetsk basin.

Family PERMAESCHNIDAE Martynov, 1931

Anterior margin sharply concave; apical section of wing distinctly set apart by a notch at the termination of MA; pterostigma large; medial area with numerous veins; no fewer than 20 veins terminate on wing margin. Permian. One genus.

Permaeschna Martynov, 1931. Genotype—*P. dolloi* Martynov, 1931; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Cross veins numerous in all areas of wing; 13 to 15 rows of cells on anal margin of apical lobe of wing. Length of wing 55–60 mm (Fig. 139). Two species. Upper Permian of Arkhangelsk province.

Suborder Zygoptera. Damselflies

(PROTOZYGOPTERA)

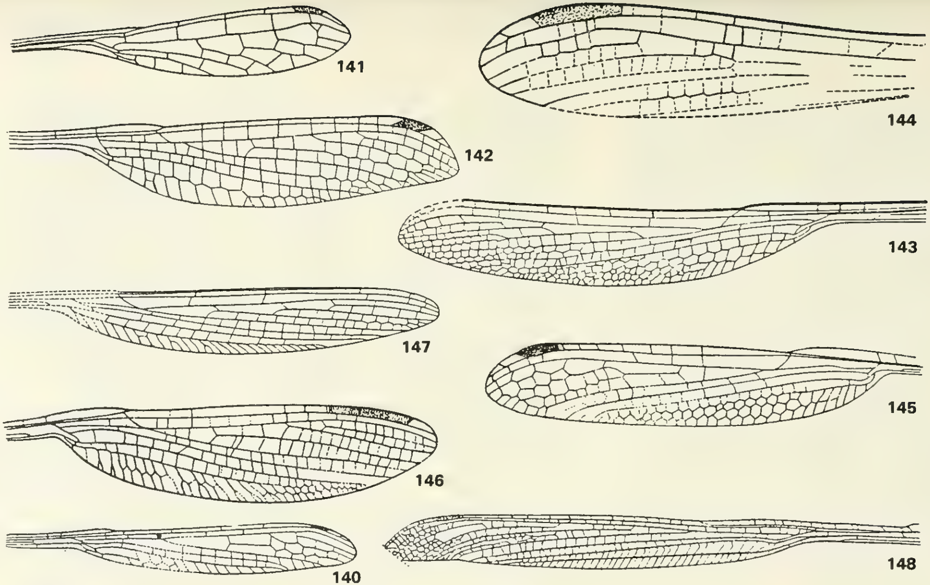
Wings sharply narrowed at base; base often in the form of a petiole. Wings similar in size and shape. Hindwings hardly broadened; discoidal cell fused with medial, or quite often separate, but never divided into triangles. Body thin. Abdomen cylindrical. Eyes set wide apart. Nymphs bear three large foliaceous gills at end of abdomen. Permian to Recent. Seven superfamilies: Kennedyidea, Permagrionidea, Permepallagidea, Protomyrmeleontidea, Hemiphlebiidea, Coenagrionidea, Agrionidea.

SUPERFAMILY KENNEDYIDEA

Nodus not seen; nodular and subnodular veins absent; costal area with few cross veins; discoidal cell not separated from medial. Permian. One family.

Family KENNEDYIDAE Tillyard, 1923

Anterior margin of wing straight, anal margin convex; all cross veins in costal



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Figs. 140–148. Suborder Zygoptera; superfamilies Kennedyidea, Permagrionidea and Permepallagidea.

140. *Kennedya mirabilis* Tillyard; wing, × 1.4. Lower Permian, North America (Tillyard, 1928). 141. *Progoneura nobilis* Carpenter; wing, × 4.6. Lower Permian, North America (Carpenter, 1947). 142. *Permagrion falklandicum* Tillyard; wing, × 2.3. Upper Permian, Falkland Islands (Tillyard, 1928). 143. *Permolestes gracilis* Martynov; wing, × 2. Upper Permian, Arkhangelsk province (Martynov, 1931). 144. *Sushkinia parvula* Martynov; wing, × 4.7. Upper Permian, Pre-Urals (Martynov, 1930). 145. *Scytolestes stigmalis* Martynov; wing, × 3. Upper Permian, Southern Urals (Martynov, 1937). 146. *Epilestes kargalensis* Martynov; wing, ×2.4. Upper Permian, Southern Urals (Martynov, 1937). 147. *Solikamptilon remuliforme* G. Zalessky; wing, × 1.7. Lower Permian, Urals (Yu.Zalessky, 1948). 148. *Permepallage angustissima* Martynov; wing, ×1. Upper Permian, Arkhangelsk province (Martynov, 1938).

and radial areas straight; not more than two antenodal cross veins; three to six postnodal veins; anal-cubital area with one row of cells. Permian. Two genera.

Kennedya Tillyard, 1925. Genotype— *K. mirabilis* Tillyard, 1925; Lower Permian, North America (Kansas). Pterostigma not prominent, not large; radial area equal to costal area or somewhat wider; four to five postnodal cross veins; seven to eight cross veins between branches RS_5 and MA, and eight or nine between MA and CuP; cubital area with 12 to 18 cross veins. Length of wing 34–45 mm (Fig. 140). Permian. Four species from Lower Permian of North America.

Progoneura Carpenter, 1931. Genotype—*P. minuta* Carpenter, 1931; Lower Permian, North America. Pterostigma prominent, moderately elongate; radial area considerably wider than costal; three or four postnodal cross veins; 77 three cross veins between RS_5 and MA and two between MA and CuP; cubital area with two or three cross veins. Length of wing 13–17 mm (Fig. 141). One species from Upper Permian of Arkhangelsk province and two species from Lower Permian of North America.

SUPERFAMILY PERMAGRIONIDEA

Costal area with two or three antenodal cross veins; nodus rudimentary; costal vein without fracture; nodular and subnodular cross veins slanting and touching one another; discoidal cell not separate from medial. Permian. Three families: Permagrionidae, Permolestidae, Solikamptilonidae.

Family PERMAGRIONIDAE Tillyard, 1928

Eight postnodal cross veins exactly match corresponding cross veins in radial area; basal part of Cu absent in petiole; anal vein distinctly seen, reaching wing margin; anal area with one row of cells. Length of wing 34 mm (Fig. 142). Permian. One genus from Upper Permian of Western Europe.*

Family PERMOLESTIDAE Martynov, 1931

Five to seven postnodal cross veins which do not correspond with cross veins of radial area; basal part of Cu usually clear; anal area with two or three rows of numerous small cells. Length of wing 25–50 mm. Permian. Four genera.

Permolestes Martynov, 1931. Genotype—*P. gracilis* Martynov, 1931; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Costal and radial areas in middle of wing of equal width; pterostigma not distinct; postnodal veins firm and distinct, MA and CuP do not reach margin of wing but 78 are transformed into thin auxiliary veins between innumerable small cells. Length of wing 48 mm (Fig. 143). One species. Upper Permian. Arkhangelsk province.

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* Editor's note: Should read South-Atlantic (Falkland Islands).

Sushkinia Martynov, 1930. Genotype—*S. parvula* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Pterostigma long and prominent; postnodal cross veins of varying thickness, firm and not very distinct, radial area markedly wider than costal; MA and CuP reach margin. Length of wing 28–33 mm (Fig. 144). Two species. Upper Permian of Urals.

Scytolestes Martynov, 1937. Genotype—*S. stigmalis* Martynov, 1937; Upper Permian, Orenburg province (Kargala). Pterostigma prominent, short and convex; postnodal cross veins distinct, radial area distinctly wider than costal; MA and CuP reach margin. Length of wing 25 mm (Fig. 145). One species. Upper Permian of Southern Urals.

Epilestes Martynov, 1937. Genotype—*E. kargalensis* Martynov, 1937; Upper Permian, Orenburg province (Kargala). Anal margin of wing markedly convex; pterostigma long; postnodal cross veins weak; radial area almost equal to costal in width; MA and CuP reach margin. Length of wing 31 mm (Fig. 146). One species. Upper Permian of southern Urals.

Family SOLIKAMPTILONIDAE G. Zalessky, 1948

Wing tapering toward apex; two postnodal cross veins corresponding to two cross veins in radial area; anal vein sturdy, reaches wing margin; anal area with one row of cells. Permian. One genus.

Solikamptilon G. Zalessky, 1948. Genotype—*S. remuliforme* G. Zalessky, 1948; Lower Permian, Urals (Solikamian salts: Lower Moshevo). Pterostigma not distinct; all branches of RS, M, Cu and main trunk of A parallel. Length of wing about 45 mm (Fig. 147). One species. Lower Permian of Urals.

SUPERFAMILY PERMEPALLAGIDEA

Costal area with a large number of cross veins—more than 15 antenodal and 25 postnodal. Nodus not prominent; discoidal cells not separated from medial ones; basal part of A_1 distinctly seen in stalk. Permian. One family.

Family PERMEPALLAGIDAE Martynov, 1938

Wing narrow and long with straight anterior and anal margins; cubital-anal area with a strong, long A_1; cross veins numerous in all areas. Permian. One genus.

Permepallage Martynov, 1938. Genotype—*P. angustissima* Martynov, 1938; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Auxiliary longitudinal veins lie between branches of RS. Length of wing about 90 mm (Fig. 148). One genus. Upper Permian of Arkhangelsk province.

SUPERFAMILY PROTOMYRMELEONTIDEA
(ARCHIZYGOPTERA)

Nodus not prominent; antenodal cross veins absent; postnodal veins numerous;

SC very short; discoidal cell not separate from medial; shortened veins absent in basal part of wing. Mesozoic. One family.

Family PROTOMYRMELEONTIDAE Handlirsch, 1906

Wing with very short petiole; pterostigma prominent; radial veins occupy large part of wing; MA and CuP simple; anal veins absent. Mesozoic. Three genera.

Protomyrmeleon Geinitz, 1887. Genotype—*P. brunonis* Geinitz, 1887, Lower Jurassic, Western Europe (Upper Lias). Four distinct branches of RS present; RS_4 not isolated; more than 10 veins terminate between RS_2 and RS_3 on margin of wing. Length of wing is 22–24 mm (Fig. 149). Two species from Upper Jurassic of Kazakhstan (Karatau) and one from Lower Jurassic of Western Europe.

Outside the USSR: *Triassagrion* Tillyard, 1922 (Upper Trias of Australia) and *Tillyardagrion* Martynov, 1927 (Lower Jurassic of England).

SUPERFAMILY HEMIPHLEBIIDEA

Nodus and its cross veins fairly well developed; two distinct antenodal cross veins; postnodal veins five in number, located at different levels from cross veins of radial area; discoidal cell open. Wings of small size. Length of wing 10–12 mm (Fig. 150). One Recent family, Hemiphlebiidae, with one genus.

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SUPERFAMILY COENAGRIONIDEA

Nodus and its cross veins well developed; two distinct antenodal veins present; postnodal veins located exactly at levels of corresponding cross veins in radial area; discoidal cell separate from medial. Neogene to Recent. Ten families in Recent fauna, of which the following four are known also in fossil form: Megapodagrionidae, Lestidae, Coenagrionidae, Platycnemididae.

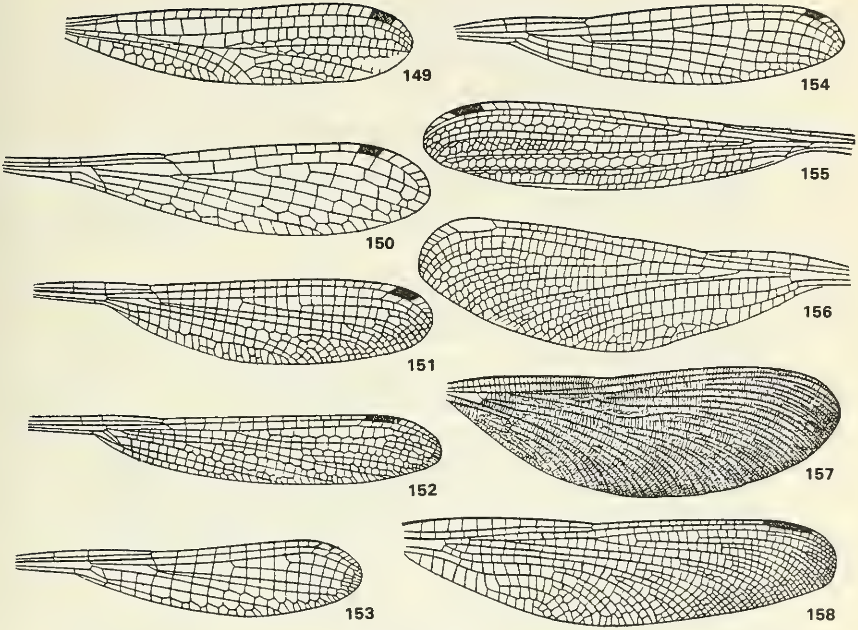
Family MEGAPODAGRIONIDAE Tillyard, 1917

Numerous auxiliary branches between RS and M terminate on wing margin; only one branch of RS branches out proximally at level of subnodal cross veins; discoidal cell with wide distal end (Fig. 151). Neogene to Recent. 13 genera, from the Miocene of North America and Western Europe.

Family LESTIDAE Calvert, 1901

Demoiselles

Two branches of RS leave main trunk proximally at level of subnodal cross veins; auxiliary branches of RS present. Discoidal cell with narrow distal end (Fig. 152). Neogene to Recent. Nine genera in Recent fauna, of which one (*Lestes* Leach) also known from the Neogene, besides two extinct genera from the Neogene of North America.



Figs. 149–158. Suborder Zygoptera; superfamilies Protomyrmeleontidae, Hemiphlebiidea, Coenagrionidea and Agrionidea.

149. *Protomyrmeleon brunonis* Geinitz; wing, × 3.7. Lower Jurassic, Western Europe (Handlirsch, 1906). 150. *Hemiphlebia mirabilis* Selys; wing, × 6.8. Recent (Tillyard, 1938). 151. *Agriolestes icteromelas* Selys; wing, × 2. Recent (Tillyard, 1926). 152. *Austrolestes cingulatus* Burmeister; wing, × 2.7. Recent (Tillyard, 1926). 153. *Pseudagrion australasiae* Selys; wing, × 2.1. Recent (Tillyard, 1926). 154. *Platycnemis pennipes* Pall; wing, × 3.1. Recent (Munz, 1919). 155. *Steleopteron deichmuelleri* Handlirsch; wing, × 1.9. Upper Jurassic, Western Europe (Handlirsch, 1925). 156. *Phenacolestes mirandus* Cockerell; wing, × 2.5. Miocene, North America (Handlirsch, 1925). 157. *Agrion virgo* Linnaeus; wing, × 2.2. Recent (Munz, 1919). 158. *Epallage fatima* Carpenter; wing. × 2. Recent. (Munz, 1919).

80 Family COENAGRIONIDAE Tillyard, 1918

Auxiliary branches of RS absent; discoidal cell with an acute distal end; RS_3, MA and A_1 zigzag at end; CuP and A_1 present (Fig. 153). Neogene to Recent. One genus in the Miocene of North America and about 40 genera in Recent fauna, of which three are also from the Neogene.

Family PLATYCNEMIDIDAE Jacobson and Bianchi, 1905

Additional branches of RS absent; CuP and A_1 present; discoidal cell with a blunt distal end; MA, CuP and A_1 with their ends in a zigzag fashion (Fig. 154). Neogene to Recent. About 10 genera in Recent fauna, of which two are also from the Miocene of North America.

SUPERFAMILY AGRIONIDEA

Wings without petiole, or stalk very short; nodus and its cross veins well developed; five or more antenodal cross veins. Jurassic to Recent. Seven families, of which Zacallitidae, Amphipterygidae, Agrionidae and Epallagidae are known in fossil form.

Family ZACALLITIDAE Fraser, 1943

Antenodal cross veins number 10. Discoidal cell closed. One genus from the Eocene of Western Europe.

Family AMPHIPTERYGIDAE Tillyard, 1917

Wing with a petiole; antenodal cross veins nine; general trunk of RS_1 not bent 81 at the base and not close to R; cross veins on wing not numerous, not particularly close together. Mesozoic to Recent. Five genera in Recent fauna and five extinct genera (Figs. 155, 156): *Steleopteron* Handlirsch, 1908 from the Upper Jurassic of Western Europe and the other four genera from the Paleogene and Neogene of North America.

Family AGRIONIDAE Kirby, 1890

Wings not petiolate; antenodal cross veins always more than 12; common trunk of RS often close to R; cross veins numerous and closely packed (Fig. 157). Paleogene to Recent. Nearly 15 genera in Recent fauna, of which one is also from the Paleogene of Europe (Baltic amber).

Family EPALLAGIDAE Needham, 1903

Wing not petiolate; antenodal cross veins number 11 or more; common trunk of RS often close to R at base; anal vein without recurrent branch; cross veins numerous (Fig. 158). Upper Jurassic to Recent. Eight genera in Recent fauna, of which two are also from the Upper Jurassic of Western Europe and one also from the Paleogene of North America.

Suborder Anisozygoptera

Wings not petiolate, moderately narrow toward base; both pairs of wings almost similar; discoidal cell in forewing not divided into triangles; in hindwing discoidal cell variable. Body thin. Abdomen cylindrical and sometimes bulging toward the end. Eyes usually wide apart. Jurassic to Recent. Two superfamilies: Heterophlebiidea, Tarsophlebiidea.

SUPERFAMILY HETEROPHLEBIIDEA

Fore- and hindwings differ markedly in form; discoidal cell of hindwing wider than that of forewing, its distal anterior angle usually pointed. Jurassic to Recent. Five families: Progonophlebiidae, Archithemistidae, Liassophlebiidae, Heterophlebiidae, Epiophlebiidae (Fig. 159). Last family found only in Recent fauna.

Family PROGONOPHLEBIIDAE Tillyard, 1925

Subnodal and nodal cross veins not located in one line; in both wings discoidal cell short and not divided; A not developed, and between discoidal cell and posterior margin of wing there is a large expanse. Length of wing 35–44 mm (Fig. 160). Lower Jurassic. One genus from Lias of Western Europe.

Family ARCHITHEMISTIDAE Tillyard, 1917

(Selenothemidae Handlirsch, 1939)

Antenodal cross veins numerous; subnodal and nodal cross veins lie in one line at middle of wing; in both wings discoidal cell not divided; anal vein present (Fig. 161). Jurassic. Seven genera.

Sogdothemis Martynov, 1937. Genotype—*S. modesta* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab). Wing elongate with slightly convex anal margin; pterostigma prominent; MA terminates at level of pterostigma; not fewer than 20 cross veins between pterostigma and nodal cross vein. Length of wing about 37 mm (Fig. 162). One species. Lower Jurassic of Central Asia.

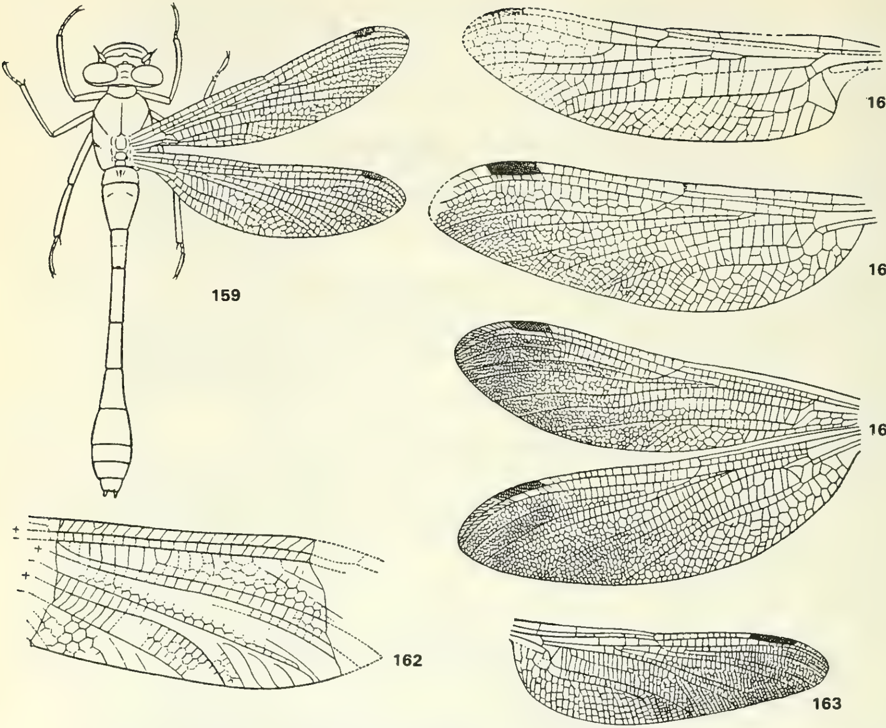
Outside the USSR: *Diastatommites* Handlirsch, 1906; *Archithemis* Handlirsch, 1906; *Selenothemis* Handlirsch, 1920; *Heterothemis* Handlirsch, 1906; *Liadothemis* Handlirsch, 1906; and *Oryctothemis* Handlirsch, 1906.

Family LIASSOPHLEBIIDAE Tillyard, 1925

Antenodal cross veins two or three; subnodal and nodal cross veins arranged in one line; in both wings discoidal cell not divided. Length of wing 60–70 mm (Fig. 163). Lower Jurassic. Two genera from Lias of Western Europe.

Family HETEROPHLEBIIDAE Handlirsch, 1906

Antenodal cross veins five, of which two prominent and others weak; subnodal and nodal veins lie in one line; discoidal cell of hindwing divided into



Figs. 159–164. Suborder Anisozygoptera, superfamily Heterophlebiidea.

159. *Epiophlebia superstes* MacLachlan; general view, × 1.7. Recent (Handlirsch, 1925). 160. *Progonophlebia woodwardi* Tillyard; wing, × 2. Lower Jurassic, Western Europe (Tillyard, 1925). 161. *Selenothemis liadis* Handlirsch; wing, × 2.8. Lower Jurassic, Western Europe (Handlirsch, 1925). 162. *Sogdothemis modesta* Martynov; wing, × 4.4. Lower Jurassic, Central Asia (Martynov, 1937). 163. *Liassophlebia magnifica* Tillyard; wing, × 0.85. Lower Jurassic, Western Europe (Tillyard, 1925). 164. *Heterophlebia dislocata* Brodie and Westwood; wing, × 0.68. Lower Jurassic, Western Europe (Handlirsch, 1925).

triangles and supertriangles. Length of wing about 30 mm (Fig. 164). Lower Jurassic. Four genera from Lias of Western Europe.

SUPERFAMILY TARSOPHLEBIIDEA

Fore- and hindwings almost identical in form; discoidal cells narrow with blunt distal angles. Abdomen long and slender. Jurassic through Paleogene. Five families: Tarsophlebiidae, Karatawiidae, Stenophlebiidae, Isophlebiidae, Sieblosiidae.

82 **Family TARSOPHLEBIIDAE Handlirsch, 1906**

Pterostigma prominent; discoidal cell fused with medial cell and together with latter forms a characteristically curved and pointed area without cross veins. Anal area almost reaches middle of posterior margin, and bears a few rows of cells in its posterior part. Body very slender. Upper Jurassic. One genus.

Tarsophlebia Hagen, 1866. Genotype—*Heterophlebia eximia* Hagen, 1862; Upper Jurassic, Germany (Malm). Between main branches of RS at middle of wing large cells present. Length of wing 35–60 mm (Fig. 165). Jurassic. One species from Lower Jurassic of Western Europe, three species from Upper Jurassic of Western Europe and one species from Upper Jurassic of Kazakhstan.

Family KARATAWIIDAE Martynov, 1925

Pterostigma absent; discoidal cell not separated from medial cell; because of
83 very short A, anal area very small and narrow, occupies less than one-fourth
of length of wing. One genus from Upper Jurassic.

Karatawia Martynov, 1925. Genotype—*K. turanica* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). MA transformed into thin zigzag vein at middle of wing, does not reach wing margin. Length of wing 48 mm (Fig. 166). One species. Upper Jurassic of Kazakhstan.

Family STENOPHLEBIIDAE Handlirsch, 1906

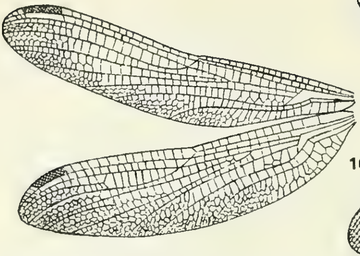
Discoidal cell markedly isolated, pointed, directed backward; in both wings it is divided by two cross veins; anal area large and well defined by strong anal vein, with distinct curve. Length of wing 30–80 mm (Fig. 167). One genus from Upper Jurassic of Western Europe.

Family ISOPHLEBIIDAE Handlirsch, 1906

Wings very narrow with pointed apices; discoidal cell shaped like a trapezium, not curved; anal area prominent, supported by a sharply curved anal vein. Length of wing 70–100 mm (Fig. 168). Three genera from Middle and Upper Jurassic of Western Europe.

Family SIEBLOSIIDAE Handlirsch, 1906

Wings slightly elongate with blunt apices. Antenodal cross veins not distinct, discoidal cell shaped like a large trapezium. Length of wing about 40 mm (Fig. 169). Paleogene. One genus from Oligocene of Western Europe.



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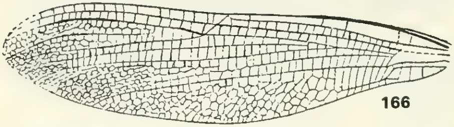

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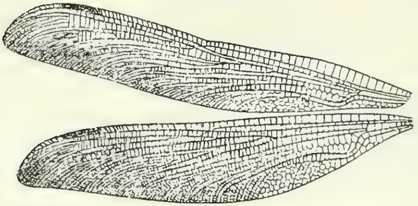

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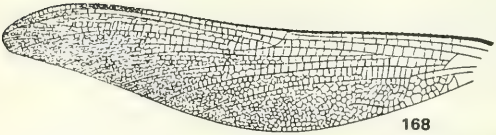

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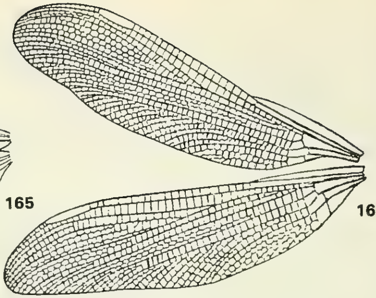

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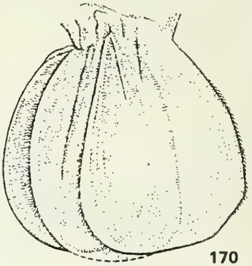

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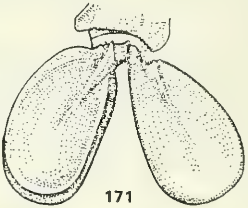


171

82 Figs. 165–171. Suborder Anisozygoptera: superfamilies Tarsophlebiidea and Anisozygoptera incertae sedis.

165. *Tarsophlebia eximia* (Hagen); wings, × 2.1. Upper Jurassic, Western Europe (Handlirsch, 1925). 166. *Karatawia turanica* Martynov, wing, × 1.6. Upper Jurassic, Kazakhstan (Martynov, 1925). 167. *Stenophlebia latereilli* Germar; wings, × 1.3. Upper Jurassic, Western Europe (Handlirsch, 1925). 168. *Anisophlebia helle* Hagen; wing, × 1.2. Upper Jurassic, Western Europe (Handlirsch, 1925). 169. *Sieblosia jucunda* Hagen, wings, × 1.7. Oligocene, Western Europe (Handlirsch, 1925). 170. *Samarura gigantea* Brauer, Redtenbacher and Ganglbauer; appendages at end of abdomen of nymph, × 6.8. Lower Jurassic, East Siberia (original drawing). 171. *S. minor* Brauer, Redtenbacher and Ganglbauer; appendages at end of abdomen of nymph, × 9.5. Lower Jurassic, Irkutsk province (original drawing).

Anisozygoptera Incertae sedis

To this suborder belong some poorly-studied genera whose relationships are not clear.

Samarura Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*S. gigantea* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province (Cheremkovian series, Ust-Bailey). Nymph: rudiments of wings reach anterior edge of third tergum of abdomen. Abdomen elongate and flexible. Three leaflike gills occur at end of abdomen. Length of gill lamellae 2.7–5.5 mm (Figs. 170, 171). Lower Jurassic. Five species from Siberia.

Outside the USSR: From Triassic of Western Europe—*Pirontetia* Meunier, 1907. From Lower Jurassic of Western Europe—*Campterophlebia* Bode, 1907; *Pterothemis* Handlirsch, 1906; *Systellothemis* Handlirsch, 1939; *Rhabdothemis* Handlirsch, 1939; *Temnostigma* Handlirsch, 1939; *Pycnothemis* Handlirsch, 1939; *Anomothemis* Handlirsch, 1906; *Parelthothemis* Handlirsch, 1906; *Petrophlebia* Tillyard, 1925. From Triassic of Australia —*Mesophlebia* Tillyard, 1916; *Periassophlebia* Tillyard, 1918; *Triassophlebia* Tillyard, 1922; *Triassolestes* Tillyard, 1918.

Suborder Anisoptera. Dragonflies

Wings not petiolate, with a broad base. Hindwings differ considerably from forewings, being much wider; nodal cross vein always at middle of anterior margin; in both wings discoidal cells transformed into typical triangles. Body relatively massive. Abdomen not slender, sometimes widens at end. Nymphs without foliaceous gills. Jurassic to Recent. Two superfamilies: Aeshnidea and Libellulidea.

SUPERFAMILY AESHNIDEA

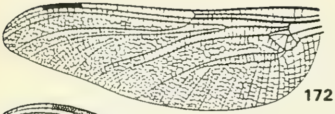
Antenodal cross veins of costal and subcostal areas irregularly distributed, lying at different levels; triangle in hind and forewings far removed from medial area. Jurassic to Recent. Five families: Liassogomphidae, Petaluridae, Gomphidae, Aeshnidae, Aeschnidiidae.

Family LIASSOGOMPHIDAE Tillyard, 1935

Triangle divided by one vein which runs longitudinally; anal area of hindwing divided by branches of anal vein into easily distinguished, radially diverging sectors. Length of hindwing 37 mm (Fig. 172). Jurassic. Five genera from Lower Jurassic of Western Europe.

Family PETALURIDAE Needham, 1903

Triangle of forewing high or wide and subdivided by irregular cross veins into two to six cells; triangle of hindwing disposed longitudinally, with one cross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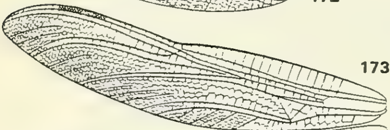
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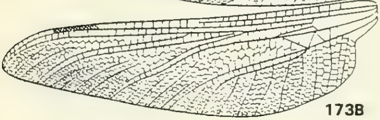
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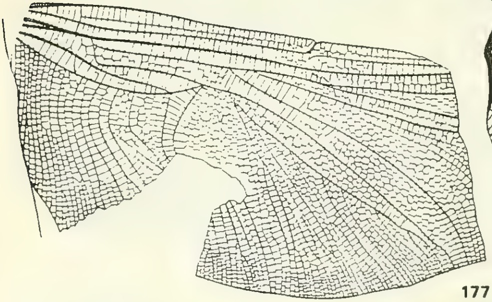
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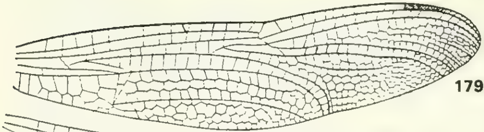
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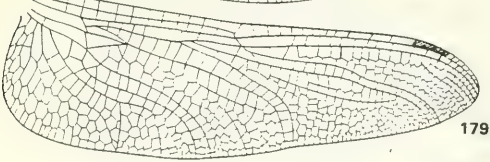
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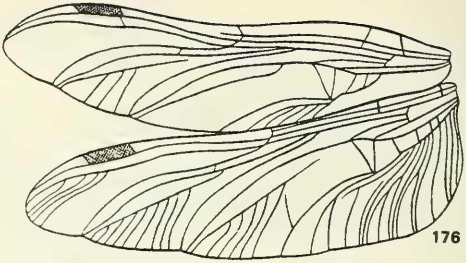
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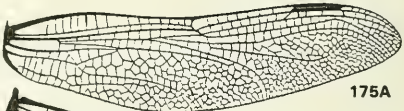
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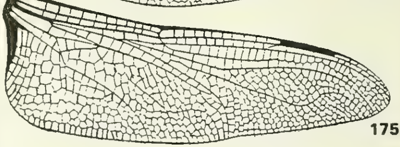
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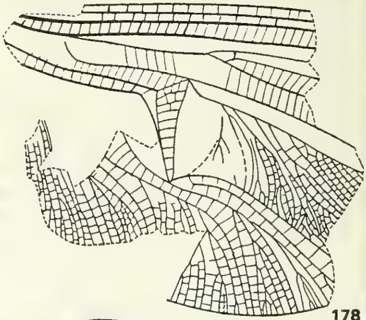
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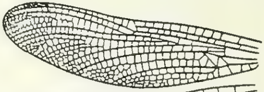
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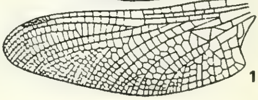
174B

vein; anal area of hindwing without looplike vein. Ovipositor protruding (Fig.
85 173). Upper Jurassic to Recent. Three genera from Upper Jurassic of Europe and some genera in Recent fauna, of which one is known to occur also in Oligocene of Western Europe.

Family GOMPHIDAE Brauer, 1856

Anal area without a loop; pterostigma short and wide; triangle of forewing equilateral, on hindwing triangle longitudinal, often both devoid of cross veins. Ovipositor reduced (Fig. 174). Upper Jurassic to Recent. Five genera from the Upper Jurassic of Western Europe and numerous genera in Recent fauna, of which two are also known to occur in the Paleogene of Europe (Baltic amber) and the Upper Oligocene of Western Europe.

Family AESHNIDAE Leach, 1815

(Aeschnidae auctorum)

Triangles of both wings disposed longitudinally and divided by cross veins; anal area of hindwings with prominent loops. Eyes in contact with each other dorsally. Ovipositor not developed (Fig. 175). Paleogene to Recent. Three genera from the Oligocene of Eastern Kazakhstan and the Miocene of North America. Numerous genera in Recent fauna, of which five are also known to occur in the Oligocene of eastern Kazakhstan and the Miocene of the Caucasus and North America.

Family AESCHNIDIIDAE Handlirsch, 1906

Costal area of wing with two rows of cross veins; pterostigma moderately elongate; triangles of both wings lie transversely and are subdivided into numerous cells; anal area of hindwing has no looped vein and has rows of cells. Ovipositor markedly elongated (Fig. 176). Jurassic to Cretaceous. Four genera.

Aeschnidiella G. Zalessky, 1953. Genotype—*A. kabanovi* G. Zalessky, 1953; Cretaceous, Povolzhe (Aptian). Anterior part of triangle with cells; posterior end of triangle narrow and pointed; arculus not complete;

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84 Figs. 172–179. Suborder Anisoptera.

172. *Liassogomphus brodiei* Buckland; wing, × 1.5. Lower Jurassic, Western Europe (Tillyard, 1925). 173. *Protolindenia wittei* Giebel: A—forewing, B—hindwing, × 1.3. Upper Jurassic, Western Europe (Handlirsch, 1925). 174. *Lanthus parvulus* Selys: A—forewing, B—hindwing, × 0.8. Recent (Handlirsch, 1906). 175. *Anax junius* Drury: A—forewing, B—hindwing, × 1.5. Recent (Comstock, 1918). 176. *Aeschnidium densum* Hagen; wing, × 1.7. Upper Jurassic, Western Europe (Handlirsch, 1925). 177. *Aeschnidiopsis flindersiensis* Woodward; wing, × 3. Cretaceous, Australia (Tillyard, 1917). 178. *Aeschnidiella kabanovi* G. Zalessky; part of wing, × 5.2. Cretaceous, Povolzhe (Yu. Zalessky, 1955). 179. *Scapanea* sp.: A—forewing, B—hindwing, × 2. Recent (Handlirsch, 1925).

subtriangle small but distinct. Length of wing about 40 mm (Fig. 178). One species. Cretaceous of Povolzhe.

Outside the USSR: From Jurassic of Western Europe—*Aeschnidium* Westwood, 1854; *Urogompus* Handlirsch, 1906. From Cretaceous of Australia—*Aeschnidiopsis* Tillyard, 1917 (Fig. 177).

SUPERFAMILY LIBELLULIDEA

Antenodal cross veins lie regularly, those of costal and subcostal areas opposite to each other; triangles formed differently in the two wings. Forewing triangle transversely disposed; in the hindwing it is equilateral or longitudinal (Fig. 179). Paleogene to Recent. Two families in Recent fauna: Libellulidae and Corduliidae. One genus of latter family known from the Miocene of North America. A rather large number of species of this superfamily, not accurately identified, are reported from many sites of the Oligocene and Miocene of Western Europe and North America.

Anisoptera Incertae sedis

Besides those mentioned, some genera of Upper Jurassic dragonflies from Western Europe belong to this suborder, whose precise taxonomic relationships are not clear. They are: *Cymatophlebiopsis* Handlirsch, 1939; *Morbaeschna* Needham, 1907; *Mesogomphus* Handlirsch, 1939 and *Aeschnopsis* Handlirsch, 1939.

Infraclass NEOPTERA

(B.B. Rohdendorf)

Wings can be folded back over the body while at rest, lie in one plane over the abdomen and partly overlap. Only in some groups of Neoptera is the paleopterous wing character secondarily developed, i.e., these insects are incapable of folding the wings and thrusting them back. In the majority of Neoptera the posterior most jugal veins (Ju) well developed. Mouth parts variable. Metamorphosis proceeds under different conditions, in most cases through terrestrial stages, rarely, in water. Devonian to Recent. Four cohorts: Archaeneoptera, Polyneoptera, Paraneoptera, Holometabola (=Oligoneoptera).

Phylogenetic relationships of cohorts are still not sufficiently known. Solution of these problems is particularly difficult due to lack of knowledge of morphology of primitive Devonian insects. The appearance of Neoptera is directly linked with the appearance of the first winged insects, which almost certainly belong to this infraclass of Pterygota. In this process, besides the
86 formation of paranotal expansions and their transformation into wings, more important is the retention of the primary density of paranota by the wing, which

subsequently becomes the basis for development of integumentary adaptations by the flight organs. Along this line of evolution the Archaeneoptera arose the primitive cohort of Neoptera, which was ancestral to the cohort Polyneoptera evolved parallel to the infraclass Palaeoptera. Many-veined Neoptera (Polyneoptera), which are ancestral to two other cohorts, are characterized by primitive body morphology (particularly including head characters) and absence of a resting period (pupa) during their development. The cohort Paraneoptera appeared as a result of development of adaptations associated with feeding on the sap of plants. Their mouth parts were modified for piercing tissues of live plants. The last cohort—Holometabola or Oligoneoptera—appeared as a result of perfection in metamorphosis which proceeded in altogether different media. This led to the appearance of the peculiar resting stage, i.e., the pupal stage. During this stage reorganization into the adult insect (which is completely different in form from the juvenile stage or larva) takes place.

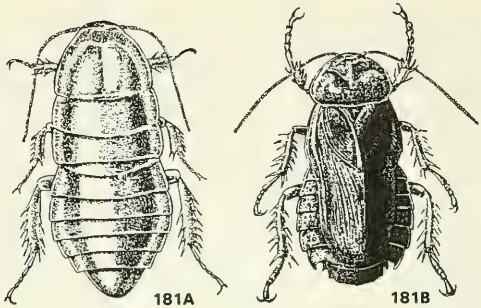
Cohort ARCHAEONEOPTERA

Wing very thick and shining, its surface marked by irregular transverse wrinkles and small pits, particularly in its middle region; anal area devoid of veins, fairly narrow. Shape of wing triangular with prominent apical margin, without venation. Instead, wing bears folds at this margin which function as veins. Structure of body not known. Upper Devonian. Single order: Archaeoptera.

Phylogenetic relationships are not sufficiently known. The thick wings and absence of venation distinguish this cohort from other Neoptera. This cohort is very close to some Paraneoptera in the weak development of the anal area of wings. Similarly, there is a distinct similarity between this cohort and many Polyneoptera and certain cockroaches (Blattodea) in the shape of the wing. Still, the absence of extensive venation distinguishes Archaeoneoptera from other Neoptera. The Devonian Archaeoneoptera undoubtedly illustrate one of the primary stages of evolution of winged insects and the appearance of wings at the base of the paranotal expansion on the dorsal side of the thoracic segments. Such primary wings acquired the capacity to beat perfectly and evolved into an adaptation for flight. But these wings were still thick and the venation had not developed into the strong skeleton of the wing plate.

Order ARCHAEOPTERA

Wings with a weakly convex anterior margin, distinct, and a fairly blunt apex; apical margin convex, anal margin straight, separated from one another by anal angle; tough convex C and flat SC in the narrow costal area; a few simple longitudinal veins present in middle of wing; a sharply convex and curved Cu occupying posterior part of wing, isolated from the narrow anal region. Middle veins of wing flat, slightly convex posteriorly (Fig. 180). Devonian. One family: Eopteridae.



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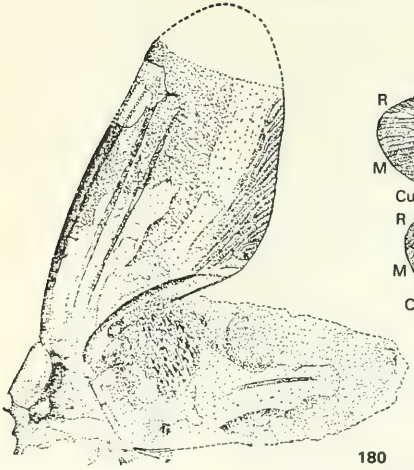

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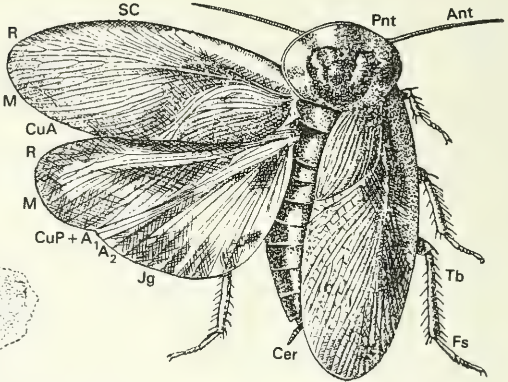

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87 Figs. 180–182. Orders Archaeoptera and Blattodea.

180. *Eopterum devonicum* Rohdendorf; general view, × 8. Upper Devonian, Northern Urals (Rohdendorf, 1961). 181. A—*Cryptocercus relictus* Bei-Bienko; general view from above, × 3.7. Recent. Family Panestiidae. Affiliated to relict Tertiary flora (Bei-Bienko, 1950). B—*Panestia spadicea* Shiraki; general view from above, × 1.3. Recent. Family Panestiidae (Bei-Bienko, 1950). 182. *Blabera atropos* Stoll; general view from above, × 1.7. Recent. Family Blattidae (Brunner, 1865).

Family EOPTERIDAE Rohdendorf, 1961

Vein C convex at its anterior edge and flat at its posterior margin, merging into wing membrane; two simple veins, R and M, located in middle part of wing, running toward basal part where they parallel each other; R gradually running toward anterior margin of wing and connected with SC and C by indistinct cross veins near wing apex; M straight, parallel to R at base, but diverging toward distal part of wing; a large part of wing lying distally to Cu and behind M and this part is without venation; goffering along apical margin conspicuous. One genus from Upper Devonian.

Eopterum Rohdendorf, 1961. Genotype–*E. devonicum* Rohdendorf, 1961; Upper Devonian, Komi ASSR (Fransian–Famenian stages, Voi-Vozh). Costal area and middle of wing brown, rest of wing yellowish brown; goffering at apical margin forms 23 distinct folds; interval between R and M nearly three times width of M; Cu dark, projects sharply. Length of wing 11 mm, width 5 mm (Fig. 180). One species. Upper Devonian of Komi ASSR.

88 Cohort POLYNEOPTERA

Heavily sclerotized wing plate consisting of numerous longitudinal and usually a large number of cross veins or prominent archedictyon. Some jugal veins present. Mouth parts always of chewing type. Development without pupal stage. Nymphs and young insects living in same medium as adults. Sometimes development proceeding in water (Plecopteroidea). Developmental stages usually without special adaptations in structure. Immature insects called nymphs differ from adults in possessing underdeveloped genital organs and wings. Lower Carboniferous to Recent. Three superorders: Blattopteroidea, Plecopteroidea, Orthopteroidea.

The phylogenetic relationships of the superorders are known only in a general sense. Blattopteroidea and Plecopteroidea are the most ancient superorders, and proceeded in two different directions of evolution: in Blattopteroidea strong development of a protective function of forewings, development maturation in a completely terrestrial environment; in Plecopteroidea the preservation of similarity between both pairs of wings or slight sclerotization of anterior wings, absence of any peculiar adaptation in individual development and aquatic habitat of nymphs are peculiar. The last superorder, Orthopteroidea, is characterized by the development of saltatorial locomotion involving hindlegs modified for jumping.

SUPERORDER BLATTOPTEROIDEA
Cockroach-like insects

Wings dissimilar, forewings thick and hindwings expanded and membranous; anojugal fan of hindwings supported primarily by jugal veins; anal veins shifted forward; venation of forewings not specialized; often radial veins not separated from anterior branches; subcostal vein large and many-branched. Body flattened. Legs adapted for running. Developmental stages underground, like in adult insects. Lower Carboniferous to Recent. Six orders: Blattodea, Manteodea, Isoptera, Dermaptera, Protelytroptera, Protoblattodea.

Phylogenetic relationships: This primitive superorder undoubtedly is the ancestral group for other superorders and probably other cohorts. Evolution in this superorder proceeded along different lines. The general trend was toward reproductive adaptations such as with protective arrangements for eggs (ootheca of cockroaches, underground nests of earwigs) or further elaboration toward a communal life style (termites). Perfection was also attained in metabolism and nutrition. Moreover, a large number of symbiotic microorganisms became widely distributed in the intestines and body cavities of many blattopteroids. These were responsible for the more efficient processing of vegetative matter (cellulose) and supply of vitamins essential for nutrition.

Order BLATTODEA. Cockroaches

(E.E'. Bekker-Migdisova)

Forewings developed into thick tegmina, usually with convex anterior margin, rounded apex and very dense venation comprising closely spaced longitudinal veins; costal area wide, with branching or, rarely, simple SC; R, M and CuA usually many-branched; CuP curved, joined with anterior branch of A_1, forming a prominent anal furrow which demarcates anal region of tegmina; usually archedictyon or numerous thin cross veins present. Hindwing always
89 wide and membranous, with straight anterior margin, rich venation and bent or folded anojugal region. Body flat. Head hypo- or opisthognathous and usually not seen from above, beyond pronotum. Antennae long, many-segmented. Legs designed for running, with large coxae. Large spines on tibia and femur. Cerci usually segmented, often short. Ovipositor sometimes long, more often absent, eggs usually encased in capsules called oothecae. Warmth-loving* insects living in sheltered spots: soil, vegetative remains or thickets (Figs. 181, 182). Carboniferous to Recent.

Nine families: Archimylacridae, Mylacridae, Neorthroblattinidae, Poroblattinidae, Blattidae, Corydiidae, Panestiidae, Diplopteridae, Oulopterigidae. The last three are found only in Recent fauna.

Family ARCHIMYLACRIDAE Handlirsch, 1906

(Spiloblattinidae Handlirsch, 1906)

Tegmina with archedictyon: wing base not widened; point of attachment on thorax close to anterior margin; SC long with a row of branches; R and RS often separate; R, RS and M directed toward front; R and M uniformly developed;

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*Editor's note: No proof of this.

CuA pectinate, forming from one-fourth to three-fourths of wing length; anojugal area in hindwings folded back but not folded like a fan. Head projecting slightly in front of pronotum. Pronotum semicircular. Cerci segmented. Ovipositor long, consisting of three pairs of valves. Middle Carboniferous to Jurassic. Two subfamilies: Archimylacrinae and Spiloblattininae.

Subfamily Archimylacrinae Handlirsch, 1906

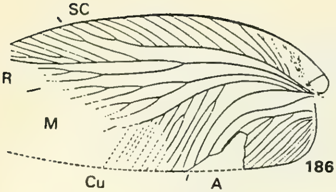
[nom. transl. Cockerell, 1927 (ex Archimylacridae Handlirsch, 1906)]

Length of tegmina 2–2.8 its width; SC 0.50–0.75 × length of tegmina, with a large number of branching and simple secondary branches; R well developed; CuA does not reach apex of wing; cubital area wide; archedictyon prominent. Middle Carboniferous to Jurassic. Most primitive group among Blattodea. About 70 genera.

Caenoblatta M. Zalessky, 1931. Genotype—*C. angaridensis* M. Zalessky, 1931; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Cheremichkino). Tegmina long; length of tegmina 2.8 × their width; apex of tegmen extended; anterior and anal margins symmetrically convex; SC slightly bent, with a large number of parallel branches; R divided into two branching trunks; M pectinate with branches directed forward; CuA terminating on anal margin more basally than R, which terminates on anterior margin; base of anal area one-half of width of basal part of tegmen. Length of tegmen 27.5 mm (Fig. 183). One species. Middle Carboniferous of Kuznetsk basin.

Phyloblatta Handlirsch, 1906 (*Tomioblatta* Martynov, 1931). Genotype—*Blattina schroteri* Geibel, 1857; Upper Carboniferous, Germany. Tegmina elliptical; costal area band-shaped; SC 0.5–0.66 of length of tegmen; R without distinctly isolated RS, with a row of dividing branches, always occupying anterior half of wing; distal branch of R terminates on anterior margin of wing at level of terminating of distal branch of CuA on anal margin, or somewhat more distally; CuA gently sloping with six to 12 branches terminating on anal margin close to apex of wing; cubital area in distal part narrow; length of anal area one-third of length of tegmen; a row of parallel anal veins which do not unite. Length of tegmen 11–35 mm (Fig. 184; Pl. III, Fig. 1; Pl. IV, Figs. 1, 2). About 190 species from Carboniferous and Permian of Western Europe, and North and South America known. Three species from the Middle Carboniferous of Kuznetsk basin and three species from the Upper Permian of Urals. Middle Carboniferous to Upper Permian.

Aissoblatta Handlirsch, 1904. Genotype—*A. rossica* Handlirsch, 1904; Permian, Orenburg province (Kargala). Tegmen ellipsoid, elongated, its length 2.25 times of its width; costal area slightly widened toward apex; SC 0.7 of length of tegmen, with many parallel branches; R and M originating almost at the same point, pectinately branched, with forwardly directed branches; M bent



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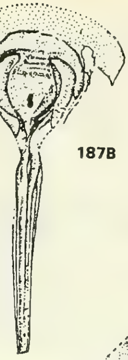

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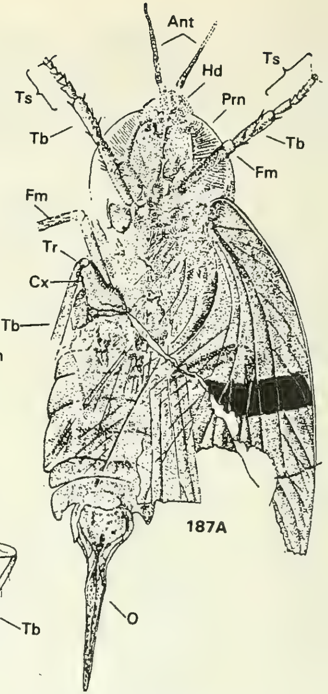

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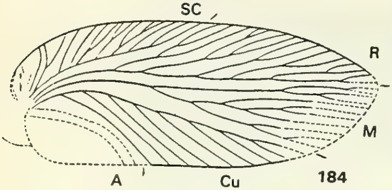

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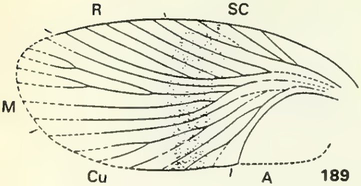

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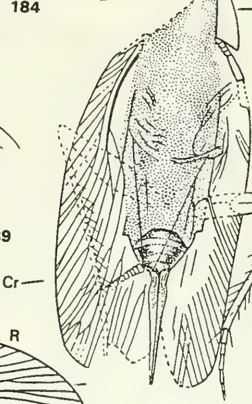

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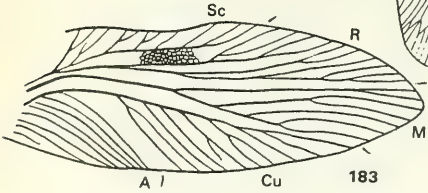

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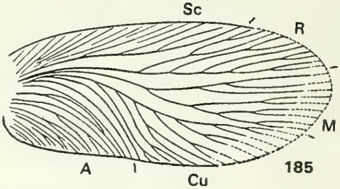

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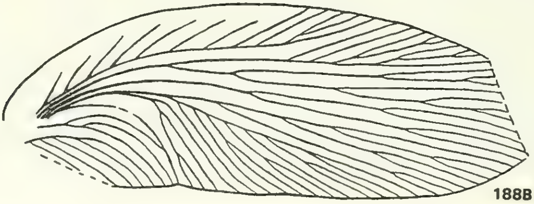

188B

sigmoidally; CuA adjoining some branches of posterior trunk of M in form of independent trunk; anal area 0.6 of width at base. Length of tegmina 30–36 mm (Fig. 185). Three species. Permian of Urals.

Kunguroblattina Martynov, 1930. Genotype—*K. arcuata* Martynov, 1930; Lower Permian, Perm province (Kungurian stage, Barda). Tegmen with convex anterior margin. R and M divided into two stems at same level, both exhibiting dichotomous branching; anal area short, wide, wider than one-half of basal part of tegmen; anterior anal vein simple, and posterior, pectinate. Length of tegmen 53–55 mm (Figs. 186, 187A, B). Two species. Lower Permian of Urals.

91 *Patrodoron* G. Zalessky, 1955. Genotype—*P. auspicatum* G. Zalessky, 1955; Lower Permian, Orenburg province (Kungurian stage, Aya-Koshelevka). Tegmen with convex anterior margin, its length 2.8 times its width; SC 0.7 of length of tegmen; R and CuA originating from the same point, i.e., posterior trunk of M connected to CuA; cubital area narrowing distally; anal area short and wide, wider than one-half of basal part of tegmen and less than one-third of length of tegmen; both anal veins pectinate. Length of tegmen 50–55 mm (Fig. 188B). Two species. Lower Permian of Urals.

Uraloblatta G. Zalessky, 1939. Genotype—*U. insignis* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Barda). Tegmen oval with slightly convex anterior margin; distal part of costal area slightly expanded; SC 0.6 of wing length, with simple parallel branches; R and RS many-branched, showing a backward bend in middle of tegmen; areas between SC and R, and M and Cu narrow. Ovipositor long. Length of wing 15 mm (Fig. 188A). Two species. Lower Permian of Urals.

Kisylblatta Martynov, 1937. Genotype—*K. unifasciata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Tegmen rounded, its length 2.2 times its width; SC reaching middle of tegmen, four-branched; branches of R simple, directed forward; M originating somewhat more distally than R, arcuately bent backward, pectinate, its branches directed forward; CuA markedly bent backward, many-branched, branches long; anal area 0.27 of length of tegmen and 0.6 of width of its basal part. Length of tegmen 6.6 mm (Fig. 189). One species. Lower Jurassic of Central Asia.

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90 Figs. 183–189. Family Archimylacridae, subfamily Archimylacrinae.

183. *Caenoblatta angaridensis* M. Zalessky; tegmen, × 2.7. Middle Carboniferous, Kuznetsk basin (M. Zalessky, 1931). 184. *Phyloblatta distincta* Martynov; tegmen, × 2.5. Middle Carboniferous, Kuznetsk basin (Martynov, 1933). 185. *Aisoblatta rossica* Handlirsch; tegmen, × 1.5. Permian, Southern Urals (Handlirsch, 1904). 186. *Kunguroblattina arcuata* Martynov; tegmen, × 1.5. Lower Permian, Urals (Martynov, 1930). 187. *K. microdictya* Bekker-Migdisova and Vishnyakova: A—general view, × 2.7; Ant—antennae, Cx—coxa, Fm—femur, Hd—head, Tb—tibia, Tr—trochanter, Ts—tarsus, O—Ovipositor; B—Ovipositor, × 4. Lower Permian, Urals (Bekker-Migdisova, 1957). 188. A—*Uraloblatta insignis* G. Zalessky; general view, × 2.2. Lower Permian, Urals (Yu. Zalessky, 1939). B—*Patrodoron auspictum* G. Zalessky; tegmen, × 1. Lower Permian, Urals (Yu. Zalessky, 1955). 189. *Kisylblatta unifasciata* Martynov; tegmen, × 9. Lower Jurassic, Central Asia (Martynov, 1937).

Balachonoblatta Bekker-Migdisova, 1961. Genotype—*B. zheltojarica* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Tegmen short, its length 1.7 times its width; distally bluntly rounded and basally narrow; anterior and anal margins almost straight; costal area uniformly wide; SC long and almost reaches apex; R and M uniformly developed; M sharply bent toward anal margin, pectinate, branches directed forward; cubital area wide; CuA convex, sometimes with many dividing branches; anal area small, less than one-half of length of tegmen. Length of tegmen 25–30 mm (Fig. 190; Pl. III, Fig. 2). Two species. Middle Carboniferous of Kuznetsk basin.

Hemimylacrela Handlirsch, 1922. Genotype—*Hemimylacris ramificata* Handlirsch, 1922; Middle Carboniferous, North America. Tegmen with wide, short costal area; SC short, with few branches, equal to or less than one-half of length of tegmen, convex on its posterior edge; M terminating on apex of wing; radial and cubital areas wide; CuA enriched with branches; anal area round with three anal veins. Length of tegmen 21–39 mm (Fig. 191). Four species, including one from the Kuznetsk basin. Middle Carboniferous of Kuznetsk basin, Western Europe and North America.

Sibiroblatta Bekker-Migdisova, 1961. Genotype—*S. flexuosa* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Length of tegmen 2.7 times its width; costal area long and broad, 0.8 length of tegmen; R and M weakly developed, symmetrically arranged: R occupies anterior margin and M, anal margin at wing apex; R with two trunks and three branches in all; M divides at middle of tegmen with long bifurcations located at same level and four parallel branches; cubital area triangular; CuA gently sloping with close branches, one branch directed forward. Length of wing 25–28 mm (Fig. 192). Two species from Middle Carboniferous of Kuznetsk basin and Western Europe.

Grypoblattites Bekker-Migdisova, 1961. Genotype—*G. flabellatus* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Tegmen elliptical with convex anterior margin; length of tegmen 2.5 times its width; costal area long, more than one-half of length of tegmen, slightly expanded at base; SC with many inclined, irregularly distributed and often forked branches; R_1 slightly distinct and somewhat shifted toward base, with long branches; M arcuately bent in middle and convex on its posterior edge; CuA arcuate and occupies 0.3 or less of length of tegmen, with five to seven branches drawn together; A_1 usually three-branched. Length of tegmen 25–30 mm (Fig. 193; Pl. III, Fig. 3). Two species. Middle Carboniferous of Kuznetsk basin.

Archaeotiphites Bekker-Migdisova, 1961. Genotype—*A. petroblattinoides* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Tegmen with convex anterior margin and straight anal margin; costal area occupying 0.6 of length of tegmen; SC forming

93 many gently sloping, irregularly distributed branches; R occupying part of anterior half of tegmen, pectinate or divided into two trunks and forming six branches; M occupying whole of apex and one-third of anal margin, split into two dichotomously branching trunks; CuA branches at the same level as R, sharply arcuate and forming four or five branches drawn close together; CuP arcuate; branch A with bifurcations. Length of tegmen 27–30 mm (Fig. 194; Pl. III, Fig. 4). Two species. Middle Carboniferous of Kuznetsk basin.

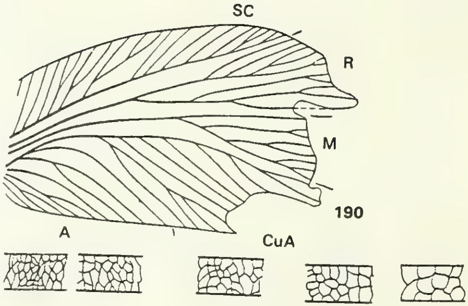
Miaroblatta Handlirsch, 1906. Genotype—*M. elata* Handlirsch, 1906; Upper Carboniferous, France. Tegmen with pectinate SC and long costal area, 0.66–0.77 of length of tegmen; R with four to six gently inclined branches, almost reaching apex of tegmen with straight branches directed forward; CuA convex, with its branches close and of almost equal length, distal branch connected to trunk in front, gently sloping at top; cubital area high; anal area large, 0.4 of length of tegmen, with 11 parallel branches. Length of tegmen 35–40 mm (Fig. 195). Two species, including one from Kuznetsk basin. Middle Carboniferous of Kuznetsk basin and Upper Carboniferous of Western Europe.

Ignaroblatta Bekker-Migdisova, 1961. Genotype—*I. panda* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Anterior margin of tegmen convex, in the form of a hump at basal half; costal area short and wide, 0.55–0.6 of length of tegmen; SC with frequently dividing branches; R rich, occupying whole apex of tegmen, divided into two trunks, or the first branches converging at base; M branching off into two and occupying part of anal margin at apex; CuA nearly straight or gently
94 convex with six or seven branches, some of which are divided; anal veins many-branched. Length of tegmen 25–30 mm (Fig. 196). Three species. Middle Carboniferous of Kuznetsk basin.

Aphthoroblattina Handlirsch, 1906. Genotype—*Blattina fascigera* Scudder, 1876; Middle Carboniferous, North America. Length of tegmen 2.5 times its width; costal area narrow and long, 0.6 of length of tegmen; branches of SC appearing tuftlike; R_1 with five short branches directed forward; RS divided into four to six branches; M divided into four branches at middle of tegmen; CuA with seven or eight branches directed toward anal margin; anal area long. Length of tegmen 24–38 mm (Fig. 197). Seven species. Middle Carboniferous of Kuznetsk basin, Western Europe and North America.

Tomacblatta M. Zalessky, 1929. Genotype—*T. baschkirica* M. Zalessky, 1929; Upper Permian, Urals (Kazanian stage, Vyaza River). Hindwing with SC running close to and along the margin; R occupying whole space up to apex of wing, divided into two trunks—a small branched R_1 or PR and a pectinate RS; M also with few branches and splitting into two trunks. Length of hindwing 14 mm (Fig. 198). One species. Upper Permian of Urals.

Sardycblatta M. Zalessky, 1928. Genotype—*S. tikhvinskii* M. Zalessky, 1928; Upper Permian, Urals (Kazanian stage, Sardyk River). Hindwing with fairly wide costal area; SC slightly arcuate with long branches; R pectinate; R_1



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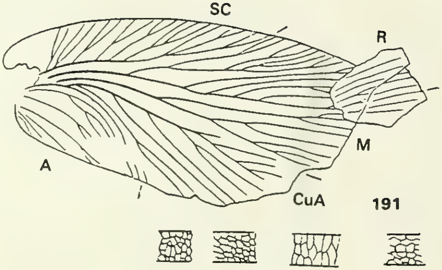

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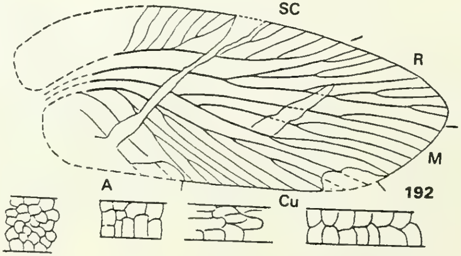

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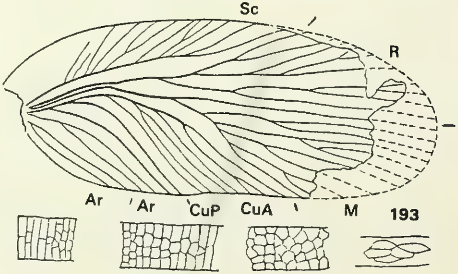

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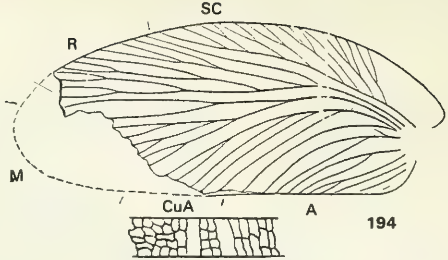

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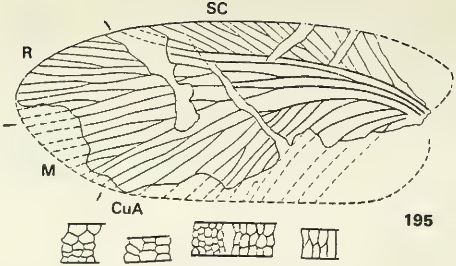

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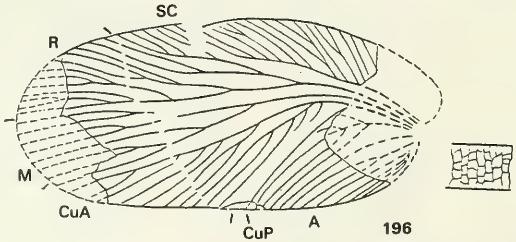

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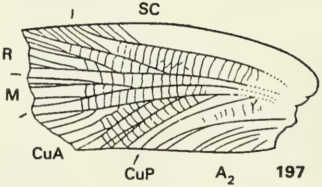

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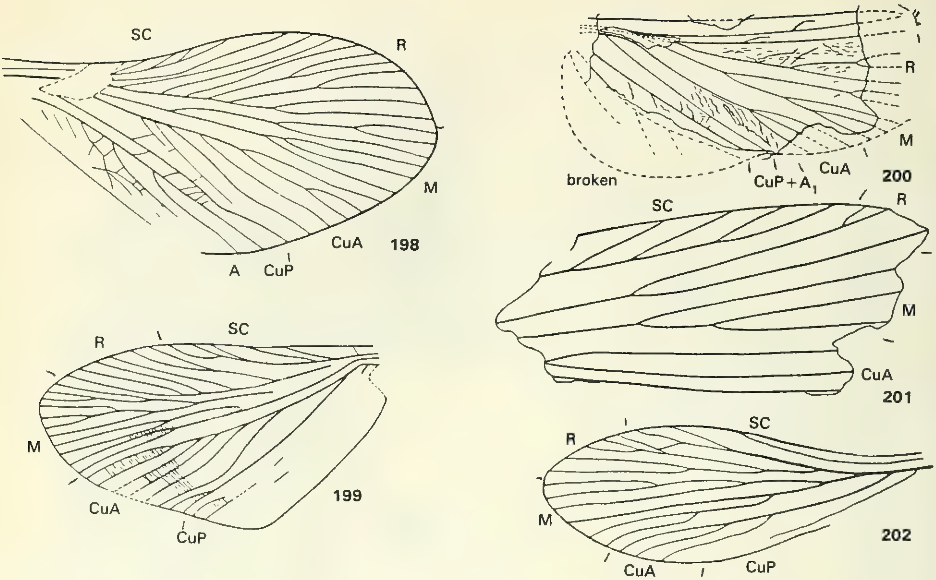
Figs. 190–197. Family Archimylacridae, subfamily Archimylacrinae.

190. *Balachonoblatta zheltojarica* Bekker-Migdisova; tegmen, × 1.8 and archedictyon, × 15. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 191. *Hemimylacrella leptophlebiopsis* Bekker-Migdisova; tegmen, × 7.6. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 192. *Sibiroblatta flexuosa* Bekker-Migdisova; tegmen, × 2.46. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 193. *Grypoblattites flabellatus* Bekker-Migdisova; tegmen, × 3.45. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 194. *Archaeotiphites petroblattinoides* Bekker-Migdisova; tegmen, × 1.93. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 195. *Miaroblatta balachonensis* Bekker-Migdisova; tegmen, × 2.53. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 196. *Ignaroblatta panda* Bekker-Migdisova; tegmen, × 2.16. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 197. *Aphthoroblattina fascigera* (Scudder); tegmina, × 1.4. Middle Carboniferous, North America (Handlirsch, 1906).



93 Figs. 198–202. Family Archimylacridae, subfamily Archimylacrinae and forms of incertae sedis.

198. *Tomacblatta baschkirica* M. Zalessky; hindwing, × 5.3. Upper Permian, Urals (M. Zalessky, 1929). 199. *Sardycblatta tikhvinskii* M. Zalessky; hindwing, × 5.7. Upper Permian, Urals (M. Zalessky, 1928). 200. *Ungoneurites paucinervis* Martynov; hindwing, × 3.3. Middle Carboniferous, Kuznetsk basin (Martynov, 1931). 201. *Oiratia valida* Martynov; hindwing, × 6.2. Middle Carboniferous, Kuznetsk basin (Martynov, 1931). 202. *Parapanorpa ungensis* M. Zalessky; hindwing, × 3.3. Middle Carboniferous, Kuznetsk basin (M. Zalessky, 1931).

parallel to branches of RS, terminating on anterior margin close to apex; M well developed, divided into two branching trunks. Length of hindwing 13 mm (Fig. 199). One species. Upper Permian of Urals.

Outside the USSR: *Acoblatta* Cockerell, 1927; *Acosmoblatta* Handlirsch, 1906; *Actinoblatta* Pruvost, 1912; *Adeloblatta* Handlirsch, 1906; *Amblyblatta* Handlirsch, 1906; *Amoeboblatta* Handlirsch, 1906; *Amorphoblatta* Handlirsch, 1906; *Anomoblatta* Handlirsch, 1906; *Anthracoblattina* Scudder, 1879; *Apempherus* Handlirsch, 1906; *Aphthoroblattina* Handlirsch, 1906; *Apotypoma* Handlirsch, 1906; *Archaeotiphe* Pruvost, 1919; *Archimylacris* Scudder, 1868; *Archoblattina* Sellards, 1903; *Asemoblatta* Handlirsch, 1906; *Atimoblatta* Handlirsch, 1906; *Auxanoblatta* Handlirsch, 1906; *Barroisiblatta*

Pruvost, 1919; *Bertrandiblatta* Laurentiaux, 1950; *Boltonopruvostia* Strand, 1929; *Bradyblatta* Handlirsch, 1906; *Cebenniblatta* Laurentiaux, 1950; *Cobaloblatta* Cockerell, 1919; *Compsoblattula* Strand, 1929; *Coraloblatta* Cockerell, 1918; *Crokoblattina* Guthorl, 1933; *Dictyoblatta* Handlirsch, 1906; *Dimoblatta* Cockerell, 1927; *Discoblatta* Handlirsch, 1906; *Distatoblatta* Handlirsch, 1906; *Dromoblatta* Handlirsch, 1906; *Dysmenes* Handlirsch, 1906; *Elaphroblatta* Handlirsch, 1906; *Eneriblatta* Laurentiaux, 1949; *Etoblattina* Scudder, 1879; *Eumorphoblatta* Handlirsch, 1906; *Exochoblatta* Handlirsch, 1906; *Flabellites* Fritsch, 1895; *Friciella* Kukalova, 1955; *Gondwanoblatta* Handlirsch, 1906; *Gongyloblatta* Handlirsch, 1906; *Grypoblattina* Pruvost, 1919; *Gyroblatta* Handlirsch, 1906; *Hesperoblatta* Handlirsch, 1906; *Kajar* Handlirsch, 1920; *Kinklidoblatta* Handlirsch, 1906; *Kinklidoptera* Handlirsch, 1906; *Leptoblattina* Handlirsch, 1906; *Liparoblatta* Handlirsch, 1906; *Livetiblatta* Laurentiaux, 1950; *Loxoblatta* Cockerell, 1927; *Manoblatta* Pruvost, 1919; *Mesitoblatta* Handlirsch, 1906; *Metachorus* Handlirsch, 1906; *Metaphyloblatta* Kukalova, 1955; *Metapoblatta* Cockerell, 1927; *Metaxys* Handlirsch, 1906; *Pachyblatta* Cockerell, 1927; *Parelthoblatta* Handlirsch, 1906; *Penetoblatta* Handlirsch, 1906; *Petrablattina* Scudder, 1885; *Phauloblatta* Handlirsch, 1906; *Phoberoblatta* Handlirsch, 1906; *Phyloblatta* Handlirsch, 1906; *Plagioblatta* Handlirsch, 1906; *Platyblatta* Handlirsch, 1906; *Platyblattina* Laurentiaux, 1950; *Polyctoblatta* Handlirsch, 1906; *Prantlites* Kukalova, 1955; *Procoptoblatta* Handlirsch, 1920; *Progonoblattina* Scudder, 1879; *Schizoblatta* Handlirsch, 1906; *Schizoblattina* Sellards, 1904; *Scuderulla* Handlirsch, 1920; *Sellardsula* Handlirsch, 1920; *Sooblatella* Handlirsch, 1920; *Sphaleroblattina* Schlechtendal, 1879; *Stephanoblatta* Handlirsch, 1906; *Sterzelia* Handlirsch, 1906; *Stigetoblatta* Handlirsch, 1906; *Sulcoboltonia* Strand, 1929; *Symphyoblatta* Handlirsch, 1906; *Syncoptoblatta* Handlirsch, 1906; *Xenoblatta* Handlirsch, 1906.

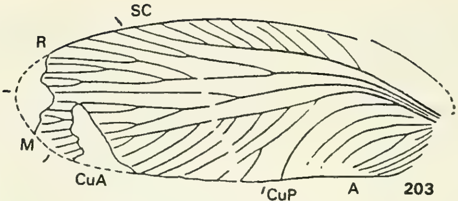
Archimylacrinae Incertae sedis

Hindwing incompletely preserved. Genera: *Ungonevrites* Martynov, 1931 (Fig. 200); *Oiratia* Martynov, 1931 (Fig. 201); and *Parapanorpa* M. Zalessky, 1931 (Fig. 202) from Carboniferous of Kuznetsk basin.

Subfamily Spiloblattininae Handlirsch, 1906

[nom. transl. Bekker-Migdisova, 1961 (ex Spiloblattinidae Handlirsch, 1906)]

Tegmen with parallel anterior and anal margins, its length 2.5–3.5 × its width; areas between SC and R, R and M, and CuA isolated up to margin of tegmen, weakly sclerotized and widened in middle; SC long, with a row of parallel
95 branches; CuA long, almost reaching apex, with parallel branches; cubital area narrow; archedictyon weak, often observed only along veins. Carboniferous to Lower Permian. Upper Carboniferous of Kuznetsk basin; Lower Permian of



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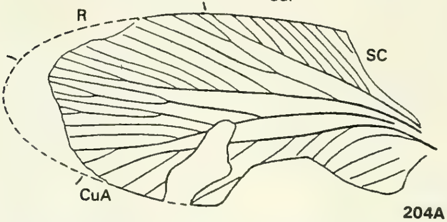

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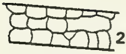

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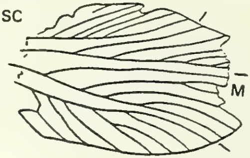

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Figs. 203–205. Family Archimylacridae, subfamily Spiloblattininae.

203. *Sysciophebia zavijalovensis* Bekker-Migdisova; tegmen, × 2.9. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 204. *Olethroblatta tomiensis* Bekker-Migdisova; A—tegmen, × 2.9; B and C—Details of archedictyon, × 15. Upper Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 205 *Zavjaloblatta rotundata* Bekker-Migdisova; tegmen, × 2.8. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961).

European USSR; Upper Carboniferous and Lower Permian of Western Europe and North America. Twelve genera.

Sysciophlebia Handlirsch, 1906; Genotype—*Blattina englyptica* Germar, 1851; Upper Carboniferous, Germany. Tegmen elliptically elongated or, rarely, round kidney-shaped, with convex anterior margin and straight anal margin; length 2.5 to 3.5 times its width; costal area narrow and long and measuring 0.5 to 0.75 of length of tegmen; SC running parallel to anterior margin, with many branches; R_1 not isolated or simple, without bifurcation or with a small bifurcation; R and M pectinate with branches directed forward; M occupying the whole middle part of tegmen. CuA long, with branches occupying almost the whole of the anal margin; CuA and CuP sharply arcuate at the base. Length of tegmen 11–32 mm (Fig. 203). One species from Lower Permian of Urals, one species from Middle Carboniferous of Kuznetsk basin (Zavyalovo) and more than 50 species from the Upper Carboniferous and Lower Permian of Western Europe and North America. Upper Carboniferous to Lower Permian.

Olethroblatta Handlirsch, 1906. Genotype—*O. americana* Handlirsch, 1906; Middle Carboniferous, North America. Tegmen broad and rounded with convex anterior and anal margins; length of tegmen 2 to 2.5 times its width; costal area band-like and of moderate width, its length reaching 0.5 to 0.6 of length of tegmen; subcostal, radial and medial areas slightly widened; R and M branching off at middle of tegmen or M dividing more distally than middle; branches of R and M close and brush-like; CuA convex with parallel branches; anal area occupying 0.4 of length of wing; archedictyon very delicate and in the form of wavy lines. Length of tegmen 17–25 mm (Fig. 204). Five species, of which one is from Upper Carboniferous of Kuznetsk basin. Tops of Middle Carboniferous of North America; Upper Carboniferous and Lower Permian, of Western Europe. Carboniferous to Lower Permian.

Zavjaloblatta Bekker-Migdisova, 1961. Genotype—*Z. rotundata* Bekker-Migdisova, 1961; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). Tegmen rounded, costal area bandlike; SC terminates on anterior margin at same level as termination of CuA on anal margin; R with a row of parallel, straight, nonbifurcating branches; M slanting, distally arcuate, runs inclined toward anal margin near apex, with a row of parallel curved branches directed forward with convexity toward anterior margin; cubital area wide; CuA convex and almost parallel to anal margin, its branches very widely separate; archedictyon very thin and finely reticulate, all over surface, also observed at base of CuA between first and second branch where there are six or seven cells in a cross section. Length of tegmen 20 mm (Fig. 205; Pl. IV, Fig. 3). One species. Middle Carboniferous of Kuznetsk basin.

Outside the USSR: *Ametroblatta* Handlirsch, 1906; *Atactoblatta* Handlirsch, 1906; *Doryblatta* Handlirsch, 1906; *Syscioblatta* Handlirsch, 1906; *Dicladoblatta* Handlirsch, 1906; *Pareinoblatta* Handlirsch, 1906; *Arrhythmoblatta* Handlirsch, 1906; *Permoblattina* Tillyard, 1937; *Spiloblattina* Scudder, 1885.

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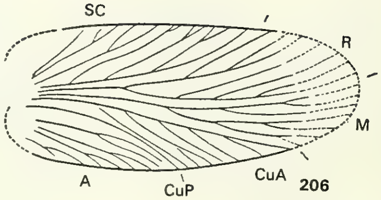
Family MYLACRIDAE Scudder, 1886

(Hemimylacridae Waterlot, 1934)

Tegmen broad, markedly sclerotized and expanded at base; point of attachment to thorax located almost exactly at center of tegmen; costal area triangular, widened at base and almost equal to length of anal area; SC straight, branching out from the base, or rarely, branching distally or pectinate, but at base always giving rise to some independent simple branches; R and CuA many-branched, anal area large and anal veins terminate on anal margin of tegmen or, rarely, on anal furrow; anojugal area of hindwing not folding like a fan, but bending under



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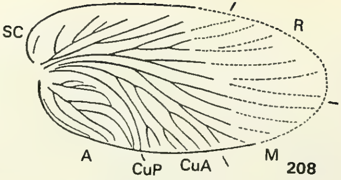

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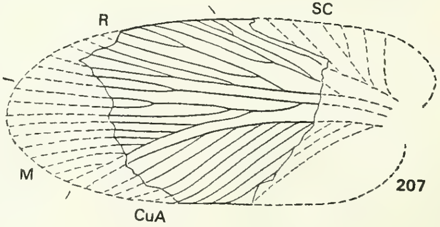

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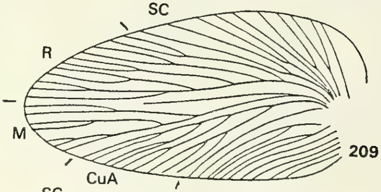

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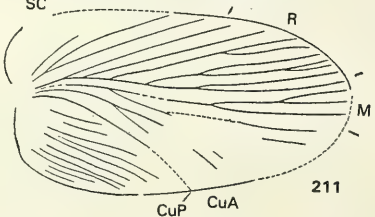

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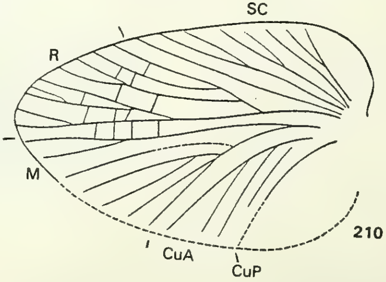

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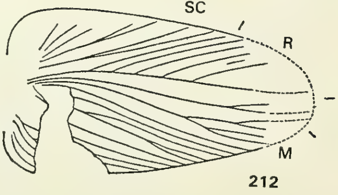

212

wing. Pronotum markedly widened and transverse with lateral outgrowths. Body broad and flat. Valves of ovipositor short. Middle Carboniferous to Upper Permian. Four subfamilies: Hemimylacrinae, Mylacrinae, Idiomylacrinae, Pteridomylacrinae.

97 Subfamily Hemimylacrinae Pruvost, 1919

[nom. transl. Bekker-Migdisova, 1961 (ex Hemimylacrides Pruvost, 1919)]
[Hemimylacridae Waterlot, 1934; Archimylacridae Handlirsch, 1906 (part.)]

Tegmen moderately expanded at base; costal area wide and triangular; SC distally pectinate with some free, simple branches at base; M weakly developed; anal veins terminating on anal margin, their distal ends not fused. Length of tegmen 19–40 (Fig. 206). Middle and Upper Carboniferous. Around 14 genera.

Metaxyblatta Handlirsch, 1906. Genotype—*M. hadroptera* Handlirsch, 1906; Carboniferous, North America. Length of tegmen is a little more than double its width; costal area wide, SC two-branched in its distal region, one trunk pectinate and running inclined toward anterior margin and second trunk with a series of parallel branches which run parallel toward anterior margin of tegmen; radial area wide; R straight with four to seven divided branches; M occupying whole apex, bent toward anal margin and pectinate with six to eight divided branches directed forward; cubital area wide with seven or eight uniformly disposed branches; anal area narrow and separated by gently sloping anal furrow. Length of tegmen 23–24 mm (Fig. 207). Two species. Upper Carboniferous of Kuznetsk basin.

Outside the USSR: *Hemimylacris* Handlirsch, 1906; *Cyphomylacris* Cockerell, 1927; *Discomylacris* Handlirsch, 1920; *Drybrookia* Bolton, 1923; *Loxoblatta* Cockerell, 1927; *Lusitanomylacris* Teixeira, 1939; *Metachorus* Handlirsch, 1906; *Oxynoblatta* Handlirsch, 1906; *Phylomylacris* Pruvost, 1914; *Sooblatta* Handlirsch, 1906; *Soomylacris* Handlirsch, 1906; *Cardioblatta* Handlirsch, 1906; *Stephanomylacris* Teixeira, 1949; *Trilophomylacris* Pruvost, 1919.

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96 Figs. 206–212. Family Mylacridae, subfamilies Hemimylacrinae, Idiomylacrinae, Mylacrinae and Pteridomylacrinae.

206. *Hemimylacris clintoniana* Scudder; tegmen, × 3.1. Middle Carboniferous, North America (Scudder, 1895). 207. *Metaxyblatta gromotuchensis* Bekker-Migdisova; tegmen, × 2. Upper Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 208. *Idiomylacris gracilis* Handlirsch; tegmen, × 3.5. Upper Carboniferous, North America (Handlirsch, 1906). 209. *Mylacris anthracophila* Scudder; tegmen, × 1.8. Middle Carboniferous, North America (Scudder, 1895). 210. *Pseudomylacris wettinensis* Schlechtendal; tegmen, × 8.25. Upper Carboniferous, Germany (Handlirsch, 1906). 211. *Neomylacris major* Handlirsch; tegmen, × 2.8. Middle Carboniferous, North America (Handlirsch, 1906). 212. *Pteriolomylacris paradoxa* Handlirsch; tegmen, × 3. Middle Carboniferous, North America. (Handlirsch, 1906).

Subfamily Idiomylacrinae Handlirsch, 1906

[non. transl. Bekker-Migdisova, hic (ex Idiomylacridae Handlirsch, 1906)]

Tegmen broad at base; SC divided into two branched trunks; anal furrow clear; anal veins branched, their branches gradually joining one another distally. Length of tegmen 15 mm (Fig. 208). Middle Carboniferous, North America. One genus—*Idiomylacris* Handlirsch, 1906.

Subfamily Mylacrinae Sellards, 1904

[nom. transl. Meunier, 1912 (ex Mylacrinariae Sellards, 1904)]

Tegmen markedly broad at base, heart-shaped, triangular or rounded; costal and anal areas symmetrical and almost equal in length; branches of SC radiating from base like a brush, anterior ones sometimes exhibiting bifurcations; M and CuA weakly developed; anal furrow distinct and arcuate. Length of tegmen 14–40 mm. Middle Carboniferous to Upper Permian. Three tribes: Mylacrini, Pseudomylacrini and Neomylacrini.

Tribe MYLACRINI Pruvost, 1919

[nom. transl. Bekker-Migdisova, hic (ex Mylacrides Pruvost, 1919)]

Tegmen triangular to heart-shaped, often asymmetrical with thin archedictyon; R many-branched: M and Cu uniformly developed, with some branches; branches of CuA occupying 0.3 of length of hindwing. Anal veins terminate on anal margin of tegmen. Length of tegmen 14–40 mm (Fig. 209). Hindwing with rounded, truncated, distal part. Pronotum with paranotal expansions. Head very small, projects slightly. Middle Carboniferous to Upper Permian: Middle and Upper Carboniferous of Western Europe and North America; Upper Permian of Southern Rhodesia. 17 genera.

Outside the USSR: *Mylacris* Scudder, 1886; *Actinomylacris* Handlirsch, 1906; *Exochomylacris* Handlirsch, 1906; *Symplicius* Handlirsch, 1920; *Anomomylacris* Handlirsch, 1906; *Chalepomylacris* Handlirsch, 1906; *Amblymylacris* Handlirsch, 1906; *Platymylacris* Handlirsch, 1911; *Ptilimylacris* Cockerell, 1918; *Aphelomylacris* Handlirsch, 1906; *Paromylacris* Scudder, 1885; *Promylacris* Scudder, 1885; *Orthomylacris* Handlirsch, 1906; *Stenomylacris* Handlirsch, 1906; *Lithomylacris* Scudder, 1879; *Brachymylacris* Handlirsch, 1906; *Rhodesiomylacris* Zeuner, 1955; *Goniomylacris* Handlirsch, 1906; *Necymylacris* Scudder, 1879; *Necymylacrodes* Strand, 1912; *Neosimplicius* Carpenter, 1934 and *Phthinomylacris* Handlirsch, 1906.

Tribe PSEUDOMYLACRINI Handlirsch, 1906

[nom. transl. Bekker-Migdisova, hic (ex Pseudomylacridae Handlirsch, 1906)]

Tegmen rounded and heart-shaped with rare cross veins; M well developed. CuA weak with two or three branches, occupying 0.25 of length of anal margin of
98 wing; anal area short and high; anal veins terminating on anal margin of wing. Length of tegmen 6.6 mm (Fig. 210). Upper Carboniferous of Western Europe. One genus: *Pseudomylacris* Schlechtendal, 1879.

Tribe NEOMYLACRINI Handlirsch, 1906
[nom. transl. Bekker-Migdisova, hic (ex Neomylacridae Handlirsch, 1906)]

Tegmen heart-shaped to rounded; cross veins absent; M weakly developed; branches of CuA occupy about 0.3 of length of anal margin of wing; some anal veins descending toward arcuate anal furrow. Length of tegmen 16–22 mm (Fig. 211). Middle and Upper Carboniferous. Upper Carboniferous of Western Europe and Middle Carboniferous of North America. One genus: *Neomylacris* Handlirsch, 1906.

Subfamily Pteridomylacrinae Handlirsch, 1906
[nom. transl. Bekker-Migdisova, hic (ex Pteridomylacridae Handlirsch, 1906)]

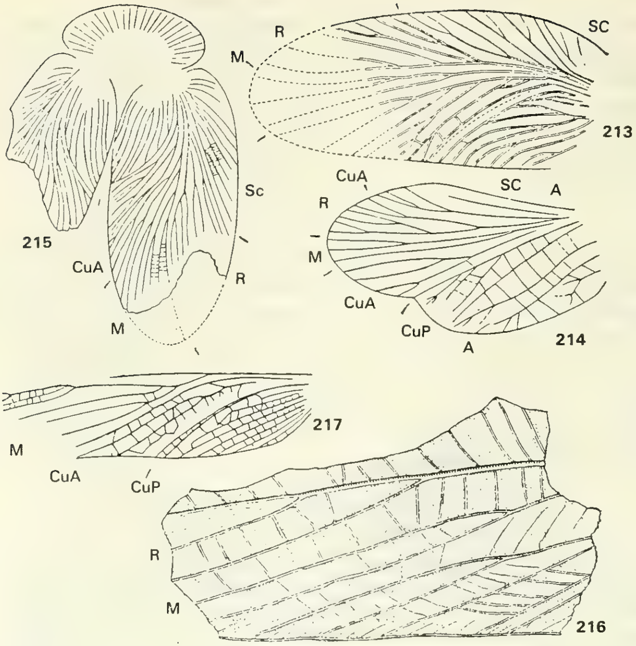
Tegmen triangular with broad base; anal margin straight; costal area wide and short; branches of SC straight and long, arising from base; R straight and pectinate; M straight and simple with only a distal bifurcation; branches of CuA long, running from base of wing; anal furrow not prominent; CuP straight and parallel to branches of CuA and anal veins; anal veins terminating on anal margin of wing. Length of tegmen about 18 mm (Fig. 212). Middle Carboniferous of North America. Two genera: *Pteridomylacris* Handlirsch, 1906 and *Sphenomylacris* Handlirsch, 1906.

Family NEORTHROBLATTINIDAE Handlirsch, 1906
(Dictyomylacridae Handlirsch, 1906)

Tegmen and hindwing with sparse, prominent cross veins; tegmen not widened sharply at base; point of attachment to thorax close to anterior margin; costal area fairly long and wide; SC pectinate; M well developed; CuA has a few long branches; anal furrow prominent and arcuate; branches of A_1 terminating on anal furrow, and branches of A_2 on anal margin of tegmina. In hindwings anojugal area not high and does not folding out like a fan but bending under wing. Upper Carboniferous to Lower Permian. Two subfamilies: Neorthroblattininae and Dictyomylacrinae.

Subfamily Neorthroblattininae Handlirsch, 1906
[nom. transl. Bekker-Migdisova, hic (ex Neorthroblattinidae Handlirsch, 1906)]

Distance between sparse cross veins in tegmen often greater than length of cross veins; costal area of moderate width; R and M sharply divided; radial area wide, straight and placed in middle of tegmen. Length of tegmen 8–9 mm (Figs. 213, 214). Upper Carboniferous to Lower Permian. Two genera: *Mylacridium* Schlechtendal, 1879 and *Neorthroblattina* Scudder, 1885.



99 Figs. 213–217. Family Neorthroblattinidae.

213. *Neorthroblattina albolineata* Scudder; tegmen, × 6.8. Lower Permian, North America (Scudder, 1895). 214. *Mylacridium germari* Schlechtendal; hindwing, × 6. Upper Carboniferous, North America (Handlirsch, 1906). 215. *Dictyomylacris poraulti* Brongniart; external view, × 2. Upper Carboniferous, France (Brongniart, 1893). 216. *Limmatoblatta permensis* Handlirsch; fragment of tegmen, × 3. Upper Permian, Urals (Handlirsch, 1904). 217. *Ideloblatta rossica* M. Zalessky; tegmen, × 2.6. Upper Permian, Urals (M. Zalessky, 1929).

Subfamily Dictyomylacrinae Handlirsch, 1906

[nom. transl. Bekker-Migdisova, hic (ex Dictyomylacridae Handlirsch, 1906)

All veins close together and cross veins often distributed on tegmen; costal area wide at base. Length of tegmen 16–20 mm (Fig. 215). Upper Carboniferous of Western Europe and North America. Single genus: *Dictyomylacris* Brongniart, 1893.

Neorthroblattinidae Incertae sedis

Limmatoblatta Handlirsch, 1904. Genotype—*L. permensis* Handlirsch, 1904; Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Fragment of tegmen with distinct cross veins. Length of fragment about 25 mm (Fig. 216). One species. Upper Permian of Pre-Urals.

Ideloblatta M. Zalessky, 1929. Genotype—*I. rossica* M. Zalessky, 1929; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Fragment of basal half of tegmen (Fig. 217) with characteristically few branches of CuA (three) and cross veins in CuA and anal areas. Length of fragment 12 mm. One species. Upper Permian of Urals.

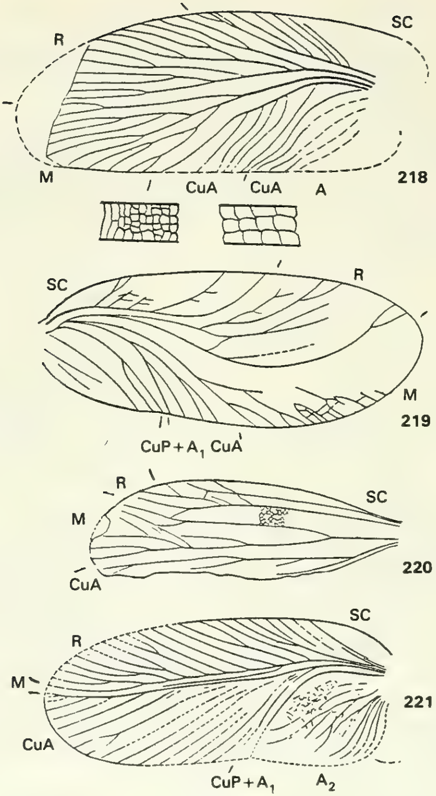
Family POROBLATTINIDAE Handlirsch, 1906

Point of attachment of tegmen to thorax close to anterior margin; costal area short occupying not more than one-half of tegmen; SC has a few simple parallel branches; system of radial veins more extensive than system of medial veins, reaching area of posterior half of tegmen with a row of parallel branches; M well developed, forming a triangle in the middle; CuA short, occupying only one-sixth 99 to one-third of anal margin, with a few perpendicular branches; anal furrow distinct; anal veins terminating on anal margin. Middle Carboniferous to Upper Triassic. Eight genera.

Ishanablattina Bekker-Migdisova, gen. nov. Genotype—*Drepanoblattina fodinensis* Bekker-Migdisova, 1961; Upper Carboniferous, Kuznetsk basin (Upper Balachonian series, Poryvai mines). Anterior margin of tegmen sharply bent at apex; close to base straight like anal margin; SC convex toward its posterior edge, reaching middle of tegmen, with six or seven parallel inclined branches; R running a little beyond middle of tegmen and occupying whole of distal half of anterior margin up to apex, pectinate; M occupying whole of distal half of anal margin, divided into two trunks; CuA convex and very short; anal region short, high; archedictyon very weak, columnar at base, in the form of closely woven crosses on distal region. Length of tegmen about 24 mm (Fig. 218, Pl. IV, Fig. 4). One species, Upper Carboniferous of Kuznetsk basin.

Amekeoblatta G. Zalessky, 1933. Genotype—*A. elegans* G. Zalessky, 1933; Permian, Orenburg province (Kargala). Tegmen broad and rounded. SC long, ending a little more distally beyond middle of tegmen, pectinate with few, indistinct branches. Costal area widened at distal part; R divided into two long trunks at basal one-fourth of tegmen; trunks sharply bent as arcs at middle of tegmen and reaching posterior half of tegmen; M and CuA joined with R at extreme base; CuA poorly branched, not reaching middle of tegmen; anal area short. Length of tegmen 8.5 mm (Fig. 219). One species. Permian of Urals.

100 Outside the USSR: *Poroblatina* Scudder, 1885; *Autoblattina* Schlechtendal, 1879; *Premnoblatta* Pruvost, 1919; *Kebaona* Handlirsch, 1906 and *Drepanoblattina* Schlechtendal, 1879.



Figs. 218–221. Families Poroblattinidae and Blattidae, subfamilies Protereminae and Diechoblattininae.

218. *Ishanoblattina fodinensis* Bekker-Migdisova; tegmen, × 2.5 and archedictyon, × 15. Upper Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1961). 219. *Amekeoblatta elegans* G. Zalessky; tegmen, × 7.6. Lower Permian, Southern Urals (Yu. Zalessky, 1933). 220. *Proterema rarinervis* Göppert; hindwing, × 3.5 Lower Permian, Germany (Göppert, 1865). 221. *Kokandoblattina analis* Martynov; tegmen, × 7.5. Lower Jurassic, Central Asia (Martynov, 1937).

Family BLATTIDAE Stephens, 1829

Tegmina leathery or semi-membranous with distinct venation; point of attachment of tegmen to thorax close to anterior margin; costal area short—less than one-half of length of tegmen; SC much reduced or, rarely, long with short branches; R straight and strongly developed, occupying anterior half of tegmen and sending a series of parallel branches to anterior margin; M free, sometimes its base fused with R or CuA; anal veins terminating on anal furrow. Hindwings, which have well developed jugal area, folding like a fan. Femur protected by spines or tarsus with arolium between claws. Clypeus without clear subdivision into posterior and anterior parts. Valves of ovipositor concealed and short. Cerci clearly segmented. Lower Permian to Recent. 12 subfamilies, of which the following nine have fossil representatives: Protereminae, Diechoblattininae, Mesoblattininae, Blattinae, Pseudomopinae, Epilamprinae, Ectobiinae, Anaplectinae, Nyctiborinae.

Subfamily Protereminae Handlirsch, 1906

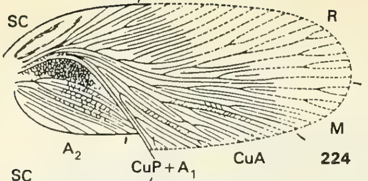
Hindwing with archedictyon and short triangular apical area; SC straight, terminating on anterior margin a little distally from middle of wing; R with two long trunks joined at base and two short branches at apex; M also with two long trunks; CuA with a few short, incomplete branches; anojugal area not preserved (probably folding like a fan). Length of hindwing about 15 mm (Fig. 220). Lower Permian of Western Europe. One genus: *Proyerema* Handlirsch, 1906.

Subfamily Diechoblattininae Handlirsch, 1906

Tegmina broad, round or slightly narrow at apex; costal area short—less than 102 one-half of length of tegmen; SC with some branches which are reduced at base; R many-branched with parallel branches, often reaching posterior half of tegmen; M joined with CuA; CuA enriched with many branches and occupying whole of posterior half of tegmen; sometimes M preserving its anterior branch, which is joined with R at base; some of branches of anal veins terminating toward anal furrow. Hindwing not known. Lower Permian to Cretaceous. Five genera.

Kokandoblattina Martynov, 1937. Genotype—*K. analis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Tegmen wide, its distal part rounded; costal area equal in length to anal; SC sending four or five branches to front; R running toward anterior half of tegmen, straight, and forming nine branches some of which branch dichotomously; M in form of short vein joined with R; CuA straight, traversing middle of tegmen, occupying its posterior half, enriched with parallel branches; anal area high; A_1 and part of branch A_2 terminating toward sharply bent anal furrow. Length of tegmen 8 mm (Fig. 221). One species. Lower Jurassic of Central Asia.

Outside the USSR: *Brephoblatta* Handlirsch, 1906; *Nepioblatta* Handlirsch, 1906; *Diechoblattina* Scudder, 1886 and *Dipluroblattina* Scudder, 1886.



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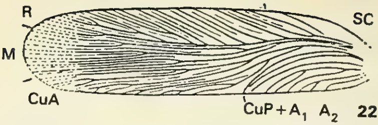

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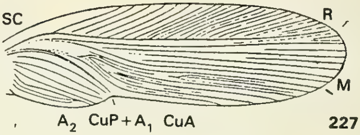

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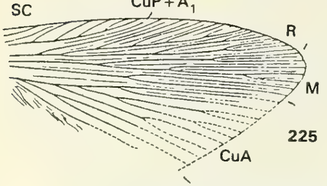

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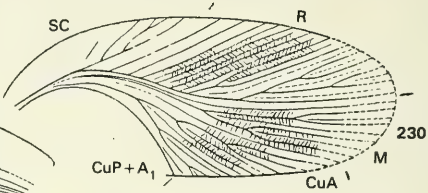

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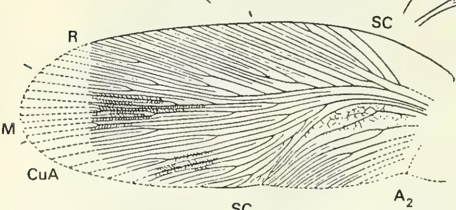

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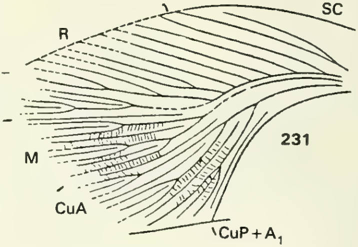

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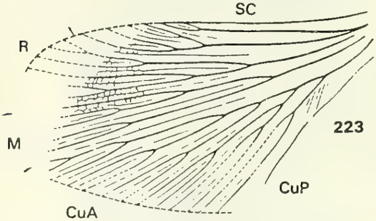

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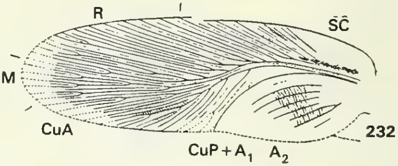

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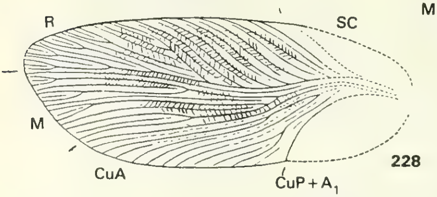

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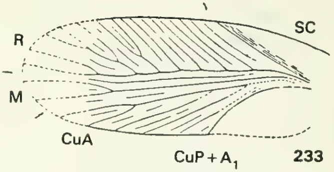

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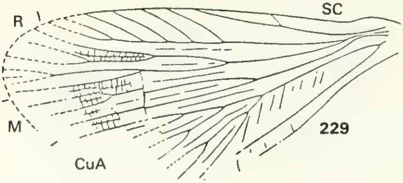

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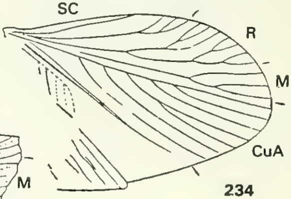

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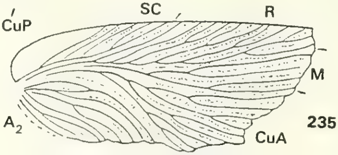

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Subfamily Mesoblattininae Handlirsch, 1908

Tegmen elongated along its length; costal area short—less than one-half of length of tegmen; SC much reduced, sometimes with two to four branches at distal part, with a distinct humeral area at basal part without any veins; R strongly developed, occupying anterior half of tegmen, sending parallel veins toward anterior margin; M and CuA not joined at base; anal area divided by anal furrow; anal veins terminating on anal margin of tegmen; anojugal area of hindwings not known. Femur armed at bottom with spines. Upper Carboniferous to Upper Jurassic. Forty-nine genera.

Sogdoblatta Martynov, 1937. Genotype—*S. robusta* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Tegmen elongated with intercalary veins and cross furrows; SC equal to or a little longer than anal area, sending three or four branches at distal part. Humeral area not large; R slightly bent. CuA richer than M, divided proximally; branches of M and CuA traversing anal margin; anal area large and extended. Length of tegmen 20–26 mm (Fig. 222). Hindwing with long SC; PR and R exhibiting dichotomous branching; M with two trunks; CuA immediately splitting into many branches (Fig. 223). Five species. Lower Jurassic of Central Asia.

Taublatta Martynov, 1937. Genotype—*T. curvata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Tegmen broad with intercalary and cross veins; SC longer than anal area, with two or three distal branches; humeral area equal to or shorter than anal area; R more distal than anal area, strongly bent backward and outward; CuA many-branched, dividing more basally than M at top of anal area. Length of tegmen 15–20 mm (Fig. 224). Hindwing with short SC and distally pectinate PR; M with two branched trunks;

100-101 Figs. 222–235. Family Blattidae, subfamily Mesoblattininae.

222. *Sogdoblatta robusta* Martynov; tegmen, × 3.4. Lower Jurassic, Central Asia (Martynov, 1937). 223. *Sogdoblatta* sp.; hindwing, × 3.7. Lower Jurassic, Central Asia (Martynov, 1937). 224. *Taublatta kisylkiensis* Martynov; hindwing, × 3.8. Lower Jurassic, Central Asia (Martynov, 1937). 225. *Taublatta* sp.; hindwing, × 3.5. Lower Jurassic, Central Asia (Martynov, 1937). 226. *Rhipidoblattina angustata* Martynov; tegmen, × 5. Lower Jurassic, Central Asia (Martynov, 1937). 227. *Mesoblattina multivenosa* Martynov; tegmen, × 5.1. Lower Jurassic, Central Asia (Martynov, 1937). 228. *Samaroblattula subacuta* Martynov; tegmen, × 5.1. Lower Jurassic, Central Asia (Martynov, 1937). 229. *Samaroblattula* sp.; hindwing, × 5. Lower Jurassic, Central Asia (Martynov, 1937). 230. *Mesoblattula shurabica* Martynov; tegmen, × 5.6. Lower Jurassic, Central Asia (Martynov, 1937). 231. *Euryblattula sparsa* Martynov; tegmen, × 1.8. Lower Jurassic, Central Asia (Martynov, 1937). 232. *Samarblatta tillyardi* Martynov; tegmen, × 3.4. Lower Jurassic, Central Asia (Martynov, 1937). 233. *Blattula turanica* Martynov; tegmen, × 8.5. Lower Jurassic, Central Asia (Martynov, 1937). 234. *Blattula* sp.; hindwing, × 6.9. Lower Jurassic, Central Asia (Martynov, 1937). 235. *Ophismoblatta sibirica* Brauer, Redtenbacher and Ganglbauer; tegmen, × 3. Jurassic, Irkutsk province (Brauer, Redtenbacher and Ganglbauer, 1889).

R, M and CuA dividing at different levels; CuA many-branched (Fig. 225). Three species. Lower Jurassic of Central Asia.

Rhipidoblattina Handlirsch, 1908. Genotype—*R. geinitzi* Scudder, 1886; Lower Jurassic, England. Tegmen narrow and long with clear intercalary and cross veins; SC with one or two branches, or simple; humeral area narrow, equal to or longer than length of anal area; R gently bent at middle part, hardly reaching middle of width of tegmen, with many inclined branches directed toward front; anterior trunk of M with two branched trunks; branches of M and CuA running parallel to anal margin and terminating toward apex; anal area elongated. Length of tegmen 8.5–13 mm (Fig. 226). Five species. Jurassic of Central Asia and England.

Mesoblattina Geinitz, 1880. Genotype—*Blattina protypa* Geinitz, 1880; Lower Jurassic, Western Europe (Lower Lias, Germany). Tegmen narrow with parallel margins; SC simple; humeral area very narrow, equal to or longer than anal area; R straight or slightly bent, not reaching middle of width of tegmen; anterior trunk of M simple, posterior trunk pectinate, without branches or with very short branches; anal area round. Length of tegmen 6 to 11.5 mm (Fig. 227). About 30 species. Jurassic of Western Europe and Central Asia.

Samaroblattula Martynov, 1937. Genotype—*S. subacuta* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Tegmen broad, of medium size, membranous with intercalary veins and cross furrows on terminal branches; SC long: length equaling that of anal area, with two or three branches;
103 R with five simple wavy branches; CuA dividing at base much earlier than M, with six or seven outwardly bent branches; anal area not high, elongated. Length of tegmen 10–12 mm (Fig. 228). In hindwing, SC arcuate with a small fork, reaching center of wing; R, M and CuA dividing at same level; PR strong and pectinate with almost vertical branches; M weakly developed; CuA many-branched (Fig. 229). Two species. Lower Jurassic of Central Asia.

Mesoblattula Handlirsch, 1906. Genotype—*Mesoblattina dobbertinensis* Geinitz, 1887; Lower Jurassic, Western Europe (Lower Lias, Germany). Tegmen broad, rounded and somewhat narrow toward end, often with intercalary veins and cross furrows; SC straight; humeral area wide and rounded; R with sharp S-shaped bend, enriched with branches; M and CuA end with two trunks and widely spaced branches; CuA branching little, with sharp bend and parallel CuP at base; anal area large and wide. Length of tegmen 6–14 mm (Fig. 230). Five species. Lower Jurassic of Western Europe and Central Asia.

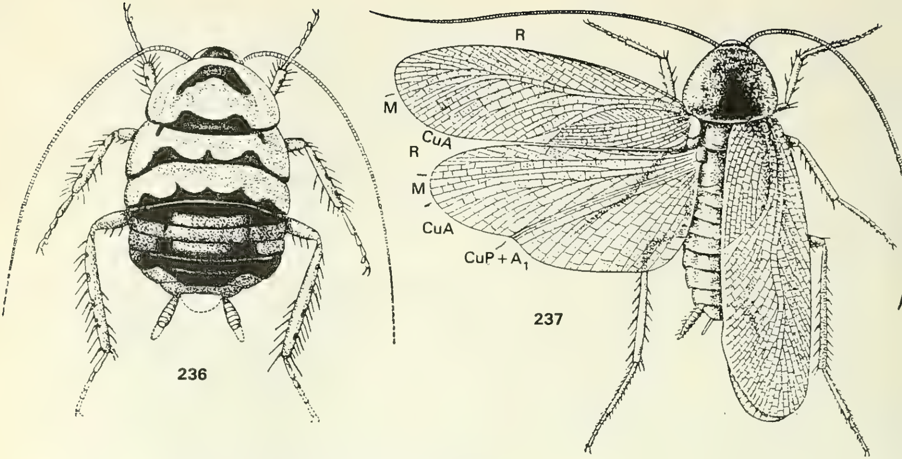
Euryblatulla Martynov, 1937. Genotype—*E. sparsa* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Tegmen broad; SC with only one branch; humeral area equal to anal area; R short, bent, with a few branches distally; CuA dividing proximal to M; branching in both weak, branches widely spaced; CuA sharply bent and parallel to CuP at base; anal area short. Length of tegmen 17 mm (Fig. 231). One species. Lower Jurassic of Central Asia.

Samaroblatta Tillyard, 1919. Genotype—*S. reticulata* Tillyard, 1919; Upper Trias of Australia. Tegmen with intercalary and close net of cross veins; SC equal to anal area in length, with two or three branches; humeral area wide; R forming an S-shaped bend at level of anal area and reaching middle of tegmen or farther; two trunks of M dividing several times, with branches directed forward; CuA dividing more basally than M, sharply arcuate at basal half; anal area long and high with cross veins in some parts. Length of tegmen 18 mm (Fig. 232). Upper Trias to Lower Jurassic. Seven species. Upper Trias of Australia and Lower Jurassic of Central Asia.

Blattula Handlirsch, 1908. Genotype—*Mesoblattina dobbertinensis* Geinitz, 1884; Lower Jurassic, Western Europe (Lower Lias, Germany). Tegmen elliptical, elongated with parallel margins; SC simple, straight and directed at an angle to the front; humeral area very broad; R almost straight, passing through middle; branches of R few and parallel; M very weakly developed, its anterior branch always simple, its posterior branch with two or three branches; CuA straight and pectinate; anal area small and rounded. Length of tegmen 6–7 mm (Fig. 233). Hindwing with straight SC; PR and M branch far distally; CuA straight and pectinate (Fig. 234). Nearly 18 species. Jurassic of Central Asia and Western Europe.

Ophismoblatta Handlirsch, 1906. Genotype—*O. sibirica* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province (Cheremchovian series, Ust-Bailey). Tegmen with broad humeral area; SC with four or five branches in distal part, of same length as anal area; R bent as a gentle arc toward anterior margin; all branches of R with bifurcations; M with two trunks and four branches; CuA many-branched; its posterior trunk sharply bent along CuP, its anterior trunk with branches parallel to anal margin, terminating on apex of tegmen; anal area large, but not high; anal veins branching. Length of tegmen 17–20 mm (Fig. 235). Two species. Jurassic of East Siberia.

Outside the USSR: *Acmeoblatta* Handlirsch, 1906; *Dichronoblatta* Handlirsch, 1906; *Nearoblatta* Handlirsch, 1906; *Haeberleoblatta* Guthorl, 1934; *Epheboblatta* Handlirsch, 1906; *Scutinoblattina* Scudder, 1885; *Austroblattula* Tillyard, 1919; *Austromylacrites* Tillyard, 1916; *Notoblattites* Tillyard, 1916; *Triassoblatta* Tillyard, 1919; *Rhaetiblattina* Handlirsch, 1908; *Hongaya* Handlirsch, 1908; *Pedinoblatta* Handlirsch, 1910; *Actinoblattula* Handlirsch, 1908; *Liadoblattina* Handlirsch, 1908; *Mesoblattopsis* Handlirsch, 1908; *Chiloblattula* Handlirsch, 1939; *Caloblattina* Handlirsch, 1908; *Ectinoblattula* Handlirsch, 1939; *Eublattula* Handlirsch, 1939; *Metablattula* Handlirsch, 1939; *Pachyneuroblattina* Handlirsch, 1908; *Parablattula* Handlirsch, 1939; *Paleoblattula* Handlirsch, 1939; *Schambeloblattina* Handlirsch, 1908; *Artitocoblatta* Handlirsch, 1908; *Blattidium* Westwood, 1854; *Ctenoblattina* Scudder, 1886; *Durdelstonia* Handlirsch, 1908; *Elisama*



104 Figs. 236–237. Family Blattidae, subfamilies Blattinae and Pseudomorphinae.

236. *Periplaneta* sp.; nymph, × 3.3. Tertiary deposits (copal), Africa (Shelford, 1911). 237. *Shelfordella tartara* Saussure; dorsal view, × 2.25. Recent, Fergana (Bei-Bienko, 1950).

Giebel, 1856; *Malmoblattina* Handlirsch, 1908; *Nannoblattina* Scudder, 1886; *Rithma* Giebel, 1856; *Apistoblattula* Bode, 1953; *Macroblattina* Bode, 1953; *Kulmbachiellon* Kuhn, 1938; *Thuringoblatta* Kuhn, 1939; *Trirhabdoblattina* Bode, 1953; *Lithoblatta* Handlirsch, 1908; *Billia* Handlirsch, 1939; *Palmoblattina* Bode, 1953; *Euglyptoblatta* Bode, 1953; *Strebloblattula* Bode, 1953; *Striatotegmen* Haughton, 1924; *Polyphleboblatta* Bode, 1953; *Plyctoblattina* Bode, 1953.

104 **Subfamily Blattinae Stephens, 1829**

[nom. transl. Handlirsch, 1925 (ex Blattidae Stephens, 1829)]

Tegmen thick and somewhat leathery with rich venation; humeral area moderately developed; SC never has posterior branches; branches of R bifurcate irregularly in costal-radial area; M many-branched and never fused with CuA; usually CuA also many-branched, its branches running at angles or parallel to anal margin of tegmen; anal area with longitudinal veins terminating on anal furrow. Hindwing always without additional field, with branching M and CuA. Parietal region of head projecting in front of pronotum. Femur with many strong spines on lower region (Figs. 236, 237). Two genera in fossil fauna—*Stantonella* Handlirsch, 1908 from the Upper Cretaceous of North America and one genus of Recent fauna from the Paleogene of Europe (Baltic amber) and from Quaternary deposits of Western Europe and copal of Africa. Cretaceous to Recent.

Subfamily Pseudomopinae Burr, 1913

[nom. transl. Bei-Bienko, 1950 (ex Pseudomopidae Burr, 1913)]

Tegmen and hindwings developed, reduced, or absent. Tegmen slender and somewhat leathery or, rarely, horny; SC simple or, rarely, with a few branches; branches of R parallel, simple, or with primary branching; M simple or branching, sometimes joined with CuA; if CuA is fused with M, then its branches are slanting or arcuate, and if CuA is free, then its branches are parallel to anal margin. Hindwing with reduced system of M; CuA lacking slanting posterior branches or with some complete and some incomplete branches; additional field always absent; cubital area narrow: less than one-half of width of antenal area. Parietal region of head not visible beyond pronotum. Femur with a few strong spines on lower part or hairlike spines on upper part (Fig. 238 and 239). Paleogene to Recent. Eleven tribes recognized in Recent fauna, of which the following are known also from Tertiary: Symplicini, Supellini, Ischnopterini, Blattellini.

Tribe SYMPLICINI Rehn, 1951

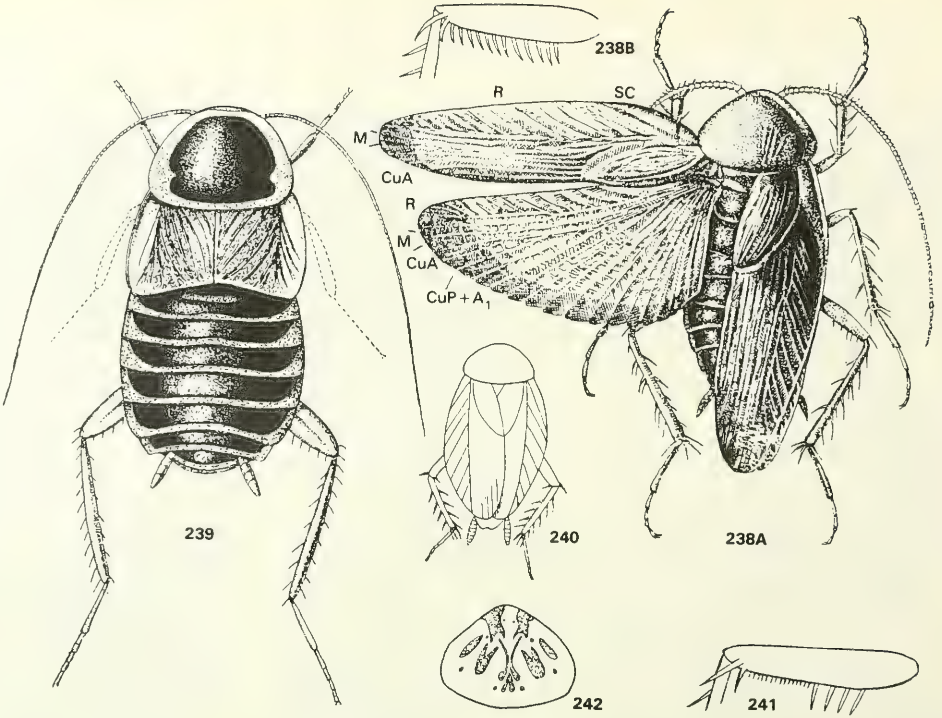
Tegmen long and rather wide; SC simple, straight and shorter than anal area; RS with a row of simple forward-directed branches; M free, with three branches: CuA divided into two trunks; branches of M and CuA run parallel to anal margin of tegmen. Hindwing with large anojugal area; SC simple, reaches 105 margin in middle of wing; R_1 and RS with short branches; CuA with four branches. Tegmina of medium size—10 to 15 mm (Fig. 240). Paleogene to Recent. One genus of Recent fauna reported also from the Paleogene of Europe (Baltic amber).

Tribe SUPELLINI Rehn, 1951

Tegmina usually elongated; if short, more or less oval; SC simple, slightly arcuate and bulging, somewhat shorter than anal area; space between R and M straight and prominent throughout its length; M and Cu joined, with series of branches at angle to anal margin. Hindwing with moderately developed anteanal and small anojugal regions; SC long and simple, reaching margin at middle of wing; R_1 and RS with short, close and distal branches; CuA with three branches. Small insects (Figs. 241, 242). Paleogene to Recent. Three genera of Recent fauna also represented from the Paleogene of Europe (Baltic amber).

106 Tribe ISCHNOPTERINI Rehn, 1951

Tegmina elongated; SC short with a few apical branches; RS many-branched; M



Figs. 238–242. Family Blattidae, subfamily Pseudomopinae.

238. A—*Simploce sinensis* Walker; dorsal view of male, × 4.9. Recent, China (Bei-Bienko, 1950); B—*S. antiqua* Shelford; fore-femur with ventral part, × 10.9. Paleogene of Europe (Baltic amber) (Shelford, 1907). 239. *Temaopteryx abissinica* Saussure and Lehnter; dorsal view, × 5. Recent (Shelford, 1907). 240. *Ceratinoptera cruenta* Shelford; male, × 3.9. Paleogene of Europe (Baltic amber) (Shelford, 1910). 241. *Margates lorenzmeyeri* Shelford; fore-femur with central part, nearly × 5. Paleogene of Europe (Baltic amber) (Shelford, 1910). 242. *M. germari* Shelford; pronotum, × 2.5 Paleogene of Europe (Baltic amber) (Shelford, 1910).

with four long, simple branches; CuA with six branches obliquely inclined to anal angle. In hindwing anojugal area moderately developed, shorter than anteanal area; SC fused with R_1; RS running parallel to R_1 and branching at apex; CuA with four simple apical branches terminating on margin of wing. Paleogene to Recent. One genus from Recent fauna also from the Paleogene of Europe (Baltic amber).

Tribe BLATTELLINI Rehn, 1951

Tegmina long; SC simple, almost straight, shorter than anal area; RS with simple, forward-directed branches; M and CuA fused with six branches; sometimes CuA reduced to one posterior branch. Hindwing with a comparatively narrow anteanal and moderately developed anojugal areas; SC simple; R_1 clear, with apical branches; RS with apical branches at the front; CuA parallel to M with two short apical branches. Paleogene to Recent. Two Recent genera known also from the Paleogene of Europe (Baltic amber).

Pseudomopinae Incertae sedis

Mesoblattina sinica Ping, 1928 from Upper Cretaceous of China and *Pseudophyllodromia* Shelford, 1911 from copal of Africa.

107 **Subfamily Epilamprinae Saussure, 1864**

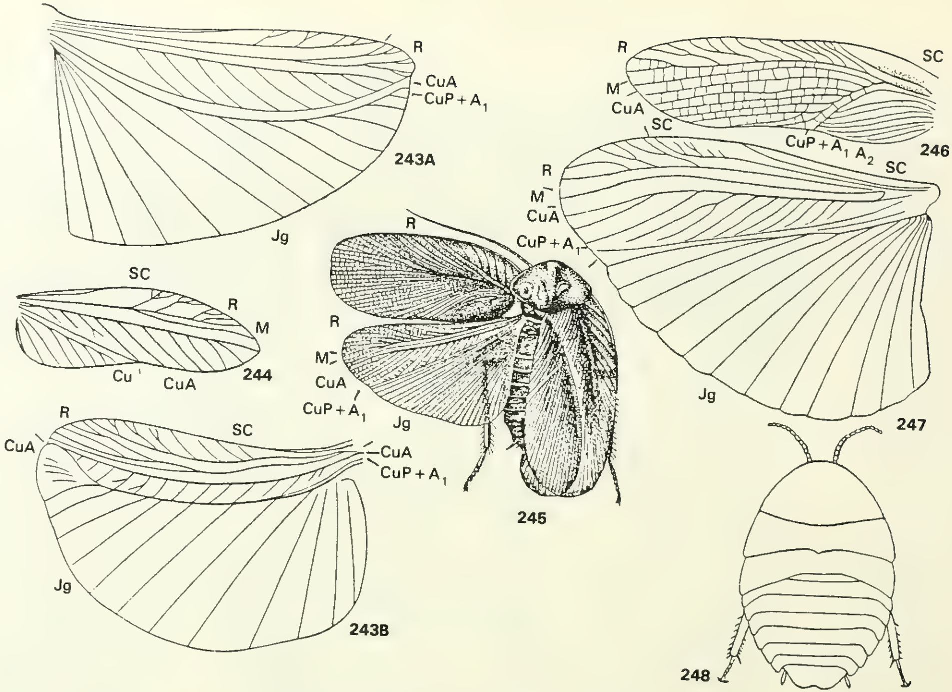
[nom. transl. Saussure, 1893 (ex Empilampriens Saussure, 1864)]

Tegmina and hindwings well developed, short, or absent; tegmina leathery or horny with wide rounded apex; SC straight, usually longer than anal area, often with branches; branches of R partly joined in front with SC and at apex with M. Hindwings with simple SC and M; cubital area wider than one-half of width of anteanal area; about one-half of numerous, incomplete, inclined branches of CuA terminate on CuP. Femur armed at bottom with spines or one apical spine (Figs. 243–248). Paleogene to Recent. 12 tribes in Recent fauna. The tribes of Tertiary deposits are Epilamprini, Panchlorini, Perisphaerini.

Tribe EPILAMPRINI Saussure, 1864

[nom. transl. Rehn, 1951 (ex Epilampriens Saussure, 1864)]

Tegmen broad; humeral area well developed; SC weak at base and often with branches at apex; R with long branches, directed forward; M very close to R at base; M and CuA many-branched, branches running parallel to anal margin. Hindwing with anojugal area equal to anteanal; SC terminates on anterior margin beyond middle of wing; R_1 with three or four apical branches; RS with simple, short apical branches; less than one-third of branches of CuA oriented toward apical margin. Femur at bottom armed with spines. Tarsi bearing pulvilli and arolium. Almost without exception circumtropical insects. Paleogene to Recent. One extinct genus from the Paleogene of Western Europe.



Figs. 243–248. Family Blattidae, subfamily Epilamprinae.

243. *Phlebonotus pallens* Serville; Recent, Malay Archipelago. A—Hindwing of male; B—shortened hindwing of female; × 4. 244. *Notolampra gibba* Thunberg; hindwing, × 2.5. Brazil (Shelford, 1907). 245. *Epilampra goliath* Shelford; general view, × 0.75. Recent, Borneo (Shelford, 1907). 246. *Panchlora cubensis* Saussure; tegmen of male, × 3.4. Recent, Central America (Hebard, 1917). 247. *Pycnoscelus surinamensis* Linnaeus; hindwing of female, × 3.8. Recent, tropics of Old and New World (Bei-Bienko, 1950). 248. *Perispherini* sp.; nymph, × 7.2. Paleogene, Europe (Baltic amber) (Shelford, 1910).

Tribe PANCHLORINI Saussure, 1864
[nom. transl. Rehn, 1951 (ex Panchloriens Saussure, 1864)]

Tegmen elongated, with parallel margins; humeral area not developed; SC often with a series of posterior branches; anterior branches of R showing bifurcations; M with two or three branches, close to R at base. Branches of CuA parallel to anal margin. In hindwing anteanal area more developed than anojugal; SC terminating on anterior margin, before middle of wing; CuA with about 12 branches, of which one-third terminate on apical margin; apical triangle absent or weakly visible. Femur with one apical spine at bottom. Anterior lower edge of fore-femur often with a row of hairlike setae. Tarsi with arolia. Nearly 20 genera in Recent fauna. Paleogene to Recent. One Recent genus also known from the Paleogene of Western Europe.

Tribe PERISPHAERINI Saussure, 1870
[nom. transl. Rehn, 1951 (ex Perispherites Saussure, 1870)]

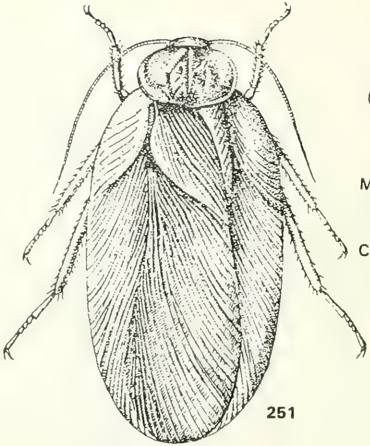
Tegmen fairly broad and short; humeral area wide; SC weak, slanting, bereft of posterior branches; R partly divided into anterior branches; M fused with CuA for some distance, with four branches; CuA many-branched, divided into two trunks; branches bent. Hindwing with clear R_1 parallel to SC and strong RS with traces of apical veins; CuA many-branched and more than one-half of its branches are oriented toward apical margin. Femur without spines at the bottom; apical and knee spines often absent. Tarsi with arolia between claws. Cerci very often short, with indistinct segmentation. Paleogene to Recent. Nymphs from the Paleogene of Europe (Baltic amber).

Subfamily Ectobiinae Saussure, 1864
[nom. transl. Kirby, 1904 (ex Ectobiens Saussure, 1864)]

Tegmen moderately leathery and narrow toward apex, often with pinnately distributed veins; SC weak, simple and equal in length to anal area; R usually extending to apex of tegmen; M and CuA joined at base and approach R, or are joined to it as well; if M and CuA are divided, M is bent and forms three branches directed at more of an angle to anal margin; anal furrow markedly bent; not more than four veins in anal area. Hindwing with large apical triangle folded at rest, which may be vestigeal; R developed, extending to apical triangle, its posterior branches absent; M straight or slightly bent; area between RS and M divided by cross veins into rows of cells; CuA simple. Hind femur with numerous spines or without spines. Size small or medium (Fig. 249). Paleogene to Recent. Three tribes: Ectobiini, Plectopterini and Chorisoneurini; the last is not found in fossil form.

Tribe ECTOBIINI Redtenbacher, 1900

Tegmen lancet-shaped; SC sigmoidal; humeral area moderately developed; R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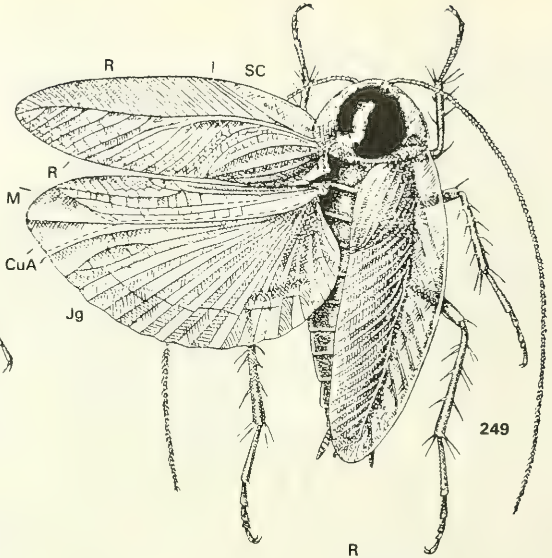

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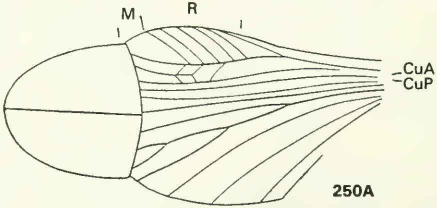

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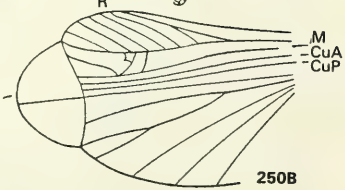

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Figs. 249–251. Family Blattidae, subfamilies Ectobiinae, Anaplectinae and Nyctiborinae.

249. *Ectobius lapponicus* (Linnaeus); general view, × 6.6. Recent, Europe (Bei-Bienko, 1950). 250. *Anaplecta* sp.: A, B—individual variation of form and venation of hind wing, × 9.6. Recent (Shelford, 1907). 251. *Megaloblatta longipennis* Walker, × 0.75. Recent, Central America.

thickened at base; M and CuA sigmoidal; M four-branched; CuA simple. 108 Hindwing with short apical triangle, with apical margin broadly rounded; cross wrinkles absent; SC simple and delicate; R_1 not separated; R, M and CuA connected together at apex; rows of irregular cells between M and R there and rows of regular and rectangular cells between M and CuA. Mid and hind femora armed with weak spines at base; rows of short hairlike spines at apex. Tarsi with asymmetrical claws (Fig. 249). A few genera in Recent fauna. Paleogene to Recent. One Recent genus also known from the Paleogene of Europe (Baltic amber).

Tribe PLECTOPTERINI Saussure, 1893

110 [nom. transl. Rehn, 1951 (ex Plectopterinae Saussure, 1893)]

Tegmen as long as hindwing; widened at base, triangular with indistinct venation; humeral area not large; R straight, lacking posterior apical branches; M and CuA fused to form a long common stalk; at middle of tegmen they divide into two branches; anal furrow straight. Hindwing with large apical triangle equal to rest of wing with provision to roll it up; R_1isolated; rows of irregular cells between M and R. Body dorsally convex. Femur at base lacks spines. Size of tegmen small. Neogene to Recent. Recent genera few including one from copal of Africa.

Subfamily Anaplectinae Walker, 1868

[nom. transl. Hebard, 1929 (ex Anaplectidae Walker, 1868)]

Small forms, outwardly resembling Coleoptera. Tegmen elongated, oval in form; humeral area elongated; SC clear with row of short branches; M with three branches running parallel to anal margin; CuA simple; R running along middle up to apex of tegmen without posterior apical branches. Hindwing with strongly developed apical triangle displaced toward top, occupying whole of distal part; veins of R and M terminating abruptly at edge of latter; SC simple and long; R with isolated R_1 and some branches directed backward. Armor of femur weak (Fig. 250). Neogene to Recent. Five Recent genera, including one from copal of Africa.

Subfamily Nyctiborinae Saussure, 1893

(Nyctiboridae Brunner, 1893; Nyctiborides Sharp, 1895)

Tegmina and pronotum covered with silken furlike setae. Tegmen oval; costal area veinless or with traces of SC distally; R with many irregular anterior branches; M and CuA many-branched; the undivided branches slanting, run parallel to anal margin; base of M close to bases of R and CuA. Hindwing with well developed anteanal area and clear R_1; R with many anterior and apical branches and a divided posterior apical branch; M simple, close to RS; CuA with many irregular branches, one-half or two-thirds of which terminate on apical margin, the reminder, on CuP; anojugal area shortened. Head projecting slightly in front of pronotum. Cerci long. Femur with spines. Size of tegmina large (Fig. 251). Paleogene to Recent. One Recent genus also from the Paleogene of Europe (Baltic amber).

Blattidae Incertae sedis

Besides these, the little-studied genera from the Lower Cretaceous of China, *Sinoblatta* Grabau, 1923 and *Layangia* Grabau, 1923, belong to Blattidae.

Family CORYDIIDAE Saussure, 1864

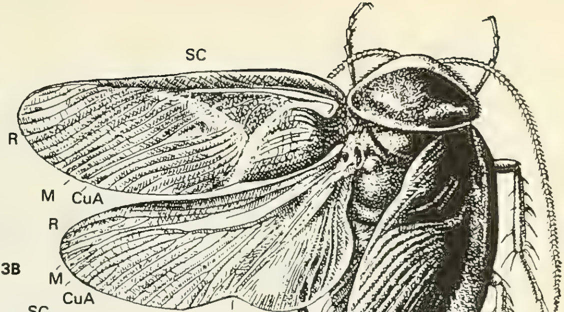
[nom. transl. Handlirsch, 1925 (ex Corydiens Saussure, 1864)]
[Polyphagidae Walker, 1868; Melander-Brues, 1932; Archimylacridae Karny, 1923 (pars)]

Tegmina and hindwings particularly in female, usually absent, when body is strongly arcuate. Point of attachment of tegmen to thorax close to anterior margin. Venation either identical to similar Archimylacridae or with marked specialization: either completely sclerotized or with marked reduction of veins and development of pterostigma; SC often reaching middle of costal border, with slanting branches and a lobe at base; R without isolated R_1. Hindwing with large anteanal area; anojugal area small; only bending and not folding like a fan. Clypeus sharply demarcated from frons and divided into anterior and posterior parts. Femur lacking spines at bottom or with one or two spines. Paleogene to Recent. Five subfamilies in Recent fauna: Corydiinae, Holocompsinae, Euthyrrhaphinae, Latindiinae, Tiviinae. Last two not known as fossil.

108-109 Figs. 252–258. Family Corydiidae, Subfamilies Corydiinae, Holocompsinae and Euthyrrhaphinae; Blattodea incertae sedis (family Cainoblattinidae).

252. *Corydia nuptialis* Gerstatter, × 1.6. Recent India (Brunner, 1865). 253. *Polyphaga saussurei* Dohrn: A—dorsal view of male, × 2; B—Head of female, × 6. Recent, Central Asia (Bei-Bienko, 1950). 254. *P. fossilis* Shelford; nymph, × 15. Paleogene of Europe (Baltic amber) (Shelford, 1910). 255. *Hypercompsa fieberi* Brunner: A—Forewing, B—Hindwing, × 10. Recent, America (Brunner, 1865). 256. *Holocompsa fossilis* Shelford; male, × 6.3. Paleogene, Europe (Baltic amber) (Shelford, 1910). 257. *Euthyrrhapa pacifica* Coquebert; fore and hindwings, × 10. Recent, tropics (Brunner, 1865). 258. *Cainoblattinopsis fushunensis* Ping; general view, × 3. Oligocene, China (Eushun Amber) (Ping, 1931).

253B



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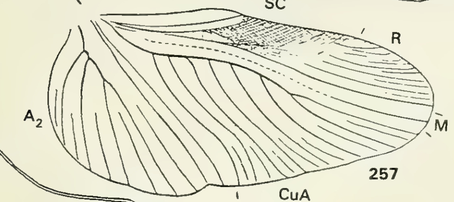

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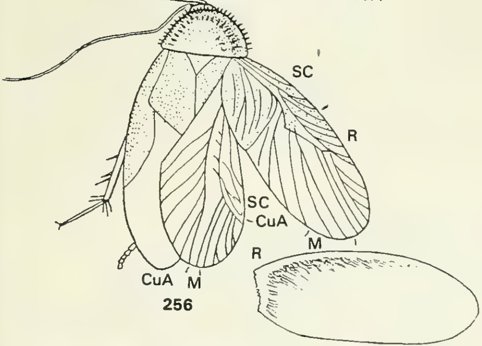

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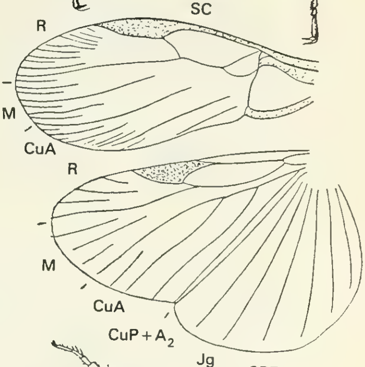

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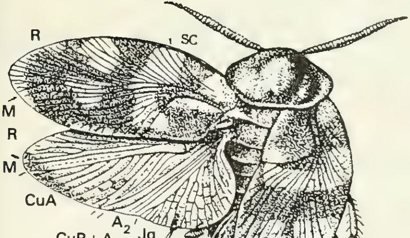

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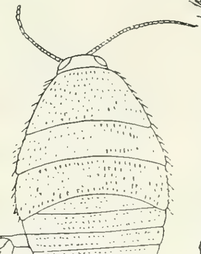

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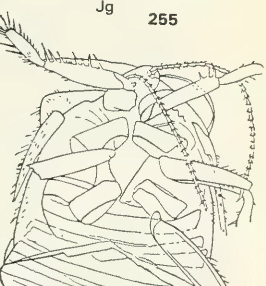

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Subfamily Corydiinae Saussure, 1870

[nom. transl. Saussure, 1893 (ex Corydites Saussure, 1870)]
(Polyphaginae Kirby, 1904; Karny, 1921; Rehn, 1951)

Tegmina and hindwings exhibiting rich venation; humeral area moderate; SC in tegmen long with a few parallel branches; R_1 repeatedly divided; M with three or more branches; CuA well developed; anal furrow sharply bent. Hindwing transparent with complete venation; SC and R_1 simple or, rarely divided; RS with irregular anterior and apical or apical and posterior branches; M with three or more branches. Anterior femur often with one apical spine. Fairly large forms 111 (Figs. 252–254). Paleogene to Recent. Two tribes in Recent fauna: Corydiini and Polyphagini, of which one genus is also known from the Paleogene of Europe (Baltic amber).

Subfamily Holocompsinae Handlirsch, 1925

[nom. transl. Rehn, 1951 (ex Holocompsini Handlirsch, 1925)]

Tegmina transparent in distal part; basal part thickens markedly; venation incomplete; distal branches terminating midway; SC strongly sclerotized, simple; R with a series of short branches at distal part; RS incomplete; M and CuA joined basally to form thick, short stalk; anal furrow vertical; anal area without veins or with traces of veins. Hindwing with simple, short SC; isolated R_1, and RS joined with M to form a pseudo-stigma; CuA clear at base, terminating distally with two branched trunks (Figs. 255, 256). Paleogene to Recent. A few genera in Recent fauna, of which one is known also from the Paleogene of Europe (Baltic amber).

Subfamily Euthyrrhaphinae Handlirsch, 1925

Tegmen strongly sclerotized, preserving only traces of SC and R, wide at base, broadly rounded at apex; anal furrow having form of slightly bent line. Hindwing longer than tegmen; SC simple, short and basally joined with R; R_1isolated; at base branches of R thickening to form a pseudo-stigma, from which springs distal part of four branches of R; M three-branched; CuA with eight slanting branches. Head spherical, without a distinct bulge in lower part. Postclypeus large. Femur with long apical spines. Tarsi sometimes with pulvilli. Small forms (Fig. 257). Neogene to Recent. A few genera in Recent fauna, of which one is also known from copal of Africa.

Blattodea Incertae sedis

Outside the USSR: Little-studied genera *Cainoblattinopsis* Ping, 1931 (Cainoblattinidae Ping, 1931, Fig. 258) from Lower Cretaceous of China; *Paralellophora* Haupt, 1956 (*Paralellophoridae* Haupt, 1956) from Tertiary deposits of Western Europe; and *Lygobius* Mitchell, 1908 (Lygobiidae Mitchell, 1908) from Lower Cretaceous of North America.

Order MANTEODEA. Praying mantids

(O.M. Martynova)

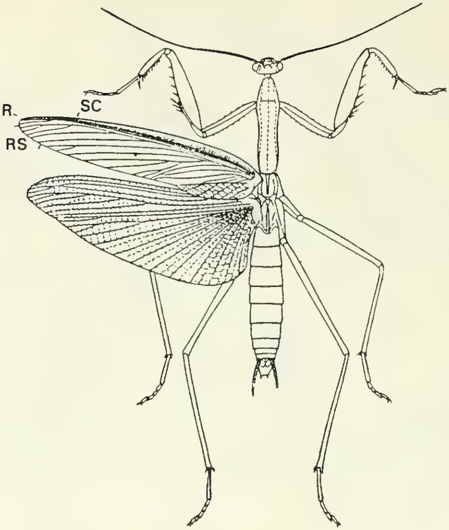
Large and medium insects, often with shortened wings. Forewing: free costal veins absent; SC long, pressing on anterior branches of R which has no basal part; rest of R also long and parallel to SC; branches of M small, directed at an angle backward and outward; Cu many-branched; anal veins usually fewer than in cockroaches; the many cross veins sometimes are transformed archedictyons. Posterior wing with large anojugal fan.

Head agile and opisthognathous. Mouth parts of biting type. Antennae not longer than body, threadlike. Eyes compound, three ocelli. Prothorax usually markedly elongated, longer than other two segments of thorax, not covering head. Forelegs prehensile. Coxa much enlarged, almost equal to length of wide femur, which has a row of spines on inner edge. Tibiae shorter and also with spines along edge. Middle and hind legs slender, long and cursorial. Five-segmented tarsi. Cerci short and segmented. Eggs enclosed in thick ootheca.
112 Tropical or subtropical (Fig. 259). Paleogene to Recent. About 1500 species in Recent fauna. There are also two remains of uncertain systematic position from the Paleogene of Europe (Baltic amber), one species from the Miocene of Europe and three species related to two genera from the Miocene of North America.

Order ISOPTERA. Termites

(O.M. Martynova)

Small and medium sized, living in large colonies. Markedly polymorphic: normal sexual individuals—winged males (''kings''), females (''queens'') —and wingless sterile workers and soldiers of different forms. Two pairs of long similar wings. Sometimes hindwings with expanded marginal area (Mastotermitidae). Venation rich but delicate, consisting of numerous branching longitudinal veins. Cross veins scarcely developed, rarely, weak and slender. Usually SC short, R simple or with many forward-directed branches. M also simple or with three to six branches directed backward. Cu well developed, bearing innumerable branches directed backward. Usually anal area very short. Basal part of wing isolated in form of a scale (along the edge of this scale, the wings break off during the transformation of a winged individual into a subterranian form). Head hypognathous. Mouth parts of biting type. Antennae short with 10 to 30 segments. Sexual forms with compound eyes and two ocelli. Thoracic segments almost similar. Legs cursorial, slender, Tarsi four-, or rarely five-segmented. Cerci short, one- or three-segmented or, rarely, eight-segmented. Living in soil, timber or special abodes—termitaria. Herbivores. In tropical countries causing damage to wood, destroying old buildings, furniture



111 Fig. 259. Order Manteodea.

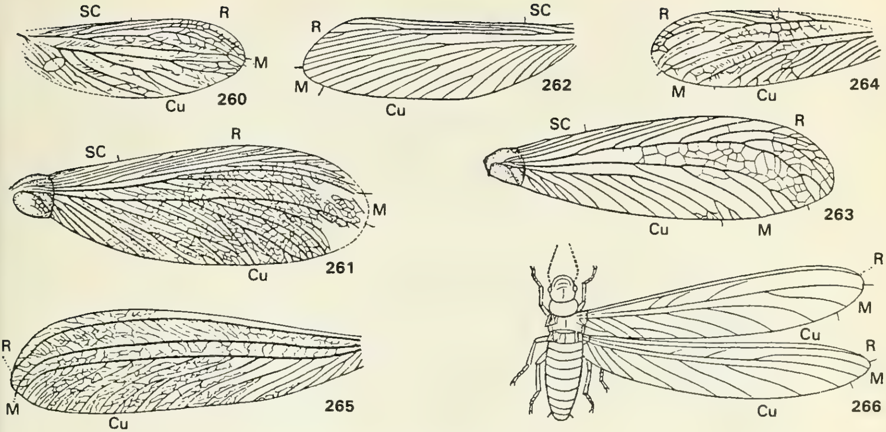
Paratenodera sinensis Saussure; dorsal view, × 1. Recent (Essig, 1947).

and other wood articles. Tropical, subtropical and temperate. Tertiary remains of wood with traces of termite damage are known. Paleogene to Recent. Five families: Mastotermitidae, Calotermitidae, Hodotermitidae, Rhinotermitidae, Termitidae.

113 Family MASTOTERMITIDAE Desneux, 1904

[nom. transl. Silvestri, 1909 (ex Mastotermitinae Desneux, 1904)]

Forewing with short C; SC terminating more distally than midway point of wing, giving rise to long branches; R almost straight, with branches starting almost at base of wing; branches long and directed forward; M approaching R and bearing three to four branches; medial area wider than cubital; Cu running to apex of wing, with its system of branches occupying whole posterior half of wing. In hindwing basal cell absent; anojugal area wide; tarsi five-segmented. These termites build nests in soil and destroy roots and trunks of trees. Recent fauna known in Australia (Figs. 260, 261). Paleogene to Recent. Six genera in the Paleogene of Europe, Central Asia and North America, of which one (*Mastotermes*) is also Recent.



Figs. 260–266. Order Isoptera.

260. *Diatermes sibiricus* Martynov; forewing, × 2.5. Oligocene, Eastern Kazakhstan (Martynov, 1929). 261. *Mastotermes anglicanus* Rosen; forewing, × 3. Oligocene, England (Rosen, 1913). 262. *Eotermes grandaeva* Statz; forewing, × 1.2. Oligocene, Germany (Statz, 1939). 263. *Termopsis bremii* (Heer); forewing, × 4. Paleogene, Europe (Baltic amber) (Rosen, 1913). 264. *Ulmeriella cockerelli* Martynov; forewing, × 2.8. Oligocene, eastern Kazakhstan (Martynov, 1929). 265. *Parastylotermes washingtonensis* (Snyder); forewing, × 5. Neogene, North America (Snyder, 1931). 266. *Constrictotermes tenuirostris* Desneux; dorsal view, × 11. Recent, Mexico (Handlirsch, 1925).

Family KALOTERMITIDAE Enderlein, 1909

Forewing with costal vein along anterior margin; SC short, terminating at beginning of second quarter of wing, lacking branches; R simple or with long branches directed to the front; M close to R, its branches not distinct; radial and medial areas of equal width; branches of Cu occupying much of width of wing; basal cell seen in both wings. Ocelli present. Tarsi four-segmented. Cerci short, two-segmented or sometimes five-segmented. One extant species. Living in Australia in dry, arid areas.* Workers absent (Fig. 262). Paleogene to Recent. Two subfamilies with seven genera from the Oligocene of Europe, the Miocene of North America and the Pleistocene of East Africa.

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* Editor's note: Only one extant species of *Mastotermes* lives in Australia; other species are found in other parts of the world.

Family HODOTERMITIDAE Desneux, 1904

[nom. transl. Snyder, 1925 (ex Hodotermitini Desneux, 1904)]

Scales of forewings shorter than those of hindwing; SC ending proximal to middle of length of wing; branches of SC short; R bent toward posterior region in distal part and terminating at anal margin of apical part of wing; M passing close to Cu with two to five branches; radial area wider than medial. Ocelli absent. Tarsi four-segmented. Cerci short (Figs. 263, 264). Paleogene to Recent. Two subfamilies in Recent fauna with five genera from the Oligocene of Europe and the Miocene of North America.

Family RHINOTERMITIDAE Froggat, 1896

[nom. transl. Light, 1921 (ex Rhinotermitinae Froggat, 1896)]

Scales of forewing longer than those of hindwing; SC absent; R with innumerable short branches or with none at all; M without branches or with short branches directed forward; medial area a little wider than radial; Cu terminating at apex of wing, its branches occupying one-half of width of wing. Fontanel present. Tarsi four-segmented. Cerci two-segmented (Fig. 265). Paleogene to Recent. Four subfamilies in Recent fauna with five genera from the Tertiary of Europe and Central* America and the Pleistocene of East Africa.

Family TERMITIDAE Latreille, 1802

Scales of forewing short; SC absent; R passing close to anterior margin of wing, without branches; M located close to Cu, many-branched; radial area wider than medial; Cu short, devoid of branches or, if long, one- or two-branched with branches of Cu occupying a large part of width of wing. Tarsi four-segmented. Nests large (Fig. 266). Paleogene to Recent. Four subfamilies in Recent fauna with six genera from the Eocene of Western Europe and the Pleistocene of East Africa.

Order DERMAPTERA. Earwigs

(O.M. Martynova)

Winged or wingless. Forewings leathery and devoid of venation, much shortened, not covering abdomen. Hindwings fanlike folding up longitudinally in rest position, with two additional transverse folds, and concealed under tegmina. Head prognathous. Mouth parts of biting type. Antennae short. Legs short. Femur widened. Tarsi three-segmented (Mesozoic forms, with four or 114 five segments). Abdomen with simple or segmented cerci forming forceps. Sterna and terga joined, forming a lateral zigzag line. Primarily nocturnal insects (in the daytime they hide in damp, secluded places—under stones, fallen

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* Editor's note: North and South America.

leaves, bark or decaying wood). Omnivorous. Jurassic to Recent. Suborders: Archidermaptera and Eudermaptera.

Suborder Archidermaptera

Tegmina fairly long, reaching middle of second segment of abdomen, with a few longitudinal ribs which apparently are veins. Antennae with long second segment, equal in length to third. Tarsi four or five segmented. Cerci short, slender, segmented. Jurassic. Family: Protodiplatidae.

Family PROTODIPLATIDAE Martynov, 1925

Tegmina not broad, oblong with four or five brown cross stripes. Segments of antenna number 17 or 18. Segments of cerci five or six. Jurassic. One genus.

Protodiplatys Martynov, 1925. Genotype—*P. fortis* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Kara-Tau). First segment of cercus equal in length to second and third together, fourth and fifth considerably shorter, sixth only rudimentary. Length of body 20 mm (Fig. 267). One species. Upper Jurassic of Kazakhstan.

Suborder Eudermaptera

(Forficulina)

Winged or wingless. Tegmina short, usually reach up to abdomen (except in *Semenoviola*), always without longitudinal ribs; only in certain forms a longitudinal lateral keel present. Antennae with second segment shorter than third. Tarsi three-segmented. Cerci usually with single segment, large and transformed into forceps. Include overwhelming majority of Recent species. Jurassic to Recent. Superfamilies: Protodermaptera and Forficulidea.

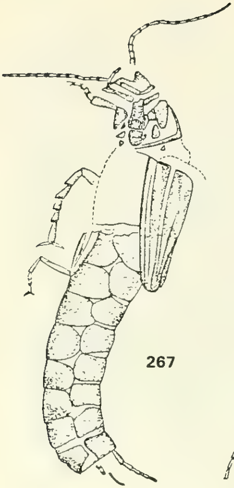
SUPERFAMILY PROTODERMAPTERA

Ocelli often present. Genitalia of male with a pair of penes. Pygidium simple. Nymphs of some genera with segmented cerci. Miocene to Recent. Three families in Recent fauna, of which only Labiduridae (Fig. 268) is also known
115 from Tertiary deposits. One genus known from Burmese amber and another from Argentina.

SUPERFAMILY FORFICULIDEA

(Eudermaptera)

Ocelli absent. Genitalia of male simple, penis not paired. Pygidium often armed with spines and outgrowths. Cerci not segmented. Jurassic to Recent. Families: Labiidae and Forficulidae.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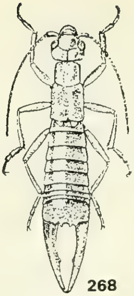
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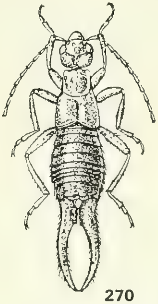
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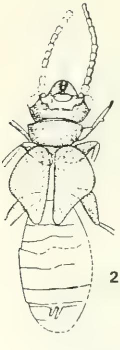
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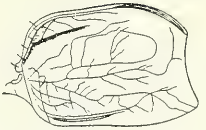
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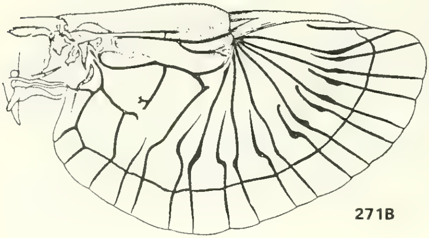
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Figs. 267–271. Order Dermaptera.

267. *Protodiplatys fortis* Martynov; general view, × 3.3. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 268. *Labidura riparia* (Pallas); dorsal view, × 2. Recent (Bei-Bienko, 1936). 269. *Semenoviola obliquotruncata* Martynov; dorsal view, × 4.3. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 270. *Forficula kaznakovi* Semenov; general view, × 2.6. Recent, Caucasus (Bei-Bienko, 1936). 271. *F. auricularia* Linnaeus: A—forewing, B—hindwing, × 15. Recent, Europe (Martynov, 1938).

Family LABIIDAE Burr, 1909

Very small to moderately large. Tegmina always developed, sometimes with keels. Antennae 10 to 23 segmented. Second segment of tarsus simple and cylindrical. Genitalia of male with pointed mataparamerae at apex. Jurassic to Recent. Two subfamilies in Recent fauna, of which Labiinae also occurs in fossil form.

Subfamily Labiinae Verhoeff, 1902

Small or very small. Many Recent genera typical and exclusive to tropics of the Old and New Worlds, of which three known from the USSR. One genus known to occur as fossil. Jurassic to Recent.

Semenoviola Martynov, 1925. Genotype—*S. obliquotruncata* Martynov, 1925. Upper Jurassic, Chimkent province (Malm, Kara-Tau). Tegmina reaching up to end of first segment of abdomen, exhibiting a somewhat rounded projection on outside in middle region and narrow at distal part. Segments of antennae uniform, length of each segment a little more than its width. Length of body 8.5 mm. Greatest width of tegmen 1.5 mm (Fig. 269). One species. Upper Jurassic of Kazakhstan.

Family FORFICULIDAE Stephens, 1829

Medium or large sized, winged or wingless. Antennae 10- to 15-segmented, cylindrical. Second segment of tarsus expanded. Genitalia of male with rounded metaparamerae at apex (Figs. 270, 271). Mesozoic to Recent. Five genera in Recent fauna, of which four are also from Tertiary deposits of Europe and North America.

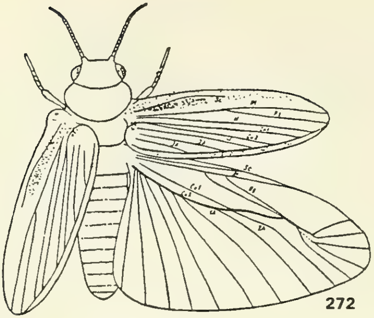
Outside the USSR: *Mesoforficula* Ping, 1928 (Cretaceous of China).

Order PROTELYTROPTERA

(B.B. Rohdendorf)

Forewings in the form of thick, convex, oval tegmina with a few straight, partly branching veins. Hindwings membranous, very wide, longer than forewings. In resting position apical part folded across and whole wing covered by tegmen; venation of hindwings in form of numerous radial diverging veins. Body short and thick with short legs, five-segmented tarsi, wide head and multi-segmented, short antennae. Without cerci (Fig. 272). Life history and development not known. Permian. Five families known: Protelytridae, Megalytridae, Blattelytridae, Archelytridae, Elytroneuridae. The first is known from territories of the USSR.

Phylogeny not resolved. Probably affiliated to ancestral forms of earwigs. Evolution by elaboration of covering tegmina and widening of folded, membranous hindwings. (This order undoubtedly is an example of parallel evolution with the order Dermaptera.)



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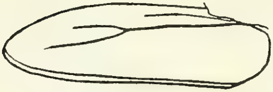

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Figs. 272–273. Order Protelytroptera.

272. *Protelytron perminum* Tillyard; (reconstruction); × 5.8. Lower Permian, North America (Carpenter, 1933). 273. *Uralelytron martynovi* Rohdendorf; tegmen, × 7.5. Lower Permian, Urals (Rohdendorf, 1939).

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Family PROTELYTRIDAE Tillyard, 1931

Forewing with a prominent rim along anal margin; RS well developed; CuA simple, without branches. Lower Permian. Four genera.

Uraleytron Rohdendorf, 1939. Genotype—*U. martynovi* Rohdendorf, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). RS branching more distally, beyond middle of wing; M, Cu and A indistinct; anal margin slightly concave. Length of tegmen 6.5 mm and width 2 mm (Fig. 273). One genus. Lower Permian of Urals.

Outside the USSR: *Protelytron* Tillyard, 1931; *Protelytropsis* Tillyard, 1931 and *Permelytropsis* Carpenter, 1933.

Order PROTOBLATTODEA

(A.G. Sharov)

Two pairs of well developed wings lying flat on dorsal side of body when insect is at rest; venation rich; RS distinctly separated from R and its branches spread to apical and anal margins of wing; M forming two or three branches, rarely five; trunks of MA and MP weakly differentiated; anal area of forewings divided by a deep furrow which is convex toward the front; CuP running along face of furrow; sparse network of remains of archedictyon or simple cross veins marking region between longitudinal veins. Hindwings have well developed anal fan.

117 Head pointed in front, not covered by pronotum. Thorax and abdomen wide, thickened dorsoventrally. Legs of cockroach type, designed for running. Well developed conical coxa, large femur and tibia armed with numerous strong spines. Five-segmented tarsi, elongate, the first segment being largest; fifth segment next largest in size, fourth segment smallest. Females with ovipositor projecting beyond abdominal end. Carboniferous to Recent. 22 families as listed below; the first five are encountered within the limits of the USSR. Families: Aenigmatodidae, Asiopompidae, Balttinopsidae, Euryptilonidae, Epimastacidae, Stenoneuridae, Eoblattidae, Aetophlebiidae, Asyncritidae, Epideigmatidae, Cheliphlebiidae, Eucaenidae, Gerapompidae, Adiphlebiidae, Anthracothermmidae, Taeneopteridae (?), Protophasmidae, Fayoliellidae (?), Stenoneurellidae, Anthracoptilidae, Prostenoneuridae (?), Kliveriidae.

Family AENIGMATODIDAE Handlirsch, 1906

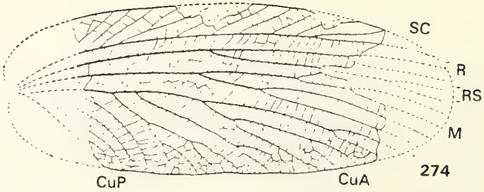
Costal area wide; R without branches in distal part; RS forming one to three branches; simple cross veins and areas with a network between longitudinal veins. Carboniferous. Two genera.

Aenigmetalla Sharov, 1961. Genotype—*A. comparabilis* Sharov, 1961; Middle Carboniferous, Kuznetsk basin (Lower Palachonian series, Zheltyi Yar). In costal area 15 to 18 branches of subcosta, leaving costal area at angles of less than 45°, sometimes also branching; M passing along middle of wing as though dividing it into two symmetrical halves, giving off a few branches which, approaching anal margin of the wing, split into a large number of smaller veins; cross veins simple for most part. Length of forewing 42 mm (Fig. 274). One species. Middle Carboniferous of Kuznetsk basin.

Outside the USSR: *Aenignatodes* Handlirsch, 1906.

Family ASIOPOMPIDAE Sharov, 1961

SC short; RS leaving R close to base of wing, with numerous (up to eight) branches distributed pectinately, with some branching again not far from wing margin; M branching dichotomously, forming up to 11 branches which terminate over a considerable part of the anal margin of wing; CuA much shortened; with not more than 10 non-branching veins running backward in form of a comb; RS, M and CuA disposed almost parallel; ends of MP and CuA slightly bent toward apex of wing; cross veins absent. Carboniferous. One genus.



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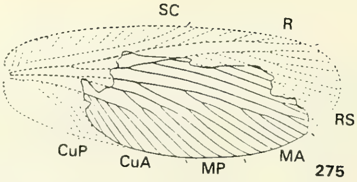

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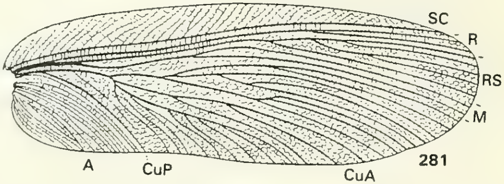

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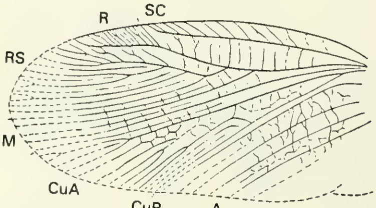

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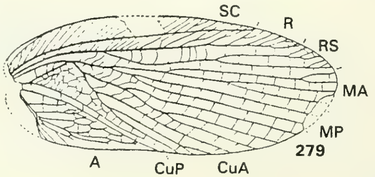

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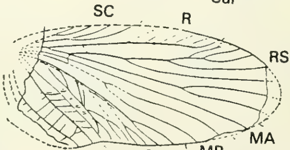

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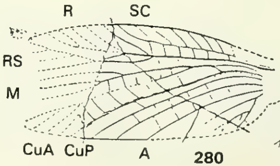

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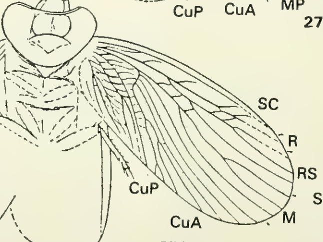

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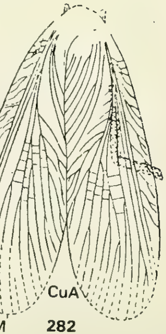

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Asiopompus Sharov, 1961. Genotype—*A. tomicus* Sharov, 1961; Upper Carboniferous, Kuznetsk basin (Upper Balachonian series, Ishanovian subseries, Poryvaiian Mines). Forewing broad, oval, narrowing basally; origins of RS, MA and MP located approximately at one level; branches of MP about one-half in size of branches of MA. Length of forewing about 40 mm (Fig. 275). One species. Upper Carboniferous of Kuznetsk basin.

Family BLATTINOPSIDAE Bolton, 1925

Forewings oval and broad; R with marked curve, at the point of divergence with RS, with numerous veins running toward anterior margin in distal part; RS also many-branched; MA isolated from MP, originating from R or RS; CuA almost straight with branches running toward anal margin. Carboniferous to Permian. Eight genera.

Sindon Sellards, 1909. Genotype—*S. speciosa* Sellards, 1909; Lower Permian, North America (Kansas). Forewing: anterior margin uniformly rounded; apex blunt; number of branches of RS varying from 10 to 12; M simple or two-branched; network strongly expressed, traversing cross veins in distal part of wing. Length of forewing 7 to 12 mm (Fig. 276). Three species. Lower Permian of Urals and North America and Upper Permian of Urals (Kazanian stage).

Sindonopsis Martynov, 1928. Genotype—*S. subcostalis* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). SC much reduced with a few branches; R long; RS arising close to base of wing, with up to seven branches; MA simple; MP with two branches; anal area widened with a few anal veins. Length of forewing 7–8 mm (Fig. 277). Two species. Upper Permian, Arkhangelsk province.

Outside the USSR: *Blattinopsis* Giebel, 1867; *Glaphyrophlebia* Handlirsch, 1906; *Microblattina* Scudder, 1895; *Rhipidioptera* Brongniart, 1885; *Pursa* Sellards, 1909 and *Glaphyrocoris* Richardson, 1956.

Family EURYPTILONIDAE Martynov, 1940

Forewing oval, broad; R with short, inclined branches in subcostal area; RS short, with a few branches; M similarly short, with a few branches; CuA sharply 118

116 Figs. 274–282. Order Protoblattodea.

274. *Aenigmatella comparabilis* Sharov; forewing, × 1.9. Carboniferous, Kuznetsk basin (Sharov, 1961). 275. *Asiopompous tomicus* Sharov; forewing, × 1.3. Carboniferous, Kuznetsk basin (Sharov, 1961). 276. *Sindon uralensis* Martynov; forewing, × 6.5. Lower Permian, Urals (Martynov, 1940). 277. *Sindonopsis subcostalis* Martynov; forewing, × 5.8. Upper Permian, Arkhangelsk province (Martynov, 1928). 278. *Euryptilon blattoides* Martynov; forewing, × 4. Lower Permian, Urals (Martynov, 1940). 279. *Euryptilodes cascus* Sharov; forewing, × 3.5. Lower Permian, Kuznetsk basin (Sharov, 1961). 280. *Epimastax parvulus* Martynov; forewing, × 4.5. Upper Permian, Urals (Martynov, 1928). 281. *Stenoneura fayoli* Brongniart; forewing, × 1.6. Upper Carboniferous, Western Europe (Handlirsch, 1925). 282. *Anrgetus cubitalis* Handlirsch; general view of the impression, × 0.9. Middle Carboniferous, North America (Handlirsch, 1911).

curved at base: A_1 strong; A_2 branching like a tree. Permian. Two genera.

Euryptilon Martynov, 1940. Genotype—*E. blattoides* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing with narrow costal area, without branches of SC; RS with three branches. M curved in the form of an S, with three branches, completely joined with CuA at base of wing; CuA after leaving M, forming three parallel branches which divide dichotomously twice; A_1 two- or three-branched. Length of forewing about 11 mm (Fig. 278; Pl. V, Fig. 1). One species. Lower Permian of Urals.

Euryptilodes Sharov, 1961. Genotype—*E. cascus* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Forewing with wide costal area containing numerous inclined branches of SC; RS branching into two halfway along its length, each of these branches while approaching apex of wing branching into three short veins; A_1 not branching at all, running almost parallel to CuP. Length of forewing 16 mm (Fig. 279; Pl. V, Fig. 2). Two species, of which one is *E.* (?) *horridus* Sharov, 1961, a nymph of which has been described. Lower Permian, Kuznetsk basin.

Family EPIMASTACIDAE Martynov, 1928

Forewing broad and short; SC short with seven or eight branches in costal area; RS diverging from R at middle of wing; M branching at level of apex of SC and more distally than origin of RS; CuA fused with M for a short distance; anal area large and wide with a few (five or six) anal veins. Permian. One genus.

Epimastax Martynov, 1928. Genotype—*E. parvulus* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Forewing: origin of RS close to origin of first inclined branch of R running toward anterior margin; six cross veins between SC and R; A_1 simple. Length of forewing about 11 mm (Fig. 280). One species. Upper Permian of Pre-Urals.

Family STENONEURIDAE Handlirsch, 1906

Forewings broad, with blunt apex; costal area very broad, with pectinate branches of SC; RS diverging from R almost at base of wing; CuA extensive; anal area of forewing broad, with a large number (15–16) of branches; A_2 often branching secondarily; thin network of cells present between longitudinal veins. Length of forewing 40–50 mm (Fig. 281). Carboniferous. Two genera from outside the USSR.

Family EOBLATTIDAE Handlirsch, 1906

Costal area narrower in forewing than in family Stenoneuridae; branches of SC exhibiting further branching; simple cross veins between longitudinal veins; anal veins numbering seven or eight. Length of forewing about 60 mm (Fig. 282). Carboniferous. Two genera from outside the USSR.

SUPERORDER PLECOPTEROIDEA.
Stonefly-like insects

(B.B. Rohdendorf)

Venation in forewing markedly specialized; anterior branch of radial veins sharply demarcated as R, posterior branch as RS; anojugal fan of hindwings medium sized, primarily composed of branches of anal veins. Dissimilarity of wings very slight, usually evident only in widening of anal fan. Wing plate of forewing differing little from that of hindwing. Often similarity of wings observed; winglessness rare. Body elongated, cylindrical, and moderately stout. Legs of running type. Development often in aquatic environment in which nymphs live, and rarely underground. (This is primarily a fossil group.)

Recent fauna include only Embioptera and Plecoptera, the majority of other orders are almost exclusively Paleozoic. Phylogenetic links are with primitive cockroach-like forms, close to order Protoblattodea. Evolution of Plecopteroidea was apparently guided by the development of immature stages in water or soil. Middle Carboniferous to Recent. Five orders: Paraplecoptera, Embioptera, Plecoptera, Miomoptera, Caloneurodea.

Order PARAPLECOPTERA

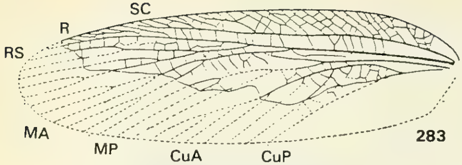
(A.G. Sharov)

Two pairs of well developed wings. Forewing: SC with regular row of inclined branches, extending toward anterior margin of wing, sometimes with additional branching; M branching very early (usually at beginning of RS), usually into two or sometimes three branches; anal area sharply differentiated from remainder of wing by deep furrow; CuP, which traverses the area, not branching; A_2 forming a few branches. In hindwing M also branching out proximally to beginning of RS; A_1 simple; A_2 pectinate.

Head prognathous. Body elongated, thickened dorsoventrally. Wings in resting position lying flat on dorsum of abdomen. Legs of running type with sparse spines. Tarsi normally five-segmented. Ovipositor usually well developed in females. Cerci long, many-segmented. Carboniferous to Jurassic. Six superfamilies; Ideliidea, Cacurgidea, Geraridea, Strephocladidea, Liomopteridea, Megakhosaridea.

SUPERFAMILY IDELIIDEA

Forewings usually leathery, rarely membranous, broad, sometimes have either well developed archedictyon or more or less developed network between longitudinal veins with cellular structure; hairlike setae absent from surface of wings; simple cross veins, if present, occur only distally and rarely over most of wing; costal area usually wide with numerous branches of SC, including a



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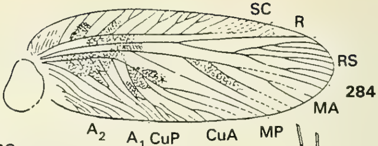

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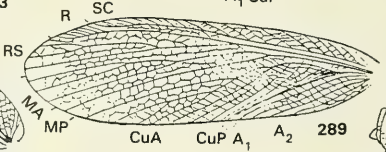

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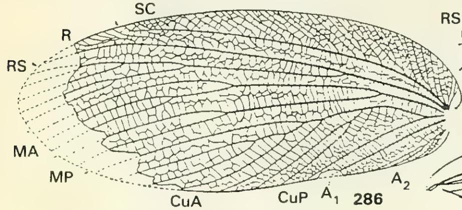

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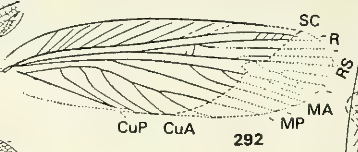

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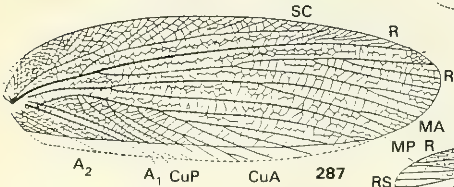

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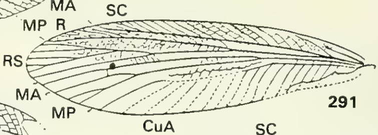

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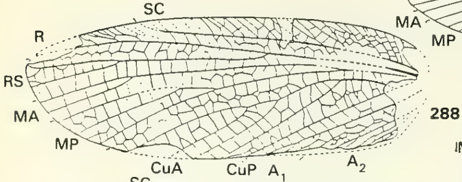

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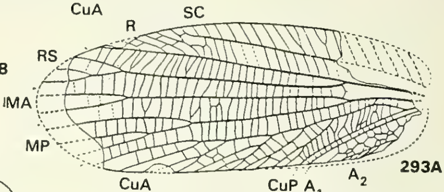

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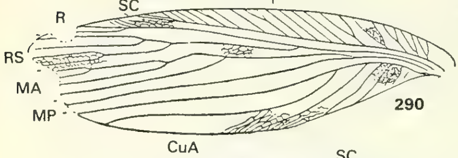

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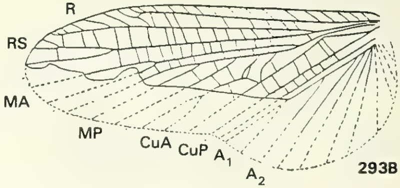

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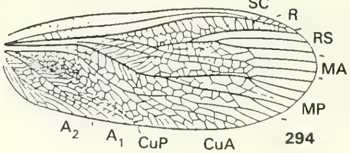

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network of archedictyons or cross veins; costal area rarely narrow; R almost reaching apex of wing, forming a series of inclined branches directed anteriorly; CuA parallel to anterior margin at base, then abruptly deflected toward anal margin to form a 'hump'; from inner part of hump a few short branches originating, resting against CuP or traverse at some angle to CuP; most proximal branch of CuA not isolated from remaining branches; CuP straight or slightly bent; anal area extended.

Body broad. Head small. Pronotum with wide paranotal expansions. Legs of running type; coxae large- or medium-sized as in cockroaches. Ovipositor long. Carboniferous to Triassic. Five families: Ideliidae, Archiprobnisidae, Camptoneuritidae, Demopteridae, Chelopteridae. Last two occur outside the USSR.

Family IDELIIDAE M. Zalessky, 1929

(Rachimentomidae G. Zalessky, 1939)

Forewing: costal area wide with numerous branches of SC, many exhibit secondary branching; no anastomosis between branches of RS and MA; MA branching in distal half of wing; MP often not branching; CuA with largest number of branches; costal area projects in the form of rounded lobe at base of wing. Carboniferous to Triassic. Eleven genera.

Kortshakolia Sharov, 1961. Genotype—*K. ideliformis* Sharov, 1961; Upper Carboniferous, Kuznetsk basin (Upper Balachonian series, Korchakol). Forewing elongated; RS originating approximately at wing midpoint; radial area narrow, with simple cross veins or veins forming separate twin cells; no more than six branches of CuA. Length of forewing approximately 30 mm (Fig. 283). One species. Upper Carboniferous of Kuznetsk basin.

Sylvidelia Martynov, 1940. Genotype—*S. latipennis* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing with small archedictyon; costal area broad; R almost straight; RS with up to seven

128 Figs. 283–294. Superfamily Ideliidea.

283. *Kortshakolia ideliformis* Sharov; forewing, × 3.3. Upper Carboniferous, Kuznetsk basin (Sharov, 1961). 284. *Sylvidelia latipennis* Martynov; forewing, × 1.3. Lower Permian, Urals (Martynov, 1940). 285. *Rachimentomon reticulatum* G. Zalessky; general view of impression, × 1.9. Lower Permian, Urals (Yu. Zalessky, 1939). 286. *Archidelia ovata* Sharov; forewing, × 1.4. Lower Permian, Kuznetsk basin (Sharov, 1961). 287. *Aenigmidelia incredibilis* Sharov; forewing, × 1.4. Lower Permian, Kuznetsk basin (Sharov, 1961). 288. *Paridelia pusilla* Sharov; forewing, × 2.2. Lower Permian, Kuznetsk basin (Sharov, 1961). 289. *Metidelia kargalensis* Martynov; forewing, × 2.1. Permian, Southern Urals (Martynov, 1937). 290. *Stenaropodites permiakovae* (M. Zalessky); forewing, × 1.7. Upper Permian, Urals (M. Zalessky, 1929). 291. *Permotermopsis roseni* Martynov; forewing, × 1. Upper Permian, Arkhangelsk province (Martynov, 1937). 292. *Kolvidelia curta* G. Zalessky; forewing, × 2. Upper Permian, Urals (Yu. Zalessky, 1950). 293. *Archiprobnis repens* Sharov: A—forewing, B—hindwing, × 3.4. Lower Permian, Kuznetsk basin (Sharov, 1961). 294. *Camptoneurites recticulatus* Martynov; forewing, × 3.3. Upper Permian, Urals (Martynov, 1928).

branches. Length of forewing approximately 40 mm (Fig. 284). One species. Lower Permian of Urals.

Rachimentomon G. Zalessky, 1939. Genotype—*R. reticulatum* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewings with small archedictyons; RS distinctly bent forward; RS with four branches. Length of forewing 26 mm (Fig. 285; Pl. VI, Fig. 1). One species. Lower Permian of Urals.

Archidelia Sharov, 1961. Genotype—*A. elongata* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Forewings with a network of cross veins rarely observed between longitudinal veins; costal area broad with numerous comb-like veins of SC, branching once or twice; subcostal area with two or three rows of cells; CuA forming more than six branches. Length of forewing greater than 50 mm (Fig. 286; Pl. V, Fig. 3). Two species. Lower Permian of Kuznetsk basin.

121 *Aenigmidelia* Sharov, 1961. Genotype—*A. incredibilis* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Forewings with a network of cross veins usually absent between longitudinal veins; a false costal vein originating from proximal part of SC usually present; SC leaving radial trunk more proximally than beginning of RS; subcostal and radial area with three rows of cells; simple cross veins present in wing apex. Length of forewing approximately 50 mm (Fig. 287; Pl. V, Fig. 4). One species. Lower Permian. Kuznetsk basin.

Paridelia Sharov, 1961. Genotype—*P. pusilla* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetskian series, Kaltan). Forewings with numerous simple cross veins between longitudinal veins; two series of cells present only in proximal part of subcostal area, radial area, a small part of medial area, distal part of submedial area, and proximal part of cubital area; MP with fewer than five branches; anal area comparatively large and elongated; three rows of cells between A_1 and A_2. Length of forewing approximately 30 mm (Fig. 288). One species. Lower Permian of Kuznetsk basin.

Metidelia Martynov, 1937. Genotype—*M. kargalensis* Martynov, 1937; Permian, Orenburg province (Kargala). Costal area of forewing comparatively narrow. A network rarely present between longitudinal veins in wing apex, forming regular honey comb-like cells; branches of SC simple; MA with two or three branches. Length of forewing 24–28 mm (Fig. 289). Two species. Lower Permian of Kuznetsk basin; Permian of Urals.

Stenaropodites Martynov, 1928 (*Idelia* M. Zalessky, 1929). Genotype—*S. reticulata* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Network of wing small and close to archedictyon; costal area broad; some branches of SC forked; R branching dichotomously more distally than initial branching of MA, forming four to five parallel branches; MA branching pectinately, forming up to four branches; MP not branching. Length of forewing 45 mm (Fig. 290; Pl. VI, Fig. 2). Two species. Upper Permian of Urals.

Permotermopsis Martynov, 1937. Genotype—*P. roseni* Martynov, 1937; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Network strongly expressed; costal area less broad than in *Stenaropodites*, but broader than in *Metidelia*; SC not distinctly reaching apex of wing, its branches lacking bifurcations; R simple; RS with six or seven branches; MP branched. Length of forewing 47–55 mm (Fig. 291). Two species. Upper Permian. Arkhangelsk province.

Kolvidelia G. Zalessky, 1955. Genotype—*K. curta* G. Zalessky, 1955; Permian, Perm province (Pochka). Costal area of forewings broad; branches of SC simple; R bifurcated; MP simple. Length of forewing approximately 30 mm (Fig. 292). One species. Permian of Urals.

Outside the USSR: *Austroidelia* Rick, 1954 (Trias of Australia).

Family ARCHIPROBNISIDAE Sharov, 1961

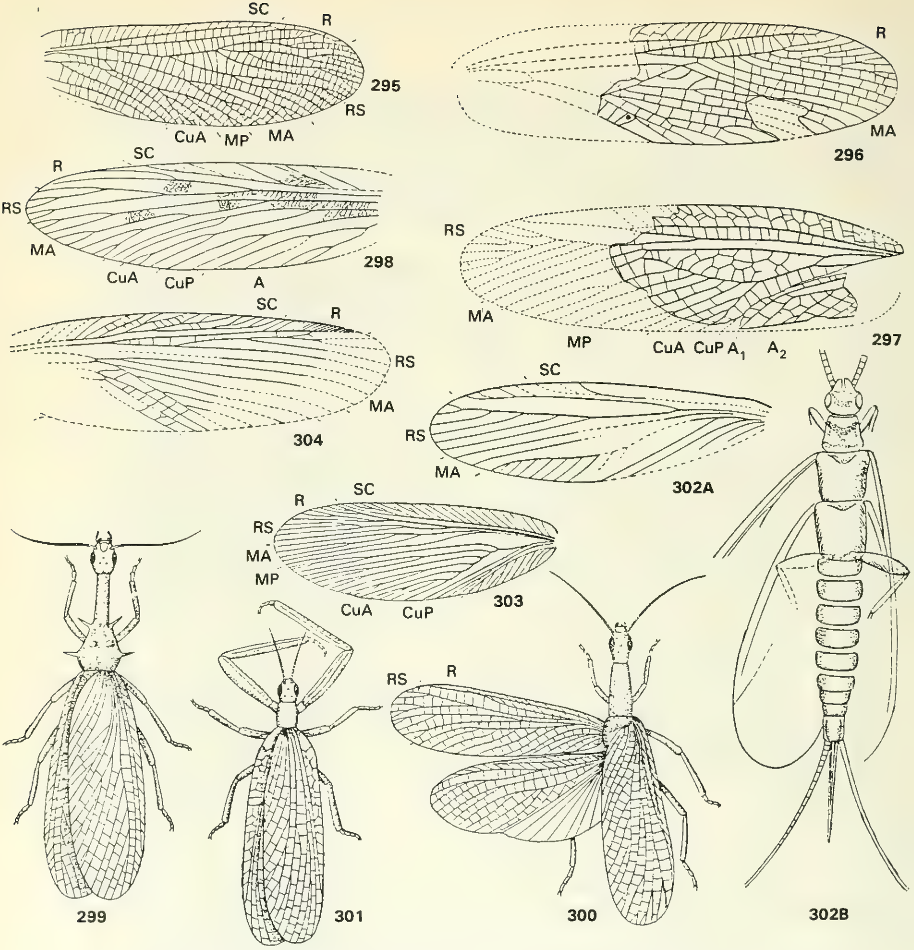
Forewings broad with broad costal area; subcostal area also wide with a regular series of simple or few forked cross veins, slightly inclined toward apex; areas between R, RS, MA MP and CuA very broad and filled with regular rows of primarily simple, closely placed parallel cross veins; branches of MA and MP few: more than five or six taken together; an inclined vein leaves M toward CuA, giving the impression of another branch of M fused with CuA; branches of CuA deflected toward anal margin of wing and very closely spaced, each branch bifurcates two or three times to form a general complex of seven to 13 branches; anal area small; A_1 passes close to CuP; A_2 sharply bent toward anal margin and forms six to eight short, weak forks. One genus.

Archiprobnis Sharov, 1961. Genotype—*A. repens* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewings broad, oval with rounded apex; cells formed by cross veins narrow and high; RS forms up to five short branches; two or three rows of cells between A_1 and A_2. Length of forewings 20–22 mm (Fig. 293). Three species. Lower Permian of Kuznetsk basin.

Family CAMPTONEURITIDAE Martynov, 1928

Costal area of forewings narrow; RS originates at one-third the length of wing from base; anastomosis between branches of RS, MA and MP, close to apex of wing; CuA branches at distal half and is bent toward anal margin. Permian. One genus.

122 *Camptoneurites* Martynov, 1928. Genotype—*C. reticularatus* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Forewings broad, but narrowed somewhat toward base; network stands out strongly; simple cross veins in apical part of wing; branches of RS, MA and MP straight and parallel to distal longitudinal axis of wing. A_1 often with two branches; A_2 with four or more branches. Length of forewing 16 mm (Fig. 294; Pl. VI, Fig. 3). One species. Upper Permian of Urals.



Figs. 295–304. Superfamilies Cacurgidea, Geraridea and Strephocladidea.

295. *Heterologus langfordorum* Carpenter; forewing, × 0.8. Middle Carboniferous, North America (Carpenter, 1943). 296. *Narkemina angustata* Martynov; forewing, × 2.1. Middle Carboniferous, Kuznetsk basin (Sharov, 1961). 297. *N. angustiformis* Sharov; forewing, × 1.8. Middle Carboniferous, Kuznetsk basin (Sharov, 1961). 298. *Homoeodictyon elongatum* Martynov; forewing, × 0.9. Southern Urals (Martynov, 1937). 299. *Gerarus danielsi* Handlirsch; (reconstruction), × 0.9. Middle Carboniferous, North America (Handlirsch, 1925). 300. *Spaniodera ambulans* Handlirsch; (reconstruction), × 1. Middle Carboniferous, North America (Handlirsch, 1925). 301. *Cnemidolestes woodwardi* Brongniart; (reconstruction), × 0.6. Upper Carboniferous, Western Europe (Handlirsch, 1925). 302. *Tillyardembia brevipes* Martynov; Lower Permian, Urals: A—forewing, × 4.8. (original drawing). B—general view of impression, × 5.3. (Martynov, 1940). 303. *Mesorthopteron locustoides* Tillyard; forewing, × 1.4. Upper Trias, Australia (Tillyard, 1922). 304. *Strephoneura robusta* Martynov; forewing, × 1.4. Lower Permian, Urals (Martynov, 1940).

SUPERFAMILY CACURGIDEA

Wings usually membranous, rarely leathery, elongated with acute apex; hairlike setae absent from surface of wings; M branches more proximally than origin of RS, forming MA and MP, latter branch joins with CuA very early; veins often branch not far from margin, as in Neuroptera. Hindwings slightly broad at base, sometimes forming a small fan. Carboniferous to Triassic?. Families: Paoliidae, Stygneidae, Cacurgidae (Fig. 295), Homalophlebiidae (Anhomalophlebiidae), Narkemidae, Thoronysidae, Pachytylopsidae, Protokollariidae, Prototettigidae, Coseliidae, Omaliidae, Stenaroceridae? Mixotermitidae, Laspeyresiellidae, Adeloneuridae?, Klebsiellidae?, Homoeodictyidae, Triassomanteidae?, Xenopteridae?, Mesotitanidae?. All families except Narkemidae and Homoeodictyidae found outside the USSR.

Family NARKEMIDAE Handlirsch, 1911

SC of forewings terminating at R; RS with two or three parallel proximal branches further; MA with two or three branches; anterior branch of MP fused with MA or its posterior branch; trunk MP, after leaving CuA, runs obliquely; wide closed area between MA, MP + CuA and MP; simple cross veins characterize distal half of wing between longitudinal veins. Carboniferous. Two genera.

Narkemina Martynov, 1930. Genotype—*N. angustata* Martynov, 1930; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alykaevian subseries, Verkhotomskoe). RS of forewings originates at midpoint of wing and forms two or three simple parallel branches, which are deflected toward anal margin of wing and then branched dichotomously, forming a total of nine to 11 branches; MA branched with two parallel veins near point of termination of SC on R; three branches originate from oblique trunk of MP. Length of forewing approximately 40 mm (Figs. 296, 297, Pl. VI, Fig. 4). Three species. Middle Carboniferous of Kuznetsk basin.

Outside the USSR: *Narkema* Handlirsch, 1911.

Family HOMOEODICTYIDAE Martynov, 1937

Forewings narrow and long with well-developed archedictyons; SC terminates on costal margin; R with distal bifurcation at end; CuP also with a bifurcation; A_1 with two dichotomous branches. Permian. One genus.

Homoeodictyon Martynov, 1937. Genotype—*H. elongatum* Martynov, 1937; Permian, Orenburg province (Kargala). Forewings large. Costal area broad; SC forms seven or eight inclined branches, RS with five branches. Length of forewing approximately 60 mm (Fig. 298). One species. Permian of Urals.

SUPERFAMILY GERARIDEA

Wings narrow and elongated; RS or CuA (sometimes both) pectinate; M branches more distally than origin of RS, forming a few branches; anal area of forewings narrow with a few (not more than four) anal veins. In hindwing anal area slightly wide and does not form a separate fan; network absent; simple cross veins usually present between longitudinal veins. Body narrow and elongated. Head prognathous with mandibles projecting forward. Pronotum always longer than broad and sometimes extremely elongated, lateral borders (paranota) are very narrow or insignificant. Sometimes forelegs are strongly developed and transformed into prehensile limbs. Ovipositor long. Carboniferous to Permian. Ten families: Geraridae, Spanioderidae, Cnemidolestidae, Hapalopteridae, Cymenophlebiidae, Ischnoneuridae, Hadentomidae?, Emphylopteridae, Kliveriidae, Tillyardembiidae. All except the last known from the USSR.

Family GERARIDAE Handlirsch, 1906

SC of forewings terminates at C; RS pectinate and extensive, leaves R close to base of wing; M well developed: Length of forewings 40–65 mm (Fig. 299). Middle Carboniferous. Five genera outside the USSR.

124 Family SPANIODERIDAE Handlirsch, 1906

SC of forewings terminates at R; area of M markedly brief; CuA well developed and pectinate. Length of forewings 26–35 mm (Fig. 300). Middle Carboniferous. More than 10 genera outside the USSR.

Family CNEMIDOLESTIDAE Handlirsch, 1906

SC of forewings terminates at C; CuA extensive. Forelegs predatory, considerably larger than middle and hind legs; two rows of strong spines on inner surface of femur and tibia. Length of forewings 50–90 mm (Fig. 301). Upper Carboniferous. Two genera outside the USSR.

Family TILLYARDEMBIIDAE G. Zalessky, 1938

(Permocapniidae Martynov, 1940)

M of forewings with not more than two branches; distal half of CuA almost parallel to anal margin of wing, forming a series of pectinate branches directed toward margin. Pronotum moderately elongated. Femur of forelegs usually enlarged. Permian. One genus.

Tillyardembia G. Zalessky, 1937. *(Permocapnia* Martynov, 1938). Genotype—*T. biarmica* G. Zalessky, 1937; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing elongated, oval. Apex of wing narrow; branches of RS not fewer than five; radial area has lancet. Meso- and metathorax rectangular, longer than broad. Length of forewing 11–12.5 mm (Fig. 302A, B). Four species. Lower Permian of Urals.

SUPERFAMILY STREPHOCLADIDEA

Costal area of forewings broad; branches of RS, M and CuA long, parallel and usually not branching near margin of wing; CuA branches pectinately proximally; anterior branch of CuA almost reaches wing apex. Carboniferous to Triassic. Families: Strephoneuridae, Strephocladidae, Mesorthopteridae? (Fig. 303). Last two occur outside the USSR.

Family STREPHONEURIDAE Martynov, 1940

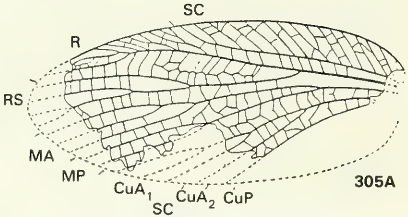
SC of forewings branches dichotomously distally; R has a comb of short veins; three or four branches of RS arranged comb-like; branches of CuA comb simple. Permian. One genus.

Strephoneura Martynov, 1940. Genotype—*S. robusta* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewings narrow and long; SC reaches distal one-third of wing; short cross veins between branches of SC; R strong and straight; M approaches CuA at base, and is connected with it by a short cross vein; branches of M and CuA do not branch in distal half of wing. Length of forewings 50 mm (Fig. 304). One species. Lower Permian of Urals.

SUPERFAMILY LIOMOPTERIDEA

Forewing broad, oval, sometimes with sharp often membranous apex, usually partly or completely covered with dense, small hairlike setae, which may be rarely absent; M with rare exceptions starts branching more proximally than origin of RS; MP not fused with or without anastomosis with CuA; most proximal branch of CuA, labelled CuA_2, is almost separate from other branches of CuA and is parallel to CuP; simple cross veins predominate, particularly in distal portion of wing, but exceptions, include Phenopteridae and Sylvaphlebiidae where two rows of cells occur between longitudinal veins in major part of wing. Hindwings have sharply differentiated, extensive anal fan.

Head prognathous. Prothorax has projecting lateral expansions (paranota) which extend toward anterior and posterior margins of pronotum and form a ring around notum (Pl. VI, Figs. 5, 6). In these lobes dark veins are sometimes observed, suggesting wing venation. Ovipositor shortened, occasionally much reduced. Carboniferous to Jurassic. Families: Palaeocixiidae, Roomeriidae, Reculidae, Phenopteridae, Stereopteridae, Probnisidae, Protembiidae, Germanopriscidae, Chaulioditidae?, Liomopteridae, Stegopteridae, Euremiscidae, Sylvaphlebidae, Lemmatophoridae, Atactophlebiidae, Tomiidae, Geinitziidae. First nine from outside the USSR.



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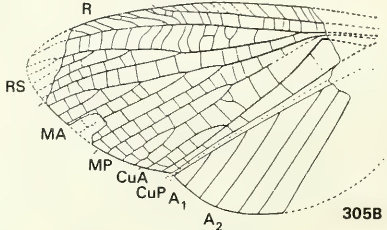

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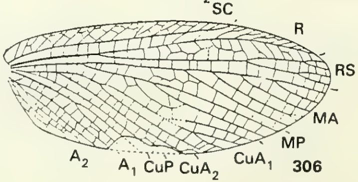

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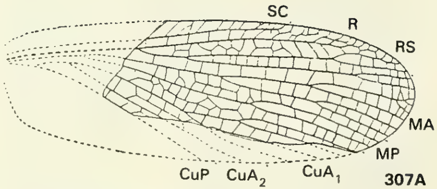

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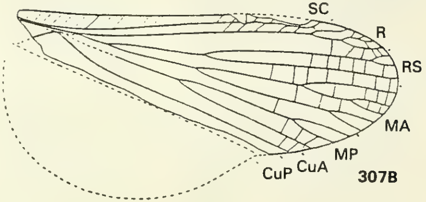

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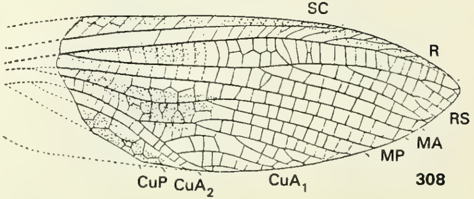

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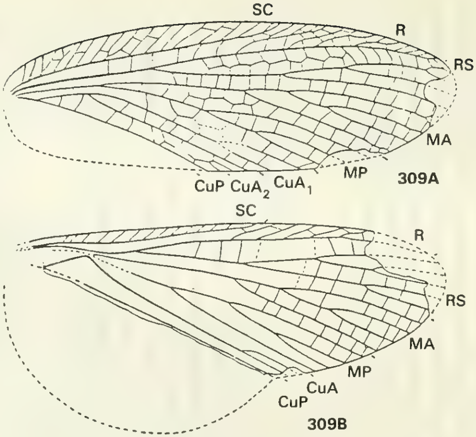

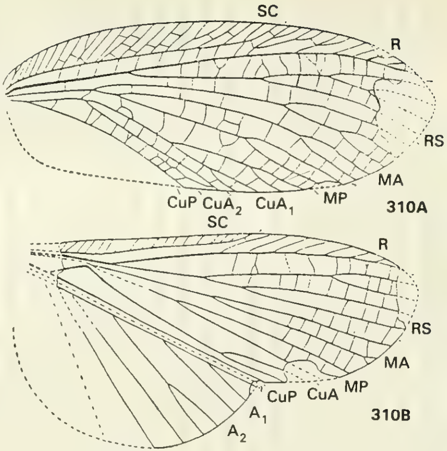

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Figs. 305–310. Superfamily Liomopteridea, Family Liomopteridae.

305. *Parapermula sibirica* Sharov; A—forewing, B—hindwing, × 2.4. Lower Permian, Kuznetsk basin (Sharov, 1961). 306. *Abashevia suchovi* Sharov; forewing, × 2.1. Permian, Kuznetsk basin (Sharov, 1961). 307. *Climaconeurites asiaticus* Sharov: A—forewing, B—hindwing, × 3.2. Lower Permian, Kuznetsk basin (Sharov, 1961). 308. *Ornaticosta magna* Sharov; forewing, × 1.8. Lower Permian, Kuznetsk basin (Sharov, 1961). 309. *Liomopterella vulgaris* Sharov; A—forewing, B—hindwing, × 3.6. Lower Permian, Kuznetsk basin (Sharov, 1961). 310. *Kaltanella lata* Sharov: A—forewing, B—hindwing, × 3.5. Lower Permian, Kuznetsk basin (Sharov, 1961).

Family LIOMOPTERIDAE Sellards, 1909

[Khosaridae Martynov, 1937 (pars); Climaconeuridae Handlirsch, 1919]

Wings membranous, partly or completely covered with small hairlike setae, sometimes with a pattern of dark spots and stripes; costal area relatively broad, normally broader than subcostal area; M branches more proximally than origin 126 of RS; MP has two, rarely three branches; A_1 usually simple, but occasionally with distal bifurcation; A_2 with four or more branches; in distal half of wing, with exception of area between R and RS, simple cross veins always present. Carboniferous to Permian. Nineteen genera.

Parapermula Sharov, 1961. Genotype—*P. sibirica* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing egg-shaped, with strongly convex anterior margin; costal area broad, with regularly spaced, usually simple branches of SC, one or two sometimes with two branches; subcostal area very narrow contains 10 to 15 simple cross veins; radial area wide with two rows of cells with separate isolated cells between them, forming a kind of third series; RS forms two to six branches, MA three to five, MP two or three and CuA three to five. Wings often patterned with large spots and dark stripes along veins. Hindwings wide with wide radial area. Length of forewing 27–31 mm (Fig. 305; Pl. VII, Fig. 1). Lower Permian of Kuznetsk basin.

Abashevia Sharov, 1961. Genotype—*A. suchovi* Sharov, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Abasheva). Costal area of forewings broad basally and proximally, forming a small lobe which is sharply rounded at extreme base; proximal branch of CuA_1 isolated, branching close to origin of and parallel with CuA_2. Length of anal area equal to one-half wing length. Length of forewing 27 mm (Fig. 306). One species. Upper Permian of Kuznetsk basin.

Climaconeurites Sharov, 1961. Genotype—*C. asiaticus* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing: distal branches of SC and R sharply bent apically toward anterior margin of wing; apex of wing blunt, broad and rounded; RS leaves R near base of wing and branches near apex; anterior branches of MA terminate at wing apex; MA with two major trunks, anterior one anastomoses with RS for some distance; sometimes base of anterior trunk of MA resembles a cross vein, which gives the impression that RS branches into two parallel trunks very early; branches of A_2 four or five, long and strong. In hindwings MA joined with RS for some distance. Length of forewing 21–22 mm (Fig. 307; Pl. VII, Fig. 2). One species. Lower Permian, Kuznetsk basin.

Ornaticosta Sharov, 1961. Genotype—*O. magna* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing with a markedly convex anterior margin in distal half; anterior margin of costal area strongly pigmented, resembling a belt; RS pectinate; MP bent toward anal margin of wing; branches of CuA_1 do not extend far forward, but lie almost parallel to anal margin of wing; A_2 forms five to seven long parallel branches. In hindwings MA does not anastomose with RS. Length of forewing 30–50 mm

(Fig. 308). Four species. Lower Permian of Kuznetsk basin.

Liomopterella Sharov, 1961. Genotype—*L. vulgaris* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewings elongated, with moderately pointed apex; costal area broader than radial, with cross veins between branches of SC; radial area and area between MA and MP with double rows of cells; RS, MA and MP branch at distal half of wing; A_1 occasionally bifurcated distally, A_2 with four or five branches. In hindwings MA does not anastomose with RS. Length of forewings 20–35 mm (Fig. 309, Pl. VII, Fig. 3). Two species. Lower Permian of Kuznetsk basin.

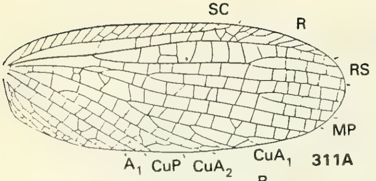
Kaltanella Sharov, 1961. Genotype—*K. lata* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewings broad, with blunt apex; two main stems of MA present; double rows of cells absent from all areas of wing; along with simple cross veins, only Y-, H- and Π-shaped cross veins present. In hindwing MA does not anastomose with RS; anal fan very wide. Length of forewing approximately 20 mm (Fig. 310, Pl. VII, Fig. 4). One species. Lower Permian of Kuznetsk basin.

Liomopterites Sharov, 1961. Genotype—*L. expletus* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Costal area of forewings narrower than radial area, with 15 to 25 short branches of SC without cross veins between them; RS forms one to four branches, MA two or three, MP one to three and CuA three to five; A_1 does not branch, A_2 with four to seven branches. Wing surface covered with dense short hair-like setae throughout. In hindwing MA anastomoses with RS. Length of forewing 8–25 mm (Fig. 311). Nymphs slim, with small free margins of pronotum and small expansions on abdominal segments; cerci shorter than abdomen (Fig. 312). Six species. Lower Permian of
128 Kuznetsk basin.

Sibirella Sharov, 1961. Genotype—*S. paucinervis* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Anterior margin of forewing markedly convex; costal area almost as broad as subcostal area, distinctly narrowing toward base; subcostal area with inclined cross veins; branches RS, M and CuA bent toward anal margin; dark spots on cross veins. Length of forewings approximately 15 mm (Fig. 313). One species. Lower Permian of Kuznetsk basin.

Sarbalopterum Sharov, 1961. Genotype—*S. ignorabile* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala II). Forewings with convex anterior margin; costal area broad, narrowing sharply toward base, with a regular row of acutely sloping branches of SC; cross veins few, exceptionally simple. Length of forewings approximately 10 mm (Fig. 314). One species. Lower Permian of Kuznetsk basin.

Kaltanympha Sharov, 1961. Genotype—*K. thysanuriformis* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Prothorax of nymph with wide paranotal expansions. Legs long, with coxal segments as long as femora. Fore-femora with apical spines. Cerci with long segments. Length of nymph without processes 14 mm (Fig. 315; Pl. VII, Fig. 5). One species. Lower Permian of Kuznetsk basin.



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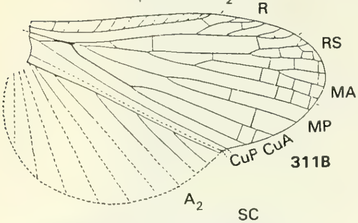

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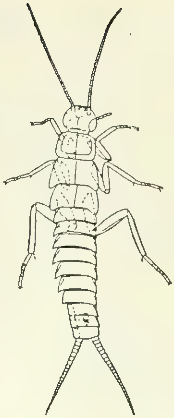

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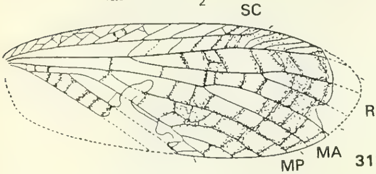

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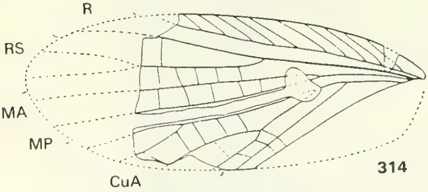

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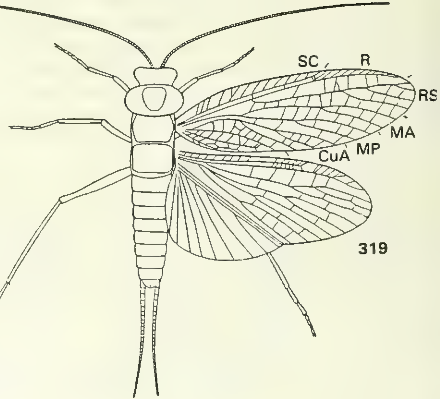

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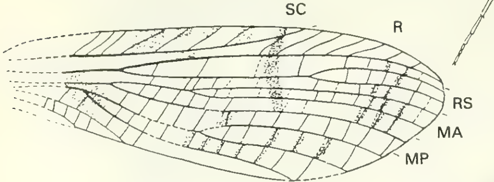

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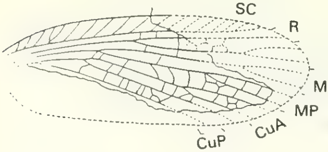

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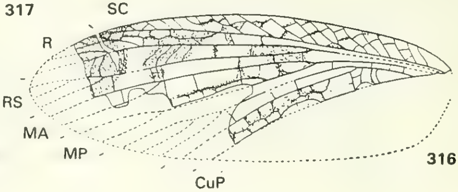

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Paraliomopterum Sharov, 1961. Genotype—*P. paulum* Sharov, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Sureikovo I). Anterior margin of forewing markedly convex; costal area with 15 to 17 branches of SC; two rows of distal cells in subcostal area; RS with a few branches; simple cross veins present in radial area, two rows of medial cells, anterior row larger and higher; similar cells in two rows also present between CuA_2 and CuP, dark spots, mostly along cross veins. Length of forewings approximately 30 mm (Fig. 316). One species. Upper Permian of Kuznetsk basin.

Khosara Martynov, 1937. Genotype—*K. permiakovae* Martynov, 1937; Permian, Orenburg province (Kargala). Forewings with slightly convex anterior margin; cross veins always simple; RS leaves R close to base of wing and branches very late into two branches; MA branches at the proximal half of wing; MA, MP and CuA_1 form not more than two branches. Length of forewings 25 mm (Fig. 317). One species. Permian of Pre-Urals.

Kazanella Martynov, 1930. Genotype—*K. rotundipennis* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Costal area of forewing considerably broader than subcostal area, narrowing distinctly toward base; in subcostal area, short cross veins occur at right angle to longitudinal veins; radial area with two rows of cells; area between MA and MP contain simple cross veins. Length of forewings 17–18 mm (Fig. 318). Two species. Upper Permian of Urals.

Outside the USSR: *Climaconeura* Pruvost, 1912; *Permula* Handlirsch, 1919; *Liomopterum* Sellards, 1909 (Fig. 319); *Tapopterum* Carpenter, 1950; *Semopterum* Carpenter, 1950 and *Ideliopsis* Carpenter, 1948.

Family STEGOPTERIDAE Sharov, 1961

Forewing leathery, with tubercular sculpturing; hair-like setae absent on wings; RS and its branches bent toward anterior margin of wing; venation reminiscent of family Liomopteridae; all cross veins simple. One genus. Permian.

Stegopterum Sharov, 1961. Genotype—*S. hirtum* Sharov, 1961; lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing: SC short; costal

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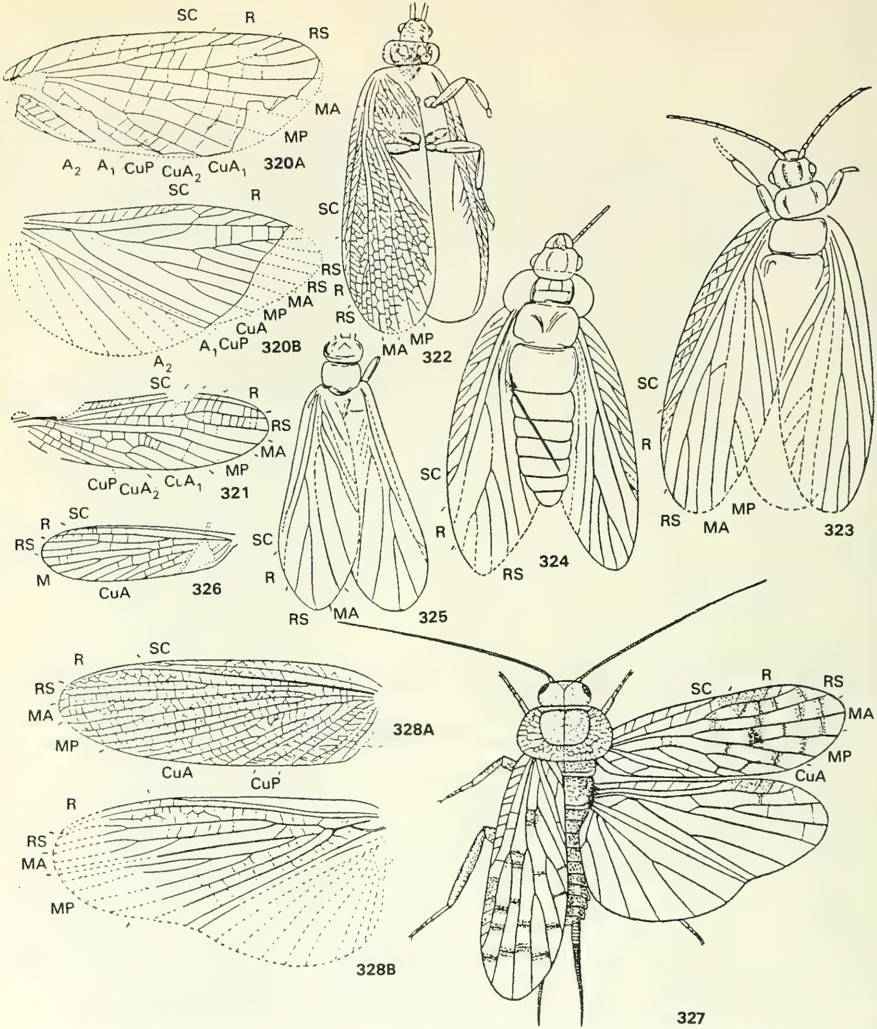
27 Figs. 311–319. Superfamily Liomopteridea, family Liomopteridae.

311. *Liomopterites comans* Sharov: A—forewing, B—hindwing, × 5. Lower Permian, Kuznetsk basin (Sharov, 1961). 312. *L. gracilis* Sharov; nymph, × 4.6. Lower Permian, Kuznetsk basin (Sharov, 1961). 313. *Sibirella paucinervis* Sharov; forewing, × 4. Lower Permian, Kuznetsk basin (Sharov, 1961). 314. *Sarbalopterum ignorabile* Sharov, forewing, × 6.1. Lower Permian, Kuznetsk basin (Sharov, 1961). 315. *Kaltanympha thysanuriformis* Sharov; (reconstruction), × 1.7. Lower Permian, Kuznetsk basin (Sharov, 1957). 316. *Paraliomopterum paulum* Sharov; forewing, × 2.5. Upper Permian, Kuznetsk basin (Sharov, 1961). 317. *Khosara permiakovae* Martynov; forewing, × 3. Permian, Southern Urals (Martynov, 1937). 318. *Kazanella rotundipennis* Martynov; forewing, × 2.9. Upper Permian, Urals (Martynov, 1930). 319. *Liomopterum ornatum* Sellards; (reconstruction), × 2.9. Lower Permian, North America (Carpenter, 1950).



129 Figs. 320–328. Superfamily Liomopteridea, families Stegopteridae, Euremiscidae, Sylvaphlebiidae, Lemmatophoridae, Atactophlebiidae.

320. *Stegopterum hirtum* Sharov; A—forewing, B—hindwing, × 4.5. Lower Permian, Kuznetsk basin (Sharov, 1961). 321. *Euremisca splendens* G. Zalessky; forewing, × 3. Lower Permian, Urals (Yu. Zalessky, 1951). 322. *Sylvaphlebia tuberculata* Martynov; ventral view of impression, × 2.7. Lower Permian, Urals (Martynov, 1940). 323. *Sylviodes perloides* Martynov, dorsal view of impression, × 1.7. Lower Permian, Urals (Martynov, 1940). 324. *Parasylviodes tetracladus* Martynov; forewing, × 2.8. Lower Permian, Urals (Martynov, 1940). 325. *Sylvaella paurovenosa* Martynov; forewing, × 4. Lower Permian, Urals (Martynov, 1940). 326. *Paraprisca uralica* G. Zalessky; forewing, × 2.5. Lower Permian, Urals (Yu. Zalessky, 1952). 327. *Lemmatophora typa* Sellards; (reconstruction), × 5.5. Lower Permian, North America (original drawing). 328. *Atactophlebia termitoides* Martynov; A—forewing, B—hindwing, × 2. Upper Permian, Pre-Urals (Martynov, 1928).

area with nine or 10 subcostal veins, radial area with five simple cross veins; RS pectinate. In hindwing RS does not anastomose with MA. Length of forewings 12–13 mm (Fig. 320). Two species. Lower and Upper Permian of Kuznetsk basin.

Family EUREMISCIDAE G. Zalessky, 1951

Costal area very narrow, almost as wide as subcostal area and with short branches of SC. R distinctly bent at base; RS leaves R close to base; MA and MP very close proximally and approximate R, following its bend. One genus. Permian.

Euremisca G. Zalessky, 1951. Genotype—*E. splendens* G. Zalessky, 1951;
130 Lower Permian, Perm province (Kungurian stage, Chekarda). Forewings long, anterior medial margin nearly straight; two rows of cells between MP and CuA; in other areas cross veins simple. Length of forewing 14 mm (Fig. 321). One genus. Lower Permian of Urals.

Family SYLVAPHLEBIIDAE Martynov, 1940

(Sylviodidae Martynov, 1940; Sylvaelidae Martynov, 1940)

Forewings leathery, hair-like setae absent; radial area wide; branches of CuA reduced; area between CuA_2 and CuP larger than area between CuA_1 and CuA_2. Four genera. Permian.

Sylvaphlebia Martynov, 1940 (*Biarmopteron* G. Zalessky, 1953). Genotype—*S. tuberculata* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area of forewings narrow with irregular slanting branches of SC joined by cross veins; thick cross veins of radial area slope toward base of wing, interconnected by numerous veins; two rows of regular honey comb-like cells between branches of RS, MA and MP. Paranotal lobes small. Length of forewings 15–20 mm (Fig. 322). One species. Lower Permian of Urals.

Sylviodes Martynov, 1940 (*Biarmopterites* G. Zalessky, 1953). Genotype—*S. perloides* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area of forewing considerably broader than subcostal area; branches of SC simple with sparse network of simple cross veins; a sparse net of cross veins in radial area; paranotal lobes small. Length of forewings 24–26 mm (Fig. 323; Pl. VII, Fig. 6). One species. Lower Permian of Urals.

Parasylviodes Martynov, 1940. Genotype—*P. tetracladus* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area of forewing very broad; many branches of SC with bifurcations; RS branches from R at wing midpoint and is pectinate; paranotal lobes broad. Length of forewings 16 mm (Fig. 324). One species. Lower Permian of Urals.

Sylvaella Martynov, 1940. Genotype—*S. paurovenosa* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area of forewing narrow; RS originates at wing midpoint and forms not more than two branches; MA and MP do not branch; cross veins few, simple; paranotal lobes small. Length of forewing 10 mm (Fig. 325). One species. Lower Permian of Urals.

Family LEMMATOPHORIDAE Sellards, 1909

Costal area of forewing narrow, not broader than subcostal; RS forms not more than three branches, often without branches; number of branches of MA, MP and CuA small; A_2 forms not more than three branches and often does not branch. In fore- and hindwings simple cross veins sparsely distributed. In hindwings A_2 with few branches (not more than six), primarily at base of wing. Wings covered with dense, short, hair-like setae. Females with reduced ovipositors which do not extend beyond end of abdomen. Permian. Five genera.

Paraprisca Handlirsch, 1919. Genotype—*Prisca fragilis* Sellards, 1909; Lower Permian, North America (Kansas). Forewings narrow; costal area rarely one-half width of subcostal area; RS originates at proximal half of wing, simple or two-branched; MA usually unbranched, rarely two branched; MP with two or three branches. Cerci short, two-fifths length of abdomen. Legs very long and slender. Length of forewings 10–18 mm (Fig. 326). Three species. Lower Permian. Urals and North America.

Outside the USSR: *Artinska* Sellards, 1909; *Lemmatophora* Sellards, 1909 (Fig. 327; Pl. VII, Fig. 7); *Lisca* Sellards, 1909 and *Lecorium* Sellards, 1909.

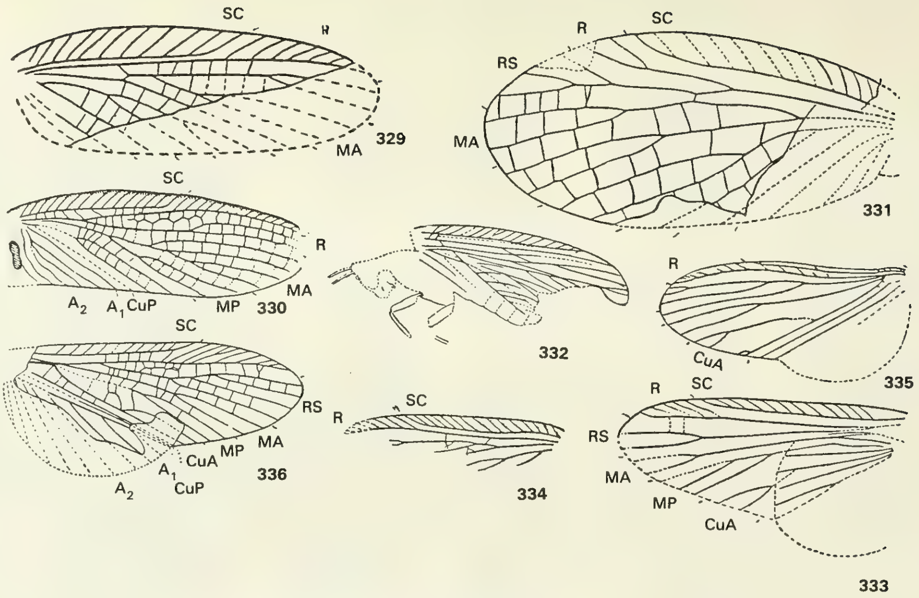
Family ATACTOPHLEBIIDAE Martynov, 1930

Short, hair-like setae absent on wings. Costal area of forewings nearly as wide as subcostal area; CuA with few weak branches and with some cross veins; in radial area and occasionally between proximal branches of CuA, two rows of cells, in other parts of wing simple, or Y-, H- and K-shaped cross veins; M branches into three major trunks, middle one always concave (actually MP?); number of branches of RS, M and CuA varies widely, with more branches in one system, and fewer in others; trunks and branches of M and CuA sometimes anastomose. Ovipositor small, but projecting beyond end of abdomen. Permian. One genus.

Atactophlebia Martynov, 1928. Genotype—*A. termitoides* Martynov, 131 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Costal area of forewing broadest basally. Radial area narrow, with simple cross veins proximally; RS originates at proximal one-third of wing and has few branches. Wing-shedding noticed in *A. termitoides* (Sharov, 1957). Length of forewing approximately 40 mm (Fig. 328; Pl. VIII, Fig. 1). One species. Upper Permian of Pre-Urals.

Family TOMIIDAE Martynov, 1936

Costal area of forewing broad, with regular row of simple branches of SC; SC pass very close to R and its most distal branch sharply deflected from R toward



Figs. 329–336. Superfamily Liomopteridea, families Tomiidae, Geinitziidae, incertae families.

329. *Kargella subcostalis* Martynov; forewing, × 4. Permian, Southern Urals (original drawing). 330. *Tomia costalis* Martynov; forewing, × 3. Triassic, Kuznetsk basin (original drawing). 331. *Shurabia ovata* Martynov; forewing, × 4.5. Lower Jurassic, Central Asia (Martynov, 1937). 332. *Aetophlebiopsis fusca* G. Zalessky; general view of impression, × 1.6. Lower Permian, Urals (Yu. Zalessky, 1955). 333. *Khosarophlebia sylvaensis* Martynov; hindwing, × 2.4. Lower Permian, Urals (Martynov, 1940). 334. *Kargalodes incerta* Martynov; forewing, × 2.3. Upper Permian, Southern Urals (Martynov, 1937). 335. *Haplopterum majus* Martynov; hindwing, × 2.1. Upper Permian, Urals (Martynov; 1928). 336. *Mitinovia dubia* Sharov; hindwing, × 2.3. Upper Permian, Kuznetsk basin (Sharov, 1961).

costal margin, resembling in position the more proximal branches; a regular distal row of simple branches of R in radial area appear as a continuation of the series of branches of SC. Permian to Triassic. Two genera.

Kargalella Martynov, 1937. Genotype—*K. subcostalis* Martynov, 1937; Permian, Orenburg province (Kargala).Forewing with markedly convex anterior margin; simple cross veins in radial area; SC ends near middle of wing and forms up to 10 branches; RS forms short anastomosis with MA; MA, MP and CuA together form not more than seven branches. Length of forewing 16 mm (Fig. 329). One species. Permian of Urals.

Tomia Martynov, 1936. Genotype—*T. costalis* Martynov, 1936; Triassic, Kuznetsk basin (Maltsevian series, Babii Kamen). Forewing elongated, with slightly convex anterior margin; radial area with two rows of cells mesally, simple cross veins in distal and remaining parts of wing; MA extensive with up
132 to four branches, CuA not branched. Length of forewings approximately 14 mm (Fig. 330). One species. Trias of Kuznetsk basin.

Family GEINITZIIDAE Handlirsch, 1908

Forewing with rounded apex located midway between anterior and anal margins; R bent toward anterior margin distally with two or three branches; branches of RS pectinate, directed forward, terminating at anterior margin of wing. Trias to Jurassic. Two genera.

Shurabia Martynov, 1937. Genotype—*S. ovata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Forewing broad, oval-shaped with markedly convex anterior margin; R with two distal branches; RS forms two or three branches; cross veins simple. Length of forewings 16–17 mm (Fig. 331). Three species. Upper Triassic of Australia; Lower Jurassic of Central Asia.

Outside the USSR: *Geinitzia* Handlirsch, 1906.

Incertae Familiae

Aetophlebiopsis G. Zalessky, 1955. Genotype—*A. fusca* G. Zalessky, 1955; Lower Permian, Perm province (Kungurian stage, Chekarda). Costal area of forewing narrow; SC parallel to R for most of its length; RS at wing midpoint. Length of forewing 27 mm (Fig. 332). One species. Lower Permian of Urals.

Khosarophlebia Martynov, 1940. Genotype—*K. sylvaensis* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Hindwing with broad costal area; R with five distal branches; MA does not anastomose with RS. Length of hindwing 23 mm (Fig. 333). One species. Lower Permian of Urals.

Kargalodes Martynov, 1937. Genotype—*K. incerta* Martynov, 1937; Permian, Orenburg province (Kargala). Forewing: SC terminates in distal half of wing; R with six or seven long apical branches; RS and MA anastomose in a small area. Length of forewing approximately 15 mm (Fig. 334). One species. Permian of Pre-Urals.

Haplopterum Martynov, 1928. Genotype—*M. majus* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Hindwing: Costal area narrow and short; branches of R short and numerous (about 10); MA fused with RS, not branch. Length of forewing approximately 20 mm (Fig. 335). Upper Permian of Pre-Urals.

Mitinovia Sharov, 1961. Genotype—*M. dubia* Sharov, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Mitina). Hindwing: apex sharp; 10 or 11 branches of SC in costal area; branches long and sometimes forked; two rows of cells in part of radial area; MA does not anastomose with RS; MA, MP and CuA form two branches each. Length of hindwings 22 mm (Fig. 336). Upper Permian of Kuznetsk basin.

Outside the USSR: *Mesonotoperla* Riek, 1954; *Mesacridites* Riek, 1954 and *Xenogryllacris* Riek, 1955.

SUPERFAMILY MEGAKHOSARIDEA

Wings narrow and long with strong, thick veins sharply demarcated from wing membrane; costal area very narrow with a few simple cross veins between C and SC. Representatives of this superfamily were perhaps the best fliers among paraplecopteres. Permian. One family.

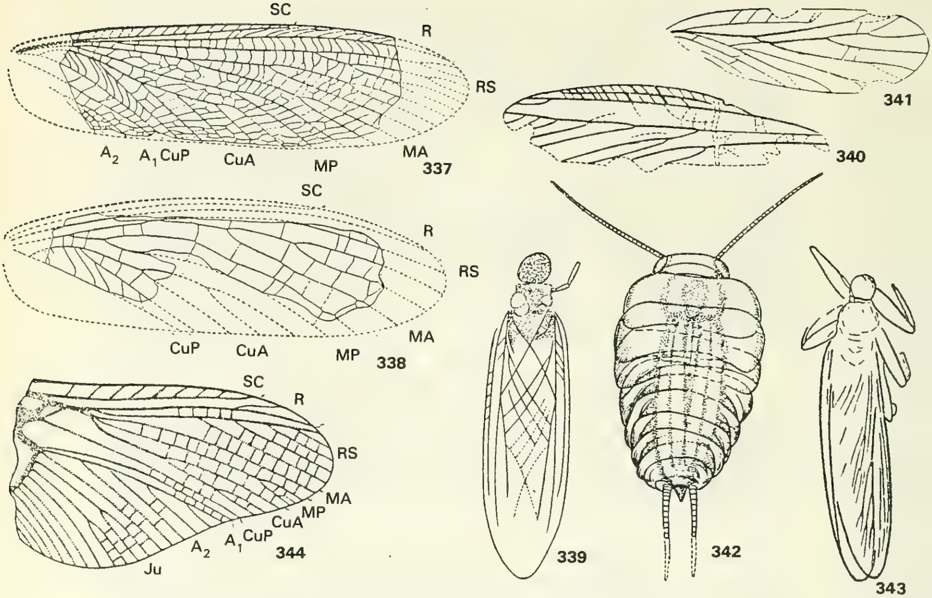
Family MEGAKHOSARIDAE Sharov, 1961

[Khosaridae Martynov, 1937 (pars)]

Forewings covered with small hair-like setae in isolated regions. An oblique vein runs from M toward CuA not far from wing base, giving the appearance of one more branch of trunk M joining CuA; CuP straight or slightly bent; regular row of slanting veins between CuA and CuP, sharply bent near intersection with CuP; anal area large, very elongated; branches of A_2 numerous, strong. In hindwing MA unites with RS for some distance; trunk of M fused with CuA at base. Permian. Two genera.

Megakhosara Martynov, 1937 (*Syndesmophora* Martynov, 1937). Genotype—*M. fascipennis* Martynov, 1937; Permian, Orenburg province (Kargala). Forewing: RS dichotomously branched; MP simple or two-branched; longitudinal veins with regular orientation, wing designed for efficient flying; numerous cross veins form two rows of cells in some areas; no anastomoses between longitudinal veins. Length of forewings 30 to 60 mm (Fig. 337; Pl. VII, Fig. 2). Five species. Lower Permian of Kuznetsk basin; Permian of Pre-Urals.

Megakhosarella Sharov, 1961. Genotype—*M. regressa* Sharov, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo I). Forewing: trunk
133 RS joined with MA for some length; MP branched in proximal half, not far from MA–MP bifurcation; longitudinal veins irregularly distributed, and sinuate;



Figs. 337–344. Superfamily Megakhosaridea, Paraplecoptera incertae sedis.

337. *Megakhosara dilucida* Sharov; forewing, × 1.8. Lower Permian, Kuznetsk basin (Sharov, 1961). 338. *Megakhosarella regressa* Sharov; forewing, × 4.3. Upper Permian, Kuznetsk basin (Sharov, 1961). 339. *Termitoides productus* G. Zalessky; general view of impression, × 2.2. Lower Permian, Urals (Yu. Zalessky, 1955). 340. *Uralotermes permianes* G. Zalessky; forewing, × 2.8. Lower Permian, (Yu. Zalessky, 1937). 341. *Sellardsiopsis conspicua* G. Zalessky; forewing, × 5.6. Lower Permian, Urals (Yu. Zalessky, 1939). 342. *Gurianovella blattoides* Martynov, nymph, × 3.3. Lower Permian, Urals (Martynov, 1940). 343. *Dyadozoarium pachypus* Handlirsch; general view of impression, × 1.2. Permian, Urals (Handlirsch, 1906). 344. *Kaltanopterodes vanus* Sharov; hindwing of nymph, × 11.4. Upper Permian, Kuznetsk basin (Sharov, 1961).

cross veins prominently placed, they are primarily simple, and only at apex of wing are they Y-shaped. Length of forewings approximately 17 mm (Fig. 338). One species. Upper Permian of Kuznetsk basin.

Paraplecoptera Incertae sedis

Termitoides G. Zalessky, 1955. Genotype—*T. productus* G. Zalessky, 1955; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewings elongated, lancets; costal area very narrow; RS originates in basal half of wing. Length of forewings 22 mm (Fig. 339). One species. Lower Permian of Urals.

Uralotermes G. Zalessky, 1937. Genotype—*U. permianus* G. Zalessky, 1937; Lower Permian, Perm province (Kungurian stage, Ust-Kishert). Forewing elongated; costal area narrow; radial area broad with cellular network; RS originates close to wing base, pectinate. Length of forewings 20 mm (Fig. 340). One species. Lower Permian of Urals.

Sellardsiopsis G. Zalessky, 1939. Genotype—*S. conspicua* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing: R bent at origin of RS; MA fused with RS; M and CuA fused at base; CuP long. Length of forewing 8 mm (Fig. 341). One species. Lower Permian of Urals.

134 *Gurianovella* G. Zalessky, 1939 (*Kirkorella* G. Zalessky, 1939; *Permella* G. Zalessky, 1939; *Czekardia* Martynov, 1940; *Mariella* G. Zalessky, 1955). Genotype— *G. silphidoides* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Nymph: head broad; antennae long and thread-like; pronotum with a small groove along anterior margin; body broad; terga with large paranotal expansions. Small styli below end of abdomen. Body length 8–13 mm (Fig. 342; Pl. VIII, Fig. 3). Five species. Lower Permian of Urals.

Dyadozoarium Handlirsch, 1904. Genotype—*D. pachypus* Handlirsch, 1904; Permian, Orenburg province (Kargala). Wings narrow, long, with numerous veins. Legs stout, similar. Length of body including wings 43 mm (Fig. 343). One species. Permian of Pre-Urals.

Kaltanopterodes Sharov, 1961. Genotype—*K. vanus* Sharov, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Zelenyi Lug). Hindwing of nymph: RS pectinate, forming five branches; MA not anastomosed with RS and not branched; MP two-branched; CuA forms three branches; in anal fan, besides pectinate A_2, nine parallel veins of jugal (?) area of the wing; all cross veins simple. Wing length 4.8 mm (Fig. 344). Upper Permian of Kuznetsk basin.

Order PLECOPTERA. Stoneflies

(A.G. Sharov)

Medium-size insects (body length 5 to 35 mm); two pairs of thin membranous wings, folding flat on back; forewings narrow and long, anterior margin straight; SC with a short distal bifurcation, anterior branch directed toward costal margin, and posterior branch toward R. Branches of R short, resembling cross veins; RS usually originates close to base of wing; one to five branches on RS. M passes close to R at base of wing, sometimes fused with it; MA with two simple branches distal to wing midpoint. MP fused with CuA and their common stem branches very late, often forming pectinately, a few short branches. Two series of simple cross veins in areas between MA, MP + CuA and CuP, rarely, two rows of cells; CuP simple; if numerous, cross veins uniformly distributed. In hindwings RS joined with M at base; anojugal area forms a fan or, rarely, is reduced; proximal part of RS from R up to anastomosis with M disappears, giving the impression that R is independent of RS.

Head prognathous, mouthparts of biting type, rudimentary; antennae thread-like, consisting of 25 to 100 segments; compound eyes small; usually with ocelli. Legs short, cursorial; hind pair a slightly longer than the others; tarsi three segmented. Abdomen flat, abdominal terga without lateral expansions, subequal in length to thorax; cerci long, usually segmented. Adults typically do not eat, but drink readily and usually inhabit banks of water bodies. Eggs are laid in water. Nymphs aquatic, predatory, live for two to two and one-half years; breathe through tracheal gills located in different parts of body in different families: on lower parts of thorax. on anterior and posterior segments of abdomen. Permian to Recent. Families: Palaeoperlidae, Perlopseidae, Taeniopterygidae, Eustheniidae, Nemouridae, Leuctridae, Perlidae, Perlodidae, Pteronarcyidae, Diamphipnoidae, Penturoperlidae, Senzillidae, Gripopterygidae, Scopuridae, Austroperlidae, Peltoperlidae, Capniidae, Chloroperlidae; first eight families known in fossil form, Eustheniidae and Perlodidae fossils are from outside the USSR.

Family PALAEOPERLIDAE Sharov, 1961

Four or five short branches of SC in subcostal area; R with three or four distal branches; two cross veins r-rs and two r-rm; cross veins between branches ofRS and MA absent; anterior branches of MP + CuA does not fuse with MA_2; anal area narrow and long; A_2 passes near the extreme anal margin and does not branch; between A_1 and A_2, S-shaped cross vein at base of wing. Permian. One genus.

Palaeoperla Sharov, 1961. Genotype—*P. exacta* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewings: RS forms two or three branches; M not fused with R at base; eight cross veins in medial area, four in cubital area. Length of forewing 10 mm (Figs. 345, 346). Two species, of which one is represented by a nymph. Lower Permian of Kuznetsk basin.

135 Figs. 345–354. Order Plecoptera.

345. *Palaeoperla exacta* Sharov; forewing, × 5.5. Lower Permian, Kuznetsk basin (Sharov, 1961). 346. *P. prisca* Sharov; nymph, × 10. Lower Permian, Kuznetsk basin (Sharov, 1961). 347. *Perlopsis filicornis* Martynov; A—general view of impression of holotype, × 3. (Martynov, 1940); B—forewing, × 3.3 (original drawing); C—tarsus, × 8.3 (original drawing). Lower Permian, Urals. 348. *Palaeotaeniopteryx elegans* Sharov; A—forewing; B—hindwing; C—nymph, × 8.3. Lower Permian, Kuznetsk basin (Sharov, 1961). 349. *Palaeonemoura clara* Sharov; forewing, × 6.5. Lower Permian, Kuznetsk basin (Sharov, 1961). 350. *Mesonemura turanica* Martynov; forewing, × 5.1. Lower Jurassic, Central Asia (Martynov, 1937). 351. *Mesotaeniopteryx elongata* Martynov; forewing, × 2.8. Lower Jurassic, Central Asia (Martynov, 1937). 352. *Nemoura cinerea* (Retzius); A—forewing, B—hindwing, × 6. Recent, Europe (Illies, 1955). 353. *Leuctra hippopus* Kempy; A—forewing, B—hindwing, × 7.7. Recent, Europe (Mosley, 1932). 354. *Perla* sp.; dorsal view, × 1.9. Recent, Europe, Asia, America (Handlirsch, 1925).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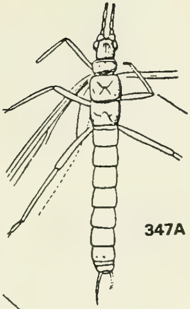
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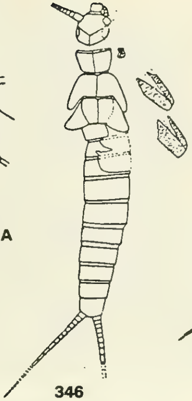
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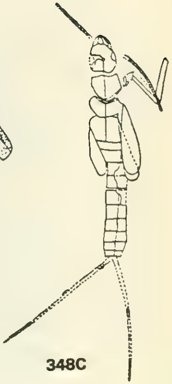
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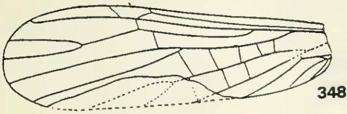
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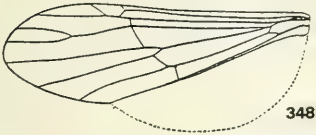
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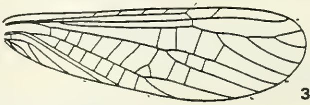
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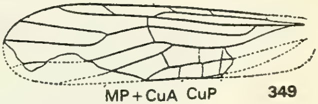

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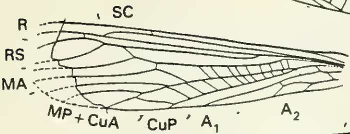

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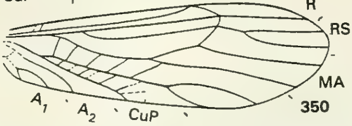

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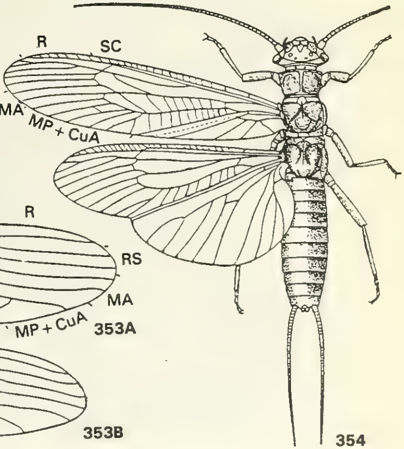

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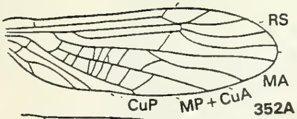

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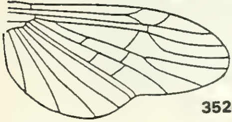
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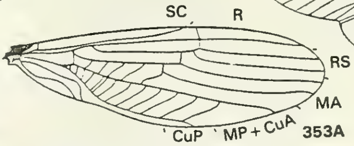

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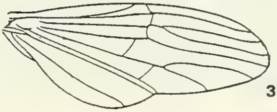

353B

136 Family PERLOPSEIDAE Martynov, 1940

Three or four short branches of SC in subcostal area; R with one branch close to end of SC; one cross vein r-rs—homologous to proximal part of r-rs of family Palaeoperlidae, and at least three r-rm, two are located more proximally to r-rs; cross veins present between branches of MA. Antennae with long segments, basal segment enlarged. Thoracic division extensive. Legs long and slender; second tarsal segment one-third length of first and third, which are of equal length. Permian. One genus.

Perlopsis Martynov, 1940. Genotype—*P. filicornis* Martynov, 1940; Lower Permian, Urals (Kungurian stage, Chekarda). Forewing: costal area as broad as subcostal in distal half, SC with four branches; cross veins r-rs located at level of end of SC; RS with four branches; MP + CuA two-branched. In impression of holotype, wing venation poorly preserved. Among numerous recently discovered impressions of this species from this site, there are specimens with well-defined venation. Length of forewings 15–17 mm (Fig. 347A, B; Pl. VIII, Fig. 4). One species. Lower Permian of Urals.

Family TAENIOPTERYGIDAE Klapalek, 1905

Not more than one branch of SC present in costal area; R usually without branches; if one branch present, it is far removed from posterior branch of SC, which causes the usual X-shaped figure to be absent. More often, RS forms two distal branches or, rarely, three or four; one to four branches extend forward from MP + CuA. Permian to Recent. Four extinct genera and a few genera in Recent fauna, of which one is known from the Paleogene of Europe (Baltic amber).

Palaeotaeniopteryx Sharov, 1961. Genotype—*P. elegans* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Part of RS between cross vein r-rs and bifurcation subequal, or slightly longer than branches of RS; M joined with R at base; between MA and MP + CuA not more than four cross veins; A_1 connected with CuP by a short cross vein, A_2 branches very early into two veins. Length of forewing 7 mm (Fig. 348A, B). Two species, one has been described as a nymph (Fig. 348b). Lower Permian of Kuznetsk basin.

Palaeonemoura Sharov, 1961. Genotype—*P. clara* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing: part of RS between r-rs and bifurcation shorter than branches of RS; branches of MA slightly bent distally toward anterior margin; MP + CuA without distal bifurcation and bent toward anal margin of wing; at least one distal cross vein between MP + CuA, CuP does not slope toward CuP, but toward anal margin of wing; CuP bent toward anal margin; anal area in the form of a long, narrow distal wedge. Length of forewing approximately 8 mm (Fig. 349). Two species. Lower Permian of Kuznetsk basin.

Mesonemura Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*M. maaki* Brauer, Redtenbacher and Ganglabauer, 1889; Lower Jurassic, Irkut province (Cheremkovian series, Ust-Bailey). Forewing: SC passes very close to C distally, anterior branch of SC very short or absent; part of RS between r-rs and bifurcation one-half or one-third length of RS branches. Tarsus long; second and third segments equal in length, first segment longest. Length of forewing 8–11 mm (Fig. 350; Pl. VIII, Fig. 5). Two species. Lower Jurassic of Irkut province and Central Asia.

Mesotaeniopteryx Martynov, 1937. Genotype—*M. elongata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Forewings narrow; SC parallels costal margin, posterior SC branch very long, terminating on R, proximal to r-rs; R with two or three branches; MP + CuA with three distal branches; two long anterior ones, situated close to one another; extend parallel to anal margin in proximal half; between MA, MP + CuA and CuP more than 10 cross veins. Length of forewing 15–21 mm (Fig. 351). Three species. Lower Jurassic of Central Asia.

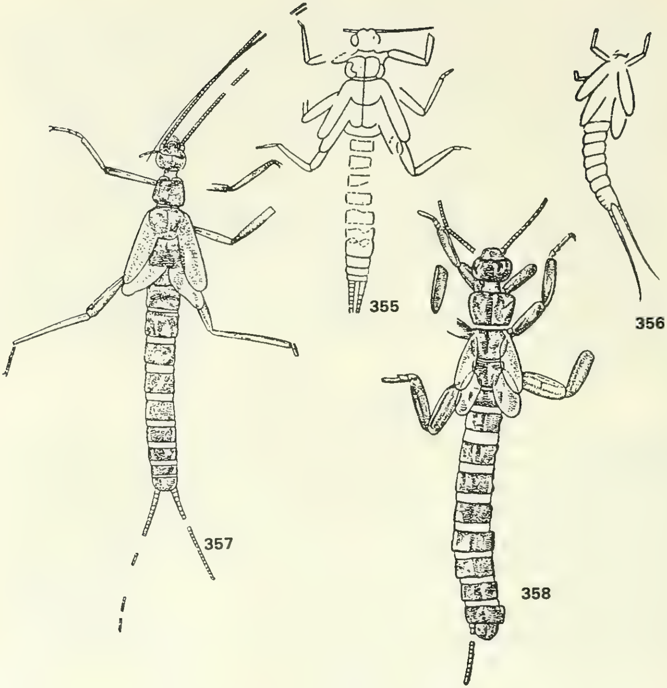
Family NEMOURIDAE Klapalek, 1905

One branch of R in fore and hindwings, starting very close to point of termination of posterior branches of SC on R, which at this point, these veins, together with rs-ma and base of RS form X-shaped pattern; r-rs located symmetrically in relation to this pattern; MA_1 and stem of MA form one straight vein from which MA_2 branches backward; occasionally proximal part of MA_2 resembles a false cross vein; MP + CuA does not branch (Fig. 352). Cretaceous to Recent. Three extinct genera from the Lower Cretaceous of China (*Sinoperla* Ping, 1928; *Perlariopsis* Ping, 1928; *Synonemoura* Ping, 1928) and a few genera in Recent fauna, one of which is also found in the Paleogene of Europe (Baltic amber).

137

Family LEUCTRIDAE Klapalek, 1905

In costal area of forewing not more than one branch of SC located at base of wing, resembling a cross vein between C and SC. SC either with a very short anterior branch, or terminating at anterior margin of wing, but its posterior branch resembles a subcostal cross vein; branches of R absent in subcostal area; branches of RS and MA straight and parallel; cross veins in area between MP + CuA and CuP nearly twice as large as those between MA and MP + CuA; CuP S-shaped, passing close to anal margin of wing in distal half bending far forward, extending parallel to the margin and reaching distal third of wing. In hindwing anojugal fan resembles a small projecting lobe with simple A_2 (Fig. 353). Paleogene to Recent. One genus in Recent fauna, known also from the Paleogene of Europe (Baltic amber) and Germany.



Figs. 355–358. Plecoptera incertae sedis.

355. *Uralonympha varica* G. Zalessky; nymph, × 3.3. Lower Permian, Urals (Yu. Zalessky, 1939). 356. *Permoleuctropsis gracilis* Martynov; nymph, × 6. Upper Permian, Southern Urals (Martynov, 1937). 357. *Mesoleuctra gracilis* Brauer, Redtenbacher and Ganglbauer; nymph, × 4. Lower Jurassic, Irkutsk province (original drawing). 358. *Platyperla platypoda* Brauer, Redtenbacher and Ganglbauer; nymph, × 3.6. Lower Jurassic, Irkutsk province (original drawing).

Family PERLIDAE Stephens, 1835

In costal area of forewings numerous short branches of SC, resemble cross veins; four or five short branches of R in subcostal area; RS forms three or four pectinate branches; between RS and MA a wide area enclosed distally by cross vein rs-ma; MP + CuA bent toward anterior margin of wing distally enclosing an area between MA and MP + CuA and forming four to six posteriorly directed pectinate branches; CuP usually straight. In hindwing, anojugal fan extensive with posterior-branching pectinate A_2 (Fig. 354). Paleogene to Recent. Few genera in Recent fauna, one of which is also known from the Paleogene of Europe (Baltic amber) and England.

138 Plecoptera Incertae sedis

Uralonympha G. Zalessky, 1939. Genotype—*U. varica* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Nymph: Pronotum wide. Wing rudiments narrow, long and placed at angle of approximately 30° to axis of body; base widely divergent, apices rounded. Cerci comparatively short. Length of body, without cerci, 10 mm (Fig. 355). One species. Lower Permian of Urals.

Permoleuctropsis Martynov, 1937. Genotype—*P. gracilis* Martynov, 1937; Permian, Orenburg province (Kargala). Nymph: wing rudiments sharply pointed, base close together. Length of cercus roughly equal to abdomen length. Length of body without cerci 5.3 mm (Fig. 356). One species. Permian of Pre-Urals.

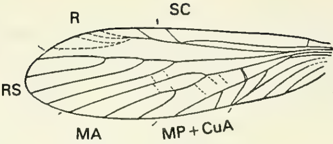
Mesoleuctra Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*M. gracilis* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province (Cheremkhovian series, Ust-Bailey). Nymph: head rounded; pronotum narrow and trapezoidal, narrower at anterior margin; wing rudiments located at a very small angle to longitudinal axis of body; legs long and slender; second tarsal segment shortest, the first a little longer and the third longest; length of cerci a little less than length of body. Length of body 18 mm (Fig. 357; Pl. IX, Fig. 1). Two species. Lower Jurassic of Irkutsk province and Kuznetsk basin. Lower Cretaceous of China.

Platyperla Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*P. platypoda* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province (Cheremkhovian series, Ust-Bailey). Nymph: Head rectangular; pronotum wide, quadrate, slightly narrow at posterior margin; wing, rudiments oval, directed at a small angle to axis of body; legs short, femur and tibia of all three pairs of legs wide and flat; first and second tarsal segment short and combined shorter than length of third; cerci long and slender. Length of body without appendages 18 mm (Fig. 358; Pl. IX, Fig. 2). One species. Lower Jurassic of Irkutsk province.

Plecopteroidea Incertae sedis

Family HYPOPERLIDAE Martynov, 1928

Small insects with membranous wings forming a sloping 'roof' in repose. Forewing: in costal area a strong cross vein extends basally between C and SC; SC terminates on R, single anterior branch extends toward anterior margin of



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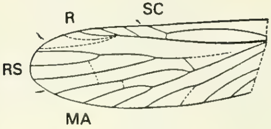

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Figs. 359–360. Family Hypoperlidae.

359. *Hypoperla elegans* Martynov; forewing, × 4.6. Upper Permian, Arkhangelsk province (Martynov, 1928). 360. *Hypoperlopsis splendens* G. Zalessky; forewing, × 3.4. Lower Permian, Urals (Yu. Zalessky, 1948).

wing; R forms two or three branches distally; RS branches pectinately; MA begins to branch approximately at a level with RS and forms up to three branches; MP fused with CuA, and the common stem forms three or four pectinate branches, proximal branches do not reach anal margin of wing; common stem slopes toward CuP. Two simple anal veins. Permian. Two genera.

Hypoperla Martynov, 1928. Genotype—*H. elegans* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: costal area broader than subcostal area in its distal half; branch of SC extends from the point of descent of SC up to R; RS with four branches; MP + CuA with four or five branches. Length of forewing approximately 10 mm (Fig. 359). One species. Upper Permian of Arkhangelsk province.

Hypoperlopsis G. Zalessky, 1948. Genotype—*H. splendens* G. Zalessky, 1948; Lower Permian, Permian province (Kungurian stage, Chekarda). Forewing: costal area narrower than subcostal area in distal half; branch of SC extends anteriorly to R from point of descent of SC; RS with three branches; MP + CuA with one or two branches. Length of forewing approximately 14 mm (Fig. 360). One species. Lower Permian of Urals.

139 Order EMBIOPTERA. Webspinners

(O.M. Martynova)

Medium or small sized insects (length of body 4–20 mm). Either wingless or with two pairs of narrow, similar wings; venation highly reduced; SC terminates approximately at wing midpoint, short and simple; RS originates at basal one-fourth of wing, either simple or with one branch; M and Cu fused at base; after separating from Cu M joins RS or branches, and then MA fused with RS for most of its length; MP an independent vein; CuA divided into a long CuA_1 extending along anal margin of wing and a short CuA_2; CuP absent; one anal vein, a few cross veins. Anal fan absent in hindwings.

Head prognathous and flat; mouthparts of biting type; antennae short, consisting of 15 to 30 segments; compound eyes weakly developed; ocelli absent. Pro- and metathorax shorter than mesothorax; legs short. Femora broad, particularly the metafemora; first segment of fore tarsus enlarged and expanded with silk glands; tarsi three segmented. Abdomen with 10 segments; cerci short; usually male cerci asymmetrical. Metamorphosis incomplete. Live in soil, under stones, bark. Herbivorous. Approximately 70 species in Recent fauna in the tropics and subtropics. Permian to Recent. Suborders: Sheimioidea and Euembiaria.

Suborder Sheimioidea

Males and females with wings equal to body length; longitudinal veins slightly bent toward distal posterior area; length of wing three times width. Female ovipositor short. Segments of cerci more than two. Permian. Family: Sheimiidae.

Family SHEIMIIDAE O.M. Martynova, 1958

Wings as long as body; SC terminates at C, slightly more distally than half of wing; free base of M longer than free base of RS, joined with RS up to bifurcation; RS leaves MA almost at midpoint of basal half of wing; Cu branches slightly more proximally than wing midpoint. Permian. One genus.

Sheimia O. Martynova, 1958. Genotype—*S. sojanensis* O.M. Martynova, 1958; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: R and RS not fused at apex; MA leaves RS at wing midpoint and is simple; CuA simple. Ovipositor as long as last three segments of abdomen. Cerci 10 to 12 segmented. Length of wing 1.8 mm (Fig. 361).

Suborder Euembiaria

Usually apterous, winged forms are only males; wings shorter than body; longitudinal veins straight; length of wing four times width. Ovipositor absent. Segments of cerci not more than two. Paleogene to Recent. Families: Clothodidae, Oligotomidae, Notoligotomidae, Embiidae. Last two from outside the USSR.

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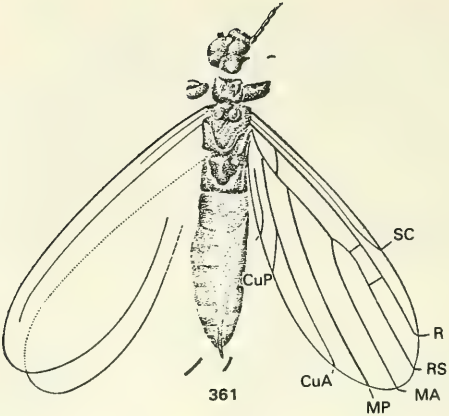
Family CLOTHODIDAE Tillyard, 1937

Males winged. Forewings: SC extends upto middle of wing; R terminates at anterior margin of wing; M branches at point of fusion with RS; MA with bifurcation; CuA_1 with one or two branches. Cerci with two segments, without



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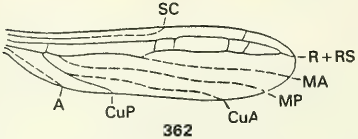

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139 Figs. 361–362. Order Embioptera.

361. *Sheimia sojanensis* O.M. Martynova; general view, × 14.5 Upper Permian, Arkhangelsk province (Martynova, 1958). 362. *Oligotoma saundersi* Westwood; forewing, × 8. Recent, Asia (Handlirsch, 1906).

modification; cerci of males symmetrical. Neogene to Recent. Two genera: one genus in Recent fauna and the other from the Miocene of North America.

Family OLIGOTOMIDAE Enderlein, 1909

Males winged. Forewings: SC extends up to middle of basal half of wing; R terminates at RS; RS simple; M does not branch until it fuses with RS; MA simple; CuA simple; long, branches at middle or basal half of wing; distal half passes close to anal margin of wing. Male cerci asymmetrical; 10th tergum bipartite; additional processes on left half of tergum and first segment of left cercus; cerci two-segmented (Fig. 362). Paleogene to Recent. Two genera in Recent fauna of Asia, North America and Australia. One genus from the Paleogene of Europe (Baltic amber) and another from the Pleistocene of East Africa.

Order MIOMOPTERA

(O.M. Martynova)

Two pairs of small, similar wings between 3.5 and 10 mm long; SC short, simple, terminates on C at approximately wing midpoint; distal end connected by cross vein with R; R with distal bifurcation; RS originates close to basal one-fourth of wing with two simple or bifurcating branches; M fused with CuA at base, separated from latter at basal one-fourth of wing; MA usually a free, sometimes without a base and connected by cross vein rs_{3+4}-ma, when it resembles a branch of RS; MP simple; Cu branches at base into a strong CuA with wide bifurcation (bufurcation absent in Permembiidae) and simple, weak CuP; two anal veins; cross veins few. In hindwing fan absent.

Head small, directed downward; antennae short and 12 or 13 segmented. Prothorax narrower than head; mesothorax approximately triangular and subequal to prothorax length; legs medium length and running type, similar; tarsi four segmented, first segment long and equal to the combined length of the other distal three segments; with two distal claws.

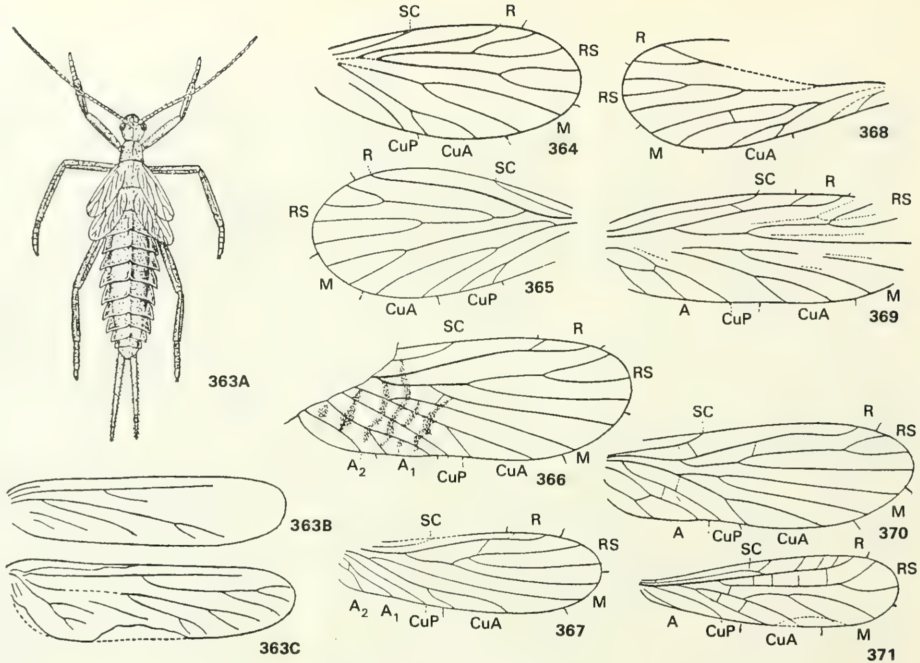
Body of nymph dorso-ventrally flattened. Head small; eyes big; antennae setaceous, many-segmented. Thorax indistinctly demarcated from abdomen; prothorax small, nearly quadrate; Meso- and metathorax subequal and have wing rudiments which are directed posteriorly; legs with tibia and femur equal; tibia flat, with short ridge along median line; tarsi five-segmented. Abdomen with 10 segments, 1–9 have lateral expansions; tenth segment with short terminal cerci, with closely fused segments. Apparently lived in running water and were predatory. Length of body up to 18 mm (Fig. 363A, B). Upper Carboniferous to Permian. Families: Archaemiopteridae, Palaeomanteidae, Permembiidae? (Fig. 371). Last encountered only outside the USSR.

Family ARCHAEMIOPTERIDAE Guthorl, 1939

Length of wing two times wing width; forewing with two branches of RS, each with a bifurcation; M leaves CuA more basally than origin of RS at wing base. Upper Carboniferous through Permian. Two genera.

Archaemioptera Guthorl, 1939. Genotype—*A. carbonaria* Guthorl, 1939; Upper Carboniferous, Western Europe (Lower Stephanian stage, Saar). R of forewings straight; terminates slightly more distally than midpoint of anterior margin; M shorter than its bifurcation, branches more proximal to central part of wing; bifurcation of CuA short. Length of wing 5.3 mm (Fig. 364). One species. Upper Carboniferous of Western Europe.

Tychtodelopterum O.M. Martynova, 1958. Genotype—*T. relictum* O.M. Martynova, 1958; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). R of forewing bent, terminates at median anterior wing margin; RS branches more distally than midpoint of basal half of wing; M branches more



Figs. 363–371. Order Miomoptera.

363. *Delopterum* sp.; nymph, A – general view, × 3; B – forewing of nymph, × 11; C – hindwing of nymph, × 11; Lower Permian, Kuznetsk basin (Sharov, 1906). 364. *Archaemioptera carbonaria* Guthorl; forewing, × 8.7. Upper Carboniferous, Western Europe (Gothorl, 1939). 365. *Tychtodelopterum relictum* O.M. Martynova; forewing, × 19. Upper Permian, Kuznetsk basin (Martynova, 1958). 366. *Miomatoneura frigida* Martynov; forewing, × 8.3. Upper Permian, Arkhangelsk province (original Fig.). 367. *Miomatoneurella reducta* O.M. Martynova; forewing, × 11.6. Upper Permian, Kuznetsk basin (Martynova, 1958). 368. *Palaeomantisca lata* Martynova; forewing, × 5. Lower Permian, Urals (Martynova, 1940). 369. *Palaeomantis schmidti* Handlirsch; forewing, × 10. Upper Permian, Pre-Urals (original Fig.). 370. *Delopterum incertum* (Martynova); forewing, × 10. Upper Permian, Pre-Urals (original Fig.) 371. *Permembia delicatula* Tillyard; forewing. Lower Permian, North America (Tillyard, 1937).

distally than wing midpoint and is twice as long as its bifurcation; bifurcation of CuA long. Length of wing 3.2 mm (Fig. 365). One species. Upper Permian of Kuznetsk basin.

141 Family PALAEOMANTEIDAE Handlirsch, 1906

(Delopteridae Sellards, 1909; Archisialidae Martynov, 1933)

Wings narrow, three times as long as wide; posterior branch of RS simple; M leaves CuA almost at same level as point of origin of RS. Permian. Five genera.

Miomatoneura Martynov, 1927. Genotype—*M. frigida* Martynov, 1927; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). RS_{1+2} of forewings with bifurcation; M joined with RS_{3+4} to form third branch of RS; base of MA resembles a cross vein. Length of wing 5 to 6.4 mm (Fig. 366). Four species. Upper Permian of Arkhangelsk province.

Miomatoneurella O.M. Martynova, 1958. Genotype—*M. reducta* O.M. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo I). Both branches of RS of forewings simple; MA fused with RS_{3+4}, without a base. Length of wing 4 mm (Fig. 367). One species. Upper Permian of Kuznetsk basin.

Palaeomantisca Martynov, 1940. Genotype—*P. lata* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Origin of RS of forewings more distal than midpoint of basal half of wing; RS_{1+2} longer, branching more distally than midpoint of wing; RS_{1+2} with bifurcation equal to
142 its length; M one-sixth length of bifurcation; MA not fused with RS; furrow absent along anal margin of wing. Length of anterior wing 9.5 mm (Fig. 368). One species. Lower Permian of Urals.

Palaeomantis Handlirsch, 1904. Genotype—*P. schmidti* Handlirsch, 1904; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). SC of forewing terminates at wing midpoint; RS originates more proximally than midpoint of basal half of wing, shorter than RS_{1+2} and branches more proximally than midpoint of wing; RS_{1+2} longer than bifurcation; MA not fused with RS, branches almost at same level; furrow absent along anal margin of wing. Length of wing 6 mm (Fig. 369). One species. Upper Permian of Pre-Urals.

Delopterum Sellards, 1909 (*Leptoneurula* Martynov, 1928; *Delopsocus* Tillyard, 1928; *Pseudomantis* Martynov, 1930; *Archisialis* Martynov, 1933). Genotype—*D. minutum* Sellards, 1909; Lower Permian, North America (Kansas). This genus differs from *Palaeomantis* in its narrower wing, presence of a small groove along anal margin of wing between apex of CuP and A and shorter SC. Length of forewing 3.5 to 10 mm (Fig. 370). 15 species. Permian of European part of the USSR, Kuznetsk basin and North America.

Order CALONEURODEA

(O.M. Martynova)

Two pairs of similar wings with almost straight, longitudinal, uniformly arranged cross veins; precostal and wedge-shaped anal area absent in forewings; SC long; R terminates at wing apex; branches of RS vary from one to seven; MA with one branch, or simple; MP, CuA and CuP simple. CuA and CuP close in family Enthygrammatidae, in all other families MP and CuA are close; MP and CuA terminate at midpoint of wing anal margin in Carboniferous species, and more distally in Permian ones.

Head medium size, hypognathous; long threadlike antennae with large, swollen basal segment. Pronotum quadrate. Legs long, similar; hindlegs slightly longer with a somewhat broad femur, jumping type. Abdomen medium size with short cerci. Middle Carboniferous to Permian. Families: Synomaloptilidae, Pleisiogrammatidae, Paleuthygrammatidae (Fig. 372), Euthygrammatidae, Caloneuridae (Fig. 373), Permobiellidae, Anomalogrammatidae, Genopterygidae. Last four occur outside the USSR.

Family SYNOMALOPTILIDAE Martynov, 1938

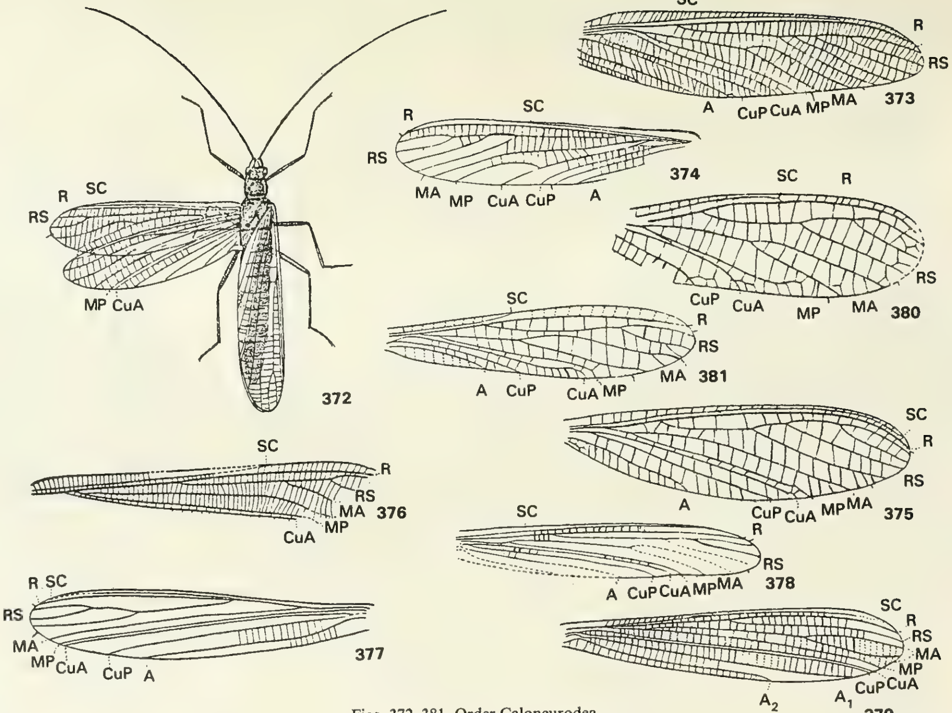
Forewing: RS originates at middle of proximal half of wing, branches more distally than wing median, with four branches; MA simple. MP and CuA fused for a considerable distance, diverge at apex and then bifurcate. Lower Permian. One genus.

Synomaloptila Martynov, 1938. Genotype—*S. longipennis* Martynov, 1938; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing; SC terminates at midpoint of anterior margin; MP terminates a little distal of SC apex; two long anal veins. Length of wing 27.5 mm (Fig. 374). One species. Lower Permian of Urals.

Family PLEISIOGRAMMATIDAE Carpenter, 1943

Forewing: SC long, terminates at wing apex, bent parallel to anterior margin of wing like R; RS originates slightly distad of midpoint of wing basal half and branches slightly distad of wing midpoint; RS with three or four branches; MA simple or with a bifurcation; MP and CuA close together, terminate slightly more proximal to midpoint of apical margin of wing; anal veins short. Lower Permian. One genus.

Pleisiogramma Carpenter, 1943; Genotype—*P. mediale* Carpenter, 1943; Lower Permian, North America (Kansas). Base of forewing narrow, petiolate; A_1 terminates more proximally than wing midpoint; A_2 short. Length of wing 15–18 mm (Fig. 375). Three species. Lower Permian of North America and Kuznetsk basin.



Figs. 372–381. Order Caloneurodea.

372. *Paleuthygramma tenuicorne* Martynov; (reconstruction), × 1.5. Lower Permian, Urals (Martynov, 1938). 373. *Caloneura dawsoni* Brongniart; forewing, × 1. Carboniferous, Western Europe (Carpenter, 1948). 374. *Synomaloptila longipennis* Martynov; forewing, × 2. Lower Permian, Urals (Martynov, 1938). 375. *Plesiogramma mediale* Carpenter; forewing. × 3.6. Lower Permian, North America (Carpenter, 1943; interpretation of venation by O.M. Martynova). 376. *Vilvia densinervosa* G. Zalessky; part of wing, × 2. Lower Permian, Urals (Yu. Zalessky, 1933). 377. *Pseudogramma aberrans* (Martynov); forewing, × 3.4. Upper Permian, Arkhangelsk province (Martynov, 1938). 378. *Vilviopsis extensa* Martynov; forewing, × 2. Upper Permian, Arkhangelsk province (Martynov, 1938). 379. *Euthygramma parallellum* Martynov; forewing, × 2.5. Upper Permian, Arkhangelsk province (Martynov, 1938). 380. *Permobiella perspicua* Tillyard; forewing, × 5. Lower Permian, North America (Carpenter, 1943). 381. *Anomalogramma parvum* Carpenter; forewing, × 6. Lower Permian, North America (Carpenter, 1943; interpretation of venation by O.M. Martynova).

Family PALEUTHYGRAMMATIDAE Carpenter, 1943

Forewing: SC long, terminates at midpoint of anterior margin of wing or slightly more distally; RS originates proximal to median, two or three branches at middle 143 of anteromedian wing area; MA with a bifurcation, or simple; MP and CuA terminate at midpoint of wing apex, or more distally; two anal veins; A_2 long. Permian. Five genera.

Paleuthygramma Martynov, 1930. Genotype—*P. tenuicorne* Martynov, 1930; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing: SC straight, not reaching wing apex; RS with a short bifurcation; A_1 terminates considerably more distally than midpoint of anal margin. Length of wing 18–22 mm (Fig. 372). Two species. Lower Permian of Urals and North America.

Vilvia G. Zalessky, 1933. Genotype—*V. densinervosa* G. Zalessky, 1933; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing: termination of SC and branching of RS in middle of upper half of wing; RS three-branched; MA simple; MP and CuA terminate more distally than SC; cross veins densely packed. Length of wing 30 mm (Fig. 376). One species. Lower Permian of Urals.

Pseudogramma Carpenter, 1943. Genotype—*Euthygramma aberrans* Martynov, 1938; Upper Permian, Arkhangelsk province (Kazanian stage, 144 Soyana). Forewing: SC terminates a slightly distad and RS branches slightly proximad than middle of upper half of wing; MA simple; MP and CuA terminate slightly proximad than SC; A_1 terminates more distally than midpoint of anal margin. Length of wing 17.5 mm (Fig. 377). One species. Upper Permian, Arkhangelsk province.

Vilviopsis Martynov, 1938. Genotype—*V. extensa* Martynov, 1938; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: SC terminates at anteromedian wing margin; RS branches slightly more proximally, with three branches; MA with bifurcation; MP and CuA terminate at midpoint of apical wing margin; A_1 terminates slightly distad of middle anal margin. Length of wing 28 mm (Fig. 378). One species. Upper Permian of Arkhangelsk province.

Outside the USSR: *Aspidoneura* Carpenter, 1943.

Family EUTHYGRAMMATIDAE Martynov, 1928

Forewing: RS simple, originating at wing midpoint; CuA and CuP close. Upper Permian. One genus.

Euthygramma Martynov, 1928. Genotype—*E. parallellum* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: MA with a bifurcation; CuA and CuP terminate on apical wing margin; A_1 terminates slightly more proximal than CuA. Length of wing 21 to 24 mm (Fig. 379). Two species. Upper Permian of Arkhangelsk province and Pre-Urals.

Family CALONEURIDAE Handlirsch, 1906

Forewing: RS originates at midpoint of proximal half of wing, branches at wing midpoint or slightly distad, with four to seven branches; MP and CuA close, originate at wing midpoint or slightly distad. Length of wing 28–50 mm (Fig. 373). Middle to Upper Carboniferous. Four genera.

Outside the USSR: *Caloneura* Brongniart, 1885; *Confusio* Handlirsch, 1919; *Homaloptilla* Meunier, 1911 and *Euthyneura* Pruvost, 1919.

Family PERMOBIELLIDAE Tillyard, 1937

Forewing: SC short, terminates at approximately midpoint of anterior margin; R parallel to anterior wing margin; RS originates slightly proximal to middle of wing and branches more distally, with three branches; MA with a bifurcation; MP and CuA diverge slightly at apex, and terminate at midpoint of anal margin; longitudinal veins slightly bent; cross veins sparse, with many inclined veins. Length of wing 11 mm (Fig. 380). One genus. Lower Permian of North America.

Family ANOMALOGRAMMATIDAE Carpenter, 1943

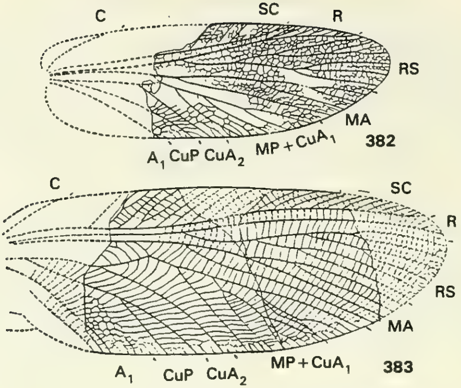
Forewing: SC short, terminates proximad to anteromedian wing margin; R almost straight and not parallel to anterior wing margin; RS originates more proximally than wing midpoint, with two branches at beginning of distal one-fourth of wing; MA with a bifurcation; MP and CuA close, terminate slightly proximad to midpoint of distal half of anal margin; cross veins sparse and straight. Length of wing 9 mm (Fig. 381). Lower Permian of North America. One genus—*Anomalogramma* Carpenter, 1943.

SUPERORDER ORTHOPTEROIDEA. Grasshopper-like insects

(B.B. Rohdendorf)

Venation of forewing highly specialized: R isolated from RS; latter vein usually with comb-like parallel branches. Dissimilarity of wings always distinct: hindwings broad, forewings narrow and thick. Anojugal fan of hindwings large, composed of branches of anal veins. Wingless and short-winged forms often encountered. Body elongated, cylindrical, or sometimes laterally compressed, rarely flat. Legs locomotory; often hindlegs modified for jumping; fore- and midlegs invariably shorter than hindlegs. Ovipositor well-developed or, rarely, reduced. Cerci normally short and unsegmented.

This ancient group is apparently related to primitive cockroach-like forms, from which it diverged during the Carboniferous period. Evolution of 145 orthopteroids was determined, apparently by associations with the vegetation among which these insects lived. Among Recent fauna, orthopteroids are one of the flourishing groups of heterometabolous insects, seen most extensively in



Figs. 382-383. Family Sthenaropodidae.
382. *Adumbratus extentus* Sharov; forewing, × 2.2. Lower Permian, Kuznetsk basin (Sharov, 1961). 383. *Kamia angustovenosa* Martynov; forewing, × 1.2. Upper Permian, Pre-Urals (Martynov, 1930).

regions with warm and sultry climate. Upper Carboniferous to Recent. Orders: Protorthoptera, Orthoptera (= Saltatoria), Phasmatodea, Glosselytrodea. The first and last are extinct.

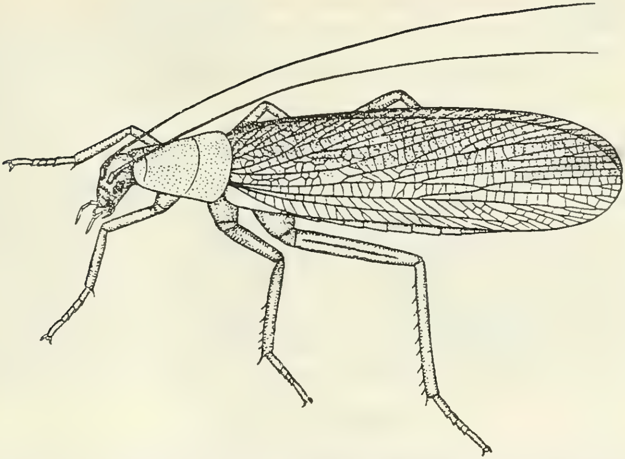
Order PROTORTHOPTERA

(A.G. Sharov)

Precostal area of forewing not large, devoid of any trace of veins. Sharply differentiated concave MA_2 absent; CuP usually branching at distal part; A_1 and A_2 branch all along length of anal area, forming many short branches. Body flattened dorsoventrally. Wings in repose lying flat on back. Pronotum longitudinally elongated. Femur of hind leg occasionally flat, but apparently of 'running' type, or very weakly saltatorial; tibia of hindlegs without regular rows of spines along posterior margin. Carboniferous of Permian. One family: Sthenaropodidae.

Family STHENAROPODIDAE Handlirsch, 1906

Wings broad; anterior margin of forewing gently convex; anterior branch of MA usually forming an anastomosis with stem of RS; anastomosing MP + CuA equidistant from anterior and anal margins of wing, or close to anterior margin;
146 stem MP + CuA short, disposed at an angle to anal margin of wing, forming four



145 Fig. 384. *Sthenaropoda fischeri* Brongniart. Reconstruction, × 1.3. Upper Carboniferous, Western Europe (Sharov, 1960a).

to six branches. Carboniferous to Permian. Nine genera.

Adumbratus Sharov, 1961. Genotype—*A. extentus* Sharov, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing with pointed apex; costal area broad; two or three rows of cells between major veins; SC terminating at some distance from apex of wing; R with many short branches at distal part, often exhibiting secondary branching; RS branching dichotomously; anastomosing MP-CuA placed equidistant from anterior and anal margins of wing. Length of anterior wings 25–27 mm (Fig. 382; P1. IX, Fig. 3). Two species. Lower Permian of Kuznetsk basin.

Kamia Martynov, 1928 (*Spongoneura* Martynov, 1928; *Permacridites* Martynov, 1930). Genotype—*K. angustovenosa* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Forewing: simple cross veins between longitudinal veins; costal area broad; SC running almost to apex of wing; R with not more than two or three branches at distal part; RS forming up to six branches; MA passing very close to R and RS, strongly compressed, forming up to four pectinately disposed branches; supporting veins along anal margin between longitudinal veins formed together with cross veins of network. Length of anterior wing 60–65 mm (Fig. 383; Pl. IX, Fig. 4). One genus. Upper Permian of Pre-Urals.

Outside the USSR: *Sthenaropoda* Brongniart, 1885 (=*Archaeacridites* Meunier, 1909) (Fig. 384); *Macrophlebium* Goldenberg, 1869; *Berlichia*

Schlechtendal, 1913; *Acridites* Germar, 1842; *Palaeoedischia* Meunier, 1914; *Nacekomia* Richardson, 1956; ? *Pseudooedischia* Handlirsch, 1919.

Order ORTHOPTERA (Saltatoria)

(A.G. Sharov)

Precostal area extensive, with numerous branches of costa and precosta. A sharply differentiated, concave; MA_2 present. CuP and A_1 not branching; A_2 branching at extreme base of wing, its branches similar to those of A_1, in form of two or three simple parallel veins. In hindwing anterior branch of A_2 simple, without comb-like veins. Body laterally compressed, or rounded in cross section; wings in repose lying along sides of body. Head hypognathous. Pronotum saddle-shaped, short, rarely, with long prolongation; hind legs of jumping type; femur elongated, stout; tibia with two rows of spines along posterior margin. Eggs laid in soil or stalks and leaves with ovipositors. Carboniferous to Recent. Suborders: Ensifera, Caelifera.

Suborder Ensifera

Antennae thread-like, longer than body, with more than thirty segments; segments weakly delimited, without any sharp boundaries. Hind femur smooth, without longitudinal keel. Ovipositor long, saber-like, adapted for piercing and pushing into substratum into which eggs are laid. Carboniferous to Recent. Three superfamilies: Oedischiidea, Gryllidea, Tettigoniidea.

SUPERFAMILY OEDISCHIIDEA

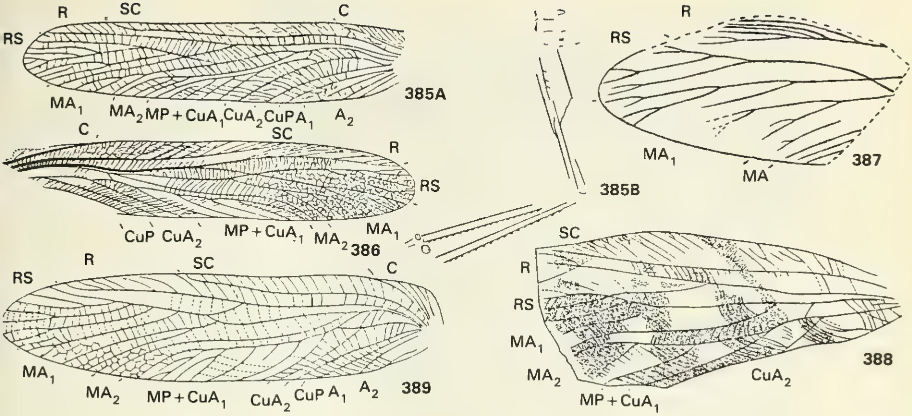
Forewings narrow, long, membranous; usually more than three branches of MA; branches of MP + CuA, if present, usually pectinate. Sound-producing organs absent, or present only in embryo. Tympanal organs absent from tibiae of forelegs. Carboniferous to Jurassic. Six families: Oedischiidae, Tcholmanvissiidae, Permelcanidae, Elcanidae, Permorhaphidiidae, Bintoniellidae. Last two occur outside the USSR.

Family OEDISCHIIDAE Handlirsch, 1906

(Pruvostitidae M. Zalessky, 1928)

Anterior branch of MA_1 forming an anastomosis with RS in forewing; proximal part of RS (up to anastomosis) in form of a long, clear longitudinal vein—base of RS; cross veins between this and R and also MA_1; MA_1 and distal
147 part of stem of RS (after anastomosis) lacking character of a single vein; MP + CuA usually with comb-like branches running toward anal margin of wing. Carboniferous to Permian. Nine genera.

Oedischia Brongniart, 1885. Genotype—*O. williamsoni* Brongniart, 1885;



Figs. 385–389. Family Oedischiidae.

385. *Oedischia williamsoni* Brongniart; A—forewing, B—hindwing, × 1.1. Upper Carboniferous, Western Europe (Handlirsch, 1906). 386. *Jasvia reticulata* G. Zalessky; forewing, × 1.2. Lower Permian, Urals (G. Zalessky, 1934). 387. *Rimnosentomon grande* G. Zalessky; fragment of forewing, × 1.4. Lower Permian, Urals (Yu. Zalessky, 1955). 388. *Pruvostites takhtachurensis* M. Zalessky; forewing, × 1.3. Upper Permian, Urals (M. Zalessky, 1928). 389. *Metoedischia magnifica* Martynov; forewing, × 2.2. Upper Permian, Arkhangelsk province (Martynov, 1928).

Upper Carboniferous, France (Stephanian stage). Costal area short, broad at base; branches of SC simple; R with six or seven short, simple branches in distal part; free branch of MA_1 forming three branches at distal part; MA_2 with three anojugal branches; $MP + CuA_1$ with five short branches which abruptly turn toward anal margin; anal area short; simple cross veins occurring between longitudinal veins. Length of forewing 62 mm (Fig. 385A, B). Two species. Upper Carboniferous of France.

Jasvia G. Zalessky, 1934. Genotype—*J. reticulata* G. Zalessky, 1934; Lower Permian, Permian province (Kungurian stage, Yazva). Costal area elongated, narrow; up to six branches of SC and R, sometimes with bifurcations; free branches of MA at distal part; MA_2 does not branch; $MP + CuA_1$ with five full branches running toward anal margin; C- and S-shaped cross veins predominate in proximal half of wing; in distal half of wing three to four rows of small cells between longitudinal veins. Length of forewing 61 mm (Fig. 386; P1. X, Fig. 1). One species. Lower Permian of Urals.

Rimnosentomon G. Zalessky, 1955. Genotype—*R. grande* G. Zalessky, 1955; Lower Permian, Perm Province (Kungurian stage, Morozkovo). Branches of R numerous, running very close together; after anastomosis with MA_1, RS bent toward anterior margin; free branch of MA_1 with broad bifurcation; branches of $MP + CuA_1$ forming dense group at distal part. Length of forewing about 80 mm (Fig. 387). One species. Lower Permian of Urals.

Pruvostites M. Zalessky, 1928. Genotype—*P. takhtachurensis* M. Zalessky, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tachtashur). Anterior margin of forewing markedly convex; some branches of SC with bifurcations; two independent branches of MA_1; MP not branching; $MP + CuA_1$ forming six or seven branches; cross veins simple or Y-shaped, running very close together. Length of forewing about 60 mm (Fig. 388). One species. Upper Permian of Pre-Urals.

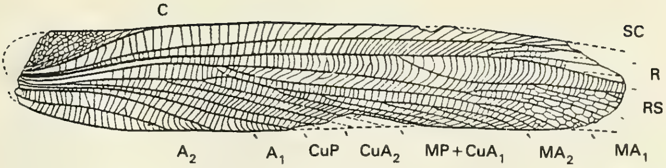
Metoedischia Martynov, 1928. Genotype—*M. magnifica* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Branches of SC and R without bifurcations; RS pectinate; independent branch of MA_1 bifurcated; MA_2 not branching; MP + CuA runs parallel to anal margin, forms
148 eight or nine branches; cross veins primarily simple, rarely inclined; two or three rows of cells lying between branches of M close to anal margin of wing. Length of forewing about 35 mm (Fig. 389; Pl. X, Fig. 2). Three species. Upper Carboniferous of Portugal; Upper Permian of Arkhangelsk province and Pre-Urals.

Also from outside the USSR: ? *Genetomum* Scudder, 1885; ? *Progenentomum* Handlirsch, 1906; *Plesioidischia* Schlechtendal, 1913; *Permoedischia* Kukalova, 1955.

Family TCHOLMANVISSIIDAE G. Zalessky, 1934

In forewing costal area short and broad; branches of SC in proximal part of costal area resembling cross veins and almost perpendicular to C and SC; SC terminating not far from wing apex; R with six to eight long branches at end, leaving R at a small angle with numerous simple cross veins between them; radial area markedly broadened at central part, with C-shaped bent cross veins forming convex region at apex, very closely packed, sometimes connected by inclined veins; RS not anastomosing with anterior branch of MA; MA_1 and MA_2 branching very late and forming two branches, or MA_1 forming three branches and MA_2 not branching; slanting S-shaped cross veins between MA_1 and MA_2; proximal anastomosis of MP + CuA resulting in two or three branches of CuA; three anal veins; cross veins between ends of these and anal margin of wing bent like a 'C' with convexity toward base of wing; two or three rows of cells between branches of RS and MA at distal part of wing and sometimes along anal margin of anal area. R and RS not anastomosing in hindwing; radial area narrow with cross veins sloping toward apex. Permian. One genus.

Pinegia Martynov, 1928 (*Thnetodes* Martynov, 1928; *Tcholmanvissia* M. Zalessky, 1929; *Kamaites* M. Zalessky, 1929, *Tillyardiella* Martynov, 1930). Genotype—*P. oknowae* Martynov, 1928; Upper Permian, Arkhangelsk



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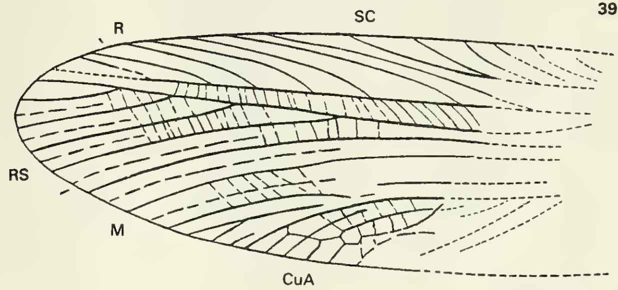

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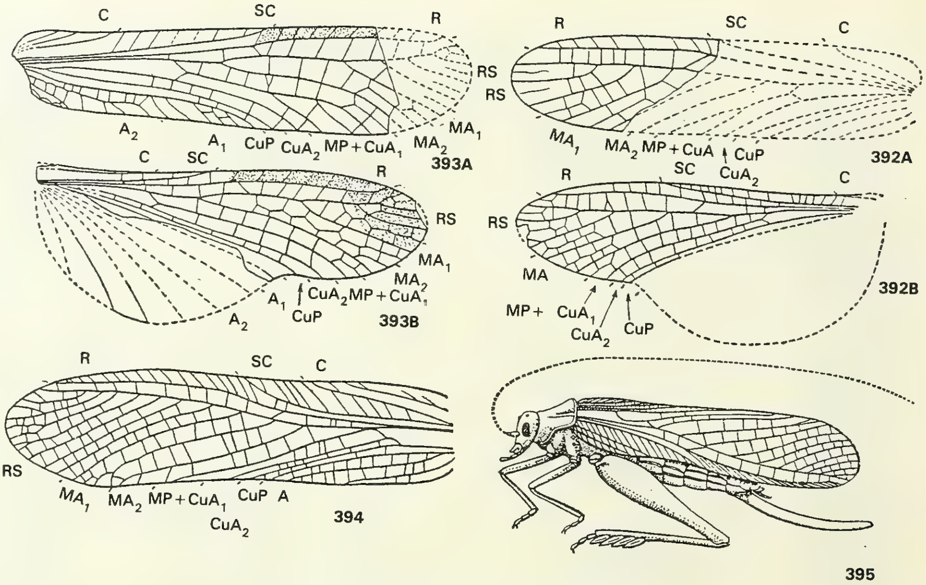
Figs. 390–391. Family Tcholmanvissiidae.

390. *Pinegia longipes* Martynov; forewing, × 1.4. Lower Permian, Urals (original Fig.). 391. *P. oknowae* Martynov; distal part of hindwing, × 4.4. Upper Permian, Arkhangelsk province (Martynov, 1928).

province (Kazanian stage, Soyana). Forewing long, narrow, with straight anterior margin in middle one-third of length; length six to seven times width; branches of SC often entering costal area, no regular rows of cross veins between them; isolated cross veins encountered; branches of MP + CuA closely packed, at a very small angle to anal margin of wing. Length of forewing 60–90 mm (Figs. 390; Pl. X, Figs. 3, 4). Five species. Lower Permian of Urals; Upper Permian of Pre-Urals and Arkhangelsk province.

149 Family PERMELCANIDAE Sharov, 1962

Small orthopterans with slender, membranous wings; SC terminating at level of origin of RS or somewhat more distally; part of subcostal area more distal than end of SC, narrow and usually pigmented, with short branches of R disposed at an angle of 60° or more; anterior branch of MA in both fore- and hindwings anastomosing with RS; proximal part of RS up to anastomosis very short, resembling inclined cross veins; no cross veins between it and R or MA; in radial area, rare simple cross veins present; MA_1 and distal part of stem of RS (after anastomosis) comprising single vein; trunk MP + CuA branching very late and forming not more than two or three branches; anal area very long, almost one-



149

Figs. 392–395. Families Permelcanidae and Elcanidae.

392. *Proelcana uralica* Sharov; A—forewing, B—hindwing, × 4.6. Lower Permian, Urals (Sharov, 1962). 393. *Permelcana sojanense* Sharovi A—forewing, × 6; B—hindwing. Upper Permian, Arkhangelsk province (Sharov, 1962). 394. *Elcana reticulata* Handlirsch; forewing, × 3.8. Lower Jurassic, Western Europe (Handlirsch, 1925). 395. *Elcana* sp.; (reconstruction), × 2.7. Lower Jurassic, Western Europe (Handlirsch, 1925).

half of length of wing; anal veins with short false branches at end arising from cross veins. In both fore- and hindwings intercalary veins predominate only in apex of wing, with large honeycomb-like cells. Lower and Upper Permian. Three genera.

Proelcana Sharov, 1962. Genotype—*P. uralica* Sharov, 1962; Lower Permian, Perm province (Kungurian stage, Chekarda). Anterior margin of forewing slightly convex; SC terminating slightly proximally to origin of RS; RS forming up to four branches: proximal branch originating close to origin of RS at a distance less than width of radial area; the two distal most branches running almost parallel and bending somewhat at their apices toward anterior margin of wing; one independent branch of MA_1. In hindwing SC terminating more distally than origin of RS; branches of RS disposed as in forewing; free branch of MA_1 absent. Length of forewing around 15 mm (Fig. 392). One species. Lower Permian of Urals.

150 *Permelcana* Sharov, 1962. Genotype—*P. sojanense* Sharov, 1962; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Anterior margin of forewing straight; precostal area narrow, with two or three branches; SC terminating at level of origin of RS; stem of RS slightly bent toward anterior margin, forming five to six branches: proximal branch originating near origin of RS and longer than width of radial area from origin of RS; two extremely distal branches divergent, directed toward apex of wing; independent branches of MA_1 absent. In hindwing SC terminating more proximally than origin of RS; branches of RS and MA occupying similar position as in forewing. Length of forewing 12–13 mm (Fig. 393; Pl. XI, Fig. 1). Two species. Upper Permian of Arkhangelsk province and Pre-Urals.

Outside the USSR: ?*Elcanopsis* Tillyard, 1918.

Family ELCANIDAE Handlirsch, 1906

Forewing: anterior and anal margins slightly concave, forming a constriction in middle of wing; in precostal area, in front of costa and parallel to it, another vein (probably precosta) present, from which short branches run forward; SC with comb-like branches at distal part, terminating more distally than origin of RS; stems of MA and RS forming a single vein from which branches of RS and MA are directed backward in form of a comb; $MP + CuA_1$ not branching or having only one or two very short offshoots toward anal margin of wing resembling cross veins; CuA leaving CuP close to origin of CuA_2; CuA_2 passing very close to CuP; anal area considerably shorter than one-half of length of wing. In hindwing R, RS, MA and their branches disposed as in anterior wing; CuA leaving CuP at base of wing; anal fan as wide as wing. Antennae long and thread-like. Hind femora strong, stout; spines along posterior margin of hind tibiae flat, platelike. Length of ovipositor equal to length of abdomen (Figs. 394, 395). Jurassic. Two genera (more than 100 species) reported from outside the USSR.

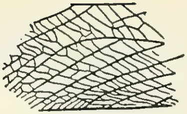


Fig. 396. *Thnetus stuckenbergi* Handlirsch; Fragment of forewing, × 2.3. Upper Permian, Urals (Handlirsch, 1906).

Oedischiidea Incertae sedis

Thnetus Handlirsch, 1904. Genotype—*T. stuckenbergi* Handlirsch, 1904; Upper Permian, Kirov province (Kazanian stage, Soyana). Fragment of forewing with part of MA and MP + CuA; at anal margin of wing between longitudinal veins two or three intercalary veins connected by cross veins, which in more proximal part are simple, Y- and K- shaped. Length of fragment of forewing 13 mm (Fig. 396). (Fragment suggests that it perhaps belongs to a representative of family Oedischiidea or family Tscholmanvissiidae.) One species. Upper Permian of Pre-Urals.

Outside the USSR: *Mesogryllacris* Riek, 1955 and ?*Proparagryllacris* Riek, 1956.

SUPERFAMILY GRYLLIDEA

Forewings usually broad; branches of MA not more than three, often two: MA$_1$ and MA$_2$; MA$_1$ sometimes two-branched; MA$_1$ not anastomosing with RS both in forewing and hindwing; occasionally MA$_1$ reduced; branches of MP + CuA usually irregularly pectinate toward anal margin of wing; three or four anal veins. Forewings of males with sound-producing mechanism, in which CuP and anal veins markedly bent toward hind margin; similar structure observed in both right and left wings; sometimes sound apparatus secondarily reduced. Tibiae of forelegs usually provided with tympanal organs. Triassic to Recent. Seven

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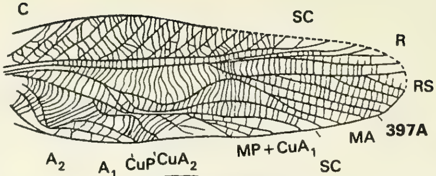
151 Figs. 397–403. Families Haglidae, Gryllacrididae and Tochorkuphlebiidae.

397. *Hagla gracilis* Giebel; forewings, × 1.5. A—of male; B—of female. Lower Jurassic, Western Europe (Zeuner, 1939). 398. *Aboilus columnatus* Martynov; A—forewing of male, × 1.5 (original Fig.); B—hindwing, × 1.3 (Martynov, 1925; damaged, but restored impression). Upper Jurassic, southern Kazakhstan. 399. *Pseudohagla pospelovi* (O.M. Martynova); forewing of female, × 1.9. Lower Jurassic, Kuznetsk basin (original Fig.). 400. *Archaboilus shurabicus* Martynov; forewing of male, × 1.1. Lower Jurassic, Central Asia (Martynov, 1937). 401. *Pseudohumbertiella grandis* (Brauer, Redtenbacher et Ganglbauer); fragment of forewing, × 2.2. Lower Jurassic, Irkutsk province (Brauer, Redtenbacher and Ganglbauer, 1889). 402. *Zeuneroptera scotica* (Zeuner); forewing, × 2.3. Tertiary deposits of Scotland (original Fig. from photograph). 403. *Tchorkuphlebia compressa* Martynov; forewing, × 2. Lower Jurassic, Central Asia (original Fig.).



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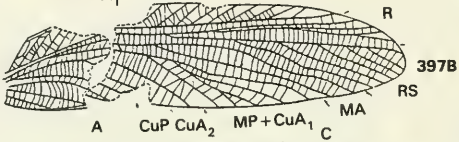

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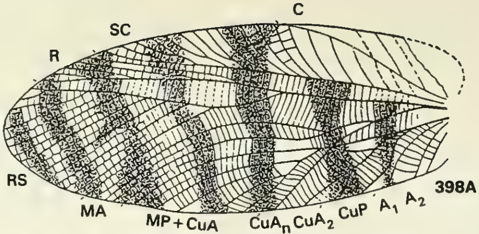

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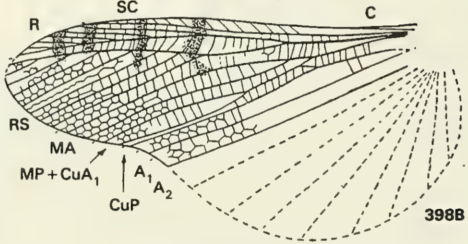

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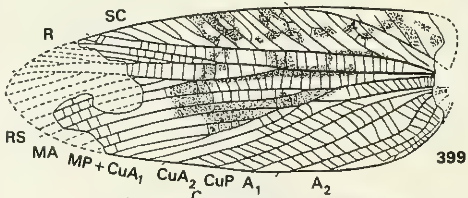

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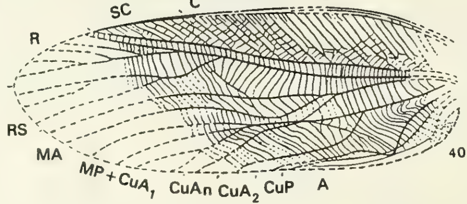

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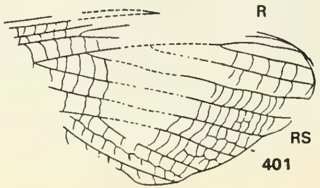

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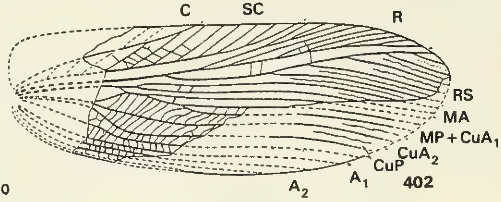

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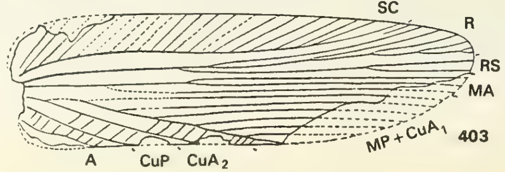

403

families: Haglidae, Gryllacrididae, Tchorkuphlebiidae, Isfaropteridae, Gryllidae, Gryllotalpidae, Schizodactylidae. Last family not known in fossil form.

Family HAGLIDAE Handlirsch, 1906

(Pamphagopsidae Martynov, 1925; Aboilidae Martynov, 1925; Prophalangopseidae Handlirsch, 1929)

R and RS always with branches; branches of RS arranged pectinately backward; MA_1 and MA_2 always present, reaching hind margin of wing; branches of MP + CuA do not exceed four; second proximal branch of CuA usually isolated from more distal branches, leaving junction of MP with CuA, or somewhat more distally; anal area short, not stretching beyond midpoint of wing; usually shorter than one-half of length of wing. Triassic to Recent. Three subfamilies: Haglinae, Prophalangopseinae, Cyrtophyllitinae.

151 Subfamily Haglinae Zeuner, 1935

(Prohaglinae Riek, 1954)

Forewing: C distinct and short; proximal branches of SC running parallel to C; different types of cross veins between distal side of C and proximal branch of SC; no regular intercalary veins between branches of SC. Strong slanting vein present between point of junction of MP and CuA; in wings of males most proximal branch of CuA absent. Triassic to Recent. Four genera, all from outside the USSR: *Prohagla* Riek, 1954; *Neohagla* Riek, 1955; *Zalmona* Giebel, 1856; *Hagla* Giebel, 1856 (Fig. 397A, B).

152 Subfamily Prophalangopsinae Caudel, 1911

Costa long, in contact with proximal branches of SC; regular intercalary veins between branches of SC absent. In wings of males a tough slanting intercubital vein arising from point of contact of MP and CuA, terminating on proximal branch of CuA. Lower Jurassic to Recent. Seven genera.

Aboilus Martynov, 1925 (*Pamphagopsis* Martynov, 1925; *Syndesmophyllum* Martynov, 1934). Genotype—*A. fasciatus* Martynov, 1925; Upper Jurassic, Chikent province (Malm, Karatau). Anterior margin of forewing markedly convex; second proximal branch of CuA originating at point of fusion of MP and CuA; between branches of RS and MA two rows of honeycomb-like or quadrangular cells; six to seven bands of cross veins come up to apex of wing. Length of forewing 45–80 mm (Fig. 398A, B; Pl. XI, Fig. 2). Four species. Lower Jurassic of Central Asia; Upper Jurassic of Kazakhstan.

Pseudohagla Sharov, gen. nov. Genotype—*Hagla pospelovi* O.M. Martynova, 1949; Jurassic, Kuznets basin (Conglomerate series, Korchakol). Proximal branches of SC terminating on C, strongly sloping toward SC and bent toward base of wing; second proximal branch of CuA leaving CuA more distally than point of fusion of MP and CuA; only simple cross veins present between branches of all veins except branches of SC. Randomly distributed small dark spots on wing. Length of forewing around 40 mm (Fig. 399, Pl. XI, Fig. 3). One species. Jurassic of Kuznetsk basin.

Outside the USSR: *Pycnophlebia* Deichmuller, 1886; *Mesogryllus* Handlirsch, 1908; *Termitidium* Westwood, 1854; *Prophalangopsis* Walker, 1871; *Cyphoderris* Uhler, 1864. Last two known to occur only in Recent fauna.

Subfamily Cyrtophyllitinae Zeuner, 1935

Costa and its branches in wings of males not distinguishable from branches of SC probably because of disappearance of C; precostal area distinct only in proximal part of wing in the form of a long narrow band, occasionally reaching midpoint of wing or a point a little more distal; costal area very wide with regular intercalary veins between branches of SC; a long cross vein sometimes passes from MA_1 toward RS, traversing over other cross veins. In wings of males a strong intercubital vein runs from junction of MP and CuA. Jurassic. Four genera.

Archaboilus Martynov, 1937. Genotype—*A. kisyl-kiensis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kisyl-Kia). Subcostal area without distinct narrowing toward proximal part; R divides very close to origin of RS and forms up to five branches; RS leaves R at an acute angle and forms three or four branches. Length of forewing 45–50 mm (Fig. 400; Pl. XI, Fig. 40). Three species. Lower Jurassic, Central Asia.

Outside the USSR: *Cyrtophyllites* Oppenheim, 1888; ?*Procyrtophyllites* Zeuner, 1935 and *Liassophyllum* Zeuner, 1935.

Haglidae Incertae sedis

Pseudohumbertiella Handlirsch, 1906. Genotype—*Humbertiella grandis* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province (Cheremchovian series, Ust-Bailey). Hindwing (fragment): branches of R running almost parallel to anterior margin of wing; RS with up to six branches; anterior branch of MA with bifurcation; two rows of cells between branches of RS and M in distal part. Length of hindwing around 50 mm (Fig. 401). One species. Lower Jurassic of Irkutsk province.

Outside the USSR: *Notopamphagopsis* Cabrera, 1928; *Zalmonites* Handlirsch, 1908; *Euspilopteron* Cockerell, 1915; *Jurassobatea* Zeuner, 1937 and *Palaeorehnia* Cockerell, 1908.

Family GRYLLACRIDIAE Stal, 1874

Forewing: C long, usually reaching midpoint of wing; many branches of SC not reaching anterior margin of wing, but terminating at C and usually resembling cross veins between C and SC. In wings with the most archaic venation (Fig. 402) R and RS of the type encountered in family Haglidae; in most representatives of Recent fauna R and RS with few branches or none at all; MP + CuA forms not more than three branches; MA branching off MP + CuA, CuP and anal veins running farther forward and passing almost parallel to anal margin of wing; anal area extending almost to apex of wing; simple cross veins predominating. Sound producing organs absent. Tympanal organs on anterior tibiae usually absent, rarely rudimentary or distinct. Often wingless. Recent. Species living primarily in tropics and subtropics. Paleogene to Recent. Subfamilies: Palaeorehniinae Stenopelmatinae, Rhaphidophorinae, Lezininae, Gryllacridinae, Henicinae, Deinacridinae; only the first three families known to have fossil representatives. First two occur outside of the USSR.

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Subfamily Palaeorehniinae Zeuner, 1937

C comparatively short, not reaching midpoint of wing; R forming six or more branches; two or three branches of RS terminating short of apex of wing; two rows of cells between branches of RS; MA two-branched; MP + CuA_1 forming three long branches; CuP with a sharp bend. Tertiary to Recent. One genus.

Zeuneroptera Sharov, gen. nov. Genotype—*Palaeorhenia scotica* Zeuner, 1939; Tertiary deposits, Scotland. Forewing: most proximal branch of R branching secondarily; stem of RS bent like an "S"; with up to six branches; $MA_1 + MA_2$ exhibits wave-like bend; wide area between MP + CuA_1 and proximal branch of CuA with sloping, straight or S-shaped cross veins; area between proximal branch of CuA and CuP of almost the same width with analogous cross veins; branches of A_2 densely packed, nearly straight. Length of forewing around 32 mm (Fig. 402). One species. Tertiary deposits of Scotland.

Subfamily Rhaphidophorinae Kirby, 1906

Area between bases of antennae with a groove or compressed. Tympanal organ absent. Tarsi compressed from sides. Forms wingless. Paleogene to Recent. Few genera in Recent fauna, one extinct genus from the Paleogene of Europe (Baltic amber).

Family TCHORKUPHLEBIIDAE Martynov, 1937

Anterior margin of forewing weakly convex; costa not distinguishable from branches of SC; costal area broad with numerous simple branches of SC; R starts branching very close to origin of RS and forms four to six long pectinately disposed branches; RS has two branches; MA with three parallel branches; base of stem of MP up to anastomosis with CuA resembling a cross vein or is absent; MP + CuA_1 with four to seven parallel pectinately disposed branches on the anterior side of the trunk, running without branching to apical margin of wing. Jurassic. One genus.

Tchorkuphlebia Martynov, 1937. Genotype—*T. compressa* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Branches of RS terminating at apex of wing; base of MP absent; seven branches of MP + CuA. Length of forewing 35–40 mm (Fig. 403). One species. Lower Jurassic of Central Asia.

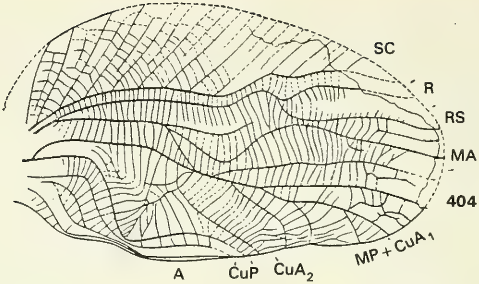
Family ISFAROPTERIDAE Martynov, 1937

Wings short; anterior margin of forewing markedly convex; costa and its branches not differing from branches of SC; costal area broad; with regular intercalary veins between branches of SC; R and RS not branching; MA_1 short, 154 rudimentary, not reaching up to apex of wing, terminating amid cross veins at level of origin of RS; MA_2 S-shaped; two long branches running from stem of MP + CuA toward apical margin; three or four short branches bent toward anal margin of wing. In wings of males an intercalary vein running through area between CuA_2 and CuP in form of a diagonal vein going toward angle of bend of CuP; base of CuA_2 proximal to intercalary and diagonal vein disappearing, most probably transforming into a cross vein between CuA and intercubital vein. Tympanate area on forewing absent. Jurassic. One genus.

Isafaroptera Martynova, 1937. Genotype—I. *grylliformis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Costal area narrowing sharply toward apex; R with wave-like bend; MA_1 isolated from MA_2; MA_2 approaching RS not far from origin of latter. Length of forewing of male 26 mm (Fig. 404). One species. Lower Jurassic of Central Asia.

Family GRYLLIDAE Latreille, 1802. Crickets
[nom. transl. Stal, 1875 (ex Grylliae Latreille, 1802)]

Forewings broad, short, covering abdomen but not reaching up to ends of cerci; often shorter than hindwings; costa and its branches not differing from branches of SC; costal area markedly widened; branches of SC long and gently sloping; R and M compressed; R does not branch; RS absent; M with two or three short branches; cubital-anal area much expanded, occupying more than one-half of posterior part of wing, held flat on the back; costal-subcostal region located toward sides of body at right angles to cubito-anal area. Wing surface bent at M and R; diagonal vein well developed in sound-producing apparatus of males, in front of which lies the membranous resonator or the tympanate area. Base of CuA_2 absent; CuA_2 leaves diagonal vein. Tarsi three-segmented; hind tibiae with long spines. Cerci long. Ovipositor stylet-like with reduced inner valves. Triassic to Recent. 12 subfamilies: Protogryllinae, Gryllinae, Pteroplistinae, Trigonidiinae, Eneopterinae, Oecanthinae, Mogoplistinae, Myrmecophilinae, Scleropterinae, Cachoplistinae, Pentacentrinae, Phalangopsinae. First six



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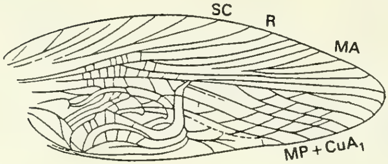

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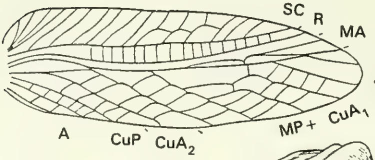

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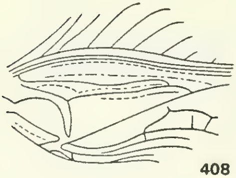

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153 Figs. 404–408. Families Isfaropteridae, Gryllidae and Gryllacrididae.

404. *Isfaroptera grylliformis* Martynov; forewing of male, × 2.9. Lower Jurassic, Central Asia (Martynov, 1937). 405. *Protogryllus acutipennis* Handlirsch; forewing of male, × 6.8. Lower Jurassic, Western Europe (Handlirsch, 1925). 406. *P. minor* Bode; forewing, × 6.8. Lower Jurassic, Western Europe (Zeuner, 1939). 407. *Gryllotalpa* sp.; foreleg, × 4. Recent. Europe (Sharp, 1910). 408. *G. prima* Cockerell; forewing of male, × 6. Paleogene, Western Europe (Zeuner, 1939).

known in fossil form. Protogryllinae (Figs. 405, 406), Oecanthinae and Trigonidiinae occur outside the USSR.

Subfamily Gryllinae Kirby, 1906

Head large and rounded. Tarsi compressed; second segment of tarsus small; hind tibia without teeth, but protected by movable or immovable spines along posterior margin. Paleogene to Recent. Few genera, of which five are from the Paleogene of Europe, including two from Baltic amber.

Subfamily Pteroplistinae Chopard, 1936

Hind tibiae covered with hair-like setae. Spines well developed. Ovipositor lamellate. Paleogene to Recent. Two genera, of which one is extinct and known from the Paleogene of Europe (Baltic amber).

Subfamily Eneopterinae Kirby, 1906

Head with projecting parietal region. Hind tibiae toothed and armed with spines; tarsi short. Paleogene to Recent. Few genera in Recent fauna, of which two are from the Paleogene of Europe (Baltic amber). Extinct genera in the Paleogene of Europe, of which one is from Baltic amber.

Family GRYLLOTALPIDAE Brunner, 1882. Mole crickets

Forewings reduced, covering only base of abdomen in most species. Costa and its branches not differing from branches of SC; costal area very broad; R not branching; RS in the form of short non-branching veins, forming anastomosis with anterior branch of M. Structure of sound-producing organs of males as in crickets, but 'tympanate' area absent. Head small. Eyes small. Antennae not longer than body. Pronotum long, covering prothorax on sides. Tarsi three-segmented. Forelegs short, fossorial (Fig. 407). Cerci long. Ovipositor reduced. Paleogene to Recent. Six genera, of which one from the Paleogene (Fig. 408), and another from the Neogene of Western Europe have fossil representatives.

SUPERFAMILY TETTIGONIIDEA. Long-horned grasshoppers

Forewings varying from narrow, lancet-shape to wide, leaf-like shape; leathery, often with a secondary archedictyon between longitudinal and cross veins; costal area long with pectinately-arranged branches leaving C, sometimes forming a sparse network along with secondary archedictyon; R with a few branches at distal part; MA and MP usually absent, replaced by pectinate MP + CuA. Sound-producing organ present in forewings of males; its structure differing on right and left wings; a resonating membrane or tympanate area present on right
155 wing at a lower level, but absent on left wing. Hindwings membranous, a small part of secondary archedictyon present occasionally at distal part; anterior

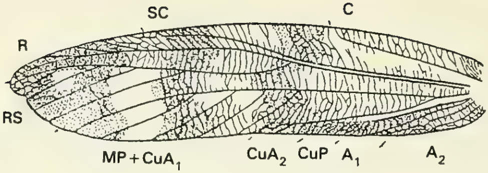


Fig. 409. *Pseudotettigonia amoena* (Henricksen).

Forewing, × 1.2. Paleogene, Western Europe (Henricksen, 1929; interpretation of venation has been modified).

branch of $MA + MA_1$ forming anastomosis with RS; posterior branch of MA_2 free. Tibiae of hindlegs with tympanal organs; tarsi four-segmented. Ovipositor compressed from sides, smooth and saber-shaped, with all three pairs of valves well developed. Paleogene to Recent. One family—Tettigoniidae.

Family TETTIGONIIDAE Krauss, 1902. Katydids, Bush-crickets

R with three or four branches at end or without any branch; CuA descending toward CuP at one-half of length of anal area or more distally; CuA_2 running toward branches of MP + CuA at an angle, often cutting across them; Paleogene to Recent. Twenty-six subfamilies: Pseudotettigoniinae, Rammeinae, Conocephalinae, Decticinae, Phaneropterinae, Tympanophorinae, Ephippigerinae, Pycnogastrinae, Acridoxeninae, Pterophyllinae, Pseudophyllinae, Meconeminae, Mecopodinae, Phyllophorinae, Tettigoniinae, Saginae, Salomoninae, Agraepterinae, Prochilinae, Simoderinae, Aspidonotinae, Moristinae, Phasmodinae, Bradyporinae, Deracanthinae, Hetrondinae. Only first six known as fossils; first five known to occur outside the USSR.

Subfamily Pseudotettigoniinae

Sharov, subfam. nov.

Sparse network of archedictyons only along anal margin and apex of wing; often prevailing over simple cross vein; inclined veins between CuA_2 and CuP (base of CuA) usually absent, most probably transformed into cross vein. Four anal veins not anastomosing with one another or with CuP; primarily simple cross veins between them. Paleogene to Neogene. Three genera outside the USSR: *Pseudotettigonia* Zeuner, 1937 (Fig. 409); *Arctolocusta* Zeuner, 1937 and *Lithymnetes* Scudder, 1890.

Subfamily Tympanophorinae Brunner, 1893

[nom. transl. Kirby, 1906 (ex Tympanophoridae Brunner, 1893)]

Head rounded, short, broad, flat at top between eyes. Eyes spherical, protruding. Pronotum saberlike or semicylindrical. Foretibiae short with short, strong spines at bottom. Wings rudimentary. Paleogene to Recent. 11 genera, of which two occur in fossil form in the Paleogene of Europe (Baltic amber); one of these is extinct.

Suborder Caelifera

Antennae usually not longer than body, with fewer than 30 segments; segments distinct, separated by sharp constrictions; length of segments two to three times their width. Hindfemora with longitudinal keels; number of segments in tarsi in fore-, middle and hindlegs 3–3–3, 2–2–3 and 2–2–1, respectively. Ovipositor short, toothed, with teeth on side of dorsal and ventral valves; inner valves rudimentary; rarely, ovipositor absent; while digging dorsal and ventral valves work opposite to each other. Triassic to Recent. Three superfamilies: Locustopseidea, Acrididea, Tridactylidea; last has fossil representatives, whose authenticity is questionable.

SUPERFAMILY LOCUSTOPSEIDEA

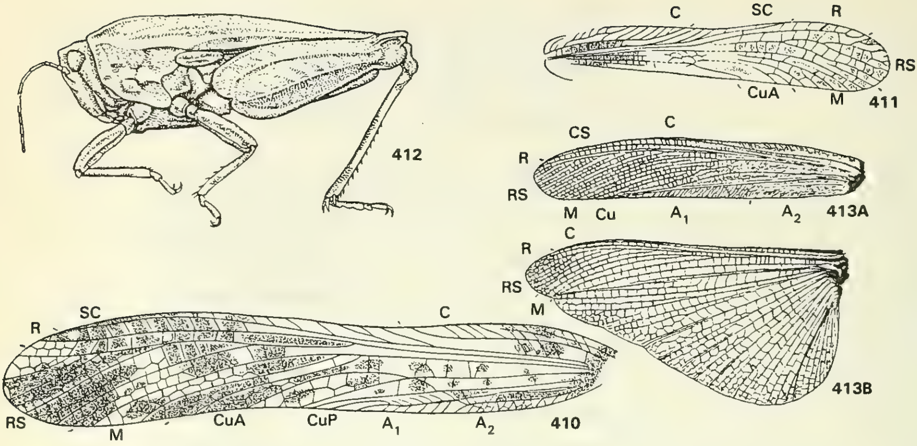
Costa running for a considerable distance parallel to anterior margin of wing, giving rise to comb-like branches; sometimes shorter than precosta; costal area at distal end of SC sharply narrowed; RS pectinate; M with three branches, posterior one with short veins at distal one-third; CuA with two or three branches. Triassic to Jurassic. One family—Locustopseidae.

Family LOCUSTOPSEIDAE Handlirsch, 1908

Branches of R short, resembling cross veins, proximal ones terminating on SC; 156 radial area narrow with simple cross veins in most part; two regular rows of cells between branches RS, M and CuA, either rectangular or honeycomb-like; anal veins two with short branches originating from cross veins. Triassic to Jurassic. Four genera.

Locustopis Handlirsch, 1908 (*Brodiana* Zeuner, 1942). Genotype—*L. elegans* Handlirsch, 1908; Lower Jurassic, Germany (Lower Lias, Meklenburg). SC almost reaching apex of wing; RS with up to five branches; between M, before branching simple or Y-shaped cross veins with Cu. Length of forewing ranging from 10 to 30 mm (Fig. 410). Lower Jurassic of Europe and Central Asia. Nineteen species.

Parapleurites Brauer, Redtenbacher and Ganglbauer, 1889. Genotype—*P. gracilis* Brauer, Redtenbacher and Ganglbauer; Lower Jurassic, Irkutsk province (Cheremchovian series, Ust-Bailey). SC terminating far short of apex of wing at level of branching of RS; two series of right-angled cells between branches PS, M, and CuA confined to margin of wing; two series of cells between M, before it branches, and Cu. Length of forewing about 16 mm (Fig. 411). One species. Lower Jurassic of Irkutsk province.



Figs. 410–413. Families Locustopseidae, Tetrigidae and Acrididae.

410. *Locustopsis magnifica* Handlirsch; forewing, × 4.7. Lower Jurassic, Western Europe (Handlirsch, 1925). 411. *Parapleurites gracilis* Brauer, Redtenbacher and Ganglbauer; forewing, × 4.2. Lower Jurassic, Irkutsk province (Brauer, Redtenbacher and Ganglbauer, 1889). 412. *Tetrix nutans* Hagenbach; general view, × 4.9. Recent, Southern Europe (Bei-Bienko and Mishenko, 1951). 413. *Schistocerca* sp.; A—forewing, B—hindwing, × 1.1. Recent, Africa, Southwest Asia, South America (Handlirsch, 1906).

Outside the USSR: *Triassolocusta* Tillyard, 1922; *Conocephalella* Strand, 1928.

SUPERFAMILY ACRIDIDEA. Short-horned Grasshoppers

Forewing: costa usually long, reaching or extending beyond considerable part of distal half of wing; SC and R without branches; RS pectinate, running very close to R; sometimes base of RS fused with R; M with two free branches; CuP straight; anal area as long as the wing or exceeding one-half of length of wing; two anal veins. Sometimes forewings rudimentary. In hindwing MA fused with RS at base; CuA not branching or anastamosing with M or its branches; A_1 simple or with not more than two branches; anojugal fan wide. Occasionally wingless forms encountered. Stridulation by rubbing hind femur against forewings or abdominal segments. Tympanal organs along sides of first abdominal segment, sometimes absent. Frons vertical; three ocelli. Cerci short. Eggs laid in clusters in egg sacs in soil. Tertiary to Recent. Five families: Tetrigidae, Eumastacidae, Acrididae, Pneumoridae, Proscopidae. Only the first three have fossil representatives.

157 Family TETRIGIDAE Rambur, 1938. Pygmy Grasshoppers

[nom. transl. Walker, 1870 (ex Tetrigides Rembur, 1938)]

Forewings extremely short, in form of small scales with reduced venation. Hindwings long; wing surface narrow with reduced venation; major part of wing occupied by anojugal fan. Pronotum with long backward outgrowth covering wings and abdomen (Fig. 412). Neogene to Recent. More than 100 genera, of which two from the Neogene of Western Europe are found as fossils.

Family EUMASTACIDAE Burr, 1889

[nom. transl. Burr, 1903 (ex Eumastacides Burr, 1889)]

Precostal area comparatively short, projecting into anterior margin of wing; RS with a few branches; inclined vein (MP) between M and CuA absent; CuA not branching. Often wingless. Antennae very short, usually shorter than fore tibiae. Tympanal organs absent on first segment of abdomen. Neogene to Recent. About 10 species, primarily from tropics, out of which one is found as fossil from the Neogene of Western Europe; two genera from Western Europe and North America are extinct.

Family ACRIDIDAE Latreille, 1825

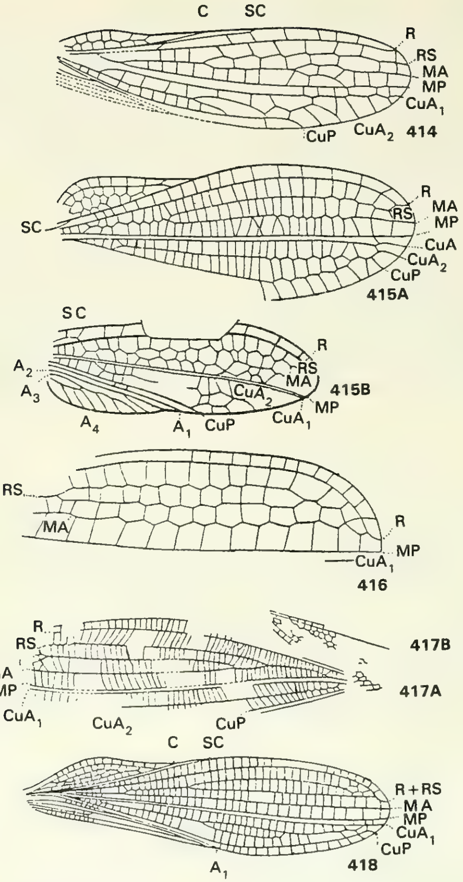
[nom. transl. Brunner, 1900 (ex Acridites Latreille, 1825)]

Wings well developed. In forewing RS with many branches; between M and CuA there is an inclined vein—the base of MP; CuA with two or three branches. In hindwing M fused with RS at base (Fig. 413). Antennae longer than hind femur. Tympanal organs on first abdominal segment. Over 100 genera, of which eight from Tertiary and Quaternary deposits of Western Europe and North America are in fossil form. Only one species, of undetermined generic affinity—gen? *kudiana* (Cockerell, 1927)— has been reported from the territory of the USSR, from the Lower Miocene deposits of the Primorye region (Amaru). Tertiary to Recent.

Order GLOSSELYTRODEA

(O.M. Martynova)

Two pairs of nearly similar wings, with straight longitudinal veins and many cross veins arranged in rows. Forewing: precostal area convex, anal area wedge-like; strong R and CuP running parallel to anterior and anal margins of wing, their distal ends approaching apical part along contour of wing (Mesozoic); MP and CuA_1 usually close (except in large forms), simple; CuA_2 with branches; on all veins traces of attachment of hair-like setae observed. In hindwing precostal area absent; anal area resembling reduced fan; CuP never joined with R. Head directed downward. Mouth parts of biting type. Antennae comparatively small, thread-like. Thoracic segments uniformly developed. Legs of running type and



Figs. 414–418. Families Archoglossopteridae and Jurinidae.

414. *Archoglossopterum shoricum* O.M. Martynova; forewing, × 8. Lower Permian, Kuznetsk basin (Martynova, 1958). 415. *Eoglosselytrum kondomense* O.M. Martynova; A—forewing, B—hindwing, × 13. Lower Permian, Kuznetsk basin (Martynova; 1952). 416. *Surijoka grandicella* O.M. Martynova; anterior half of forewing, × 12. Upper Permian, Kuznetsk basin (Martynova, 1958). 417. *Protojurina cellulosa* O.M. Martynova; forewing, × 8. Upper Permian, Kuznetsk basin; A—wing; B—torn off and reversed precostal area (Martynova, 1958). 418. *Jurina Marginata* Martynov; forewing, × 6. Upper Permian, Arkhangelsk province (Martynova, 1958).

nearly similar. Herbivorous. Living in damp conditions in subtropical and temperate regions. Lower Permian to Triassic. Families: Archoglossopteridae, Permoberothidae, Jurinidae, Glosselytridae, Uskatelytridae, Polycytellidae.

Outside the USSR: Permoberothidae.

Family ARCHOGLOSSOPTERIDAE O.M. Martynova, 1958

Forewing: precostal area with one vein which does not run parallel to margin; MP and CuA_1 close; R short, not curving to run parallel to apical margin; no longitudinal vein, terminating at R; CuP short, terminating almost at midpoint of distal half of wing; cross veins irregularly spaced, varied, not forming row of regular cells. Lower Permian. One genus.

Archoglossopterum O.M. Martynova, 1958. Genotype—*A. shoricum* O.M. Martynova, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing: precostal area longer than anal area and 10/13th of length of tegmen; SC terminating a little more distally than midpoint of wing; RS and MA not branched; CuA_2 not branched. Length of wing 7.5 mm (Fig. 414). One species. Lower Permian of Kuznetsk basin.

158 Family JURINIDAE M. Zalessky, 1928

(Eoglosselytridae O.M. Martynova, 1952)

Precostal area with a few longitudinal veins, including one parallel to margin; MP and CuA_1 close, dividing wing into two unequal parts, anterior half wider than posterior; R curved and parallel to anterior margin, but not reaching apex of wing; RS terminating on R; CuP terminating more distally than midpoint of apical half of wing; cross veins form more or less regular rows of cells. Permian. Four genera.

Eoglosselytrum O.M. Martynova, 1952. Genotype—*E. kondomense* O.M. Martynova, 1952; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Cells formed by cross veins of different shapes, their width not exceeding one-half their height. Length of tegmen 5–6.5 mm (Fig. 415A, B). Six species. Lower Permian of Kuznetsk basin.

Surijoka O.M. Martynova, 1958. Genotype—*S. grandicella* O.M. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Cells formed by cross veins large, varied in shape, their width slightly exceeding or equalling their height. Length of tegmen about 7 mm (Fig. 416). One species. Upper Permian of Kuznetsk basin.

Protojurina O.M. Martynova, 1958. Genotype—*P. cellulosa* O.M. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Cells formed by cross veins narrow and high, their height exceeding their width by three or four times. Length of tegmen 7–8 mm (Fig. 417). Four species. Upper Permian, Kuznetsk basin.

Jurina M. Zalessky, 1929 (*Anorthoneura* Martynov, 1938—according to description of hindwing). Genotype—*J. scutulata* M. Zalessky, 1929; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie gory). All cross veins straight and regularly spaced; width of cells 0.2–0.3 mm height equals or greater than width. Length of tegmen 7.2–11 mm (Fig. 418). Four species. Upper Permian of Urals and Arkhangelsk province.

Outside the USSR: *Permoberothella* Riek, 1953.

Family GLOSSELYTRIDAE Martynov, 1938

Forewing: vein running parallel to anterior margin of precostal area absent; precostal veins distributed like fan; MP and CuA_1 not close; apical part of R not preserved; CuP terminating more proximally than midpoint of apical half of wing; cross veins forming rows of small quadrangular cells. Upper Permian. One genus.

159 *Glosselytron* Martynov, 1938. Genotype—*G. multivenosum* Martynov, 1938; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing with many branches of CuA_1. Length of forewing 16–19 mm (Fig. 419). One species. Upper Permian of Arkhangelsk province.

Family USKATELYTRIDAE O.M. Martynova, 1952

Vein running parallel to anterior margin in precostal area present; anal area considerably longer than precostal area; MP and CuA_1 not close; apical part of R not preserved; anterior branch of RS terminating on R; apical part of CuP not preserved; cross veins short, running at an angle, forming rows of small cells. Upper Permian. One genus.

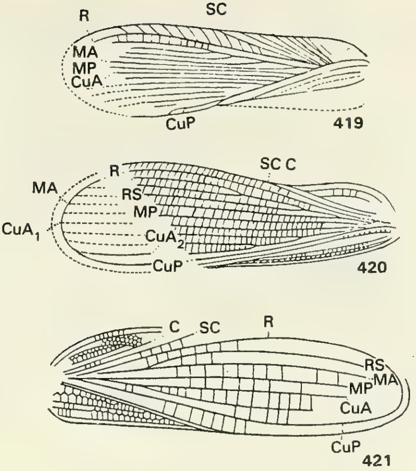
Uskatelytrum O.M. Martynova, 1952. Genotype—*U. sibiricum* O.M. Martynova, 1952; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). Forewing: anal veins long, straight; CuA_2 and RS with three branches. Length of forewing 16 mm (Fig. 420). One species. Upper Permian of Kuznetsk basin.

Family POLYCYTELLIDAE O.M. Martynova, 1952

Vein present, parallel to anterior margin in precostal area; MP and CuA_1 joined to form single strong vein, dividing wing into two equal halves; R and CuP fused at apex of wing. Triassic. Two genera.

Mesojurina O.M. Martynova, 1943. Genotype—*M. sogjutensis* O.M. Martynova, 1943; Upper Triassic, Issyk-Kul province (Raetian stage, Issyk-Kul). Precostal and anal areas of equal length; cells formed by cross veins wide and low, as in genus *Jurina*. Length of forewing 4.7 mm (Fig. 421). One species. Upper Triassic of Issyk-Kul province.

Outside the USSR: *Polycytella* Tillyard, 1922.



Figs. 419–421. Families Glosselytridae, Uskatelytridae and Polycytellidae.

419. *Glosselytron multivenosum* Martynov; forewing, × 2.7. Upper Permian, Arkhangelsk province (Martynov, 1938). 420. *Uskatelytrum sibiricum* O.M. Martynova; forewing, × 4. Upper Permian, Kuznetsk basin (original drawing). 421. *Mesojurina sogjutensis* O.M. Martynova; forewing, × 11. Upper Triassic, Central Asia (Martynova, 1943).

Order PHASMATODEA. Stick insects and leaf-insects

(O.M. Martynova)

Medium or large sized insects. Both winged and wingless forms included. In Recent forms one pair of wings reduced to size of scales; in Mesozoic forms both pairs of wings developed. Forewing: precostal area small; on long, narrow wings, straight, almost parallel veins with few branches; in costal area branches of SC slanting; branches of R also slanting; veins close and parallel to wing margin absent. Hindwing: anojugal area well developed.

Head small, prognathous. Mouth parts of biting type. Antennae thread-like; segments of antennae ranging in number from eight to 100. Compound eyes, not large. Ocelli often absent. Pronotum always shorter than pterothorax. Legs long, similar, adapted for climbing. Tarsi five-segmented. Cerci unsegmented. Ovipositor rudimentary. Herbivorous. Around 2,000 species in present-day fauna, primarily in the tropics. Triassic to Recent. Two suborders: Chresmododea, Euphasmatodea.

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Suborder Chresmododea

Forewings well developed. Mesozoic. Families: Aerophasmatidae, Necrophasmatidae, Aeroplanidae, Chremodidae. Last two families occur outside the USSR.

Family AEROPHASMATIDAE Martynov, 1928

Forewing not narrow toward apex; RS starting considerably more proximally than midpoint of length of wing; R with three short anterior branches; M branching at basal one-fourth of wing; both branches of M with long bifurcations; Cu long, unbranched; A_1 terminating at apical part of wing; cross veins many. Jurassic. One genus.

Aerophasma Martynov, 1928. Genotype—*A. prynadai* Martynov, 1928; Upper Jurassic, Chimkent province (Malm, Karatau). Precostal area of forewings broad; SC terminating more distally than midpoint of wing; R and A_1 terminating at apical part of wing, their apical part straight; A_2 and A_3 terminating on preceding veins, forming loops. Length of forewing 26 mm (Fig. 422). One species. Upper Jurassic of Kazakhstan.

Family NECROPHASMATIDAE Martynov, 1925

Forewing narrowing toward apex; apex pointed; RS simple, starting around midpoint of wing; M with two simple branches arising almost at wing base, more proximally than origin of RS; CuA with branches; CuP simple; A_1 terminating more proximally than midpoint of wing; cross veins few. Jurassic. One genus.

Necrophasma Martynov, 1925. Genotype—*N. shabarovi* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Precostal area of forewing narrow and short; SC reaching near middle of wing; R reaching up to apex of wing, its distal end bending backward; CuA with three pectinately arranged branches; A_2 with three branches. Length of forewing 21.5 mm (Fig. 423). One species. Upper Jurassic of Kazakhstan.

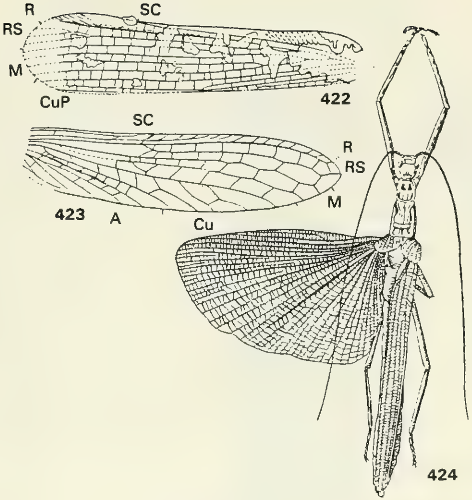
Suborder Euphasmatodea

Forewings almost always rudimentary. Paleogene to Recent. Two recent families: Phyllidae, Phasmatidae, latter with fossil representatives.

Family PHASMATIDAE Leach, 1815

[nom. transl. Serville, 1839 (ex Phasmida Leach, 1815)]

Winged or wingless forms with forewings reduced to scales. Thoracic segments long and narrow (Fig. 424). Paleogene to Recent. Three genera from the Paleogene of Europe (Baltic amber) and North America.



Figs. 422–424. Order Phasmatodea.

422. *Aerophasma prynadai* Martynov; forewing, × 2.3. Upper Jurassic, Southern Kazakhstan (Martynov, 1928). 423. *Necrophasma shabarovi* Martynov; forewing, × 3. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 424. *Calvisia atrosignata* Stal; general view, Recent. (Brunner, 1893).

Cohort PARANEOPTERA

(B.B. Rohdendorf)

Venation of wings normally poor; jugal area of moderate size, usually with one, branching jugal vein. Hindwings usually broad, often shorter than forewings. Wings almost always dissimilar. Dipterygia often developed. At times forewings 161 thickened, or as size of insects decreases, with long hair-like setae and fringed. Many secondarily wingless forms. Head usually with a strong sucking pump and mouth parts in the form of a piercing segmented proboscis or different types of biting jaws. Incomplete metamorphosis. A hibernating stage during development occasionally in some specialized forms (certain Rhynchota and thrips). Nymphs resemble adult insects, there are no specialized larvae. Lower Carboniferous to Recent. Three superorders: Rhynchota, Psocopteroidea, Thysanopteroidea.

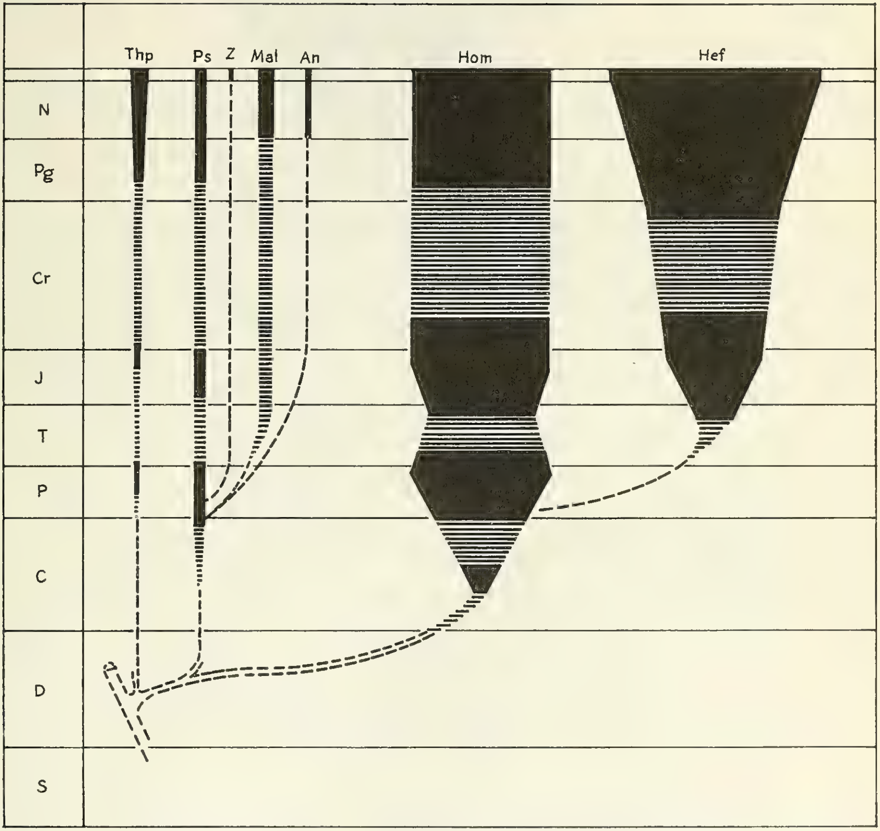
The phylogenetic relationships of Paraneoptera with other cohorts of winged insects are not clear. The lines of evolution of the superorders of Paraneoptera were determined by varying degrees of parasitism, and above all by mode of food-intake and structure of mouth parts. First superorder, Rhynchota, characterized by the evolution of a piercing, segmented proboscis in the phytophagous insects, is closely related to the second, probably ancestral, superorder Psocopteroidea.The latter is quite heterogeneous, but characterized by primitive characters (biting mouth parts of most representatives of this superorder) and highly specialized features (due to parasitism in many groups). Still more peculiar is the evolution of the last superorder, such as the development of the small thrips and the nature of their primitive type of feeding, probably based on the sucking in of pollen grains (Fig. 425). The great antiquity and peculiarity of this cohort of superorders on the one hand reveal the direct connection of these neopterans with some groups of palaeopterans (such as Palaeodictyoptera, some of which have a segmented proboscis) and Blattopteroidea and, on the other hand, they cast doubt on the integrity and phylogenetic unity of this whole complex of otherwise isolated superorders and orders. Obviously, if these opinions and suggestions prove correct, it will be necessary to reexamine the scheme of taxonomic relationships of groups of Neoptera as a whole. At present, for lack of phylogenetic data, we can only state and cannot hope to solve the problem.

SUPERORDER RHYNCHOTA. Insects with proboscis

(E.E'. Bekker-Migdisova)

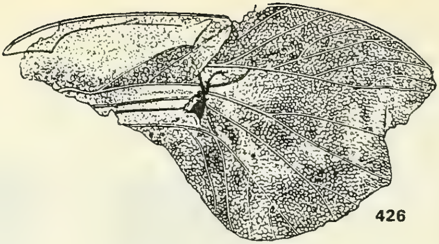
Head with bifid clypeus and sucking mouth parts consisting of stylets formed from maxillae and mandibles, enclosed in a long, segmented proboscis formed by the labium. Antennae short, four- or five-segmented, rarely long and many-segmented. Usually with two pairs of wings; rarely, hindwings reduced; many short-winged and wingless forms. Forewings often transformed into thick tegmina; sometimes a part of this remains membranous. Vein CuP straight, and divides triangular anal area. Herbivores, parasites on vertebrates, predators and a few saprophages. Lower Carboniferous to Recent. Two orders: Homoptera, Heteroptera.

First order ancestral, known from the Carboniferous, the second, in the opinion of some scientists, is a branch of the first which separated during the Permian. Evolution of Rhynchota was influenced by their broadening and increasing association with plants in one direction and in another direction by their omnivorous and predatory nature. The development of phytophagy continued in the order Homoptera and led to the formation of highly specialized phytophages, namely the present-day coccids and aphids. Predatory habits, linked with various modifications led to the appearance of bed bugs and other parasitic bugs.



162 Fig. 425. Phylogenetic relationships of orders of Paraneoptera; period of geological distribution and phylogenetic relationships have been superimposed on geochronological scale.

Thp—Thysanoptera, Ps—Psocoptera, Z—Zoraptera, Mal—Malophaga, An—Anoplura, Hom—Homoptera, Het—Heteroptera (Rohdendorf, Bekker-Migdisova, Martynova and Sharov, 1961).



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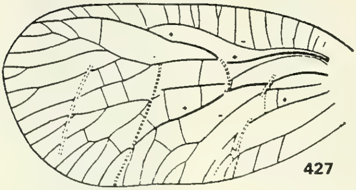

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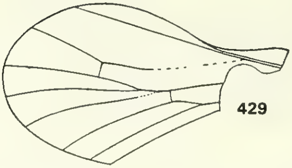

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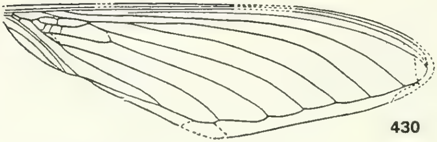

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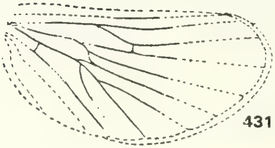

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162 Order HOMOPTERA

(E.E'. Bekker-Migdisova)

Tegmina membranous or sclerotized, held slanted like a roof while at rest, rarely held flat; usually with a posterior part called "clavus" sharply demarcated by the vein CuP. Sometimes membranous distal part of tegmina separated by a socalled dividing line, and with broken longitudinal veins. Hindwings with a broad anojugal area; occasionally this area is reduced. Short-winged and wingless forms not uncommon. Head hypognathous or opisthognathous, usually compact and fused with thorax, sometimes independent. Gular plate
163 always absent. Compound eyes usually well developed; ocelli present. Mesothorax larger than metathorax. Legs of cursorial type; often posterior pair of jumping type; occasionally legs highly reduced; tarsi one to three segmented. Often sound-producing and auditory organs located on abdomen. Abdomen composed of eight to 11 segments. Life cycle occasionally includes an immobile stage. Almost always herbivorous, associated with various ground biocenoses. Lower Carboniferous to Recent. Three suborders: Auchenorrhyncha, Sternorrhyncha, Coleorrhyncha.

Suborder Auchenorrhyncha

Wings always dissimilar. Forewings transformed into thick tegmina or membranous. Hindwings with expanded anojugal area, rarely rounded with weakly developed jugal area. Proboscis stout, blends with head. Antennae short. Lower Carboniferous to Recent. Four infraorders: Blattoprosbolomorpha, Cicadomorpha, Cicadellomorpha, Fulgoromorpha.

Infraorder Blattoprosbolomorpha

Veins of tegmina independent up to base, do not form common stem. Carboniferous. Families: Blattoprosbolidae, Protoprosbolidae.

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163 Figs. 426–431. Families Blattoprosbolidae, Protoprosbolidae, Mesogereonidae, Homoptera insertae sedis.

426. *Blattoprosbole tomiensis* Bekker-Migdisova; elytron, × 3.8. Middle Carboniferous, Kuznetsk basin (Bekker-Migdisova, 1958). 427. *Protoprosbole straeleni* Laurentiaux; elytron, × 4.3. Lower Carboniferous, Belgium (Laurentiaux, 1952). 428. *Permodunstania prosboloides* Bekker-Migdisova; elytron, × 7.1. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 429. *Kaltanocicada dunstanioides* Bekker-Migdisova; hindwing, × 14. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 430. *Mesogereon superbum* Tillyard; forewing, × 1.6. Upper Trias, Australia (Tillyard, 1921). 431. *M. affine* Tillyard; forewing, × 4.6. Upper Triassic, Australia (Tillyard, 1921).

Family BLATTOPROSBOLIDAE Bekker-Migdisova, 1958

SC, R, M and CuA set apart at base of tegmen; C thickened, with hook-like expansion at base; SC long, branching; CuA pectinate. Upper Carboniferous. One genus.

164 *Blattoprosbole* Bekker-Migdisova, 1958. Genotype—*B. tomiensis* Bekker-Migdisova, 1958; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Zheltyi Yar). SC very thick, straight and long, with a row of parallel branches; R and M with a few branches; CuA pectinate. Length of tegmen 17.8 mm (Fig. 426; Pl. XII, Fig. 1). One species. Carboniferous of Kuznetsk basin.

Family PROTOPROSBOLIDAE Laurentraux, 1952

SC, R and M close at base of tegmen, but do not join up; C without hooklike expansion at base; SC many-branched and at distal part fused with R. Length of tegmen 14 mm (Fig. 427). Namurian of Belgium. One genus—*Protoprosbole* Laurentiaux, 1952.

Infraorder Cicadomorpha

Forewings usually membranous, with dense veins; R and M fused at base to form common stalk. In hindwings edge of wing margin separated from marginal veins forming a marginal border; tegulae absent. Middle coxae short and closely linked with one another. Posterior division of clypeus convex; face small and triangular. Three ocelli. Carboniferous to Recent. Superfamilies: Palaeontinidea and Cicadidea.

SUPERFAMILY PALAEONTINIDEA

SC long in forewing; M and CuA split proximally, connected by a long slanting

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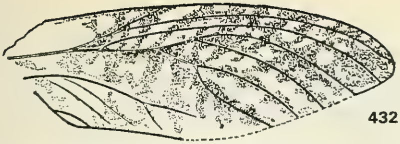
164-165 Figs. 432–444. Superfamily Palaeontinidea, family Palaeontinidae.

432. *Cicadomorpha punctulata* Martynov; tegmen, × 1.3. Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1949). 433. *Palaeontinodes schabarovi* Martynov; tegmen, × 1.2. Lower Jurassic, Central Asia (Martynov, 1937). 434. *Phragmatoecicossus shurabensis* Bekker—Migdisova; tegmen, × 2.2 Lower Jurassic, Central Asia (Bekker-Migdisova, 1949). 435. *Palaeocossus jurassicus* Oppenheim; tegmen, × 2.6. Jurassic, Irkutsk province, (Martynov, 1931). 436. *Phragmatoecites damesi* Oppenheim; tegmen, × 1.6. Jurassic, Irkutsk province (Martynov, 1931). 437. *Suljuctocossus prosboloides* Bekker-Migdisova; tegmen, × 1.3. Jurassic, Central Asia (Bekker-Migdisova, 1949). 438. *Pseudocossus zemcuznicovi* Martynov; tegmen, × 1.5. Jurassic, Irkutsk province (Martynov, 1931). 439. *Asiocossus costalis* Bekker-Migdisova; fragment of tegmen, × 4.5. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 440. *Palaeontinopsis latipennis* Martynov; tegmen, × 2.2. Jurassic, Central Asia (Martynov, 1937). 441. *Ijacossus suchanovae* Bekker-Migdisova; tegmen, × 3. Jurassic, Irkutsk province (Bekker-Migdisova, 1950). 442. *Plachutella picta* Bekker-Migdisova; hindwing, × 2.3. Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1949). 443. *Shurabocossus gigas* Bekker-Migdisova; hindwing, × 1.6. Jurassic, Central Asia (Bekker-Migdisova, 1949). 444. *Suluktaja turkestanensis* Bekker-Migdisova; hindwing, × 1.5. Jurassic, Central Asia (Bekker-Migdisova, 1949).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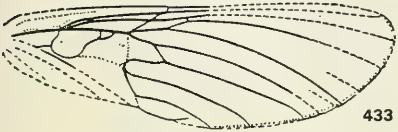
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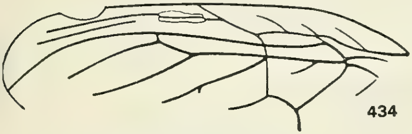
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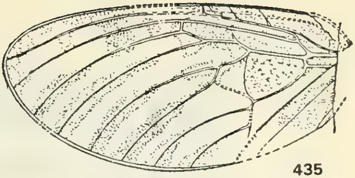
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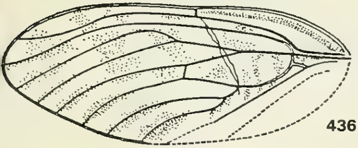
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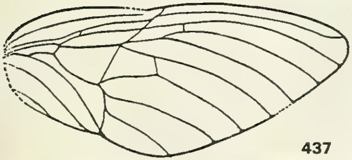
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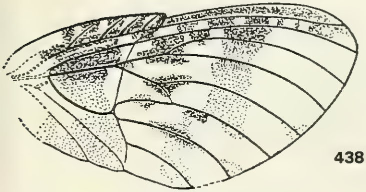
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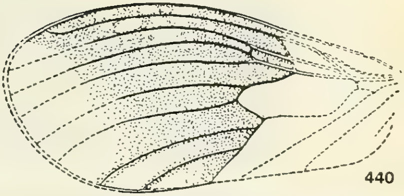
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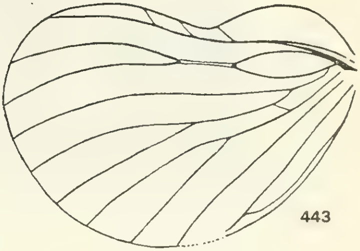
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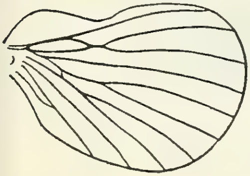
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cross vein. Hindwing rounded, without expanded anojugal area. Lower Permian to Jurassic. Families: Dunstaniidae, Mesogereonidae, Palaeontinidae.

Family DUNSTANIIDAE Tillyard, 1916

Distal membranous part of tegmen distinct from sclerotized basal series of thick, long, slanting cross veins, nodus well developed; SC long; reaches distal part of tegmen; RS with branches; M anastomoses with RS and CuA. Hindwing wide, rounded with broad, concave anterior margin. Lower Permian to Upper Triassic. Five genera.

Outside the USSR: *Dunstania* Tillyard, 1916; *Dunstaniopsis* Tillyard, 1918 and *Paradunstania* Tillyard, 1918.

Family MESOGEREONIDAE Tillyard, 1921

Forewings greatly elongated, membranous, with thick, convex veins; with marginal border and wrinkled on surface; all veins separate at base of wing; no distal branches; anterior margin strongly sclerotized; SC, R_2 and RS extend along anterior margin, very close together; costal area reduced; anal area very small; broken veins and nodus absent; basal cell closed. Hindwings one-half of forewings, rounded, with marginal border; M_4 and CuA connected by cross vein, forming closed basal cell. Length of forewing 44 mm (Figs. 430, 431). Triassic of Australia. One genus: *Mesogereon* Tillyard, 1921 (five species).

Family PALAEONTINIDAE Handlirsch, 1906

(Cicadomorphidae Evans, 1956)

Distal part of tegmen considerably larger than basal part; costal area short and narrow; stem of R short; immediately after M branches off, it divides into two branches: R_2 and RS, extending parallel to anterior margin; forks of M and CuA long. Hindwing with shallow notch on anterior margin and large hump-like protuberance; M_1 fused with RS for some distance, forming basal cell; M branches off at base of wing. Head small. Upper Triassic to Jurassic. Twenty-two genera.

Cicadomorpha Martynov, 1926. Genotype—*C. punctulata* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen narrow
166 and long. Dividing line, nodus and long slanting cross vein m_4-cu_a absent; CuA does not curve toward base of M. Head small. Pronotum trapezoidal, three times as wide as it is long; mesonotum large; metanotum shortened. Body covered with hair-like setae. Length of tegmen 54 mm (Fig. 432). One species. Upper Jurassic of Kazakhstan.

Palaeontinodes Martynov, 1937. Genotype—*P. schabarovi* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab, II). Tegmen elongate, narrow at base; dividing line and nodus distinct; a few long cross veins present between middle part of CuA and M. Length of tegmen 30–58 mm (Fig. 433). One species. Lower Jurassic of Central Asia.

Phragmatoecicossus Bekker-Migdisova, 1949. Genotype—*P. shurabensis* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Tegmen not broad at distal part, with rounded apex and straight anterior margin; nodus absent. Dividing line thick; SC with a row of parallel branches; basal bend of CuA touches base of M at top, forming small basal triangular cell. Length of tegmen 32 mm (Fig. 434). One species. Lower Jurassic of Central Asia.

Phragmatoecites Oppenheim, 1885. Genotype—*P. damesi* Oppenheim, 1885; Jurassic, Irkutsk province (Cheremkhovian series, Ust-Bailey). Tegmen elongated and elliptical; anal area reaches midpoint of wing; M branches off proximal to dividing line and is divided into two stems, nodus more or less distinct. Length of tegmen 23 mm (Fig. 436). One species. Jurassic of East Siberia.

Palaeocossus Oppenheim, 1885. Genotype—*P. jurassicus* Oppenheim, 1885; Lower Jurassic, Irkutsk province (Cheremchovian series, Ust-Bailey). Tegmen broad, with truncated anal margin distally; basal part narrows slightly; anterior margin straight. Nodus clear; costal area short and broad, with traces of branching SC, pentagonal; basal cell bordered by dense veins. Length of tegmen 38 mm (Fig. 435). Two species. Jurassic of East Siberia and Central Asia.

Suljuctocossus Bekker-Migdisova, 1949. Genotype—*S. prosboloides* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lias, Sulyukta). Anal margin of tegmen sharply truncated; apex drawn out; anterior margin straight; anal area short; dividing line thick; basal cell small and fringed by weak veins. Length of tegmen 45 mm (Fig. 437; Pl. XIII, Fig. 3). One species. Lower Jurassic of Central Asia.

Pseudocossus Martynov, 1931. Genotype—*P. zemcuznicovi* Martynov, 1931; Jurassic, Irkutsk province (Cheremchovian series, Ust-Bailey). Tegmen broad, narrows basally; nodus has a projection of costal area; dividing line clear; SC branches. Length of tegmen 41 mm (Fig. 438; Pl. XIII, Fig. 5). One species. Jurassic of East Siberia.

Asiocossus Bekker-Migdisova, 1962. Genotype—*A. costalis* Bekker-Migdisova, 1962; Upper Trias, Issyk-Kul province (Raetian stage, Issyk-Kul). Tegmen with convex anterior margin and fairly broad costal area; SC with branches, runs through middle of costal area distinctly at some distance from R; R + M and stem of R very short and of equal length; basal cell not closed, but bordered in front by thick veins. Length of tegmen about 48 mm (Fig. 439). One species. Upper Triassic of Issyk-Kul province.

Palaeontinopsis Martynov, 1937. Genotype—*P. latipennis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Tegmen broad, rounded at distal part; anterior margin convex; nodus not clear; dividing line thick; all veins close. Length of tegmen 38 mm (Fig. 440). Two species. Lower Jurassic of Central Asia.

Ijacossus Bekker-Migdisova, 1950. Genotype—*I. suchanovae* Bekker-

Migdisova, 1950; Jurassic, Irkutsk province (Cheremkhovian series, River Iya). Tegmen elongated lengthwise; anterior margin convex at base; nodus present; dividing line thick; SC with a series of parallel branches; stem of R fairly long; RS leaves at distal one-third of costal area; a few inclined veins present between middle of CuA and M. Length of tegmen about 55 mm (Fig. 441). One species. Jurassic of East Siberia.

Plachutella Bekker-Migdisova, 1949. Genotype—*P. rotunda* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Schurab II); anterior margin of hindwing straight at distal part; notch on anterior margin not very large, hump-like protuberance quite large; SC simple, terminates on wing margin, at bottom of notch; M_{1+2} and M_{3+4} in the form of two separate branches reaching up to extreme base of wing. Length of forewing 20–23 mm (Fig. 442; Pl. XIII, Figs. 4, 6). Seven species. Jurassic of Central Asia and East Siberia.

Shurabocossus Bekker-Migdisova, 1949. Genotype—*S. gigas* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Schurab III). Hindwing rounded and elongated; notch wide and deep; protuberance large and hump-shaped; SC fused along R and R_2, with a row of short branches running
167 toward notch; M_{3+4} and M_2 fuse early after fusion of latter with M_1 at base of wing. Length of hindwing 37.4 mm (Fig. 443). One species. Lower Jurassic of Central Asia.

Suljuktaja Bekker-Migdisova, 1949. Genotype—*S. turkestanensis* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lias, Sulyukta). Notch on hindwing fairly deep and moderately wide; protuberance large and hump-like; M_1 and RS fused along very small distance; M_{3+4} joined with M_2 a little after fusion of latter with M_1 and together they terminate on R. Length of hindwing 29 mm (Fig. 444). One species. Jurassic of Central Asia.

Outside the USSR: *Palaeontina* Butler, 1873; *Pachypsyche* Handlirsch, 1906; *Cyllonium* Westwood, 1854; *Limacodites* Handlirsch, 1906; *Protopsyche* Handlirsch 1906; *Archipsyche* Handlirsch, 1906; *Polystra* Oppenheim, 1888; *Eocicada* Oppenheim, 1888; *Beloptesis* Handlirsch, 1906 and *Fletcheriana* Evans, 1956.

SUPERFAMILY CICADIDEA

In tegmen SC two-branched or simple; forks of M and CuA usually short. Hindwings with wide anojugal area. Head with convex bifid clypeus. Lower Permian to Recent. Three families: Prosbolidae, Tettigarctidae, Cicadidae.

168 Family PROSBOLIDAE Handlirsch, 1904

[Scytinopteridae Tillyard, 1926 (pars)]

Distal part of tegmen usually membranous; costal area broad; SC divided into SCA, with hook-like bend at base forms thick margin, and SCP, running along

R + M and R_1; basal cell not isolated. Hindwing with deep notch and hump-like protuberance. Carboniferous to Triassic. Seventeen genera.

Prosbole Handlirsch, 1904 (*Prosbolia* Handlirsch, 1937). Genotype—*P. hirsuta* Handlirsch, 1904; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mountains). Venation usually rich. Distal part of tegmen broad; anal margin slightly truncated; dividing line and nodus present; R, M and CuA divided almost at same level. In hindwing M has four branches or more. Length of tegmen 12–35 mm (Figs. 445, 446; Pl. XII, Fig. 4). Twenty-two species. Lower Permian of Kuznetsk basin and Upper Permian of Arkhangelsk province and Urals.

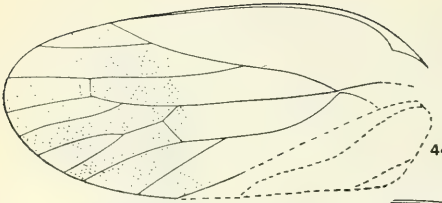
Orthoprosbole Martynov, 1935. Genotype—*O. congesta* Martynov, 1935; Upper Permian, Kuznetsk basin (Erunakovian series, Baikamskaya Listvyashka). Distal part of tegmen narrows sharply with asymmetrically truncated anal margin, dividing line and nodus; venation rich; R divides more basally than M and CuA. Hindwing with markedly arcuate distal part and many early branching veins of M and CuA. Length of tegmen 23 mm (Figs. 447, 448). Two species. Upper Permian of Kuznetsk basin.

Dictyoprosbole Martynov, 1935. Genotype—*D. membranosa* Martynov, 1935; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). Tegmen membranous, with a fine net; distal part broad; venation rich; R, M and CuA divide at same level; RS, M and CuA many-branched; R_2 and RS curved. Length of tegmen 32 mm (Fig. 449). One species. Upper Permian of Kuznetsk basin.

Sojanoneura Martynov, 1928. Genotype—*S. edemskyi* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Distal part of tegmen truncated, rounded; venation poor; R, M and CuA divide at same level: 0.57–0.65 of length of tegmen from its base; M forms three or four branches. Hindwings with gently sloping hump-like protuberance. Length of tegmen 6–11 mm (Figs. 450, 451; Pl. XII, Fig. 8). Seventy-two species. Upper Permian of Arkhangelsk province and the Urals.

Prosboloneura Bekker-Migdisova, 1961. Genotype—*P. colorata* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen truncated, rounded off in distal part; venation poor; R and CuA divide at same level, i.e. at 0.57 of length of tegmen from base; M has three branches at a point 0.66–0.77 of length of tegmen from base. Length of tegmen 6.7 mm (Figs. 452, 453; Pl. XII, Fig. 9). Three species. Lower Permian of Kuznetsk basin.

Kaltanetta Bekker-Migdisova, 1961. Genotype—*K. nigra* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen elongated, ratio of length to width being 3:1; distal part attenuate, symmetrically rounded; venation poor. R runs close to margin and terminates before apex; pterostigma absent; cell r_2-rs very broad; R divided at 0.47 and M at 0.66 of length of tegmen from base; M three-branched. Hindwing with convex



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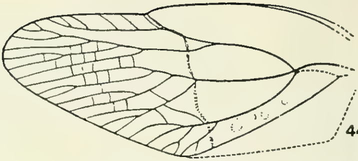

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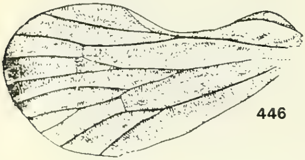

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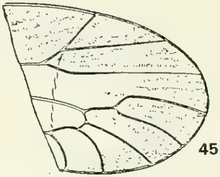

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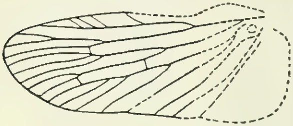

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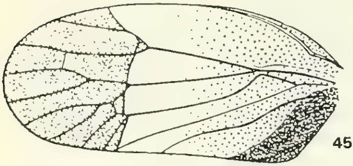

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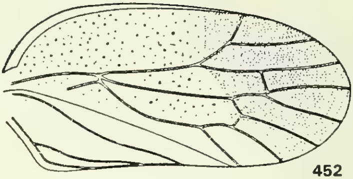

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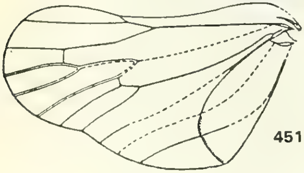

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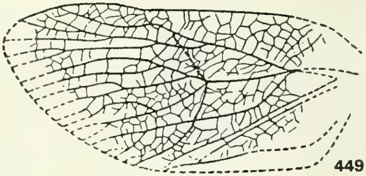

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Figs. 445–453. Family Prosbolidae.

445. *Prosbole kondomensis* Bekker-Migdisova; elytron, × 4.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 446. *P. brevialata* Bekker-Migdisova; hindwing, × 2.7. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1941). 447. *Orthoprosbole triangularis* Martynov; tegmen, × 3. Upper Permian, Kuznetsk basin (Martynov, 1935). 448. *O. congesta* Martynov; hindwing, × 3. Upper Permian, Kuznetsk basin (Martynov, 1935). 449. *Dictyoprosbole membranosa* Martynov; tegmen, × 2. Upper Permian, Kuznetsk basin (Martynov, 1935). 450. *Sojanoneura stigmata* Martynov; tegmen, × 5.4. Upper Permian, Arkhangelsk province (Martynov, 1935). 451. *S. bimaculata* Martynov; hindwing; × 4.5. Upper Permian, Arkhangelsk province (Martynov, 1935). 452. *Prosboloneura kondomensis* Bekker-Migdisova; tegmen, × 9. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 453. *P. colorata* Bekker-Migdisova; Fragment of tegmen, × 10. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961).

distal part, deep wide border, and gently sloping hump-like protuberance. Length of tegmen 8.1 mm (Fig. 454A, B; Pl. XII, Fig. 5). Two species. Lower Permian of Kuznetsk basin.

Permocicada Martynov, 1928 (*Permocicadopsis* Bekker-Migdisova, 1940). Genotype—*P. nigronervosa* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mountains). Venation poor; R branches at 0.44–0.5 and M at 0.5–0.77 of length of tegmen from base; M three- or four-branched. 170 Hindwings truncated, gently sloping; R, M and CuA branch at level of middle of slope. Length of tegmen 4–16 mm (Figs. 455–457; Pl. XII, Fig. 7). Twenty-three species. Lower Permian of Kuznetsk basin and Upper Permian of Arkhangelsk province and Urals.

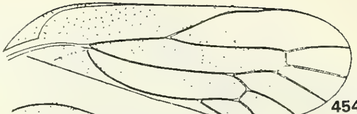
Kaltanopsis Bekker-Migdisova, 1961. Genotype—*K. ornata* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Distal part of tegmen elliptically elongated; venation poor; SCP long; pterostigma not observed; longitudinal and marginal veins very broad; R branches at 0.4 of length of tegmen from base and is considerably more basal than M and CuA; M has three to four branches. Length of tegmen 6.9 mm (Fig. 458). One species. Lower Permian of Kuznetsk basin.

Orthoscytina Tillyard, 1926 (*Anomaloscytina* Evans, 1943, non Davis, 1942). Genotype—*O. mitchelli* Tillyard, 1926; Upper Permian, Australia. Tegmen elongated; ratio of length to breadth varies from 2.6 to 2.9 : 1; distal part shortened; anal area long; R branches at 0.3 to 0.4, M at 0.6 to 0.7 of length of tegmen from base. Hindwing elongate; M and Cu branch early, but at same level; they are two-branched. Length of tegmen 7.5–8.5 mm (Figs. 459, 460; Pl. XII, Fig. 1). Fifteen species. Upper Permian of Australia and Kuznetsk basin (two species.).

Archeglyphis Martynov, 1931. Genotype—*A. crassinervis* Martynov, 1931; Middle Carboniferous, Kuznetsk basin (Lower Balachonian series, Alukaevian sub-series, Verkhotomskoe). Wing has straight anterior margin and narrow costal area; venation rich; R and R_2 in the form of straight horizontal veins; RS has bifurcation; M and CuA many-branched. Length of wing about 29 mm (Fig. 461). One species. Carboniferous of Kuznetsk basin.

Kondomoprosbole Bekker-Migdisova, 1961. Genotype—*K. pictata* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Anterior margin of hindwing convex, with deep notch and large hump-like protuberance; R_2 straight; RS leaves R considerably more distally than wing notch; M has three short branches. Length of hindwing 6 mm (Fig. 462). One species. Lower Permian of Kuznetsk basin.

Pervestigia Bekker-Migdisova, 1961. Genotype—*P. veteris* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Wing notch of hindwing absent; hump-like protuberance small and gently sloping; venation poor; cell r_2-rs fairly wide; M three-branched. Length of forewing 6.7 mm (Figs. 463, 464; Pl. XII, Fig. 6). Two species. Lower Permian of Kuznetsk basin.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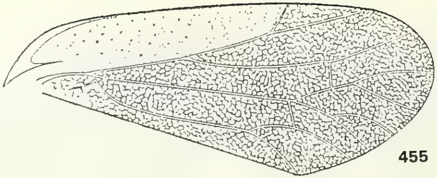
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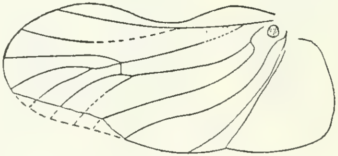
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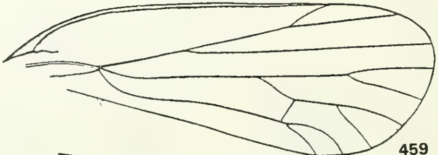
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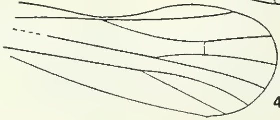
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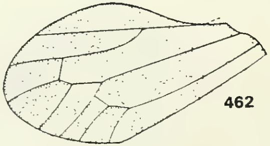
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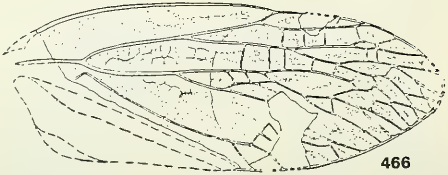
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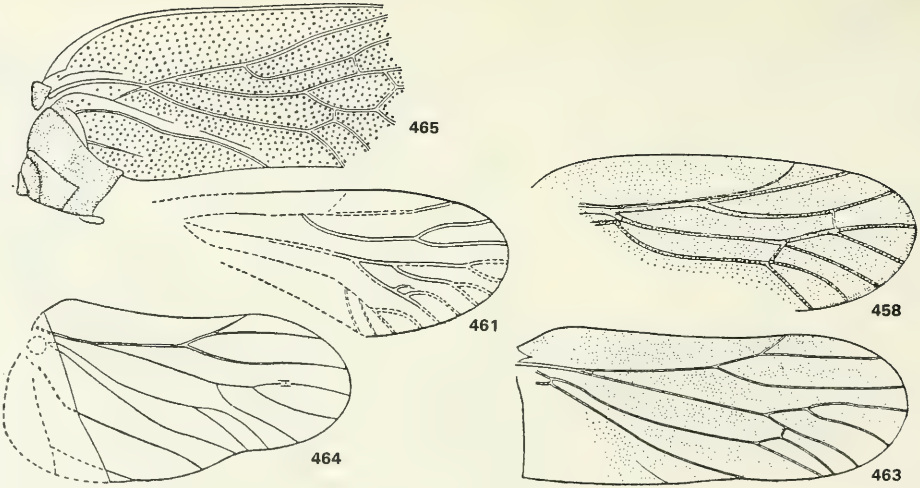


168-169

Figs. 454–466. Family Prosbolidae.

454. *Kaltanetta nigra* Bekker-Migdisova; A—tegmen, × 7.5; B—hindwing, × 10. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 455. *Permocicada nigrita* Bekker-Migdisova; tegmen, × 10.6. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 456. *P. kuznetskiensis* Bekker-Migdisova; hindwing, × 12. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 457. *P. integra* Bekker-Migdisova; (reconstruction), × 4. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1940). 458. *Kaltanopsis ornata* Bekker-Migdisova; tegmen, × 9.7. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 459. *Orthoscytina skoki* Bekker-Migdisova; tegmen, × 9.2. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 460. *O. longifurcata* Bekker-Migdisova; hindwing, × 9. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 461. *Archeglyphis crassinervis* Martynov; tegmen, × 2. Middle Carboniferous,Kuznetsk basin(Martynov, 1931). 462. *Kondomoprosbole picta* Bekker-Migdisova; hindwing, × 11.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 463. *Pervestigia fumosa* Bekker-Migdisova; forewing, × 8.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 464. *P. veteris* Bekker-Migdisova; hindwing, × 8.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 465. *Mesocicada verrucosa* Bekker-Migdisova; tegmen, × 21. Upper Triassic, Central Asia (Bekker-Migdisova, 1961). 466. *Evanscicada speciosa* Bekker-Migdisova; tegmen, × 3.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961).

Mesocicada Bekker-Migdisova, 1962. Genotype—*M. verrucosa* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul); venation poor; thick. Base of tegmen covered with tubercles; R branches considerably more basally than M and CuA and earlier than midpoint of tegmen; nodus and dividing line absent; M has four branches; fork of CuA small. Length of tegmen about 5 mm (Fig. 465). One species. Upper Triassic of Issyk-Kul province.

Evanscicada Bekker-Migdisova, nom. nov. (*Evansia* Bekker-Migdisova, 1961, nom. nud.). Genotype—*E. speciosa* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen narrow, ratio of length to width about 2.5 : 1; basal part of wing sclerotized, distal part membranous; RS with branches, leaves R more proximally than middle of tegmen and considerably more proximally than R_1; M divides at same level as R; CuA at level of origin of R_1; traces of archedictyon seen at basal part of wing; distal part with large cells or intravenous goffers. Length of tegmen 22–28 mm (Fig. 466; Pl. XII, Figs. 2, 3). Four species. Lower Permian of Kuznetsk basin.

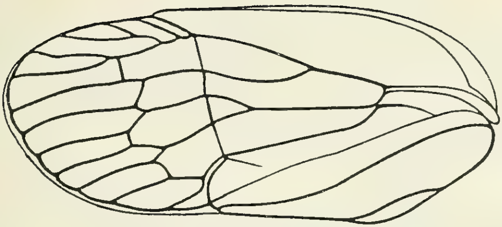
Outside the USSR: *Mitchelloneura* Tillyard, 1929; *Permodiphtera* Tillyard, 1926 and *Austroprosbole* Evans, 1943.

Family TETTIGARCTIDAE Bekker-Migdisova, 1949

Tegmen transparent, with broad sclerotized costal and triangular anal areas; marginal border very narrow; SC divides into SCA, with hook-like bend at base and forming a thick border, and SCP, which joins up with R + M, and R; distal ends of branches of veins form straight line. In hindwing notch and hump very small. Rudiments of sound-producing organs observed, in the form of round goffered surfaces along sides of abdomen. Chordotonal organs absent. Triassic to Recent. 10 genera, of which one genus is from Recent fauna of Australia.

Cicadoprosbole Bekker-Migdisova, 1947. Genotype—*C. sogutensis* Bekker-Migdisova, 1947; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Distal part of tegmen broad, with somewhat asymmetrically truncated anal margin; basal stem of R 0.75 of length of R + M; R branches at 171 0.37 and M at 0.5 of length of tegmen from base; R_2 pectinate; nodus clear; dividing line thick; apices of distal forks of veins at nearly same level; posterior branch of CuA almost equal to its anterior branch. Length of tegmen 17.8 mm (Fig. 467; Pl. XIII, Fig. 2). Two species. Upper Triassic of Issyk-Kul province.

Turutanovia Bekker-Migdisova, 1949. Genotype—*T. karatavica* Bekker-Migdisova, 1949; Upper Jurassic, Chimkent province (Malm, Karatau). Distal part of tegmen symmetrical and elliptically elongated; R_2 with a few branches; dividing line thick; distal forks of veins long, their apices not at same level, but along slope; posterior branch of fork of CuA one-third of length of anterior branch. Length of tegmen about 14 mm (Fig. 468). One species. Upper Jurassic of Kazakhstan.



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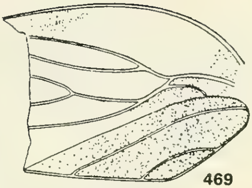

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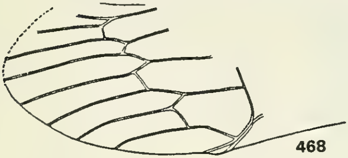

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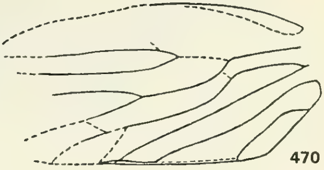

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Figs. 467–470. Family Tettigarctidae.

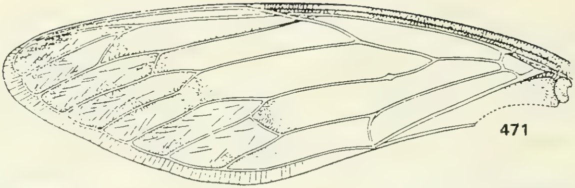
467. *Cicadoprosbole sogutensis* Bekker-Migdisova; tegmen, × 4.7. Upper Triassic, Central Asia (Bekker-Migdisova, 1947). 468. *Turutanovia karatavica* Bekker-Migdisova; tegmen, × 8.7. Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1949). 469. *Shuraboprosbole plachutai* Bekker-Migdisova; tegmen, × 10. Jurassic, Central Asia (Bekker-Migdisova, 1949). 470. *Kisylia psylloides* Martynov; tegmen, × 3.7. Jurassic, Central Asia (Martynov, 1937).

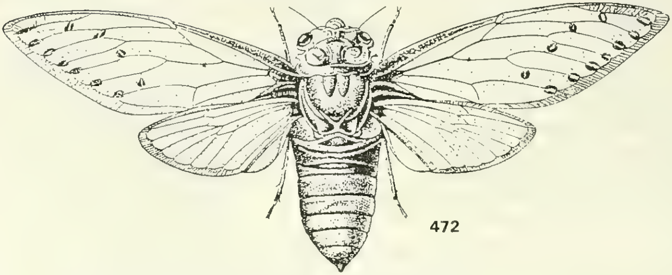
Shuraboprosbole Bekker-Migdisova, 1949. Genotype—*S. plachutai* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Schurab II). In tegmen basal stem of R one-half of length of R + M; R branches more proximally and M at midpoint of length of tegmen; CuA with a small branch from the place where it curves towards M in the basal region, which fuses with the latter; basal end of CuA free and curved toward region of CuP. Length of tegmen 35–40 mm (Fig. 469). One species. Jurassic of Central Asia.

Kisylia Martynov, 1937. Genotype—*K. psylloides* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Dividing line and nodus absent; general stem of R three-fourths of length of R + M; RS branches more proximally and M at midpoint of length of tegmen; R_1 absent; RS does not branch; R_2 and RS parallel; fork of CuA small, its branches of same length. Length of tegmen 17–20 mm (Fig. 470). One species. Jurassic of Asia.

Probably the genus *Diphtheropsis* Martynov, 1937 from Lower Jurassic of Central Asia, also belongs to this family.

Outside the USSR: *Hylaeoneura* Lameere and Severin, 1897; *Eotettigarcta* Zeuner, 1944; *Mesodiphthera* Tillyard, 1919; *Meshemipteron* Cockerell, 1916; one genus from the Paleogene of East Europe and the Recent relict genus *Tettigarcta* White.





172 Figs. 471–472. Family Cicadidae.

471. *Tymocicada gorbunovi* Bekker-Migdisova, tegmen, × 2.3. Miocene, East Siberia (Bekker-Migdisova, 1954). 472. *Pomponia merula* Distant; dorsal view, × 0.75. Malay archipelago (Distant, 1912).

Family CICADIDAE Latreille, 1802

[nom. transl. Westwood, 1940 (ex Cicadae Latreille, 1802, 1804)]

Forewing sclerotized; R_2 drawn close to margin; costal area absent or replaced by chitinous strip; apices of distal forks of veins form one straight line; anal area narrow, short and considerably less than one-half of length of tegmen; basal cell 172 sharply demarcated. Hindwing without notch or hump. Sound-producing and chordotonal organs present. Tertiary to Recent. Four subfamilies: Cicadinae, Platypleurinae, Tettigadinae, Tibicininae. Last two not known in fossil form.

Subfamily Platypleurinae Handlirsch, 1925

Tympanate membranes, covering sound apparatus, developed. Length of forewing 2–60 mm (Fig. 471). Numerous genera in Recent fauna. Paleogene to Recent. Three genera in fossil form: one genus from the Paleogene of North America, one from the Miocene of West Siberia and one from the Paleogene of Western Europe and North America and the Neogene of Western Europe.

Subfamily Cicadinae Latreille

Tympanic covers weakly developed, do not completely cover sound apparatus.

Length of forewing 10–17 mm (Fig. 472). Neogene to Recent. Three genera in fossil form. One genus from the Neogene of Western Europe, the other two from the Neogene of North America.

Liassocicada Bode, 1953 from Upper Lias of Germany also belongs to Cicadoidea incertae sedis.

Cicadomorpha Incertae sedis

Permodunstania Bekker-Migdisova, 1961. Genotype—*P. prosboloides* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen shows poor venation; SC long, does not branch; RS with fork; R_2, RS and M curve toward margin of distal part and have long, thick sloping cross veins forming a thick dividing line; M_4 free, not joined distally with M_3. Length of wing 16–20 mm (Fig. 428). One species. Lower Permian of Kuznetsk basin.

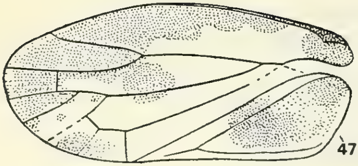
Kaltanocicada Bekker-Migdisova, 1961. Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Hindwing with broad rounded distal part and broad notch on anterior margin; R_2 straight, in continuation of R; radial cell (r_2-rs) very broad; RS sharply bent distally toward anal margin; ends of R_2 and RS and similar branches of M exhibit distal divergence; fork of CuA long. Length of hindwing about 7 mm (Fig. 429). One species. Lower Permian of Kuznetsk basin.

Infraorder Cicadellomorpha (Jassidomorpha)

Tegmina usually leathery, with weak veins; R and M joined at base to form common stem. In hindwings marginal border separated by marginal veins. 173 Tegulae absent. Middle coxae short and closely linked together. Posterior division of clypeus large, not always convex, often not demarcated from frons. Only two simple ocelli present. Lower Permian to Recent. Two superfamilies: Cicadellidea, Cercopidea.

SUPERFAMILY CICADELLIDEA
(Jassoidea)

Tegmina sclerotized, rarely membranous with marginal vein; branches of M and CuA short; some exclusive inner cells between R, M and CuA characteristic. Hindwing sometimes has very small projection at base of anterior margin; RS usually short or absent; M with branches; CuA simple; A_1 and A_2 fused at base of wing. Head with flat clypeus, often fused with frons. Anterior arms of tentorium not connected with the posterior arms. Posterior coxae transverse with broad sides. Posterior tibiae without spurs, but armed with spine-like setae. Lower Permian to Recent. Families: Scytinopteridae, Biturritidae, Cicadellidae, Eurymelidae, Membracidae, Aetalionidae, Hylicidae.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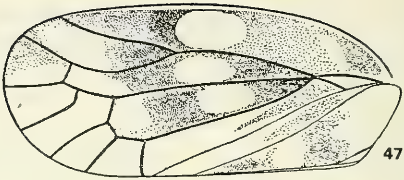
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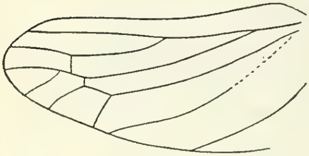
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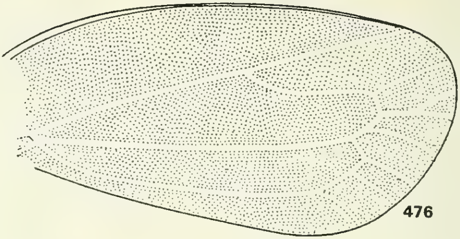
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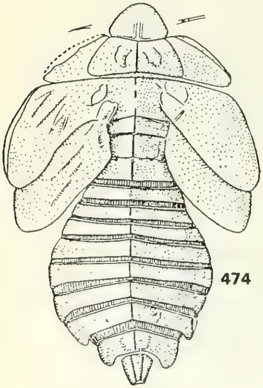
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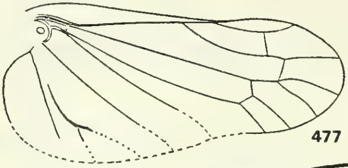
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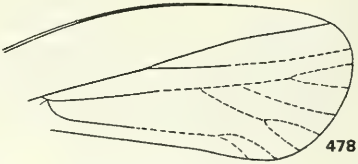
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Figs. 473–478. Family Scytinopteridae, subfamily Scytinopterinae.

473. *Scytinoptera kaltanica* Bekker-Migdisova; A—tegmen, B—hindwing, × 11. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 474. *Scytinoptera* sp.; nymph, × 15. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 475. *S. picturata* Bekker-Migdisova; tegmen, × 9.7. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 476. *Sarbaloptera sarbalensis* Bekker-Migdisova; elytron, × 8.8. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 477. *Permolamproptera grandis* Bekker-Migdisova; hindwing, × 6.3. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 478. *Tychtoscytina kuznetskiensis* Bekker-Migdisova; tegmen, × 10.5. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1952).

Family SCYTINOPTERIDAE Handlirsch, 1904

Tegmen completely sclerotized; venation poor; SC not clear. Hindwing without hump-like protuberance and notch. Permian to Triassic. Four subfamilies: Scytinopterinae, Ivaiinae, Permojassinae, Ingruinae.

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Subfamily Scytinopterinae Bekker-Migdisova, 1960

In tegmen SCP short, extends only along R + M. Base of hindwing with broad anojugal area; SC terminates on anterior margin, gives off an inclined vein from its distal part, which is directed backward toward R_{1+2} (Fig. 473A, B). Lower Permian to Triassic. Nine genera.

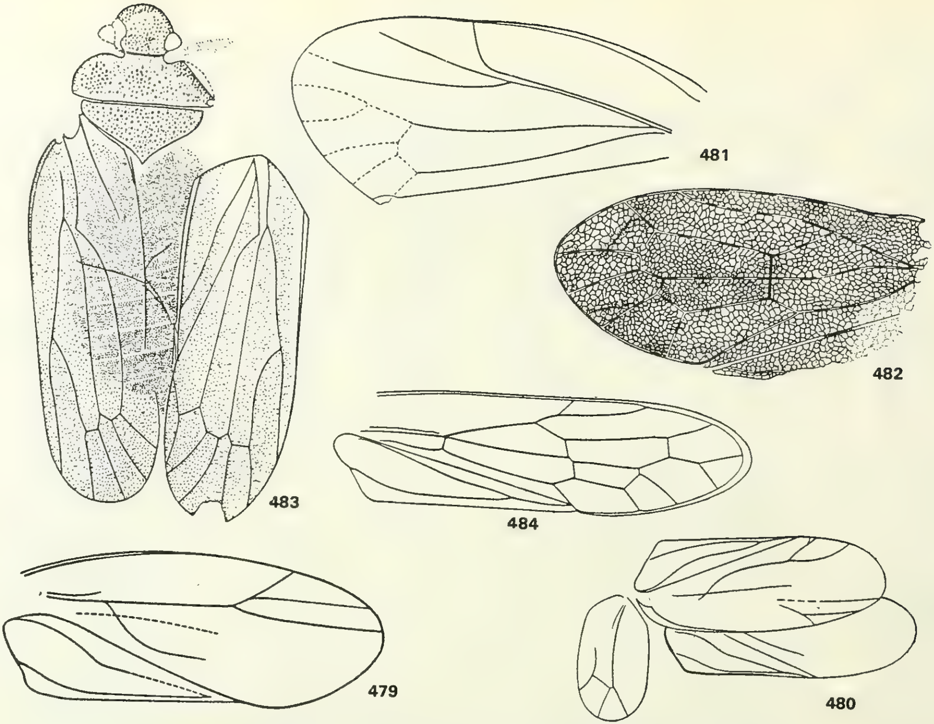
Scytinoptera Handlirsch, 1904 (*Anomoscyta* Martynov, 1928; *Permocixius* Martynov, 1928; *Scytinopterula* Handlirsch, 1937). Genotype—*S. kokeni* Handlirsch, 1904; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mountains). In tegmen SCP has small, sharp bend at level of middle part of R + M; M and CuA, dividing distally, forming a row of small cells; anojugal area markedly broad. Pronotum has lateral outgrowths. Scutellum long. Length of tegmen 6.2–8.4 mm (Figs. 474, 475; Pl. XIV, Figs. 1, 2). Eight species from the Kazanian stage of Arkhangelsk province and Urals and from the Lower and Upper Permian of Kuznetsk basin. Permian of Arkhangelsk province, Urals, and Kuznetsk basin.

Sarbaloptera Bekker-Migdisova, 1961. Genotype—*S. sarbalensis* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala II). Tegmina large, broad, length 1.8–1.9 times of breadth; costal area broad. Length of tegmen 8.8 mm (Fig. 476). One species. Lower Permian of Kuznetsk basin.

Permolamproptera Bekker-Migdisova, 1961. Genotype—*P. grandis* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Upper Kaltan). Hindwing large—about 10 mm long; anterior margin with small protuberance at base; distal part broad and rounded; R_1 short; R_2 and RS arcuately bent (Fig. 477, Pl. XIV, Fig. 3). One species. Lower Permian of Kuznetsk basin.

Tychtoscytina Bekker-Migdisova, 1952. Genotype—*T. kuznetskiensis* Bekker-Migdisova, 1952; Lower Permian. Kuznetsk basin (Erunakovian series, Sokolova). Tegmen with wide costal area; R branches more basally than middle of tegmen; M somewhat more distal, with five branches. Length of tegmen 5.8 mm (Fig. 478.) One species. Upper Permian of Kuznetsk basin.

Outside the USSR: *Homaloscytina* Tillyard, 1926; *Elliptoscarta* Tillyard, 1926; *Anomaloscytina* Davis, 1942 (non *Anomaloscytina* Evans, 1943); *Triassoscytina* Evans, 1956. Taxonomic position of genus *Stenoscytina* Tillyard, 1926 not clear.



Figs. 479–484. Family Scytinopteridae, subfamilies Ivaiinae, Permojassinae and Ingruinae.

479.*Ivaia indistincta* Bekker-Migdisova; tegmen × 14.4. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 480. *Anaprosbole ivensis* Bekker-Migdisova; tegmina and hindwing, × 10.8. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 481. *Surijokovia lata* Bekker-Migdisova; tegmen, × 12.5. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 482. *Ingruo smolenskui* Bekker-Migdisova; tegmen, × 15.7. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 483. *Kaltanospes kuznetskiensis* Bekker-Migdisova; tegmina and body of insect, × 12. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 484. *Permododa membracoides* Bekker-Migdisova; tegmen, × 8.7. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961).

Subfamily Ivaiinae Bekker-Migdisova, 1960

Tegmen: SCP short; M and CuP often form a false cross at base; distal part of M and CuA indistinct; CuP very weak. Hindwing with rounded distal part and broad anojugal area. Upper Permian. Two genera.

Ivaia Bekker-Migdisova, 1960. Genotype—*I. indistincta* Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). M and CuA form a false cross at base of tegmen; often M indistinct; CuP very weak. Length of tegmen 6.3 mm (Fig. 479). Two species. Upper Permian of Arkhangelsk province.

Anaprosbole Bekker-Migdisova, 1946. Genotype—*A. ivensis* Bekker-Migdisova, 1946; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Tegmen with asymmetrically truncated anterior margin; costal area broad; R_2 with branches; branches of M and CuA weak; M four-branched. Hindwing reduced to small scale. Length of tegmen 10.8 mm (Fig. 480). One species. Upper Permian of Arkhangelsk province.

Outside the USSR: *Triassoscelis* Evans, 1956; *Triassoscytinopsis* Evans, 1956; *Mesonirvana* Evans, 1956; *Mesothymbris* Evans, 1956.

Subfamily Permojassinae Bekker-Migdisova, 1960

Tegmen: SCP long, runs along whole length of R + M, R and R_1 and terminates on anterior margin. Hindwing with straight anterior margin and somewhat broad anojugal area; SC long and approaches R + M and R; SC terminates on anterior margin at midpoint of wing; branches of R short. Upper Permian. Two genera.

Surijokovia Bekker-Migdisova, 1961. Genotype—*S. lata* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian Suriekovo). Tegmen with wide costal area; SCP runs for some distance along R + M and RS and is bent at a right angle where R branches, before terminating on anterior margin; R_2 and RS long. Length of tegmen 4.9 mm (Fig. 481). One species. Upper Permian of Kuznetsk basin.

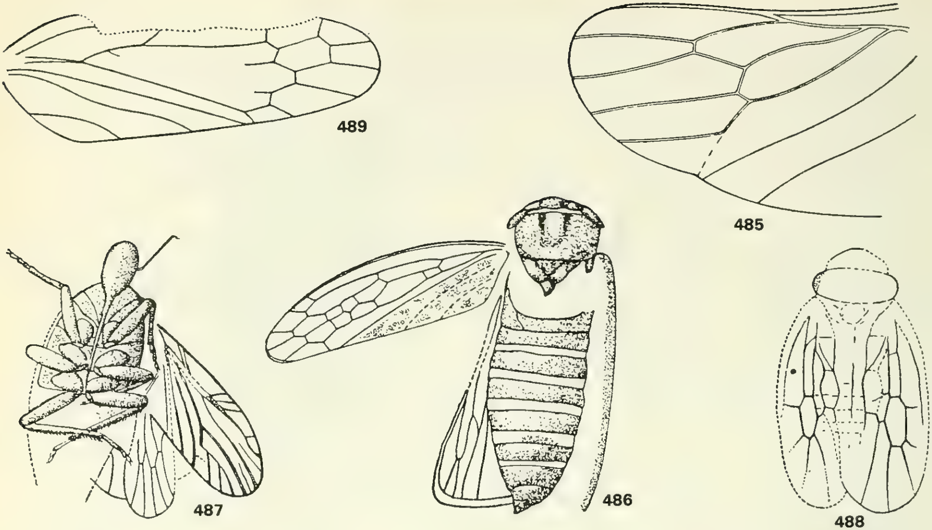
175 Outside the USSR: *Permojassus* Tillyard, 1926 (*Permojassula* Handlirsch, 1937).

Subfamily Ingruinae Bekker-Migdisova, 1946

[nom. transl. Bekker-Migdisova, 1952 (ex Ingruidae Bekker-Migdisova, 1946)]

Tegmen not very large, narrow with slender costal area; SCP short but distinct along R + M, fused with R; M branches considerably more distally than R. Hindwing with narrowing distal part and markedly broad anojugal part; anterior margin straight. Pronotum with lateral growths. Scutellum twice as broad as it is long. Permian. Three genera.

Ingruo Bekker-Migdisova, 1960. Genotype—*I. lanceolatus* Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage,



Figs. 485–489. Families Biturritidae, Cicadellidae and Eurymelidae.

485. *Absoluta distincta* Bekker-Migdisova; hindwing, × 15. Upper Triassic, Central Asia (Bekker-Migdisova, 1962).486. *Durgades miocenica* Bekker-Migdisova; body and wings, × 11.2. Miocene, Central Asia (Bekker-Migdisova, 1951). 487. *Karajassus crassinervis* Martynov; body and wings, × 20. Upper Jurassic, Southern Kazakhstan (Martynov, 1926). 488.*Karabasia paucinervis* Martynov; tegmen, × 13.6. Upper Jurassic, Southern Kazakhstan (Martynov, 1926). 489. *Mesojassus ipsviciensis* Tillyard; tegmen, × 11. Upper Triassic, Australia (Evans, 1956).

Soyana). In tegmen RS and CuA divide almost at same level; fork of CuA very large; M branches more distally than CuA. Length of tegmen 3–3.5 mm (Fig. 482). Four species. Upper Permian of Arkhangelsk province.

Kaltanospes Bekker-Migdisova, 1961. Genotype—*K. kuznetskiensis* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series,
176 Kaltan). In tegmen M and CuA divide almost at same level; R considerably more basal; fork of CuA wide, but moderately long. Length of tegmen 4.3–5.1 mm (Fig. 483; Pl. XIV, Fig. 4). Three species. Lower Permian of Kuznetsk basin.

Permododa Bekker-Migdisova, 1961. Genotype—*P. membracoides* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetskseries, Kaltan). Tegmen narrow and long with narrow marginal border, and many cells between RS and M and also between M and CuA. Length of tegmen 5.25 mm (Fig. 484; Pl. XIV, Fig. 5). One species. Lower Permian of Kuznetsk basin.

Family BITURRITIDAE Evans, 1953

(Lampropteridae Evans, 1948, nom. nud.)

Tegmen sclerotized, without marginal border; M simple; usually one row of small distal cells; radial cell divided by two cross veins. Hindwing uniformly broad, with small protuberance at base; fork of CuA very large; M simple; R fused with anterior margin. Parietal region reaches middle of frontal part of head. Pronotum with lateral outgrowths. Scutellum large, width twice its length. Triassic to Recent. Few genera in Recent fauna, of which one is also in fossil form.

Absoluta Bekker-Migdisova, 1962. Genotype—*A. distincta* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Hindwing with very thick veins; R_2 fused with margin at distal part; R branches more distally than M and CuA; CuA fused with R + M at base or approaches close to them. Length of hindwing 4 mm (Fig. 485). Two species. Upper Triassic of Issyk-Kul province.

Family CICADELLIDAE Latreille, 1825

(Jassidae Spinola, 1850)

Tegmen sclerotized, without marginal border, or only with welt along distal anal margin; with many large cells; M simple; fork of CuA broad. Hindwing narrows distally, with a broad anojugal area and wide border. Anterior margin with small 177 projection (Fig. 486; Pl. XIV, Fig. 6). Jurassic to Recent. In Recent fauna, 17 subfamilies and more than 5,000 species are known. There are about 40 fossil genera.

Karajassus Martynov, 1926. Genotype—*K. crassinervis* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen elongate, with rounded apex and elliptical shape; R branches more basad of middle of tegmen; M branches more distad; R forms a row of short branches toward anterior margin; CuA simple. Hindwing three-lobed. Fork of CuA situated at fringe of anojugal area. Length of tegmen 3.7 mm (Fig. 487). One species. Upper Jurassic of Kazakhstan.

Karabasia Martynov, 1926. Genotype—*K. paucinervis* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen oval. R extends very close to anterior margin; cells elongated lengthwise distally; between RS and M there is a large rounded central cell; between M and CuA, and CuA and CuP there are groups of small cells. Pronotum rounded and twice as wide as it is long. Length of forewing 2.75 mm (Fig. 488). One species. Upper Jurassic of Kazakhstan.

Outside the USSR: *Eurymelidium* Tillyard, 1919; *Triassojassus* Tillyard, 1919; *Mesoledra* Evans, 1956 (= *Mesojassus* Handlirsch, 1939; non *Mesojassus* Tillyard, 1916); *Jassites* Handlirsch, 1906; *Mesojassoides* Oman, 1937; *Acocephalites* Meunier, 1904; *Cicadellium* Westwood, 1854; *Homopterulum* Handlirsch, 1907.

Further, there are 15 genera from the Paleogene of Europe (Baltic amber) and North America, six genera from the Paleogene and Neogene of Western Europe and North America and three genera from the Neogene of Western Europe, North Caucasus and East Siberia.

Family EURYMELIDAE Amyot and Serville, 1843

[nom. transl. Evans, 1934 (ex Eurymelides Amyot et Serville, 1843)]

Tegmina transparent or sclerotized with simple or reticulate venation; marginal border small, but well developed; R_2 with a row of parallel branches; M divided into two stems: M_{1+2} and M_{3+4}, terminating on top of CuA with bifurcation. Hindwing with wide neala and rounded distal part; R_2 and RS present; M with two branches (Fig. 489). Triassic to Recent. About 25 genera, of which only one, *Mesojassus* Tillyard, 1916 from Triassic of Australia, is a fossil form.

Family MEMBRACIDAE Germar, 1821

[nom. transl. Dohrn, 1859 (ex Membracides Germar, 1821)]

Tegmina usually not membranous, with convex, distinct longitudinal and cross veins and usually with well-developed marginal border; cells distinctly isolated, often irregular; costal area narrow; M free at base, or branches from R + M at extreme base or joined with CuA. Pronotum and scutellum with paired and unpaired outgrowths. Triassic to Recent. In Recent fauna there are about 2,500 species in warm and temperate regions—primarily in tropical America. Thirteen subfamilies: Oxyrhachinae, Smiliinae, Darninae, Hyphinoinae, Terentiinae, Stegaspinae, Tolaniinae, Heteronotinae, Polyglyptinae, Darniopseinae, Ceresopseinae, Membracinae, Centrothinae; only the last four found as fossils.

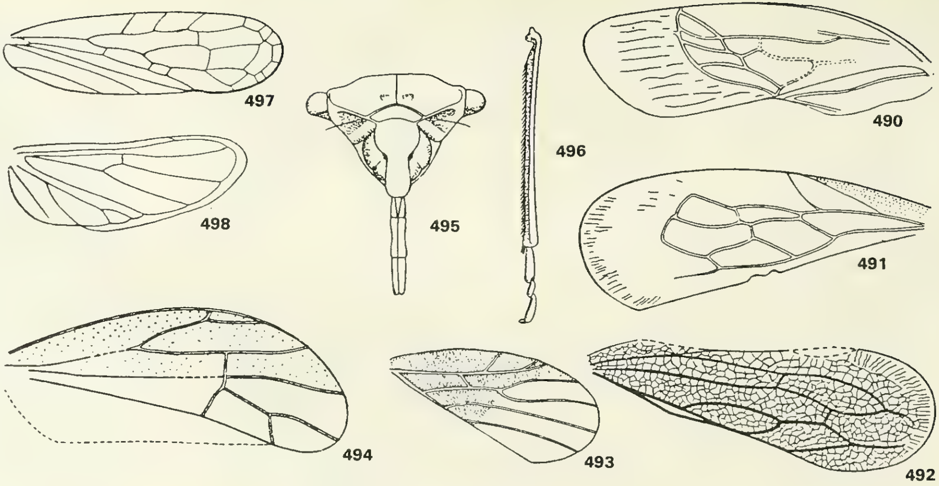
Subfamily Darniopseinae Bekker-Migdisova, 1958

Tegmen with a wide marginal border; cells close toward midpoint of tegmen, placed along its entire width; there are four apical cells; a_4 divided crosswise into two cells; RS long; M and CuA fused basally into one general stalk; anal area large, triangular, with A_1 and A_2, and with its posterior angle shifted distally. Upper Triassic. One genus.

Darniopsis Bekker-Migdisova, 1958. Genotype—*D. tragopea* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen elongated lengthwise; anterior margin slightly convex at basal half, with narrow, thick belt; marginal border occupies distal one-third of tegmen; stem of R short, R_2 breaks off at base; RS long; apical cells located vertically in a row; a_1 large and m wide and pentagonal. Length of tegmen 4.7 mm (Fig. 490). One species. Upper Triassic of Issyk-Kul province.

Subfamily Ceresopseinae Bekker-Migdisova, 1958

Tegmina broad; marginal border very wide; all cells located at center of wing;



Figs. 490–498. Families Membracidae and Aetalionidae.

490. *Darniopsis tragopea* Bekker-Migdisova; tegmen, × 12.7. Upper Triassic, Central Asia (Bekker-Migdisova, 1958). 491. *Ceresopsis costalis* Bekker-Migdisova; tegmen, × 10.7. Upper Triassic, Central Asia (Bekker-Migdisova, 1958). 492. *Sphongophoriella reticulata* Bekker-Migdisova; tegmen, × 50. Upper Trias, Central Asia (Bekker-Migdisova, 1958). 493. *Minuta heteropterata* Bekker-Migdisova; tegmen, × 19. Upper Triassic, Central Asia (Bekker-Migdisova, 1958). 494. *Maguviopsis kotchnevi* Bekker-Migdisova; tegmen, × 18. Lower Jurassic, Central Asia (Bekker-Migdisova, 1958). 495. *Aetalion reticulatum* (Linnaeus); head, × 10. Recent, South America (Evans, 1946). 496. *A. reticulatum* (Linnaeus); hind leg, × 15. South America (Evans, 1946). 497. *A. viticolle* Stall; tegmen, × 5. Recent, South America (Evans, 1946). 498. *Darthula hardwickii* Gray; hindwing, × 3. Recent South Asia (Evans, 1946).

anterior margin of tegmen with sclerotized belt; R_1 originates at basal half of wing; M and R fused into one stem; with three apical cells. Upper Triassic. One genus.

178 *Ceresopsis* Bekker-Migdisova, 1958. Genotype—*C. costalis* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen distally rounded; margin border one-fourth of length of tegmen; R_1 leaves R at margin of basal one-third of tegmen and bends toward anterior margin of wing; a_1 almost triangular in form; basal cell (rm) along its length one-third of length of tegmen. Length of tegmen 5.6 mm (Fig. 491). Three species. Upper Jurassic of Issyk-Kul province.

Subfamily Membracinae Stal, 1866

In tegmen cell m_1 almost always divided by a cross vein; cells r and m_1 bent at obtuse angles, narrowing toward base; veins R and M extends very close together; branches of R short; R_1, R_2 and RS run parallel, or ends of their branches fused to form irregular cells; M and CuA free or only touch at base, but do not fuse to form common stalk. Scutellum usually covered by pronotum, which is extended backward. Pronotum in the form of an expanded, elevated process, with its lateral lobes bearing longitudinal keels at lower margin, without keels at shoulder. Upper Triassic to Recent. Two tribes: Hypsoprorini and Membracini, latter with only Recent forms.

Tribe HYPSOPRORINI Haupt, 1929

Tegmen elongated along its length; venation much reduced; cells of extended oval shape; costal and anal areas narrow. Upper Triassic to Recent. Recent genera found in Neotropical areas. One fossil genus.

Sphongophoriella Bekker-Migdisova. Genotype—*S. reticulata* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen elongated and lancet-shaped; with three oval apical (a) and precostal cells (pc); r and m very long, not closed at base; SCP approaches R. Length of tegmen 1.2 mm (Fig. 492). One species. Upper Triassic of Issyk-Kul province.

Subfamily Centrotinae Stal, 1866

From base of tegmen two veins or, sometimes, only one arise; SC, R and M run 79 more or less parallel; M_1 usually with a bifurcation, fused with CuA at midpoint; a_3 located at apex; cell m_1 usually not divided by cross vein. Scutellum more or less distinct with sides not covered by outgrowths of pronotum. Posterior margin or pronotum with long dorsal process or, rarely, with hornlike growths; pronotum occasionally flat-dome or with a central stalk produced into a rootlike of swollen process. Femur flat in front, and with lateral rounded margins. Subfamily rich in species, inhabiting all areas. Upper Triassic to Recent. Two genera in fossil form.

Minuta Bekker-Migdisova, 1958. Genotype—*M. heteropterata* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen short, rounded, strongly sclerotized along anterior margin up to M_{1+2} distally and up to base of CuA_2 in middle; venation much reduced; all veins (R, M, CuA_1 and CuA_2) fused with CuP at base; R with small bifurcation; Mi divides at midpoint into two branches; branches of CuA long and parallel; apical cells absent. Length of tegmen 2 mm (Fig. 493). One species. Upper Triassic of Issyk-Kul province.

Maguviopsis Bekker-Migdisova, 1953. Genotype—*M. kotchnevi* Bekker-Migdisova, 1953; Lower Jurassic, Central Asia (Lower Liassic, Madygen). Tegmen rounded and bent distally abruptly truncated along anterior margin; anterior margin up to M sclerotized; R, M and CuP run close together at base, but do not fuse; M straight, simple vein which extends along middle of tegmen; R divided slightly before middle, with short branches; parallel to M; CuA joined with CuP a little more distally than middle of tegmen. Length of tegmen 3.3 mm (Fig. 494). Lower Jurassic of Central Asia.

Family AETALIONIDAE Spinola, 1850

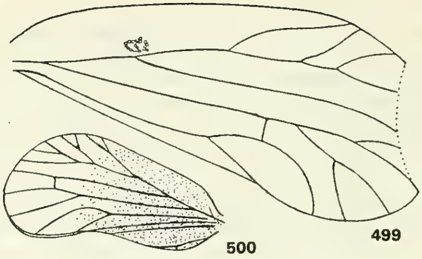
[nom. transl. Dohrn, 1859 (ex Aethalionoideae Spinola, 1850)]

Tegmen with clear veins, forming many cells or a network; R simple, does not divide into distinct stems, has a row of short branches running toward apex of wing; M three- or four-branched; CuA simple, venation varies widely. R not branched in hindwing. Head short, does not project behind border of pronotum. Anterior division of clypeus not separated from small posterior division. Lobes of frenum large. Postfrontal and frontal sutures form a continuous line behind frons. Antennae short. Ocelli located near coronal suture. Tibiae straight and cylindrical; hind tibia—long, flat, often with a row of bristles. Pronotum very well developed, with curved posterior margin, which grows over mesonotum and extends up to the long, narrow, scutellum. Length of body 5–28 mm (Figs. 495–498). Adults and nymphs lead communal life and are visited by ants. Females lay eggs on plants in special secretions and die. Their bodies protect the eggs. Polyphages. Paleogene to Recent. Two genera in Recent fauna from Southeast Asia and tropical America and also from the Paleogene of Western Europe.

SUPERFAMILY CERCOPIDEA

(Aphrophoroideae Spinola, 1850; Handlirsch, 1925)

Tegmina always sclerotized; SC usually long; cells normally located along margin or, if small, they occupy entire distal part of tegmen; M and CuA joined at base, or connected by long cross vein. Prominence usually developed on anterior margin at base of hindwing. M always simple; CuA forked; A_1 and A_2 free or fused only at middle. Anterior and posterior arms of tentorium fused. Hind legs with spurs, but no spines, with short and conical coxae. Triassic to



Figs. 499–500. Family Eoscarterellidae.

499. *Eoscarterella media* Evans; tegmen, × 10.5. Upper Triassic, Australia (Evans, 1956). 500. *Prosbolopsites tillyardi* Bekker-Migdisova; tegmen, × 9.6. Upper Triassic, Australia (Bekker-Migdisova, 1960).

Recent. Five families: Eoscarterellidae, Procercopidae, Cercopidae, Clastopteridae, Machaerotidae; last family without fossil representative.

Family EOSCARTERELLIDAE Evans, 1956

Tegmina rounded; costal area broad; R_2 divided many times; anal area shifted
180 backward, anal margin of anal area and distal part of wing located at same level
(Figs. 499, 500). Upper Triassic of Australia. Three genera: *Eoscarterella* Evans,
1956; *Eoscartoides* Evans, 1956; *Prosbolopsites* Bekker-Migdisova, 1961.

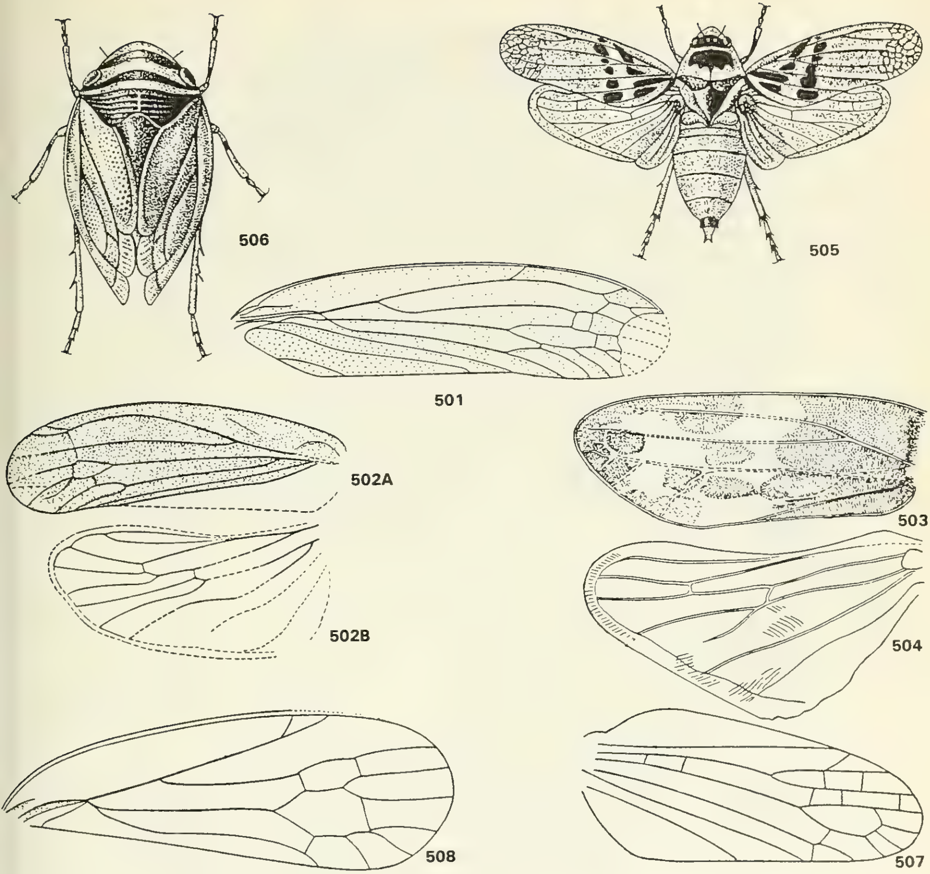
Family PROCERCOPIDAE Handlirsch, 1906

Length of tegmen exceeds its width by three- or four times; RS branches from R at basal one-third; M and CuA divide at distal one-third of tegmen, their branches are short. Hindwing with marginal border extending along its whole length and slightly widened in anojugal area; CuA branches at midpoint of wing; bifurcations of M and CuA long and narrow. Upper Permian to Lower Jurassic. Three genera.

Procercopsis Handlirsch, 1906. Genotype—*P. alutacea* Handlirsch, 1906;
Lower Jurassic, Germany. Length of tegmen almost four times its width; at
181 distal part of tegmen R_2 and M have a few short branches connected by a few
cross veins. In hindwing anterior margin almost straight. Length of tegmen 14
mm (Fig. 501). Two species: one from the Lower Jurassic of Western Europe
and the other from the Upper Triassic of Issyk-Kul province.

Procercopina Martynov, 1937. Genotype—*P. asiatica* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Length of tegmen nearly three times its width; venation poor; branches few; every two veins connected by cross vein. In hindwing distal and basal parts convex. Length of tegmen 12 mm (Fig. 502). Two species. Upper Triassic to Lower Jurassic of Central Asia.

Outside the USSR: *Stenoglyphis* Evans, 1947.



Figs. 501–508. Families Procercopidae, Cercopidae, Clastopteridae, Archijassidae and Hylicellidae.

501. *Procercopis longipenna* Bekker-Migdisova, tegmen, × 5.7. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 502. *Procercopina asiatica*Martynov; A—tegmen, × 6.4; B—hindwing, × 5.6. Lower Jurassic, Central Asia (Martynov, 1937). 503. *Megacercopis optima* Cockerell; tegmen,× 3.2. Miocene, Primorye province (Cockerell, 1921). 504. *Philagra kudiana* Cockerell; hindwing, × 3.2. Miocene, Primorye province (Cockerell, 1921). 505. *Locris areata* Walker; dorsal view, × 4.4. Recent (Lallemand, 1912). 506. *Clastoptera proteus* Fritch; dorsal view, × 9.4. Recent (Lallemand, 1912). 507. *Archijassus heeri* Handlirsch; tegmen, × 9. Lower Jurassic, Germany (Handlirsch, 1906). 508. *Hylicella colorata* Evans; tegmen, × 6.8. Upper Triassic, Australia (Evans, 1956).

Family CERCOPIDAE Leach, 1815

[nom. transl. Leach, 1818 (ex Cercopida Leach, 1815)]
(Tomaspididae Melander-Brues, 1932; Metcalf, 1934; Poisson-Pesson, 1951)

Tegmina lack distinct marginal border separated by marginal vein; RS always long; clavus pointed at apex. RS developed in hindwings. Scutellum of mesonotum shorter than pronotum. Length of tegmen 5 – 25 mm (Figs. 503–505). This family is rich in species: around 1,500, distributed over diverse areas. Upper Triassic to Recent. 25 genera in fossil record; two genera from the Upper Triassic of Australia: *Trifidella* Evans, 1956 and *Aldotrifidus* Evans, 1956; about nine genera from the Paleogene of North America, Greenland and Western Europe; about five genera from the Paleogene and Neogene of Western Europe, North Caucasus, East Siberia and North America, and about nine genera from Western Europe, North Caucasus and East Siberia.

Family CLASTOPTERIDAE Dohrn, 1859

Tegmina with marginal vein connecting distal ends of all veins, isolating marginal border; clavus sharply rounded at apex. In hindwing RS very short, often arcuate, terminating on R to form a rounded cell. Scutellum of mesonotum longer than pronotum (Fig. 506). Neogene to Recent. Tropical family, with few species. One genus from the Neogene of North America in fossil record.

Cercopidea Incertae sedis

The genus *Mesojassula* Evans, 1956 from the Upper Triassic of Australia belongs to Cercopidea (only hindwing known).

Cicadellidomorpha Incertae sedis

Family ARCHIJASSIDAE Bekker-Migdisova, 1962

Tegmen with very wide, often triangular costal area, with a long SC across it; RS always long; rows of cross veins and usually a group of isolated cells in distal part of tegmen; anal area wide and triangular. Length of tegmen 5–9.4 mm (Fig. 507). Upper Triassic to Lower Jurassic. Five genera in Australia and Western Europe: *Archijassus* Handlirsch, 1906 (*Cercopidium* Geinitz, 1880); *Atitizon* Handlirsch, 1939; *Eojassus* Handlirsch, 1939; *Liojassus* Handlirsch, 1939; *Mesoscytina* Tillyard, 1919. Also, *Mesocixiodes orthoclada*Tillyard, 1922 from the Upper Triassic of Australia possibly belongs to this family.

Family HYLICELLIDAE Evans, 1956

CuA partly fused with M at distal part of tegmen; M three- or four-branched; two or three closed cells between branches of R and M. Length of tegmen 3.5–3.8 mm (Fig. 508). Upper Triassic of Australia. Two genera: *Hylicella* Evans, 1956; *Hylicellites* Bekker-Migdisova, 1962.

Infraorder Fulgoromorpha

Tegmina membranous, rarely leathery, more often with rich venation and long SC. In hindwing marginal border and marginal vein absent; R_2 short, terminates on anterior margin before apex of wing. Tegulae present. Middle coxae elongated and articulating closer to outer margin than coxae of forelegs and capable of lateral movement; hind coxae immovable. Clypeus does not reach level of compound eyes and is flat. Frons small, with median ocellus, or not distinct; lateral ocelli located along margin of compound eyes. Permian to Recent. In Recent fauna about 6,500 species. Eighteen families: Mundidae, Pereboriidae, Dictyopharidae, Fulgoridae, Fulgoridiidae, Lophopidae, Cixiidae, Achilidae, Ricaniidae, Flatidae, Delphacidae, Issidae, Tettigomotridae, Derbidae, Achilixiidae, Acanaloniidae, Tropiduchidae, Eurybrachiidae, last six families not known to contain fossil representatives.

182 Family MUNDIDAE Bekker-Migdisova, 1960

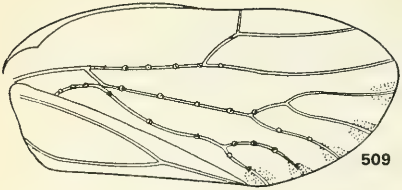
Tegmen leathery-membranous, without sculpturing; venation poor; veins convex with warts; costal area broad; anterior margin of tegmen convex; CuA branches distally; anal area broad. Upper Permian. One genus.

Mundus Bekker-Migdisova, 1960. Genotype—*M. nodosus* Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Tegmen with a rounded distal part asymmetrically truncated along anal border; R divides at middle of tegmen; R_2 and RS parallel. M and CuA divide more distally than R; anal veins thick; all veins with warts. Length of tegmen 6.1 mm (Fig. 509). One species. Upper Permian of Arkhangelsk province.

Family PEREBORIIDAE M. Zalessky, 1930

Tegmina membranous; venation rich; R_2, RS, M and CuA have many branches, not distinct in distal part, R_2 with a row of short branches, M and R divide more basally than CuA. Lower Permian to Upper Triassic. Nine genera.

183 *Pereboria* M. Zalessky, 1930. Genotype—*P. bella* M. Zalessky, 1930; Upper Permian, Komi ASSR (Kazanian stage, River Perebora). RS pectinate with many parallel branches; M many-branched and pectinate; many cross veins. Length of tegmen exceeds 40 mm (Fig. 510). One species. Upper Permian of North Urals.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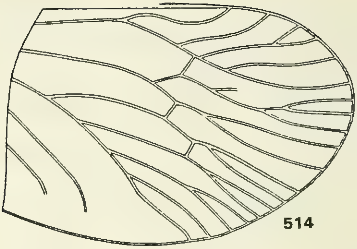
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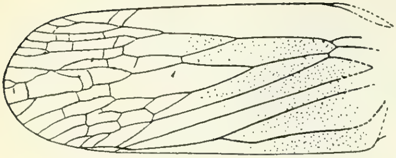
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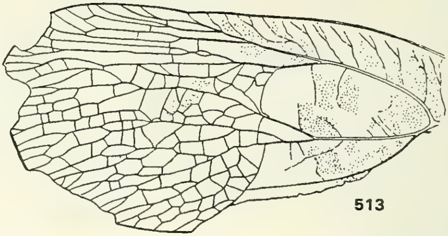
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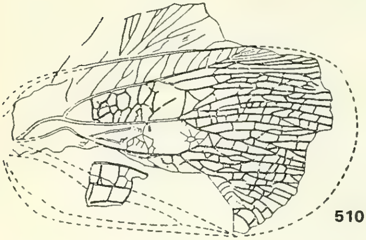
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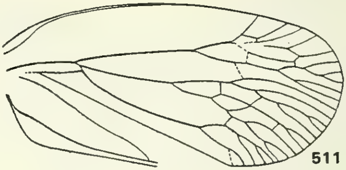
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Figs. 509–514.

Families Mundidae, Pereboriidae. 509. *Mundus nodosus* Bekker-Migdisova; tegmen, × 11. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 510. *Pereboria bella* M. Zalessky; tegmen, × 1.5. Upper Permian, Pre-Urals (original drawing after photograph by M. Zalessky). 511. *Permopibrocha ramosa* Martynov; tegmen, × 4.5. Upper Permian, Arkhangelsk province (Martynov, 1935). 512. *Scytophara extensa*Martynov; tegmen, × 9. Upper Permian, Southern Pre-Urals (Martynov, 1937). 513. *Neuropibrocha ramisubcostalis* Bekker-Migdisova; tegmen, × 3.3. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 514. *Kaltanopibroca boreoscytinoides* Bekker-Migdisova; hindwing, × 10.3. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961).

183 *Permopibrocha* Martynov, 1935. Genotype—*P. ramosa* Martynov, 1935; Upper; Permian, Arkhangelsk province (Kazanian stage, Soyana). Length of tegmen double its width; distal part of tegmen broadly rounded; anterior margin convex; M and R branch at distal half of wing, and CuA more distally; R_2 forms a row of parallel short branches terminating on anterior margin of wing. Length of tegmen 13 mm (Fig. 511). One species. Upper Permian of Arkhangelsk province.

Scytophara Martynov, 1937. Genotype—*S. extensa* Martynov, 1937; Permian, Orenburg province (Kargala). Length of tegmen 2.5 times its width; anterior border straight; M and R branch more basally than midpoint of tegmen, and CuA branches more distally; R_2 pectinate, forms long parallel branches terminating on apex of wing. Length of tegmen 7.5 mm (Fig. 512). One species. Permian of Pre-Urals.

Neuropibrocha Bekker-Migdisova, 1961. Genotype—*N. ramisubcostalis* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen rounded distally; anterior margin convex; SC completely fused with R, preserves traces of pectinate structure; long cross veins are present throughout; distal region, between R, M and CuA, R_2 with a row of parallel branches, directed toward the apex, RS distinctly demarcated, divides distally; radial area short and broad; medial area considerably narrower; both with traces of large-celled archedictyon, distally giving way to cells; M with a row of parallel branches; CuA divides more distally than M and R. Length of forewing 26–38 mm (Fig. 513; Pl. XIV, Figs. 7, 8). Two species. Lower Permian of Kuznetsk basin.

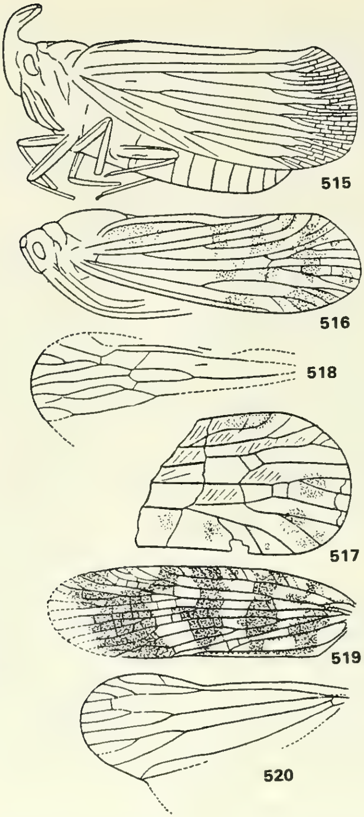
Kaltanopibrocha Bekker-Migdisova, 1961. Genotype—*K. boreoscytinoides* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Anterior margin of hindwing almost straight; R_2 bent and pectinate, its branches run parallel to R_1 toward apex of wing; RS with branches; M pectinate; anal area not wide, rounded. Length of hindwing about 10 mm (Fig. 514). One species. Lower Permian of Kuznetsk basin.

Outside the USSR: *Permobrachus* Evans, 1943 from Upper Permian of Australia. Possibly genera *Crossbella* Evans, 1956, *Mesocicadella* Evans, 1956 and *Permoglyphis* Tillyard, 1926 also belong here.

Family FULGORIDAE Latreille, 1807

[nom. transl. Stephens, 1929 (ex Fulgorellae Latreille, 1807)]
(Laternariidae Haupt, 1929; Lystridae Pascol, 1882; Rhinotharia Distant, 1911)

Tegmen and hindwing broad distally, with very rich venation; covered with a dense network of longitudinal and cross veins; in tegmen SC distinct and
184 pectinate, with a row of parallel veins along its entire length; directed toward anterior border, and with a tuft of parallel branches of RS at the apex; R branches at basal one-fourth of tegmen; CuA divides at middle of wing. Anal area with a network in hindwing. Head with different types of horns, spines or



183 Figs. 515–520. Families Fulgoridae and Fulgoridiidae.

515. *Nyctophylax uhleri* Scudder; general view, × 2.5. Miocene, North America (Scudder, 1899). 516. *Fulgoridium breviradiatum* Handlirsch; tegmen, × 6.9. Lower Jurassic, Germany (Handlirsch, 1939). 517. *Fulgoridiella rhaetica* Bekker-Migdisova; tegmen, × 8.7. Upper Triassic, Central Asia (Bekker-Migdisova, 1961). 518. *Fulgoropsis dubiosa* Martynov; hindwing, × 4. Lower Jurassic, Central Asia (Martynov, 1937). 519. *Eofulgoridium kizylkiensis* Martynov; tegmen, × 4.3. Lower Jurassic, Central Asia (Martynov, 1937). 520. *E. proximum* Martynov; hindwing, × 5.6. Lower Jurassic, Central Asia (Martynov, 1937).

outgrowths. Large forms. Length of body up to 75 mm [sic] (Fig. 515). Tropical family with few genera. Paleogene to Recent. Five genera in fossil form; one from the Paleogene of Europe (Baltic amber); three from the Paleogene and Neogene of Western Europe, North America and Australia and two from the Neogene of North America.

Family FULGORIDIIDAE Handlirsch, 1939

[nom. transl. Bekker-Migdisova, 1961 (ex Fulgoridiinae Handlirsch, 1939)]

Tegmina with slightly broad and rounded distal part; SC simple, does not branch, extends along anterior margin of wing and along R_1; R branches in middle of tegmen or a little before; CuA branches at basal one-third or before; all veins distally divide many times; cross veins very sparse. Basal cell closed. Head without cephalic process. Lower Jurassic to Recent. Eight genera.

Fulgoridium Handlirsch, 1906. Genotype—*Phryganidium balticum* Geinitz, 1880; Lower Jurassic, Germany. Tegmen with markings or transparent; elongate, distal part being slightly elongated; anterior margin straight; SC long, approaches margin, does not branch; R with a row of short branches; CuA divides at basal one-fourth of tegmen, with three long branches; basal cell closed. In hindwing RS with short branches; CuA three- or four-branched; M branches more distally than CuA. Length of tegmen 6–9 mm (Fig. 516). 108 species from Western Europe and one species from Issyk-Kul province. Upper Triassic to Lower Jurassic.

Fulgoridiella Bekker-Migdisova, 1962. Genotype—*F. rhaetica* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen with markings, distally broad; R_1 fairly long and bent, not parallel to short branch of R_2; RS simple; M and CuA with short distal branches. Length of tegmen 10 mm (Fig. 517). One species. Upper Triassic of Issyk-Kul province.

Fulgoropsis Martynov, 1937. Genotype—*F. dubiosa* Martynov, 1937; Jurassic, Central Asia (Lower Lias, Kizil-Kiya). R and RS very close in hindwing; M branches at same level as R, more basally than midpoint, and forms a central cell; branches of CuA long; veins curved. Length of hindwing about 11 mm (Fig. 518). One species. Lower Jurassic of Central Asia.

Outside the USSR: *Fulgoridulum* Handlirsch, 1939; *Metafulgoridium* Handlirsch, 1939; *Margaroptilon* Handlirsch, 1906 and *Cixiites* Handlirsch, 1906.

Family LOPHOPHIDAE Stal, 1866

[nom. transl. Melichar, 1903 (ex Lophopida Stal, 1866)]

Tegmen with rich venation; branches long, converging; SC distinct, long and branching; R, M and CuA branch earlier than M and CuA; anal area with cross veins. Head narrower than pronotum, with long cephalic process. Clypeus with lateral keels. Jurassic to Recent. Recent fauna with about 28 genera, of which one is in fossil record.

Eofulgoridium Martynov, 1937. Genotype—*E. kisylkiense* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Kizil-Kiya). Tegmen of uniform width; SC runs in middle, between C and R; R divides at basal one-third of tegmen, M at its midpoint and CuA at level of R; CuA and RS with numerous pectinate branches; M three-branched. Hindwing with short rounded distal part; R with short branches; R_1 present; M and CuA with three branches, they divide at same level. Length of tegmen 12.5 mm (Figs. 519, 520). Two species. Lower Jurassic of Central Asia.

Family CIXIIDAE Spinola, 1850

[nom. transl. Fieber, 1872 (ex Cixioideae Spinola, 1850)]

Tegmina usually transparent, with moderately rich venation and thick longitudinal and cross veins, often with warts on them; all veins converge at basal region; SC not separate, but fused with R; R divides at middle of tegmen or more basally, and M more distally; CuA straight at base. Hindwing with broad anojugal area, thick veins and truncated anterior margin. Head not extended in front. More than 780 species and about 100 genera in Recent fauna. About 20 genera have fossil forms. Permian to Recent.

Mesocixiella Martynov, 1937. Genotype—*M. asiatica* Martynov, 1937; Lower Jurassic, Central Asia (Lower Liassic, Kizil-Kiya). Anterior margin of tegmen straight; pterostigma short; branches of R_2 short; stem of R equal to or longer than R_{1+2}; RS leaves R before middle of tegmen; fork of CuA short.
185 Length of tegmen 6.5 mm (Fig. 521; Pl. XV, Fig. 1). Five species. Upper Triassic of Issyk-Kul province and Lower Jurassic of Kazakhstan.

Cycloscytina Martynov, 1926; Genotype—*C. delutinervis* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen sclerotized and elongate anterior margin straight; pterostigma with a row of branches; RS leaves R before middle; fork of CuA short. Hindwing with gently curving anterior margin; M with two long branches; anterior one pectinate and posterior one simple; fork of CuA long. Length of tegmen 9 mm (Fig. 522). Seventeen species.
186 Upper Triassic of Issyk-Kul province and Upper Jurassic of Kazakhstan.

Surijokocixius Bekker-Migdisova, 1961. Genotype—*S. tomiensis* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Tegmen distally rounded with thick convex anterior margin; R_2 and RS in the form of parallel arcs; fork of CuA long and bent. Length of forewing 4.3 mm (Fig. 523). One species. Upper Permian of Kuznetsk basin.

Permocixiella Bekker-Migdisova, 1949. Genotype—*P. venosa* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). Tegmen membranous, with thick veins, elongated along its length, with straight anterior margin; R, R_{1+2} and R_1 in the form of a continuous, straight vein; M divides at same level as CuA; dividing line present; fork of CuA with long, strong branches. Length of tegmen 10.5 mm (Fig. 524). One species. Upper Permian of Kuznetsk basin.

Scytocixius Martynov, 1937. Genotype—*S. mendax* Martynov, 1937; Permian, Orenburg province (Kargala). Tegmen narrows basally, with almost straight anterior margin; R and RS arcuately bent and simple; R and CuA branch at same level, M more distally; branches of CuA long and straight. Length of forewing 5.5 mm (Fig. 525). Two species. Upper Permian of Urals and Kuznetsk basin.

Boreocixius Bekker-Migdisova, 1955. Genotype—*B. sibiricus* Bekker-Migdisova, 1955; Lower Triassic, North Siberia. Tegmen rounded with thick convex anterior margin; common stem of R very short; RS and R_{1+2} with short branches; fork of CuA long and bent. Length of forewing 5.5 mm (Fig. 526). Two species. Lower Triassic of Issyk-Kul province.

Vitreacixius Bekker-Migdisova, 1962. Genotype—*V. elliptica* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen weakly sclerotized, elliptical in form with convex anterior margin; costal area broad; RS branches a little more proximally than in *Cixiella* ; M many-branched, divides somewhat more distally than middle of tegmen; fork of CuA small. Length of tegmen 9 mm (Fig. 528). One species. Upper Triassic of Issyk-Kul province.

Asiocixius Bekker-Migdisova, 1962. Genotype—*A. fulgoroides* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen elliptically rounded, transparent and weakly sclerotized at base; anterior margin convex; venation rich; veins close; trunk of R shorter than R_{1+2}; M and R_2 pectinate. Length of tegmen 10.9 mm (Fig. 529). One genus in Upper Triassic of Issyk-Kul province.

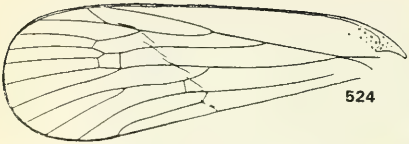
In addition to these, there are two genera from the Paleogene of Europe (Baltic amber) and one genus from the Neogene of East Siberia.

Outside the USSR: *Triassocixius* Tillyard, 1919; *Mesocixioides* Tillyard, 1919; *Mesocixius* Tillyard, 1919 from Upper Triassic of Australia and in addition to these, there are six genera from the Paleogene of Western Europe and North America, two genera from the Paleogene and Neogene of Western Europe and North America and four genera from the Neogene of Western Europe and North America.

Family ACHILIDAE Stal, 1866

[nom. transl. Melichar, 1903 (ex Tympanophoridae Brunner, 1893)]

Tegmina usually membranous, folded horizontally or like a flat roof at rest; distal region of tegmen widen beyond apices of clavus and are placed one above the other when folded; SC usually without short branches directed toward anterior margin; clavus pointed at apex. Head narrow. Clypeus with distinct lateral keels. Two ocelli. Last segment of proboscis elongated. Lateral keel of pronotum bent. Length of body 6–12 mm (Fig. 530). Paleogene to Recent.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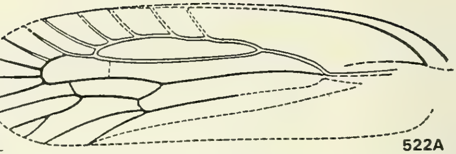
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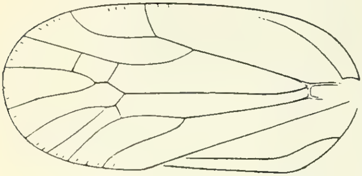
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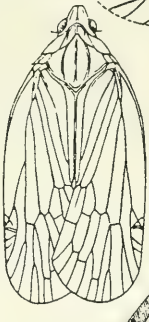
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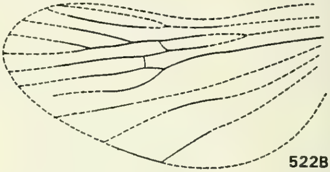
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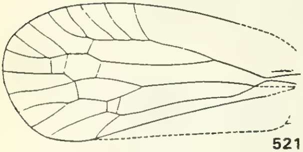
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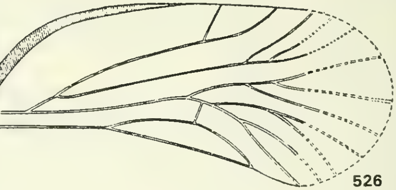
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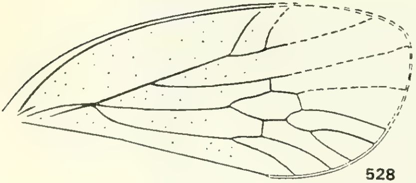
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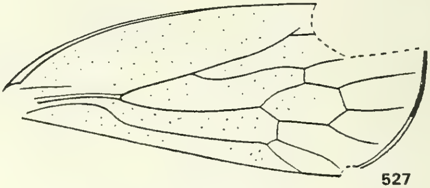
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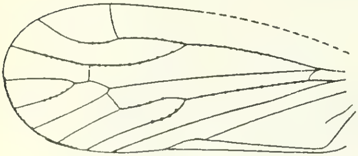
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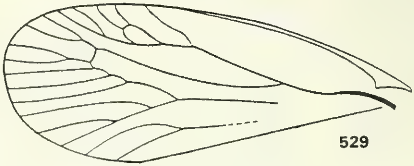
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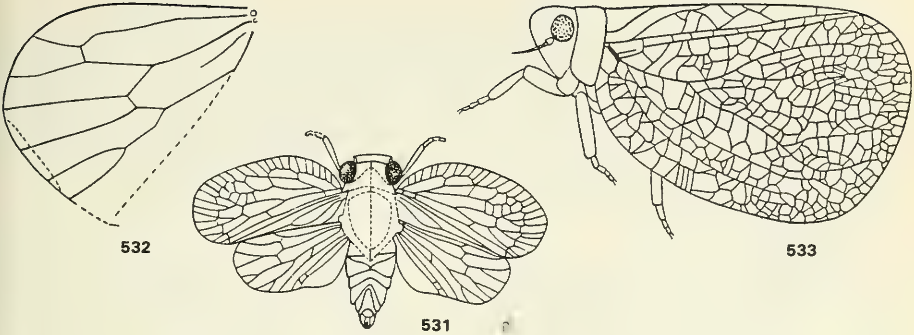

187 Figs. 531–533. Families Ricaniidae and Flatidae.

531. *Tritophania patruelis* Jakobi; dorsal view, × 13. Paleogene, Europe (Baltic amber) (Jakobi, 1937). 532. *Ludibrium ludus* Bekker-Migdisova; hindwing, × 6.3. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 533. *Ormenis* sp.; lateral view, × 3. Recent, South America (Orenberger, 1957).

Numerous (primarily tropical) genera. Three fossil genera, one from the Paleogene of Europe (Baltic amber) and two from the Neogene of North America.

Family RICANIIDAE Amyot and Serville, 1843

[nom. transl. Dohrn, 1859 (ex Ricanides Amyot et Serville, 1843)]

Tegmina large and usually variable or triangular in shape, with extended conical apex; numerous longitudinal and cross veins; row of cross veins in distal area
187 located at one level, forming a transverse line; SC long with a row of numerous parallel branches; R and M branch immediately after branching of M from R;

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185 Figs. 521–530. Families Cixiidae and Achilidae.

521. *Mesocixiella asiatica* Martynov; tegmen, × 8. Lower Jurassic, Central Asia (Martynov, 1937). 522. *Cycloscytina extensa* Martynov; A—tegmen, × 9; B—hindwing, × 6.6. Lower Jurassic, Central Asia (Martynov, 1937). 523. *Surijokocixius tomiensis* Bekker-Migdisova; tegmen, × 14. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 524. *Permocixiella venosa* Bekker-Migdisova; tegmen, × 6.5. Upper Permian, Kuznetsk basin (Bekker-Migdisova 1961). 525. *Scytocixius mendax* Martynov; tegmen, × 12. Upper Permian, Southern Urals (Martynov, 1937). 526. *Boreocixius sibiricus* Bekker-Migdisova; tegmen, × 13. Lower Triassic, North Siberia (Bekker-Migdisova, 1955). 527. *Cixiella reducta* Bekker-Migdisova; tegmen, × 14. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 528. *Vitreacixius ellipticus* Bekker-Migdisova; tegmen, × 8. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 529. *Asiocixius fulgoroides* Bekker-Migdisova; tegmen, × 6.8. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 530. *Helicoptera* sp.; dorsal view, × 8. Recent (Haupt, 1935).

anal area without warts. Hindwing small, without widening of anojugal area. Head almost equal to pronotum (Fig. 531). Upper Triassic to Recent. Many genera in Recent fauna of tropics. Ten genera in fossil form.

Ludibrium Bekker-Migdisova, 1962. Genotype—*L. ludus* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Hindwing rounded without humplike protuberance at base. R simple (only short, curved RS preserved distally; R_2 reduced); M branches into two, somewhat more basad of middle; CuA divided at base into two simple pectinate branches. Length of hindwing 7.3 mm (Fig. 532). One species. Upper Triassic of Issyk-Kul province.

Besides these there are six extinct genera: one from the Paleogene of Europe (Baltic amber), two from the Paleogene of Western Europe, one from the Paleogene of Western Europe and North America, one from the Neogene of North America, and *Ricaniites* Handlirsch, 1907 from the Jurassic of Western Europe, and three genera in Recent fauna which are also represented as fossils: one from the Tertiary deposits of Australia, one from the Paleogene of Europe (Baltic amber) and one from the Paleogene of Western Europe.

Family FLATIDAE Spinola, 1839

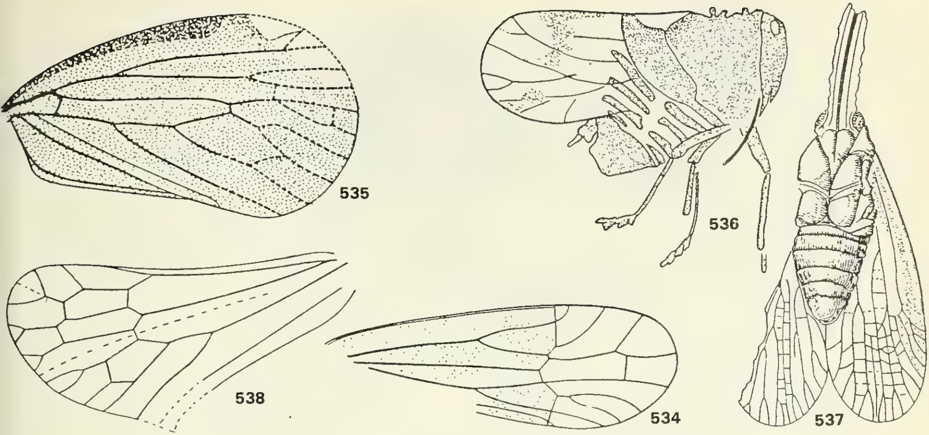
[nom. transl. Dohrn, 1859 (ex Flatoides Spinola, 1839)]

Tegmina of irregular shape, wide and often truncated anteriorly; costal area distinctly isolated; SC long with numerous short parallel branches directed toward wing margin; R divides close to base into R_2 and branching RS; M leaves a little more basad of point, where R branches off, often fused at base with RS; CuA straight and two-branched, runs close to CuP; rows of short parallel branches isolated by cross veins at distal part of tegmen; anal area with warts. Hindwing much widened distally or with irregular form (Fig. 533). Paleogene to Recent. Many tropical and subtropical genera in Recent fauna. About 11 fossil genera, comprising one Recent genus also from the Paleogene of Western Europe (Baltic amber), seven extinct genera from the Paleogene of North America, two extinct genera from the Paleogene of Western Europe and one Recent genus also from the Paleogene of Western Europe and Tertiary deposits of South America.

Family DELPHACIDAE Leach, 1815

[nom. transl. Dohrn, 1859 (ex Delphacida Leach, 1815); Araeopidae Metcalf, 1938]

Tegmina narrow, with distal part elliptically elongated; venation rich; veins thick; row of distinct cross veins separates a large distal part of tegmen. Hindwing with almost straight anterior margin; RS bent; M and CuA close at base. Hind tibia with large leaflike spur (Fig. 534). Paleogene to Recent. There
188 are about 137 genera and more than 1,000 species in Recent fauna of tropical and temperate regions. Five genera are reported in fossil record, of which one extinct



Figs. 534–538. Families Delphacidae, Issidae and Dictyopharidae.

534. *Liburnia stavropolitana* Bekker-Migdisova; tegmen, × 21. Miocene, North Caucasus (Bekker-Migdisova). 535. *Elasmoscelidium rotundatum* Martynov; tegmen, × 8.9. Upper Jurassic, South Kazakhstan (Martynov, 1926). 536. *Mesotubilustrium asiaticum* Bekker-Migdisova, insect from side, × 12.5. Upper Jurassic, South Kazakhstan (Bekker-Migdisova, 1949). 537. *Thanatodictya vishneviensis* Bekker-Migdisova; body and wings, × 4.4. Miocene, North Caucasus (Bekker-Migdisova). 538. *Dictyophora* sp.; hindwing, × 10.5. Miocene, North Caucasus (Bekker-Migdisova).

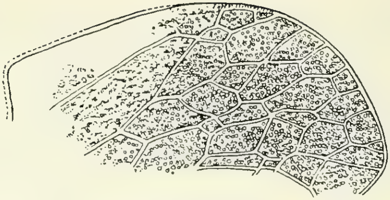
genus is from the Neogene of Primorye-province, one Recent genus also from the Neogene of the North Caucasus and the Paleogene of Baltic amber and amber from Burma, one extinct genus from the Paleogene of North America, one Recent genus also from the Paleogene of Western Europe and one Recent genus also from the Paleogene of North America and Western Europe.

Family ISSIDAE Spinola, 1839

[nom. transl. Schaum, 1850 (ex Issites Spinola, 1839)]

Tegmina strongly sclerotized and convex with convex anterior margin, often with erratic shape; SC without branch; RS simple or pectinate, arise from R at base. Hindwing sometimes divided into three equal lobes: distal, anal and anojugal, the last narrows toward base. Head equal in width to thorax or wider. Measures 3–7 mm. Many genera in Recent fauna. Upper Jurassic to Recent. Four genera in fossil record.

Elasmoscelidium Martynov, 1926. Genotype—*E. rotundatum* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen short, with distal part broad and round; SC runs parallel to anterior margin and forms a



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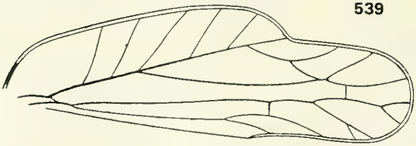

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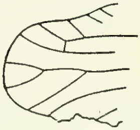

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Figs. 539–541. Fulgoridea incertae sedis and Auchenorrhyncha incertae sedis (Family Dysmorphoptilidae).

539. *Reticulocicada brachyptera* Bekker-Migdisova; fragment of tegmen, × 10.4. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 540. *Dysmorphoptiloides elongata* Evans; tegmen, × 64.4. Upper Triassic, Australia (Evans, 1956). 541. *Mesoatracis reducta* Bekker-Migdisova; hindwing, × 10. Lower Jurassic, Central Asia (Bekker-Migdisova, 1949).

reduced border; R_2 long and simple; RS and M branch distally; CuA has long branches; basal cell curved; anal area does not reach apex of tegmen. Length of forewing 7 mm (Fig. 535). Four species. Upper Jurassic of Kazakhstan and Lower Jurassic of Western Europe.

Mesotubilustrium Bekker-Migdisova, 1949. Genotype—*M. asiaticum* Bekker-Migdisova, 1949; Upper Jurassic, Chimkent province (Malm, Karatau). Tegmen fairly short, only slightly longer than abdomen, broad distally; R branches at middle of tegmen or slightly more distally; R and RS have branches; CuA simple; M has a small bifurcation. Head flat. Abdomen short and broad. Length of tegmen 4.7 mm (Fig. 536). One species. Upper Jurassic of Kazakhstan.

Besides this, there are also two genera from the Paleogene of Europe, one from Baltic amber and one from Western Europe.

Family DICTYOPHARIDAE Spinola, 1839

[nom. transl. Kirschberg, 1868 (ex Dictyopharoides Spinola, 1839)]
[Fulgorinae Haupt, 1929; Pseudophanides Amyot et Serville, 1843 (pars);
Dohrn, 1859 (pars)]

Tegmina membranous; veins thick and sparse; SC not separated; R divides more distad than middle; M and CuA divide at middle; cross veins abound only at distal part, oriented vertically. Hindwings with straight anterior margin, without marginal veins. Head elongated, with long cephalic process with usually two or three longitudinal keels; two ocelli. Legs long. Length of body 6–15 mm 189 (Figs. 537, 538). Paleogene to Recent. Few genera from regions of warm, moist climate. Three genera in fossil form—one from the Paleogene of Europe (Baltic amber), and two from the Neogene of the North Caucasus.

Fulgoromorpha Incertae sedis

Reticulocicada Bekker-Migdisova, 1961. Genotype—*R. brachyptera* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian series; Suriekovo). Tegmen very short, covered with warts, with anterior margin truncated, sloping toward apex; costal area broad; with small nodus at base of pterostigma; R_2 sends short branches toward anterior margin; a close network of cells observed between RS, M and CuA in distal part. Length of tegmen 6–7 mm (Fig. 539; Pl. XV, Fig. 2). One species. Upper Permian of Kuznetsk basin.

To Fulgoromorpha incertae sedis belong genera like *Permofulgor* Tillyard, 1917; *Homopterites* Handlirsch, 1906; *Pendodelphax* Handlirsch, 1907; *Petropteron* Cockerell, 1912. Four genera from the Paleogene of North America and one species of indistinct systematic position (*Cicadellium psocus* Westwood, 1854).

Auchenorrhyncha Incertae sedis

Family DYSMORPHOPTILIDAE Handlirsch, 1906

Tegmen of atypical shape with distinct broadening at base; strongly sclerotized, but with distinct venation; SC fused with R, but usually preserves its parallel branches directed toward anterior margin; RS very long, leaves R earlier than middle of tegmen; M simple, with short branches that terminate on apex; CuA with a bifurcation, without a sharp basal bend toward base of M; anal area with free A_1 and A_2. Length of tegmen 10–16 mm (Fig. 540). Systematic position uncertain. Handlirsch (1939) related Dysmorphoptilidae to Jassidea and Evans (1956) to Cercopidea. Bekker-Migdisova (1949) related a fragment of the wing of *Mesoatracus* to Flatidae on the basis of its peculiar form. Triassic to Jurassic. Three genera.

Mesoatracis Bekker-Migdisova, 1949. Genotype—*M. reducta*, 1949; Lower Jurassic, Central Asia (Lower Liassic, Schurab II). Distal part very short. Wing abruptly and sharply broadens toward base; traces of branches of SC preserved; RS connected with R_2 by cross vein; M three-branched, with branches of equal length. Length of wing about 10 mm (Fig. 541). One species. Lower Jurassic of Central Asia.

Outside the USSR: *Dysmorphoptila* Handlirsch, 1906 and *Dysmorphoptiloides* Evans, 1956.

Family IPSVICIIDAE Tillyard, 1919

(Stenoviciidae Evans, 1956)

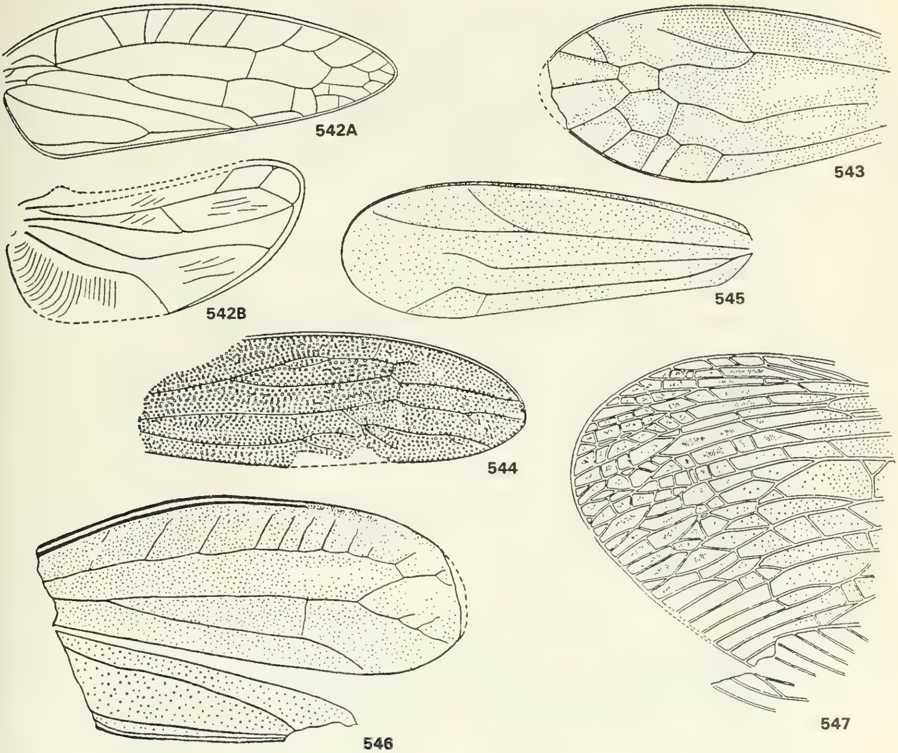
Tegmen completely sclerotized with sharply truncated rim along entire anterior margin of tegmen. SCP often transformed into a nodal line; RS or R_2 reduced, if present M fused with CuA at base; if CuA free, then R_2 or RS reduced. In hindwing R with one to three short branches; M simple and connected with R by slanting cross vein or with CuA by straight cross vein; A_1 and A_2 united at base; A_1 indistinct; jugal vein separates a small, wrinkled, jugal area. Evans divided this family of Tillyard (Evans, 1950, 1956) into three families: Paraknightiidae (*Paraknightia*), Ipsviciidae (*Ipsvicia* and *Ipsiviciopsis*) and Stenoviciidae with 190 the remaining genera. He related the first two families to Heteroptera and the third to Cicadellidomorpha. There is agreement on the status of Paraknightiidae as a separate family, but for lack of body remains we assign all the rest Ipsviciidae, as suggested earlier (Evans, 1943). Length of tegmen 6–14.2 mm (Fig. 542). Upper Permian to Upper Triassic. Fourteen genera.

Tomioscarta Bekker-Migdisova, 1961. Genotype—*T. surijokovensis* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Tegmen elliptically rounded; R_1, R_2 and RS diverge from one point; between M, CuA and RS one or more closed cells; branches of CuA short. Length of tegmen 6.8 mm (Fig. 543). One species. Upper Permian of Kuznetsk basin.

Tychticola Bekker-Migdisova, 1952. Genotype—*T. longipenna* Bekker-Migdisova, 1952; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). Tegmen narrow and long with extended apex; RS long and parallel to R_2, latter disappears before reaching apex; branches of M long; CuA branches more basally than M. Length of tegmen 7 mm (Fig. 544). One species. Upper Permian of Kuznetsk basin.

Tychtoscarta Bekker-Migdisova, 1961. Genotype—*T. sokolovensis* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova). Tegmen long and narrow; R_2 absent; R, RS and R_1 straight and with wide bifurcation; M simple, CuA with small bifurcation; M and CuA fused at extreme base. Length of tegmen 6.2 mm (Fig. 545; Pl. XV, Fig. 3) One species. Upper Permian of Kuznetsk basin.

Ipsviciella Bekker-Migdisova, 1962. Genotype—*I. asiatica* Bekker-Migdisova, 1962; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen rounded; R straight, along its length it sends a row of parallel



191 Figs. 542–547. Family Ipsviciidae and Auchenorrhyncha incertae sedis.

542. *Ipsvicia jonesi* Tillyard; A—tegmen, × 5. Triassic, Australia; B—hindwing, × 5. Upper Triassic, Australia (Evans, 1956). 543. *Tomioscarta surijokovensis* Bekker-Migdisova; tegmen, × 8.8. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 544. *Tychticola longipenna* Bekker-Migdisova; tegmen, × 9.7. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1952). 545. *Tychtoscarta sokolovensis* Bekker-Migdisova; tegmen, × 11. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 546. *Ipsviciella asiatica* Bekker-Migdisova; tegmen, × 4.8. Upper Triassic, Central Asia (Bekker-Migdisova, 1962). 547. *Borisrohdendorfia picturata* Bekker-Migdisova; hindwing, × 2.9. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959).

branches toward anterior margin; R_1, R_2 and RS absent; M with a few short branches distally; CuA simple and fused with M at base. Length of tegmen about 70 mm (Fig. 546). One species. Upper Triassic of Issyk-Kul.

Outside the USSR: *Apheloscyta* Tillyard, 1922; *Permoscarta* Tillyard, 1917; *Stanleyana* Evans, 1943; *Palaeovicia* Evans, 1943; *Stenovicia* Evans, 1943; *Permovicia* Evans, 1943; *Permagra* Evans, 1943; *Permocentrus* Evans, 1956; *Ipsvicia* Tillyard, 1918; (*Pseudipsvicia* Handlirsch, 1939); *Ipsviciopsis* Tillyard, 1922.

Incertae Familie

Borisrohdendorfia Bekker-Migdisova, 1959. Genotype—*B. picturata* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Tegmen encircled by thick marginal vein; distal part rounded-oval with dark spots, not divided by long cross veins; veins R, M and CuA difficult to distinguish distally; at distal part SC + R with a row of parallel veins directed toward anterior margin; all branches of RS, M and CuA arcuate, directed toward anal margin; R with four or five branches; M with two to four branches. Length of forewing about 40 mm (Fig. 547; P1.XIV, Fig. 9). One species. Lower Permian of Kuznetsk basin.

Besides these, Auchenorrhyncha incertae sedis also include *Permoglyphis belmontensis* Tillyard, 1926; (*Homopteron* ?) *hahni* Westwood, 1854; *Permodiphtheroides dubitans* Martynov, 1928; *Parajassus hattorfensis* Bode, 1953; *Triassoscarta* Tillyard, 1919.

Suborder Sternorrhyncha

Wings similar or dissimilar. Forewings membranous, rarely sclerotized or leathery. Hindwings membranous; jugal area absent; anal area weakly developed; distal part of wing broad or whole hindwing only slightly broader than forewing. Antennae long, many-segmented. The ancestral group, primitive Archescytinidea, has similar wings, of neuropterygid type, without jugal rudiments. Various other groups widely distributed in the Permian and Mesozoic. In the Cenozoic this suborder (related to its peak development) attains particularly wide distribution and gives rise to a series of large infraorders and superfamilies which achieve a high degree of specialization. Lower Permian to Recent. Four infraorders: Archescytinomorpha, Aphidomorpha, Coccidomorpha, Psyllomorpha.

Infraorder Archescytinomorpha

In forewings CuA with sharp bend toward R + M and long length in basal region. Wings similar, membranous and elongated in longitudinal direction. Hindwings differ from forewings in their great width and presence of free end of

CuA without bend toward R + M, or hindwings altogether absent and forewings distally broad. Abdominal end with long appendages. Permian. Two families: Archescytinidae and Boreoscytidae.

Family ARCHESCYTINIDAE Tillyard, 1926

(Maueriidae G. Zalessky, 1937; Uralosytinidae G. Zalessky, 1939; Permoscytinopsidae G. Zalessky, 1939; Maripsocidae G. Zalessky, 1939)

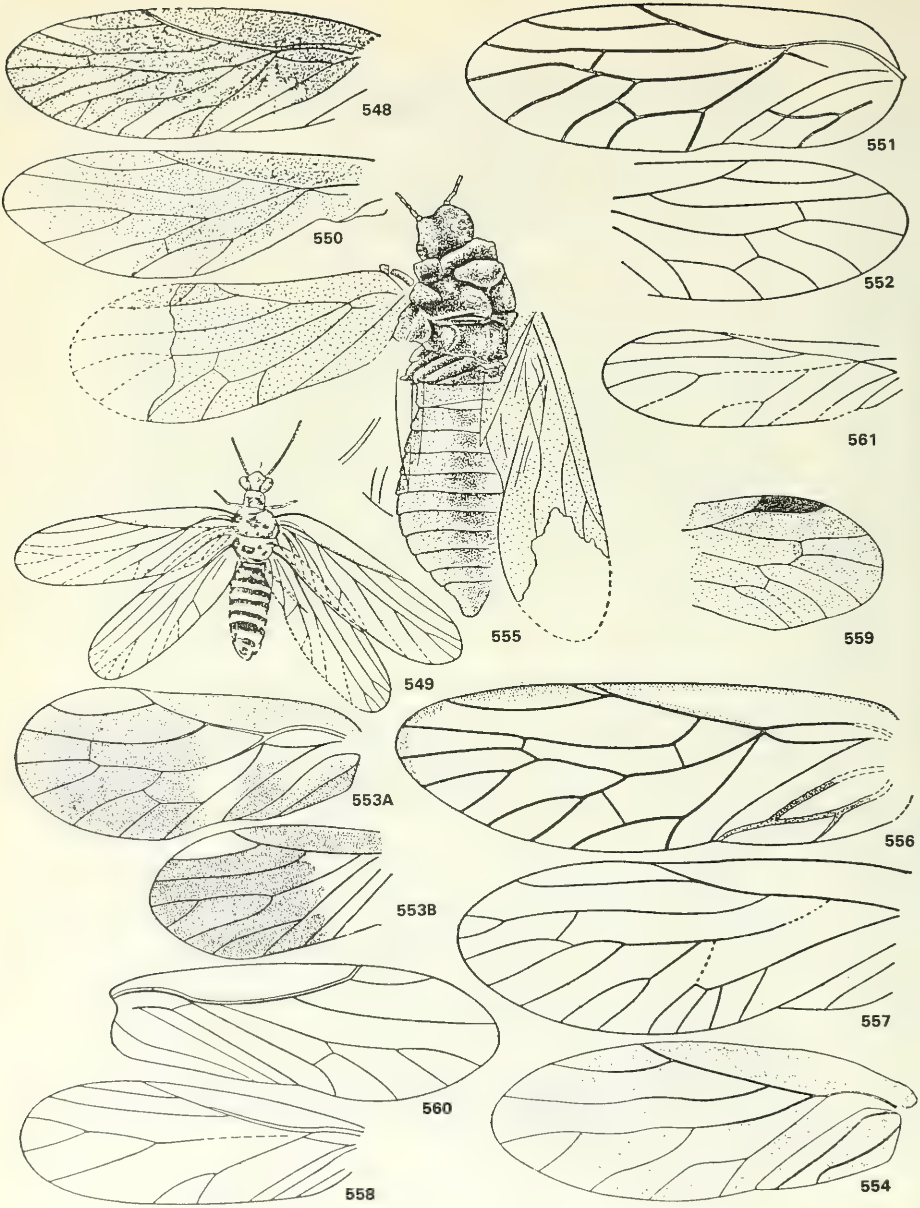
Fore- and hind pairs of wings similar. Forewings membranous, usually elongated along their length; distal part elliptically rounded and extended; costal area long; RS and R_2 parallel and reach apex of wing; RS usually simple, rarely with a small bifurcation; anal area small. Hindwings slightly more broad; basal end of CuA without bend toward base of M, terminates freely. Representatives of some genera with long appendages at end of abdomen. Permian. Sixteen genera.

Uraloscytina G. Zalessky, 1939. Genotype—*U. prosbolioides* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing long, length 3 times its width; R + M arcuate; pterostigma narrow; length of margin of wing between R_2 and RS barely one-half of distance between R_1 and R_2; stem of R up to branching equal to R_{1+2} in length and shorter than stem of M; M many-branched, with independent branch M_5; stem of M one-fourth to 192 one-sixth of length of entire system of M; basal part of CuA up to bend toward M larger than one-half of length of R + M. Large forms. Length of forewing 12–20 mm (Fig. 548). Three species. Lower Permian of Urals and Kuznetsk basin.

Maueria G. Zalessky, 1937. Genotype—*M. sylvensis* G. Zalessky, 1937; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing narrow, length 3.5 times its width; R + M weakly arcuate; pterostigma narrow; length of stem of R less than length of stem of M; M with five branches; M_4 exhibits branching; no independent M_5; trunk of M less than one-third of length of entire system of M. Small forms, length varies from 4 to 6 mm (Fig. 549). Four species. Lower Permian of Urals.

Sarbaloscytina Bekker-Migdisova, 1959. Genotype—*S. angustipennis* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala). Forewing very narrow; ratio of length to width more than 3 : 1; R + M almost straight; pterostigma narrow; length of margin of wing between R_2 and RS one-half of that between R_1 and R_2; radial cell broad at base; stem of R equal to or shorter than stem of M; M with three long branches; stem of M one-third of length of whole system of M; basal part of CuA up to bend toward M exceeds one-half of length R + M. Length of forewing 12 mm (Fig. 550). Two species. Lower Permian of Kuznetsk basin.

Archescytina Tillyard, 1926 (*Permoscytinopsis* G. Zalessky, 1939). Genotype—*A. permiana* Tillyard, 1926; Lower Permian, North America. Forewing: length 2.5 to 3 times its width; R + M arcuate; pterostigma long and



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wide; length of margin of wing between R_2 and RS from 10/17 to 2/5 of distance between R_1 and R_2; radial cell uniformly wide; stem of R of same length as or shorter than R_{1+2} and equal to one-half of length of stem of M; R almost equal to length of distal three-branched part of M. Length of forewing 8–20 mm (Figs. 551–553). Eleven species. Lower Permian of Kuznetsk basin; Upper Permian of Arkhangelsk province and Lower Permian of North America.

Kaltanoscytina Bekker-Migdisova, 1959. Genotype—*K. nigra* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing broad; ratio of length to width 2.2–2.6; R + M arcuate; pterostigma wide; length of margin of wing between R_2 and RS two-thirds to one half of distance between R_1 and R_2; radial cell broad at base; stem of R equal in length to R_1 and one-half to two-fifths of length of stems of M and R_{1+2}; M with three branches; stem of M slightly shorter than its branching part; basal part of CuA up to bend toward M exceeds one-half of distance R + M. Length of forewing 6–10 mm (Fig. 554). Three species. Lower Permian of Kuznetsk basin.

Permopsylla Tillyard, 1926. Genotype—*P. americana* Tillyard, 1926; Lower Permian, North America. Forewing with a constriction in center; R + M arcuate; pterostigma moderately long and wide; length of margin of wing between R_2 and RS one-half to two-fifths of distance between R_1 and R_2; radial cell of uniform width; R_2 and RS parallel along entire length; M three-branched; length of stem of M almost equal to length of its distal branching part; basal part of CuA up to bend toward M less than one-half of length of R + M. Small forms: 2–6 mm (Fig. 555; P1. XV, Fig. 4). Eight species. Lower Permian of Urals, Kuznetsk basin, North America and Upper Permian of Arkhangelsk province.

Sojanoscytina Martynov, 1933 (*Ivascytina* Martynov, 1933). Genotype—*S. grandis* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian

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Figs. 548–561. Family Archescytinidae.

548. *Uraloscytina multinervosa** Bekker-Migdisova; forewing, × 5.3. Lower Permian, Urals (Bekker-Migdisova, 1960). 549. *Maueria sylvensis* G. Zalessky 1937; dorsal view, × 4.8. Lower Permian, Urals (Yu. Zalessky, 1936). 550. *Sarbaloscytina angustipennis* Bekker-Migdisova; forewing, × 6. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 551. *Archescytina gunderseni* Bekker-Migdisova; forewing, × 4.3. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 552. *A. gunderseni* Bekker-Migdisova; hindwing, × 4.3. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 553. *A. fusca* Bekker-Migdisova; A—forewing; B—hindwing, × 5.2. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1959). 554. *Kaltanoscytina nigra* Bekker-Migdisova; forewing, × 9.5. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 555. *Permopsylla kuzbassensis* Bekker-Migdisova; dorsal view, × 27. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 556. *Sojanoscytina grandis* Martynov; forewing, × 5. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1933). 557. *S. ramosa* Bekker-Migdisova; hindwing, × 4. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 558. *Permopsyllopsis rossica* G. Zalessky; anterior wing, × 12. Lower Permian, Urals (Yu. Zalessky, 1939). 559. *Paleoscytina sibirica* Bekker-Migdisova; forewing, × 13.5. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 560. *P. brevistigmata* Carpenter; forewing, × 13. Lower Permian, North America (Carpenter, 1933). 561. *Maripsocus ambiguus* G. Zalessky; forewing, × 8. Lower Permian, Urals (Yu. Zalessky, 1939).

*Editor's note: Species in text is *prosbolioides*, not *multinervosa* as in legend.

stage, Soyana). Length of forewing 3 to 3.5 times its width; R + M arcuate; pterostigma narrow and long; length of margin of wing between R_2 and RS varies, 5/11 to one-fifth of distance between R_1 and R_2; radial cell broad at base; stem of R considerably shorter than R_{1+2}; stem of M about one-third of length of its distal four- or five-branched part and two to three times longer than stem of R; basal part of CuA up to the top of bend toward M exceeds one-half of length of R + M. Length of forewing 12–20 mm (Figs. 556, 557). Six species. Upper Permian of Arkhangelsk province.

194 *Maripsocus* G. Zalessky, 1939. Genotype—*M. ambiguus* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Length of forewing a little more than double its width; R + M almost straight; radial cell slightly broad toward base; stem of R almost equal to R_{1+2} and longer than stem of M; stem of M one-fourth of length of its distal four-branched part; bifurcations of M wide apart; length of basal part of CuA up to top of bend toward M more than one-half of length of R + M; CuA simple. Length of forewing about 7 mm (Fig. 561). One species. Lower Permian of Urals.

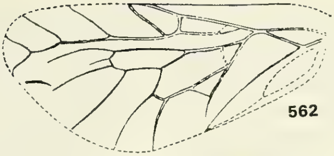
Paleoscytina Carpenter, 1933. Genotype—*P. brevistigmata* Carpenter, 1933; Lower Permian, North America. Forewing lacks constriction in middle; R + M arcuate; pterostigma very small; length of margin of wing between R_2 and RS only slightly more or less than distance between R_1 and R_2; radial cell short and distinctly broad distally; M three-branched; basal part of CuA up to top of bend toward M less than one-half of length of R + M; CuA simple, or with very close branches, and indistinct anterior branch. Length of forewing 3–4 mm (Figs. 559, 560). Two species. Lower Permian of North America and Kuznetsk basin.

Permopsyllopsis G. Zalessky, 1939. Genotype—*P. rossica* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing lacks constriction in middle; R + M arcuate; pterostigma small and without widening; length of margin of wing between R_2 and RS one-half of distance between R_1 and R_2; radial cell of uniform width; stem of R equal in length to R_{1+2} and less than one-half of length of stem of M; M three-branched; length of wing margin between M_{3+4} and anterior branch of CuA three times the distance between branches of CuA; basal part of CuA up to top of bend toward M more than one-half of length of R + M. Length of forewing 5 mm (Fig. 558). One species. Lower Permian of Urals.

Outside the USSR: *Austroscytina* Evans, 1943; *Bekkerscytina* Evans, 1958; *Eoscytina* Evans, 1958; *Lithoscytina* Carpenter, 1933; *Permoscytina* Tillyard, 1926; *Triassopsylla* Tillyard, 1917.

Family BOREOSCYTIDAE Bekker-Migdisova, 1949

Forewings markedly broad at distal part, with thin membranes and weak veins, narrow toward base with thick, convex veins; costal area short; R_2 and RS distally not parallel; R_2 terminates on anterior margin, always short of apex of



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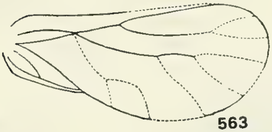

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194 Figs. 562–563. Family Boreoscytidae.

562. *Boreoscyta mirabilis* Martynov; forewing, × 6.8. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1949). 563. *Archescytinopsis smolenskii* Bekker-Migdisova; forewing, × 7.5. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1949).

wing; R_2 short and slanting; RS always with branches and sometimes pectinate; anal area very small. Hindwings apparently absent, or transformed into halteres. Family related to Archescytinidae. Upper Permian. Two genera.

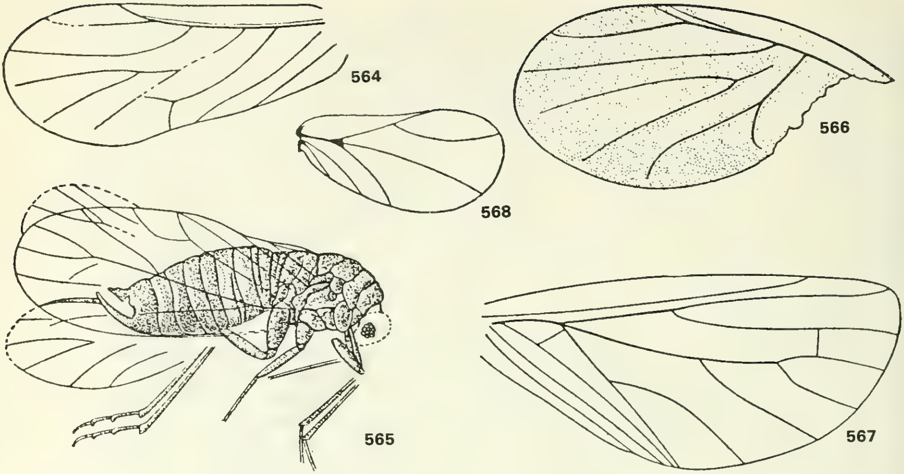
Boreoscyta Bekker-Migdisova, 1949. Genotype—*B. mirabilis* Martynov, 1937; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Distal part of forewing spread like a fan; venation extensive; basal half of anterior margin straight; R_2 short and terminates halfway along anterior wing; RS pectinate with many branches; CuA branches early: with conical bifurcation, divided by cross vein. Length of forewing 8–9 mm (Fig. 562). Three species. Upper Permian of Arkhangelsk province.

Archescytinopsis Bekker-Migdisova, 1949. Genotype—*Sojanoscytina latipennis* Martynov, 1933; Lower Permian, Arkhangelsk province (Kazanian stage, Soyana). Distal part of forewing uniformly broad; anterior margin straight; venation not extensive; R_2 terminates at midpoint of distal half of wing; RS and M with a few branches; CuA divides distally, with wide bifurcation. Length of forewing 6–7 mm (Fig. 563). Three species. Upper Permian of Arkhangelsk province.

Infraorder Aphidomorpha

(E.E'. Bekker-Migdisova and E.E. Aizenberg)

Forewings sclerotized with thick anterior margin and light anal margin. Hindwings considerably smaller than forewings, sometimes transformed into
195 halteres. Head hypognathous. Frontal sclerite not demarcated. Lobes of anterior division of clypeus not segmented. In winged forms mesothorax well developed. Legs long and of running type. Abdominal end usually with



Figs. 564–568. Families Permaphidopseidae and Pincombeidae.

564. *Permaphidopsis sojanensis* Bekker-Migdisova; forewing, × 10.2. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 565. *Tshekardaella tshekardaensis* Bekker-Migdisova; lateral view of wings and body of insect, × 9.7. Lower Permian, Urals (Bekker-Migdisova, 1960). 566. *Kaltanaphis permiensis* Bekker-Migdisova; forewing, × 1.7. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 567. *Pincombea mirabilis* Tillyard; forewing, × 24. Upper Permian, Australia (Tillyard; 1922). 568. *Eupincombea postica* Davis; hindwing, × 14. Upper Permian, Australia (Davis, 1942).

siphunculi. Ninth tergum often has a small ''tail'', or cauda. Body often with wax glands. Antennae three to six segmented with rhinaria. Upper Permian to Recent. Five families: Permaphidopseidae, Pincombeidae, Genaphididae, Phylloxeridae, Aphididae.

Family PERMAPHIDOPSEIDAE Bekker-Migdisova, 1960

Forewing somewhat larger than hindwing; SCP fused with R + M and R, forms a reduced vein; M, CuA and CuP terminate on R + SCP approximately at equal distance from one another and at angles of 50–70°; M two- or three-branched; CuA with bifurcation, or simple, with its base fused with R + M. Pronotum cylindrical. Mesothorax well developed and convex. Ninth segment of abdomen with a cauda. Siphunculi absent. Legs long, of running type with long coxae. Permian. Three genera.

Permaphidopsis Bekker-Migdisova, 1960. Genotype—*P. sojanensis*

Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Distal part of forewing broad; costal area narrow; RS and R_2 arcuate; pterostigma of medium size; radial cell wide; stem of M one-half of length of branching part; M and CuA weak; CuA simple, its anterior branch fused with M_{3+4}. Length of forewing 5.9 mm (Fig. 564). One species. Upper Permian of Arkhangelsk province.

Tshekardaella Bekker-Migdisova, 1960. Genotype—*T. tshekardaensis* Bekker-Migdisova, 1960; Lower Permian, Perm province (Kungurian stage, Chekarda). Basal part of forewing slightly narrow; distal part oval-rounded; R + M slightly arcuate; distal ends of all veins distinct; pterostigma of medium size; radial cell narrow; M with three branches; CuA with small bifurcation. Length of forewing 5.5 mm (Fig. 565). One species. Upper Permian of Urals.

Kaltanaphis Bekker-Migdisova, 1959. Genotype—*K. permiensis* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing fairly wide, rounded; R + M almost straight; pterostigma wide and long; R_2 and RS long and parallel throughout their length; radial cell long; M, 196 RS and CuA leave R + M and R at equal distance, but their bases are close; M with two long branches, divides at basal one-fourth of its whole length; base of M indistinct; CuA with short stem and very wide bifurcation. Length of forewing 5.2 mm (Fig. 566; Pl. XV, Fig. 5). One species. Lower Permian of Kuznetsk basin.

Family PINCOMBEIDAE Tillyard, 1922

Forewing considerably longer than hindwing; distinctly narrows toward base; M and CuA leave R + M at one point; anal area very narrow. Hindwing rounded and broad at distal part; M and CuA diverge at same point; length of forewing 4–5 mm (Figs. 567, 568). Upper Permian of Australia. Three genera: *Pincombea* Tillyard, 1922; *Protopincombea* Evans, 1943; *Eupincombea* Davis, 1942.

Family GENAPHIDIDAE Handlirsch, 1907

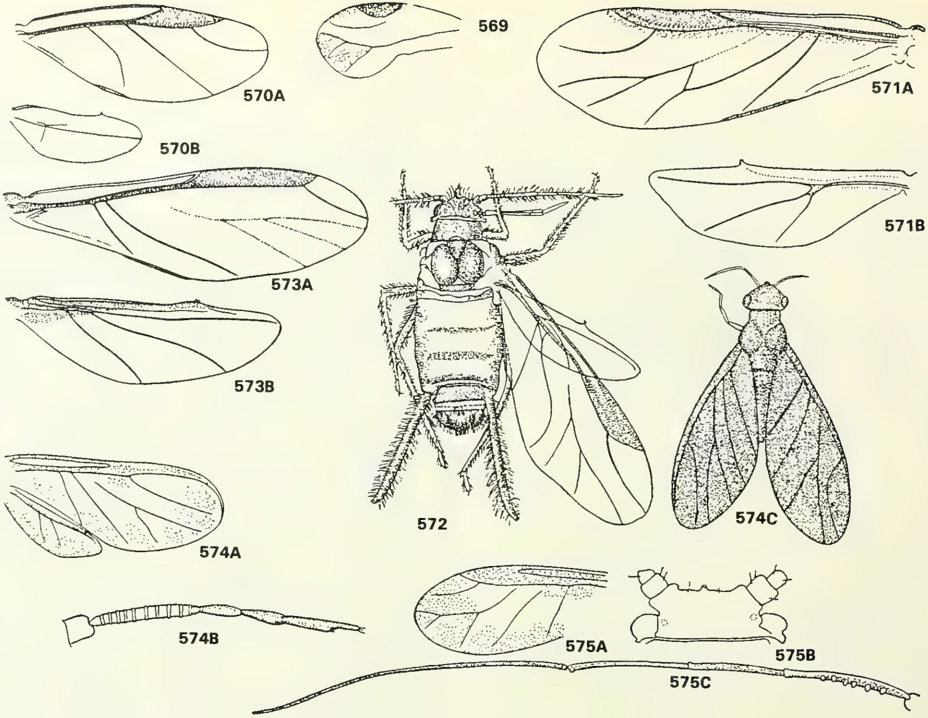
In forewing pterostigma large and rounded; RS starts in area of pterostigma; M and CuA gently sloping and never vertical, not fused with R at base; M with three short branches. Length of forewing 2 mm (Fig. 569). Upper Jurassic of Western Europe. One genus—*Genaphis* Handlirsch, 1907.

197 Family PHYLLOXERIDAE Herrich-Schaeffer in Koch, 1857

[nom. transl. Dreyfus, 1889 (ex Phylloxeridae Herrich-Schaeffer in Koch, 1857)]

(Chermesidae Herrich-Schaeffer in Koch, 1857; Adelgidae C. Border, 1930)

Forewing with strong costa; venation reduced; three simple veins running perpendicular from R are RS, M and CuA (or M, CuA and CuP). In hindwing one longitudinal vein or one inclined vein; antennae short and three- or four-



Figs. 569–575. Families Genaphididae, Phylloxeridae and Aphididae.

569. *Genaphis valdensis* (Brodie); forewing, × 12.7. Upper Jurassic, England (Handlirsch, 1906). 570. *Adelges abietis* (Linnaeus); A—forewing, B—hindwing, × 45. Recent (Mordvilko, 1934). 571. *Asiphum tremulae* Degeer; A—forewing, B—hindwing, × 30. Recent, Europe (Mordvilko, 1934). 572. *Paratrichosiphum tattakanum* Takahashi; dorsal view, × 30. Recent (Mordvilko, 1934). 573. *Cinara pinicola* Kaltenbach; A—forewing, × 30; B–hindwing, × 30. Recent (Mordvilko, 1934). 574. *Mindarus magnus* Backer; A—forewing and hindwing, × 18; B—antenna, × 100. Paleogene, Europe (Baltic amber) (Backer, 1922); C—*Mindarus transparens* Germar; dorsal view, × 21. Paleogene, Europe (Baltic amber) (Germar, 1856). 575. *Calaphis scudderi* Backer; A—forewing, × 18; B—head, × 100; C—antenna, × 100. Paleogene, Europe (Baltic amber) (Backer, 1922).

segmented, rarely with five segments*. "Cauda" and siphunculi absent. Five or six pairs of spiracles on abdomen**. Winged and wingless adult females have ovipositors. Only certain sexual individuals have proboscis. Most primitive family connected exclusively with forests. Quaternary to Recent. Two subfamilies: Adelginae, Phylloxerinae, latter not known in fossil record.

Subfamily Adelginiae[†] C. Börner, 1930. Chermes

Wings when at rest fold like a pitched roof. In hindwings one slanting vein. In winged forms antennae made up of five segments with three primary rhinaria. Sexual forms winged,[‡] with proboscis. Invariably found in coniferous forest. Very small forms. Length of forewing varies from 0.5 to 1.67 (Fig. 570). Quaternary to Recent. One genus of Recent fauna also from Quaternary deposits (African copal).

Family APHIDIDAE Latreille, 1802

[nom. transl. Herrich-Schaeffer in Koch, 1857 (ex Aphidii Latreille, 1802)]

Forewing with four slanting veins: RS, M (simple, or, often, two- or three-branched), CuA and CuP. In winged forms antennae usually five or six segmented, with two primary rhinaria. In wingless forms antennae four to six segmented, short. Compound eyes in wingless forms many-faceted, in some groups three faceted triomitidia. In many "honey dew producers" pores, tubercles or siphunculi located on fifth tergum and a cauda at end of abdomen. Seven pairs of spiracles on abdomen. Parthenogenetic females viviparous, sexual females oviparous. Inhabit trees and herbaceous plants. Paleogene to Recent. Fourteen subfamilies: Schizoneurinae, Greenideinae, Lachninae, Mindarinae, Drepanosiphinae, Aphidinae, Phloeomyzinae, Anoeciinae, Thelaxinae, Chaitophorinae, Atheroidinae, Pterocommatinae, Cervaphidinae, Schoutedeniinae, last eight families not known in fossil form.

Subfamily Schizoneurinae Herrich-Schaeffer in Koch, 1857

[nom. transl. Obenberger, 1857 (ex Schizoneuriden Koch, 1857)]
(Pemphigiden Koch, 1857; Schizoneurinae Buckton, 1883; Eriosomatinae Backer, 1920; Börner, 1930, 1952; Shaposhnikov, 1953; Aizenberg, 1956)

In hindwing M simple, not preserved in distal part, rarely with two branches. Usually in winged forms antennae six segmented; in wingless forms number of segments varies from four to six. Antennae never longer than head and thorax together. Wingless parthenogenetic females and young secrete a white waxy

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* Editor's note: In extant species, immature adelgids have 3-segmented antennae, sexuales have 4-segmented antennae, and alatae have 5-segmented antennae.

**Editor's note: All extant species have either 4 or 5 pairs of abdominal spiracles.

[†] Editor's note: Adelgidae is recognized as a valid family by all current workers.

[‡] Editor's note: In extant species, sexuales are wingless.

powder on dorsal side. Sexual individuals resemble nymphs, do not have a proboscis, in adults cauda absent, siphunculi absent or rudimentary. Inhabit trees and shrubs, move about on herbaceous plants. Length of forewing 1.4–4.5 mm (Fig. 571). Paleogene to Recent. One genus of Recent fauna also from the Paleogene of Europe (Baltic amber); one genus from the Paleogene of Western Europe and three from the Neogene of North America.

Subfamily Greenideinae Wilson, 1940

[nom. transl. Takahashi, 1931 (ex Greenideini Wilson, 1940)]

M with three branches in forewings. Usually both males and females winged. Proboscis slender, with elongated last segment. Segments of abdomen number eight or nine; behind siphunculi abdominal segment very much shortened so that their long siphunculi, covered with long hairlike setae appear to originate from end of abdomen. ''Cauda'' absent. Live on deciduous and evergreen trees. Very primitive group. Length of wing 3–4 mm (Fig. 572). Neogene to Recent. Recent fauna contains a few tropical genera of the Old World, of which one is also from the Neogene of Southern Europe.

Subfamily Lachninae Herrich-Schaeffer in Koch, 1857

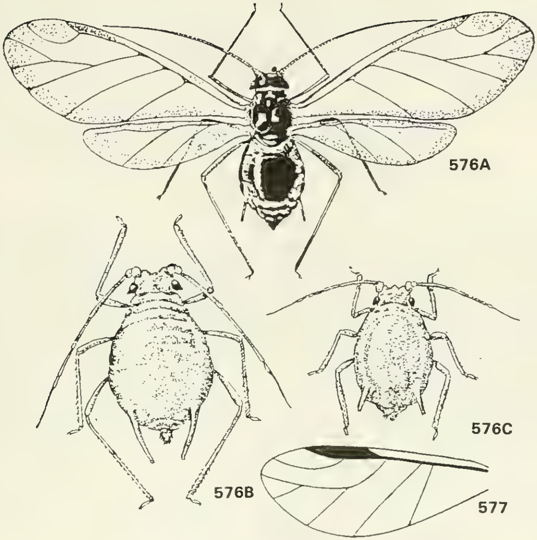
[nom. transl. Passerini, 1862 (ex Lachniden Herrich-Schaeffer in Koch, 1857)]
(Cinarinae Mordvilko, 1934)

In forewing pterostigma elongated along its length, RS usually short and straight, originates at distal end of pterostigma, rarely gently convex; M with 198 three branches, rarely, with two or without branches. Eyes of wingless forms usually many faceted. Siphunculi usually well developed, truncated-conical or cupola shaped, with side walls covered with hairlike setae, at times they exude only waxy powder and not waxy down. In adults cauda absent. Tree dwelling forms: found on bark and stems of conifers, rarely of other trees, and roots of dicotyledonous herbs. Do not migrate. Largest aphids, reach a size of 6–8 mm (Fig. 573). Paleogene to Recent. One genus in Recent fauna; also from the Paleogene of Europe (Baltic amber) and of North America.

Subfamily Mindarinae Tullgren, 1909

[nom. transl. Backer, 1920 (ex Mindarina Tullgren, 1909)]
[Rhyllaphidinae Mordvilko, 1948 (pars); Telaxidae Börner, 1952 (pars); Thelaxinae Obenberger, 1957 (pars)]

In forewing pterostigma long, crescent-shaped, reaches apex of wing; RS originates from proximal end of pterostigma and is very large; M two-branched. In resting position wings fold back over abdomen like a roof. Antennae six-segmented, with short pointed tip. In the wingless parthenogenetic females eyes are three-faceted. Wingless and young forms with six rows of wax glands, exuding dove-white waxy down. Found only on conifers (Abietinae), do not



Figs. 576–577. Family Aphidinae.
576. *Yezabura malifolii* Fitch; A—[dorsal view of] winged male, B—[dorsal view of] wingless parthenogenetic female, C—[dorsal view of] wingless sexual female [ovipara]. Recent (Beier, 1938).
577. *Aphis gurnetensis* Cockerell; forewing, × 12.8. Oligocene, North America (Cockerell, 1921).

migrate. Length of forewing about 3 mm (Fig. 574A, B). Paleogene to Recent. Only one genus in Recent fauna; also from the Paleogene of Europe (Baltic amber) and the Neogene of North America.

Subfamily Drepanosiphinae Herrich-Schaeffer in Koch, 1857

[nom. transl. Aizenberg, 1956 (ex Drepanosiphiden Herrich-Schaeffer in Koch, 1857)]

(Callipteriden Herrich-Schaeffer in Koch, 1857; Callipterinae Mordvilko, 1895; Phyllaphidinae Aizenberg, 1932; Mordvilko, 1948; Callaphinidae Börner, 1952)

In forewing RS originates from posterodistal angle of pterostigma; M three-branched, M_{1+2} and M_1 sharply bent toward anterior margin, sometimes replace RS; M_{3+4} bent toward posterior side. Wings fold like a hood in position of rest. Antennae five- or six-segmented, with short or elongated pointed tip. Siphunculi, prominences or pores present. Cauda flask-shaped, hemispherical, rarely absent. In wingless parthenogenetic females head distinct from prothorax, compound eyes many-faceted. Inhabit only deciduous trees, usually of the order Fagales and, rarely, herbs. Do not migrate. Length of forewing 2–4 mm (Fig. 575). Paleogene to Recent. About 1,000 species in all. One genus in Recent fauna; also from the Paleogene of Europe (Baltic amber).

Subfamily Aphidinae Koch, 1857

[nom. transl. Mordvilko, 1896 (ex Aphiden Koch, 1857)]
(Siphonophorini Ashmead, 1881)

In forewing M with two or three branches. Antennae five or six segmented. In wingless parthenogenetic females eyes many-faceted. Sometimes secrete a grayish-brown wax powder. Cauda long or short and triangular, digitate, saber-like or, sometimes, not prominent. Siphunculi usually well developed, rarely, like short prominences. Occasionally eighth tergum of abdomen bears an
199 outgrowth or supracaudal processes, resembling a second tail or cauda. Length of forewing 2–5 mm (Figs. 576A, B; 577). Cretaceous to Recent. In Recent fauna wide distribution of numerous genera. About 12 genera known in fossil form, including one genus, *Canadaphis* Essig, 1937, from the Cretaceous of Western America (Canadian amber), one from the Paleogene of Europe (Baltic amber) and Paleogene and the Neogene of Western Europe and about 10 from the Neogene of North America.

Aphidomorpha Incertae sedis

To this superfamily also belong *Triassoaphis* Evans, 1956 from the Upper Triassic of Australia and *Aphidulum* Handlirsch, 1939 from the Jurassic of Western Europe.

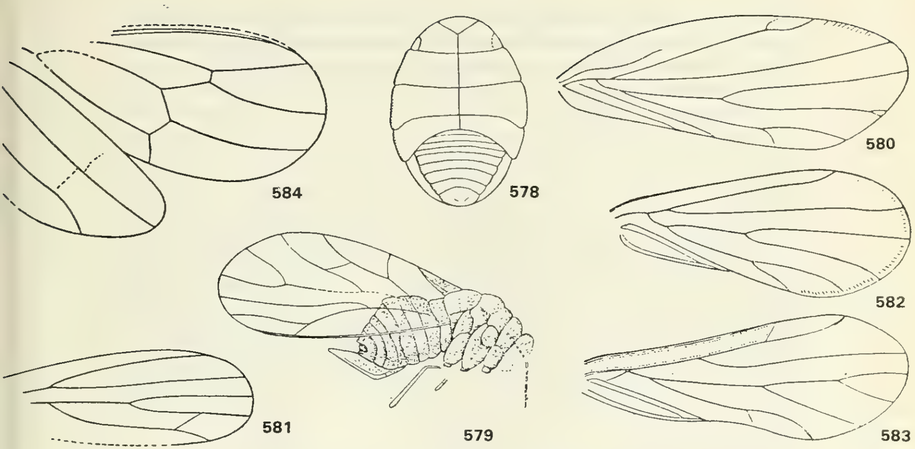
Infraorder Coccomorpha

(E.E'. Bekker-Migdisova)

Small insects. Two pairs of wings. Hindwings noticeably smaller, or with only forewings, or hindwings transformed into halteres; venation poor; four or five longitudinal veins, sometimes with distal bifurcations (R, RS, M, CuA and CuP). Females and occasionally males lack wings. Antennae in winged forms many-segmented. Eyes faceted in fossil forms and present-day males; wingless females occasionally possess only rudiments of eyes; in some groups, males only with simple eyes. Hind legs of cursorial type. Nymphs mobile, rarely sedentary. Upper Permian to Recent. Two superfamilies: Protopsyllidiidea, Coccidea.

SUPERFAMILY PROTOPSYLLIDIIDEA

Two pairs of wings. Hindwings considerably shorter. In forewing R branches; M fused with CuA at base; anal area small and reduced, with distinct anal veins,



200 Figs. 578–584. Family Protopsyllidiidae.

578. Protopsyllididae; [dorsal view of] nymph, × 21. Upper Permian, Australia (Evans, 1943). 579. *Propatrix psylloides* Bekker-Migdisova; lateral view of wing and body, × 9.1. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 580. *Cicadellopsis incerta* Martynov; forewing, × 10.5. Lower Jurassic, Central Asia (Martynov, 1937). 581. *Cicadopsyllidium elongatum* Bekker-Migdisova; forewing, × 16.6. Triassic, Central Asia (Bekker-Migdisova, 1959). 582. *Asiopsyllidium unicum* Bekker-Migdisova; forewing, × 10.4. Upper Triassic, Central Asia (Bekker-Migdisova, 1959). 583. *Tomiopsyllidium iljinskiense* Bekker-Migdisova; forewing, × 28.5. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 584. *Mesaleuropsis venosa* Martynov; forewing and hindwing, × 28. Lower Jurassic, Central Asia (Martynov, 1937).

demarcated by straight CuP. Head with compound eyes and triangular frontal sclerite. Permian to Mesozoic. One family: Protopsyllidiidae.

Family PROTOPSYLLIDIIDAE Carpenter, 1931
(Permopsyllidae Tillyard, 1926)

In forewing M and CuA exhibit branching. Head with central suture. In nymph head distinct. Compound eyes on sides of head. Triangular frontal sclerite and central suture continue into central dorsal suture; along central suture integument splits during molting. Pronotum lacks paranotal expansions, equal in size to mesonotum; metanotum smaller. Abdomen eight-segmented (Fig. 578). Upper Permian to Jurassic. Eighteen genera.

Propatrix Bekker-Migdisova, 1960. Genotype—*P. psylloides* Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewings with straight anterior margin and wide distal part; costal area wide; pterostigma long; R divides at midpoint of forewing; R and RS run parallel to anterior margin; M with three branches; fork of CuA wide; anal area short. Length of forewing about 6 mm (Fig. 579). One species. Upper Permian of Arkhangelsk province.

Cicadellopsis Martynov, 1937. Genotype—*C. incerta* Martynov, 1937; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Forewing with convex anterior margin, narrow apex; costal area wide; pterostigma very small; R divides at base of forewing; R and RS diverge distally; M divides at midpoint of forewing into two branches; fork of CuA small. Length of forewing 5.8 mm (Fig. 580). Two species. Upper Triassic to Lower Jurassic of Issyk-Kul province.

Cicadopsyllidium Bekker-Migdisova, 1959. Genotype—*C. elongatum* Bekker-Migdisova, 1959; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Forewing narrow, long and wide at distal part; veins thick; costal area narrow, with slight widening at base; pterostigma not isolated; R divides at basal one-third of forewing; R and RS almost straight; M and CuA fused at basal one-third; M with two branches; CuA simple; cross vein M_4 + CuA long. Length of forewing 2.7 mm (Fig. 581). One species. Upper Triassic of Issyk-Kul province.

Asiopsyllidium Bekker-Migdisova, 1959. Genotype—*A. unicum* Bekker-Migdisova, 1959; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Forewing membranous, expanded at distal part; costal area narrow; anterior margin straight; R branches at extreme base of forewing; pterostigma not very large or not isolated; M divides at center of forewing; CuA fused with M at level of branching of R; CuA divides a little more distally than M. Length of forewing 5 mm (Fig. 582). One species. Upper Triassic of Issyk-Kul province.

Tomiopsyllidium Bekker-Migdisova, 1959. Genotype—*T. iljinskiense*
200 Bekker-Migdisova, 1959; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Forewing transparent and membranous in distal part, with straight anterior margin; costal area narrow; R divides two-thirds of forewing margin; pterostigma of moderate length; R and RS bent, with distal ends diverging; M with three branches; CuA branches more basally than M, fused with latter for some distance; CuA fused at base with CuP. Length of forewing 2 mm (Fig. 583). One species. Upper Permian of Kuznetsk basin.

Mesaleuropsis Martynov, 1937. Genotype—*M. venosa* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Forewing rounded and widened at distal part, anterior margin with strong costa; costal area has the form of a narrow belt; R runs along margin; RS originates at extreme base, arcuate; M divides at midpoint of forewing, with two branches; CuA simple, bent distally, connected with M_{3+4} by a cross vein and basally fused with M. Hindwing one-half length of forewing; with two longitudinal veins, M and CuA. Length of forewing 2.3 mm (Fig. 584). One species. Lower Jurassic of Central Asia.

Outside the USSR: 12 genera from the Lower Permian of Australia—*Protopsyllidium* Tillyard, 1926; *Permothea* Tillyard, 1926; *Permopsyllidium*

Tillyard, 1926; *Clavopsillidium* Davis, 1942; *Permotheela* Davis, 1942; *Permopsyllidops* Davis, 1942; *Psococsytina* Davis, 1942; *Psocopsyllidium* Davis, 1942 (*Psyllidiana* Evans, 1943, *Protopsyllops* Evans, 1943); *Belpsylla* Evans, 1943; *Eopsyllidium* Davis, 1942; *Psyllidella* Evans, 1943; *Permopsylloides* Evans, 1943; *Triassothea* Evans, 1956 from the Upper Triassic of Australia.

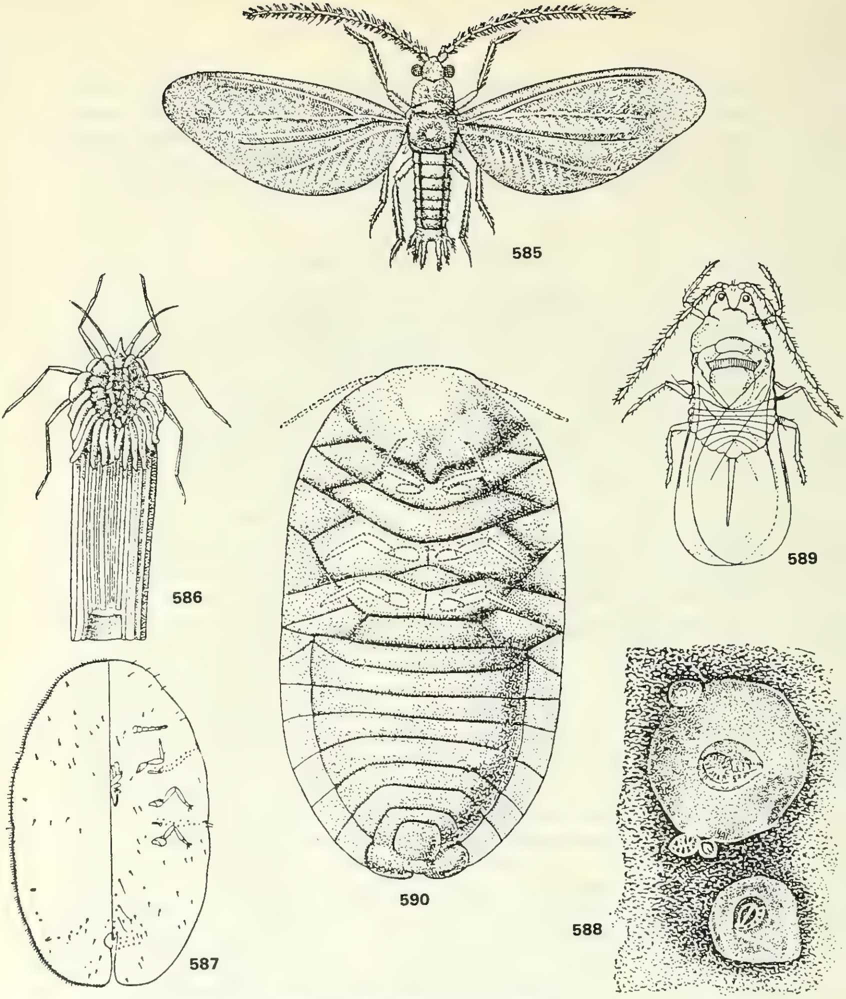
SUPERFAMILY COCCIDEA

Forms with sharply differentiated sexual dimorphism. Males with one pair of wings or, rarely, wingless; hindwings transformed into halteres; forewings with three to five simple veins; R, M and CuA do not branch; anal area transparent, reduced, not separated by a straight CuP; with compound eyes; many-segmented antennae, poorly developed mouth parts; tarsus single-segmented, rarely two-segmented, with one claw. Females wingless; sometimes thick-set with reduced legs; body not distinctly divided into head, thorax and abdomen; covered with waxy exudations or bare; dorsal surface completely or partly sclerotized; head fused with thorax; antennae, eyes and mouth parts located on
201 ventral surface of body. In Recent fauna about 3,000 widely distributed species found up to northern and southern limits of vegetation. Permian to Recent. 17 families, of which the following are also in fossil form: Margarodidae, Ortheziidae, Coccidae and Diaspididae.

Family MARGARODIDAE Neustead, 1901. Giant coccids

[nom. transl. Enderlein, 1920 (ex Margarodinae Neustead, 1901)]

Males usually winged; forewings wide at base, with four or five longitudinal non-branching veins (R, M, CuA and CuP); hindwings transformed into halteres, but occasionally, like forewings, are absent; both compound eyes and ocelli present, rarely only ocelli; sometimes segments of legs fused; penultimate segment of abdomen usually with group or row of cylindrical ducts and with waxy threads; penial sheath short. Females fixed or mobile; dorsal surface of body convex, sclerotized or with chitinous plates; segmentation of body usually distinct; sometimes with a constriction between terga of thorax; abdomen made up of eight distinct segments; proboscis two- or three- segmented or poorly developed, occasionally absent; legs well developed, occasionally with some segments fused, rarely reduced or absent; posterior end of body with anal tube developed or only with chitinous ring without setae. Paleogene to Recent. Representatives of this family most abundant as tropical forms and found in all parts of the world, living on various plants and their roots. Length of body of female 1.5–3.5 mm (Fig. 585). In Recent fauna more than 240 species recognized. Two genera of Recent forms known as fossils from the Paleogene of Europe (Baltic amber).



Figs. 585–590. Superfamily Coccoidea.

585. *Drosicha turkestanica* Archangelskaya; [dorsal view of] male, × 18. Recent (Borkhsenius, 1950). 586. *Orthezia insignis* Douglas; [dorsal view of] female with egg sac, × 7.4. Recent (Borkhsenius, 1950). 587. *Coccus hesperidium* Linnaeus; female, [dorsum on left half and venter on right half] × 10. Recent (Borkhesenius, 1950). 588. *Aspidiotus hederae* (Vallot); test of male, female and nymphs of first and second instars, × 15. Recent, Europe (Borkhsenius, 1950). 589. *Aspidiotus* sp.; [dorsal view of] winged male with long copulating organ, × 20. Recent (Betleve, 1896). 590. *Mesococcus asiaticus* Bekker-Migdisova; [dorsal view of] body of insect, × 69. Upper Triassic, Central Asia (Bekker-Migdisova, 1959).

Family ORTHEZIIDAE Amyot and Serville, 1843

[nom. transl. Enderlein, 1920 (ex Orthezides Amyot et Serville, 1843)]

Males with long narrow wings; antennae nine-segmented; legs long; penultimate segment of abdomen with a group of cylindrical ducts and waxy threads; penial sheath bent toward ventral side. Body of female oval, covered with waxy plates, not highly arched dorsally, almost flat ventrally; derm weakly sclerotized; segmentation of body distinct; abdomen eight-segmented; proboscis one or two segmented; legs longer than body; trochanter and femur fused, sometimes similarly tibia and tarsus also fused; tarsus one-segmented; anal opening surrounded by flat chitinous ring with pores and six setae; eggs in a dense waxy ovisac. Live above ground, on herbs and shrubs, rarely on trees. Length of body of female 1.5–3.5 mm (Fig. 586). Paleogene to Recent. About 45 species in Recent fauna under five widely-distributed genera, of which one is also from the Paleogene of Europe (Baltic amber).

Family COCCIDAE Fallen, 1814

[nom. transl. Stephens, 1829 (ex Coccides Fallen, 1814)]
(Lecaniidae Balachnovsky, 1915; Lecanococcidae Lindinger, 1889)

Males winged; halteres variable in form; antennae ten-segmented; two to six pairs of ocelli; legs long; penial sheath of varying length, with pointed tip. Body of female oval, rounded or egg-shaped; convex dorsally, often sclerotized; without segmentation, head, thorax and abdomen fused; antennae six- to eight-segmented, sometimes reduced; eyes small or absent; proboscis single-segmented; tarsus one-segmented; posterior end bifurcated by anal cleft; anal opening located at end of anal tube at base of cleft on dorsal side, surrounded by flat anal ring with pores and six to eight setae and also, usually, anal plates. Found on different plants and their roots in all parts of the world (Fig. 587). Paleogene to Recent. Recent fauna contains more than 800 species and numerous widely-distributed genera of which one genus is also from the Paleogene of Europe (Baltic amber).

Family DIASPIDIDAE Signoret, 1868

[nom. transl. Maskell, 1878 (ex Diaspides Signoret, 1868)]

Males usually winged*; antennae threadlike, 10-segmented; four to six ocelli; penial sheath narrow, of varying length; abdomen without wax threads, body of extremely varied shapes, covered by test formed from sloughed skin [of first instar] and secretion [of first and second instars]; [immature with] antennae reduced to tubercles with setae; eyes usually absent; proboscis single-segmented; legs usually absent; segmentation of body distinct; abdomen usually divided into an anterior segmented part and a posterior fused pygidium; on dorsal side of

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* Editor's note: Description of both adults and immatures. Antennae cannot be both threadlike and 10-segmented and also reduced to tubercles with setae.

pygidium segments IX, X and XI form region surrounding anal opening. Inhabit various trees, shrubs and, rarely, herbs. Length of body of female 0.6–2 mm (Figs. 588, 589). Neogene to Recent. In Recent fauna there are more than 1,500 species and a large number of genera, of which one is also from the Neogene of Western Europe.

203 Coccidea Incertae sedis

Mesococcus Bekker-Migdisova, 1959. Genotype—*M. asiaticus* Bekker-Migdisova, 1959; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-kul). Wingless form, not probably, that of female; body oval; head bent under thorax, indistinctly demarcated; proboscis absent; eyes absent; prothorax larger than meso- and metathorax; pleural sclerites of thorax large and indistinctly differentiated; legs reduced to insignificant appendages, short; coxae close; abdomen made up of nine segments, 10th segment reduced to the form of a small plate; anal opening present at end of abdomen. Length of body 1–2 mm (Fig. 590). One species. Upper Triassic of Issyk-Kul province.

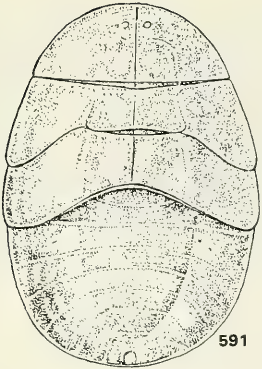
Besides this, four genera of indistinct systematic position from the Cretaceous of Western Europe: *Coccodes* Fritsch, 1901; *Puccinites* Velenowski, 1889; *Variolina* Fritsch, 1901; *Pteridophyllites* Renger, 1866.

Infraorder Psyllomorpha

Forewings and hindwings almost of equal length, with similar venation. Forewings poorly specialized as organs of flight, leathery-membranous, sometimes short and sclerotized, or leathery or almost similar to hindwings. Head hypognathous or opisthognathous. Abdomen separated from thorax by a constriction. Mesothorax well developed. Hind legs cursorial. Tarsal claws with adhesive pads. Females with ovipositors. Nymphs differ sharply from adults. Coxae of nymphs close. Permian to Recent. Three superfamilies: Aleurodidea, Cicadopsyllidea, Psyllidea.

SUPERFAMILY ALEURODIDEA

Wings membranous, almost similar. Forewings broader. Hindwings slightly narrowed at base, lack any mechanism for coupling with forewings; venation not extensive; usually one or two longitudinal veins; R and M diverge distally; CuA weak or absent; all veins weak, none reach margin of wing. Head orthognathous; compound eyes kidney-shaped, two ocelli; frontal sclerite not demarcated; parietal convexity and frontal processes absent. First segment of abdomen in form of circular peduncle. Parts of sclerite of abdomen often fused with one another. Coxae of hind legs conical, elongated. Nymphs pass through immobile pupal stage. Length of body 1–5 mm. Upper Permian to Recent. In Recent fauna about 200 widely distributed species. Two families: Permaleurodidae, Aleurodidae.



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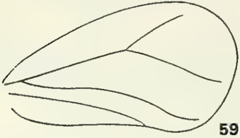

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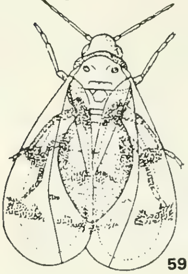

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Figs. 591–593. Superfamily Aleurodidea.

591. *Permaleurodes rotundatus* Bekker-Migdisova; [dorsal view of] nymph, × 16.1. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 592. *Aleurolobus olivinus* Silvestri; dorsal view, × 30. Recent (Silvestri, 1914). 593. *Aleurodes* sp.; A—forewing; B—hindwing, × 30. Recent (Handlirsch, 1925).

Family PERMALEURODIDAE Bekker-Migdisova, 1959

Pupa rounded and longer than broad. Head located on ventral region of body. Pronotum semidiscoidal in shape; meso- and metanotum and their wing 204 rudiments of same size; middle region of pro-, meso- and metanotum distinct, divided into two by a medium suture. Abdomen eight-segmented with distinct segmentation. Upper Permian. One genus.

Permaleurodes Bekker-Migdisova, 1959. Genotype—*P. rotundatus* Bekker-Migdisova, 1959; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Length of pronotum two-fifths of its width; middle section does not reach anterior margin; near margin of pronotum there are two pits—bases of setae. Length of body 3 mm (Fig. 591; Pl. XV, Fig. 9). One species. Upper Permian of Kuznetsk basin.

Family ALEURODIDAE Westwood, 1840

Pupa rounded or rounded and elongated dorsally. Meso- and metanotum fused, latter narrow; middle section of notum not demarcated; median suture distinct. Segmentation of abdomen indistinct, retained only medially. Length of body 1–3 mm (Figs. 592, 593). Paleogene to Recent. One genus in Recent fauna; also from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CICADOPSYLLIDEA

Dissimilarity of wings often slight. Forewings oval, poorly specialized for flight, but with thick veins, leathery-membranous or, rarely, very short and sclerotized, with widely diffused veins; costal area wide. Hindwings narrow toward base; venation resembles that of forewings; only CuA without basal bend toward M; costal area narrower and anterior margin almost straight. Head hypognathous or orthognathous; compound eyes not differentiated; parietal prominence small; frontal processes absent; lobes of posterior division of clypeus not

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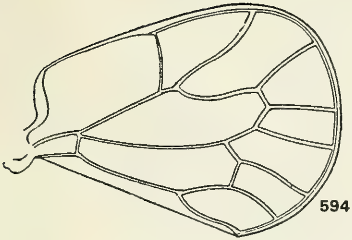
205 Figs. 594–603. Families Coleoscytidae and Cicadopsyllidae.

594. *Coleoscyta occulata* Bekker-Migdisova; forewing × 8.3. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 595. *C. eletrata* Martynov; hindwing, × 9.2. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 596. *Kaltanoscyta reticulata* Bekker-Migdisova; forewing, × 8.7. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959). 597. *Sojanopsylla brevipennis* Bekker-Migdisova; forewing, × 6. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 598. *Cicadopsylla permiana* Martynov; forewing, × 6. Upper Permian, Pre-Urals (Martynov, 1931). 599. *Scytoneura elliptica* Martynov; [lateral view of wing and body] (reconstruction), × 11.8. Upper Permian, Arkhangelsk province (original drawing by Bekker-Migdisova). 600. *S. vitripenna* Bekker-Migdisova; forewing, × 13. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 601. *Scytoneura* sp.; hindwing, × 7. Lower Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 602. *Scytoneurella major* G. Zalessky; forewing, × 8. Lower Permian, Urals (Yu. Zalessky, 1939). 603. *Cicadopsis rugosipenna* Bekker-Migdisova; forewing, × 9.3. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1959).



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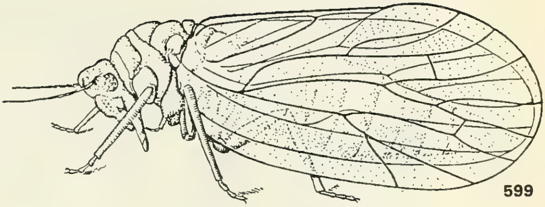

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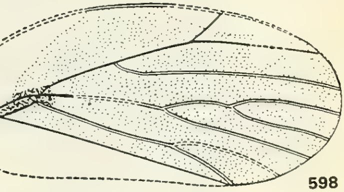

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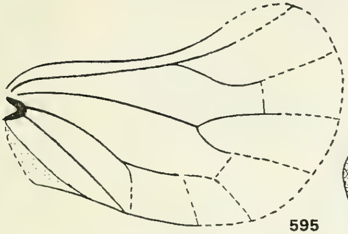

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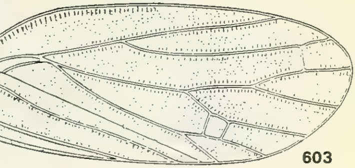

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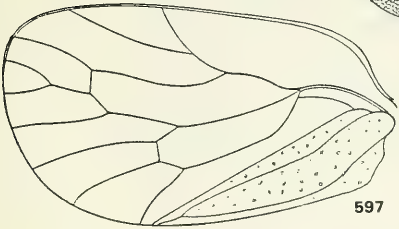

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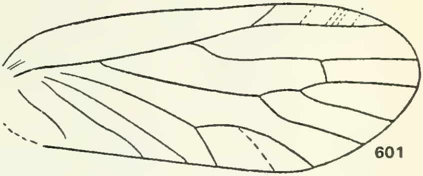

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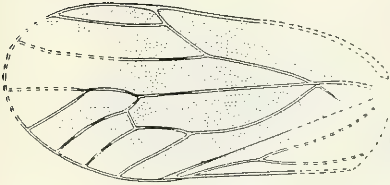

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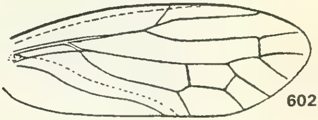

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segmented; frontal sclerite not demarcated. Coxae of hind legs large, conically elongated or of smaller size and slightly transverse. Lower Permian to Recent. Two families: Coleoscytidae, Cicadopsyllidae.

Family COLEOSCYTIDAE Martynov, 1935

Forewing short and broad, strongly sclerotized, convex and sharply truncated both distally and basally; veins often only in the form of shading or depression; R_1, R_2 and RS almost equal in length, diverge in different directions; branches of M short; fork of CuA wide; basal part of CuA short and gently sloping; anal area long; A_1 and A_2 short, join to form a long stalk. Hindwing rounded and broad at distal part; branches of R and M short; fork of CuA wide. Hind legs of jumping type. Coxae slightly transverse. Permian. Two genera.

Coleoscyta Martynov, 1935, Genotype—*C. rotundata* Martynov, 1935; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing strongly sclerotized with no remnant of primary network (archedictyon) or sculpturing; veins weak and diffused in the form of shading; branches of M short. In hindwing fork of CuA very wide, its posterior branch one-half to two-fifths of length of anterior one. Length of forewing 7–7.5 mm (Figs. 594, 595). Seven species. Upper Permian of Pre-Urals and Arkhangelsk province.

Kaltanoscyta Bekker-Migdisova, 1959. Genotype—*K. reticulata* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing strongly sclerotized, covered with a fine network forming a sculptured surface, markedly convex: apex displaced toward anterior margin; veins thin and distinct; branches of M long. Length of forewing 5–6 mm (Fig. 596; Pl. XV, Fig. *6*). One species. Lower Permian of Kuznetsk basin.

Sojanopsylla Bekker-Migdisova, 1960. Genotype—*S. brevipennis* Bekker-Migdisova, 1960; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing weakly sclerotized at base, short; anterior margin straight with truncated base; M and CuA divide at same level and more distally than R; M four-branched, branching part longer than stem; M_1 also divides; fork of CuA moderately wide. Length of forewing 11.5 mm (Fig. 597; Pl. XV, Fig. 7). Two species. Lower Permian of Kuznetsk basin and Upper Permian of Arkhangelsk province.

Family CICADOPSYLLIDAE Martynov, 1931

[nom. transl. Martynov, 1935 (ex Cicadopsyllinae Martynov, 1931)]

Forewing membranous or leathery-membranous; R and M joined at base; CuA with bend toward M, joined at base with CuP. Hindwing almost equal in length to forewing, slightly elongated; R and RS parallel, long and almost straight; bifurcation of CuA small, its basal end free. Head orthognathous; clypeus with non-segmented lobes; compound eyes with a few large facets, small parietal prominences present; frontal processes absent. Hind legs of cursorial type; coxae much enlarged and conical; trochanter large; femur slightly widened; tarsi three-segmented. Permian. Four genera.

206 *Cicadopsylla* Martynov, 1931. Genotype—*C. permiana* Martynov, 1931; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mountain). Forewing oval, with markedly convex anterior margin, membranous-leathery; costal area very wide; R, R_{1+2} and R_2 form a continuous arcuate vein; M three-branched, divides more distally than R, with branching part longer than stem; CuA divides almost at same level as M, with a narrow fork. Length of forewing 13.5 mm (Fig. 598). One species. Upper Permian of Pre-Urals.

Scytoneura Martynov, 1935. Genotype—*S. elliptica* Martynov, 1935; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing distally rounded and leathery membranous; anterior margin weakly arcuate; costal area wide; M three-branched, branching part equal to or shorter than basal stem; M branches more distally than CuA; fork of CuA narrow and bent. Hindwing narrower than forewing, slightly broadens distally, anterior margin straight; fork of CuA wide. Length of forewing 4.6–8.5 mm (Figs. 599–601). Three species. Lower Permian of Kuznetsk basin and Upper Permian of Arkhangelsk province.

Scytoneurella G. Zalessky, 1939. Genotype—*S. major* G. Zalessky, 1939; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing membranous, distally elliptically rounded; costal area somewhat narrow; anterior margin somewhat convex in middle; M with three short branches, divides more distally than CuA; fork of CuA wide. Length of forewing 4–6 mm (Fig. 602). One species. Lower Permian of Urals.

Cicadopsis Bekker-Migdisova, 1959. Genotype—*C. rugosipenna* Bekker-Migdisova, 1959; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing membranous with wrinkles, with distal part elongated, apex displaced toward anterior margin; R_{1+2} and R_2 straight continuations of R; stem of R equal to its distal three-branched part, branches at same level as CuA; fork of CuA small; anal veins from ribbed elevations. Length of forewing 7.3 mm (Fig. 603; Pl. XV, Fig. 8). One species. Lower Permian of Kuznetsk basin.

SUPERFAMILY PSYLLIDEA

Wings distinctly dissimilar. Forewings membranous or leathery-membranous, broad and oval with close convex veins; costal area wide. Hindwings slightly elongated with straight anterior margin and mechanism for coupling with anterior wing. Head opisthognathous; frontal sclerite demarcated; parietal prominences weakly developed; frontal processes well developed; three ocelli; antennae long and many-segmented. First segment of abdomen joined with metathorax to form intermediate segment; second abdominal segment forms a flat stalk. Coxae of hind legs transverse. All larval stages mobile. Jurassic to Recent. One family—Psyllidae.

Family PSYLLIDAE Latreille, 1807

Forewing membranous, rarely leathery; veins very close and convex; with a marginal vein; R, M and CuA have two branches distally, joined at base into one stem. Hindwing shorter, usually narrower than forewing, exhibits slightly broadening at distal end; R and M simple; CuA with bifurcation, all three veins joined at base. Antennae nine or 10 segmented. Tarsi two-segmented, with adhesive pad. In Recent fauna more than 1,500 species in all territories primarily in tropical and temperate zones usually associated with specific host plants. Jurassic to Recent. Nine subfamilies: Aphalarinae, Liadopsyllinae, Psyllinae, Triozinae, Liviinae, Pauropsyllinae, Ciriacreminae, Spondyliaspinae, Carsidarinae. Four subfamilies in fossil form.

Subfamily Aphalarinae Low, 1879

Forewing leathery or membranous, with diverse shapes; pterostigma may be absent. Parietal region inclined, projects in front of base of antennae; frontal sclerite long and narrow, not hidden by processes, conical frontal processes absent; median ocellus seen from dorsal side; first three segments of antennae elongate. Pronotum sloping, not longer than parietal region. Axillary sclerites present; tegulae absent. Length of body 1–4 mm (Fig. 604). Paleogene to Recent. Two Recent genera also from the Paleogene of Europe, including one from Baltic amber.

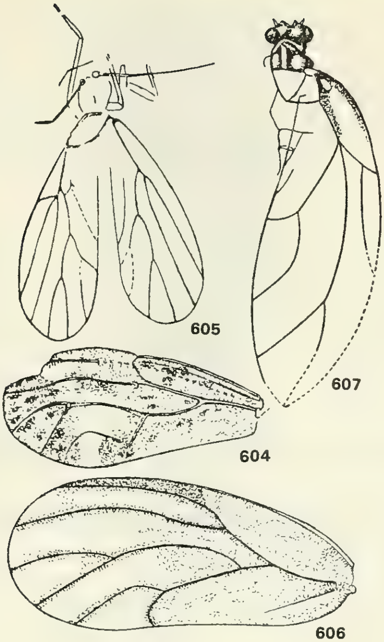
Subfamily Liadopsyllinae Martynov, 1929

Forewing membranous; costal area small, pterostigma broad and long; R_1, R_2 and RS originate at one point. Jurassic. One genus.

Liadopsylla Handlirsch, 1923. Genotype—*L. geinitzi* Handlirsch, 1925; Jurassic, Germany. Antennae shorter than forewing. Forewing oval, twice
207 longer than broad; pterostigma seven times longer than broad; radial cell straight; R_2 and RS long, straight and parallel; general stem of R very short; fork of CuA wide, anterior branch only weakly convex. Length of forewing 1.5–2 mm (Fig. 605). Few species. Jurassic of Central Asia and Western Europe.

Subfamily Psyllinae Low, 1879

Forewing with two marginal cells formed by forks of M and CuA; RS not connected to M by cross vein, latter fused basally with CuA to form a common stalk, shorter than stem of R; R_2 long; tegmen with axillary sclerites at base and with tegulae. Frontal sclerite hidden by conical frontal processes, median ocellus located at junction of frons and cheek. Length of body 2–6 mm (Fig. 606). Paleogene to Recent. Recent fauna with widely distributed genera, which include *Psylla* Goeffroy, 1762, with many species, and *Agonoscena* Enderleiw, from the Miocene of the North Caucasus; one genus from the Paleogene of Western Europe and the Neogene of North America, one genus from the Neogene of North America.



Figs. 604–607. Family Psyllidae.

604. *Agonoscena marmorea* Bekker-Migdisova; forewing, × 21. Miocene, North Caucasus (Bekker-Migdisova, 1962). 605. *Liadopsylla tenuicornis* Martynov; [dorsal view of head, thorax, and] forewing, × 17. Upper Jurassic, Southern Kazakhstan (Martynov, 1926). 606. *Psylla nigritopsis* Bekker-Migdisova; forewing, × 28. Miocene, North Caucasus (Bekker-Migdisova, 1962). 607. *Trioza karaganica* Bekker-Migdisova; [dorsal view of head and] forewing and head, × 15. Miocene, North Caucasus (Bekker-Migdisova, 1962).

Subfamily Triozinae Low, 1872

Forewing membranous, angular at apex; R, M and CuA diverge from one point; common stalk of M and CuA absent; R_{1+2} short, terminates on anterior margin; pterostigma absent. Frons hidden by conical frontal processes, median ocellus on junction of frons and cheek. Length of body 1.5–4 mm (Fig. 607). Neogene to Recent. In Recent fauna subfamily represented in all territories. Genera include *Trioza* Forster, 1848 from the Miocene of the North Caucasus.

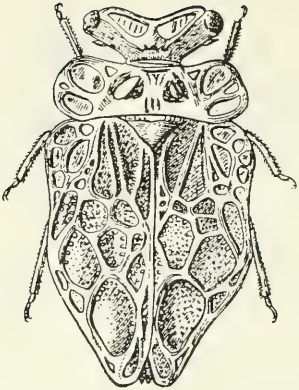


Fig. 608. Family Peloridiidae.

Hemiodoecus veitchi Hacker; [dorsal view of] body and wings; × 22. Recent, Tasmania (Hacker, 1932).

Sternorrhyncha Incertae sedis

Outside the USSR: *Tripsyllidium* Evans, 1956 from Upper Triassic of Australia.

Suborder Coleorrhyncha

Wings dissimilar. Forewings leathery, without spotted ornamentation, fold flat on back, meet along a straight line or overlap at distal part; in latter case distal part usually sharply broadened and anal margin of anal area displaced. Head small and mobile; gula absent; posterior division of clypeus with unsegmented 208 lobes; antennae short. Anal tube in both male and female cylindrical. Eleventh segment elongated, valves of ovipositor weakly developed. In Recent fauna three relict genera and eight species on southern borders or at considerable altitudes (2,000–3,000 m) of temperate zones of South America, South Australia, New Zealand, Tasmania and adjoining islands. It is possible that the first representatives of the order Heteroptera arose from Coleorrhyncha. Only relict family without known fossil forms. Actinoscytinidae (Cicadocoridae Bekker-Migdisova) Evans, belongs to Heteroptera.

Family PELORIDIIDAE Breddin, 1897

Forewings fold back flat on dorsal side of body, meet along a straight line or overlap, leathery with thick veins forming irregular, closed cells all over surface;

costal area with a row of smaller cells; anterior margin of forewing convex, and margin straight; paths of veins M and CuA indistinct; M fused with R and CuA here and there, and CuA fused with M and CuP. Head fairly large, triangular and semimobile; in adults frontal plate fused with clypeus; in nymphs frontal plate quadrate, lobes of clypeus not demarcated. Pronotum broad with lateral expansions. Scutellum small. Anal tube short. Length of body 4–5 mm (Fig. 608). Four genera in Recent fauna distributed in southern parts of Australia, South America, New Zealand and Tasmania.

Homoptera Incertae sedis

Family PROSBOLOPSEIDAE Bekker-Migdisova, 1946

Forewings weakly sclerotized or leathery; costal area wide; anterior margin convex; R_2 parallel to RS, with a row of branches; A_1 and A_2 fused to form a stalk. Head mobile or semimobile; proboscis long, reaches base of hind coxae; posterior division of clypeus small, with unsegmented lobes. Pronotum short and broad; scutellum triangular, with length equal to width. Abdomen flat. Anal tube short. Permian to Triassic. One genus.

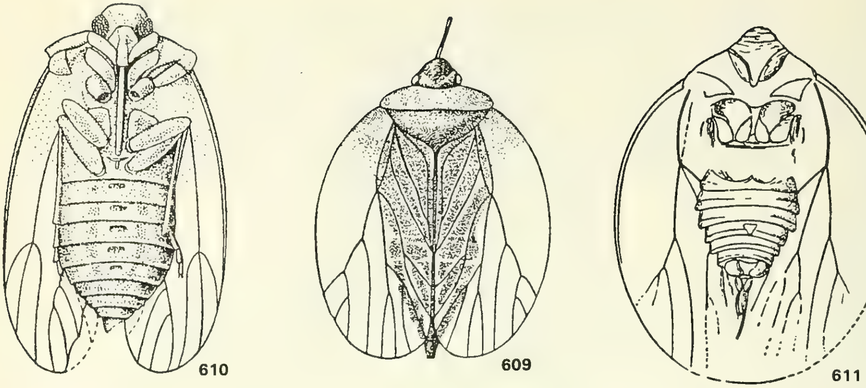
Prosbolopsis Martynov, 1935. Genotype—*P. ovalis* Martynov, 1935; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing with wide costal area, markedly convex and rounded anterior margin, perfectly straight anal margin and slightly asymmetric apex; R + M is long; R, M and CuA divide almost at same level at middle of tegmen; M three- to five-branched. Length of forewing 8.5–9 mm (Figs. 609–611). One species. Upper Permian of Arkhangelsk province.

Besides this *Eochiliocycla* Davis, 1942 (Upper Permian of Australia) belongs to Homoptera *incertae sedis*.

Order Heteroptera. True Bugs

(E.E'. Bekker-Migdisova)

Forewings folded, back flat, transformed into hemelytra, usually divided by sutures and fractures into distinctly isolated parts: membrane membranous, clavus and corium leathery; sometimes cuneus corresponding to pterostigma of other groups, and embolium to costal area of corium; in a few representatives tegmina complete, not subdivided; venation on thick parts of wing indistinct. Head free and mobile, usually prognathous. Mesonotum larger than metanotum, closely fused with it; scutellum often well developed. Odoriferous glands present on thorax in adults and on abdominal terga in nymphs. Many families inhabit water and shore vegetation, or are pelagic. Herbivores, predators, ectoparasites of vertebrates, saprophages or with combination of these food habits. Exhibit phylogenetic affinity toward primitive Homoptera,



209 Figs. 609–611. Family Prosbolopseidae.

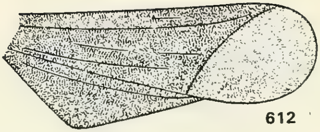
609. *Prosbolopsis ovalis* Martynov; impression of dorsal side of body, × 4.7. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1960). 610. *Prosbolopsis* sp.; impression of ventral side of body, × 6.3. Upper Permian, Arkhangelsk province (Martynov, 1935). 611. *Prosbolopsis* sp.; impression of ventral side of body, × 6.3. Upper Permian, Arkhangelsk province (Martynov, 1935).

from which they diverged in the Permian. Separation and evolution of Heteroptera continued from herbivorous to omnivorous nature and then to predation leading invariably to great mobility, which led to great variability and adaptation to prevailing biotopes and thus wide distribution. Permian to Recent.

209 Recent Heteroptera are distributed between two suborders—terrestrial bugs, Geocorisae and aquatic bugs, Hydrocorisae: but the morphological characteristics of these groups are based on structures of body that usually are difficult to observe in fossil material. Therefore, descriptions of Heteroptera begin with families; suborders and superfamilies are not treated. The order includes about 50 Recent families and 16 extinct Mesozoic ones. There are 40 families with fossil representatives.

Family APOPNIDAE Handlirsch, 1939

Forewings with very large clavus; corium thick, separated from membrane by arcuate lines, convex on outer side, with remnants of four major veins; veins indistinct in membrane. Scutellum large. Length of forewing 4 mm (Fig. 612). Possibly family related to Notonectidae. Lower Jurassic of Western Europe. One genus: *Apopnus* Handlirsch, 1939.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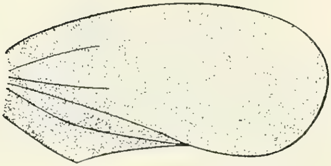
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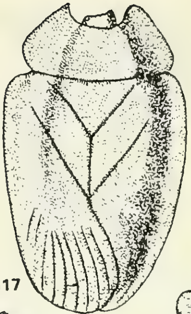
Figs. 612–614. Families Apopnidae, Aphlebocoridae and Probascanionidae.

612. *Apopnus magniclavus* Handlirsch; forewing, × 13.7. Lower Jurassic, Germany (Handlirsch, 1939). 613. *Aphlebocoris punctata* Handlirsch; forewing, × 11. Lower Jurassic, Germany (Handlirsch, 1939). 614. *Probascanion megacephalum* Handlirsch; general view, × 9.6. Lower Jurassic, Germany (Handlirsch, 1939).

Family APHLEBOCORIDAE Handlirsch, 1906

Forewings with very short, broad clavus, which projects angularly, A_1 distinct; corium and membrane not sharply isolated; corium large, thick and with visible bases of R and M; membrane small in the form of a wide border without veins. Length of forewing 5 mm (Fig. 613). Characters of tegmen resemble Naucoridae, which are probably their predecessors. Jurassic of Western Europe. One genus: *Aphlebocoris* Handlirsch, 1906.



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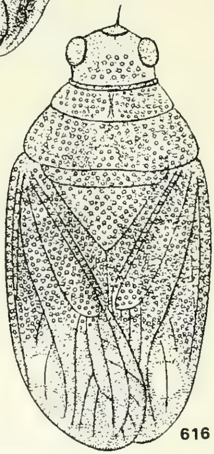

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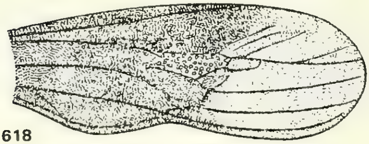

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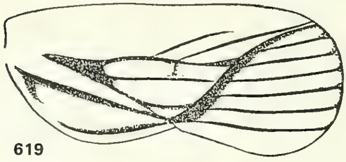

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Family PROBASCANIONIDAE Handlirsch, 1939

Forewings short, rounded with large, displaced and angular clavus. Head large, broad; eyes large and convex. Pronotum broad, cylindrical, with width double the length; scutellum like a small isosceles triangle, somewhat pointed, less than one-third of length of body. Length of forewing 6 mm (Fig. 614). Apparently related to Naucoridae. Jurassic of Western Europe. One genus: *Probascanion* Handlirsch, 1939.

Family ARCHEGOCIMICIDAE Handlirsch, 1906

Forewings with transparent membrane, not separated from corium by distinct dividing line or break; often with border; veins not reaching margin; SC long; R distally pectinate with three branches; M indistinct or fused with R at base, with three or four distal branches, which run beyond corium; anterior branch of CuA long, posterior branch often distally fused with wing margin; posterior angle of clavus shifted by one-third in distal direction. Body flat. Width of pronotum double the length; scutellum large, its length equal to width. Head broad, with compact articulation. Structurally similar to Actinoscytinidae (= Cicadocoridae). Length of tegmen 4–6 mm (Figs. 615, 616). Jurassic of Western Europe. Seven genera: *Archegocimex* Handlirsch, 1906; *Archegocoris* Handlirsch, 1939; *Anosmus* Handlirsch, 1939; *Deraiocoris* Bode, 1953; *Progonocoris* Handlirsch, 1939; *Megacoris* Bode, 1953; *Ophthalmocoris* Bode, 1953.

Family PROGONOCIMICIDAE Handlirsch, 1906

Forewings with indistinct boundary between membrane and corium, without dividing line; veins of corium indistinct. Pronotum notched in front, with rounded sides, and almost straight posterior margin; scutellum twice as wide as long, shaped like an isoscles triangle. Head of moderate size. Length of body 7 mm (Fig. 617). Jurassic of Western Europe. One genus: *Progonocimes* Handlirsch, 1906.

Family EONABIDAE Handlirsch, 1939

Clavus, corium and membrane sharply demarcated, but not differing in ornamentation; clavus small and rounded; SC well developed, looks like a line

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Figs. 615–619. Families Archegocimicidae, Progonocimicidae, Eonabidae and Eocimicidae.

615. *Archegocimex geinitzi* Handlirsch; dorsal view, × 10.2. Lower Jurassic, Germany (Handlirsch, 1906). 616. *Progonocoris pictus* Handlirsch; dorsal view, × 14.5. Lower Jurassic, Germany (Handlirsch, 1939). 617. *Progonocimex jurassicus* Handlirsch; dorsal view, × 7.6. Lower Jurassic, Germany (Handlirsch, 1906). 618. *Eonabis primitiva* Handlirsch; forewing, × 13.8. Lower Jurassic, Germany (Handlirsch, 1939). 619. *Eocimex liasinus* Handlirsch; forewing, × 10. Lower Jurassic, Germany (Handlirsch, 1906).

211 separating embolium; R and M fused basally up to midpoint of forewing, distally free. R with two series of branches in membrane; CuA with two long parallel branches at midpoint of tegmen; CuP straight, terminates on posterior branch of CuA, which continues beyond this in the form of a marginal vein. Length of forewing 4.5 mm (Fig. 618). Resemble Nabidae. Jurassic of Western Europe. Five genera: *Eonabis* Handlirsch, 1939; *Copidopus* Handlirsch, 1906; *Pronabis* Bode, 1953; *Engynabis* Bode, 1953; *Eogerridium* Bode, 1953.

Family EOCIMICIDAE Handlirsch, 1906

Forewings sharply demarcated into clavus, corium and membrane by ridges; clavus large and semicircular; corium resembles an equilateral triangle, with distinct veins; R and M joined at base with CuA; CuA divides at midpoint into two long branches; in membrane all veins in form of ribs, which erupt out from dividing ridge. Length of forewing 5.5 mm (Fig. 619). Jurassic of Western Europe. One genus: *Eocimex* Handlirsch, 1906.

Family HADROCORIDAE Handlirsch, 1939

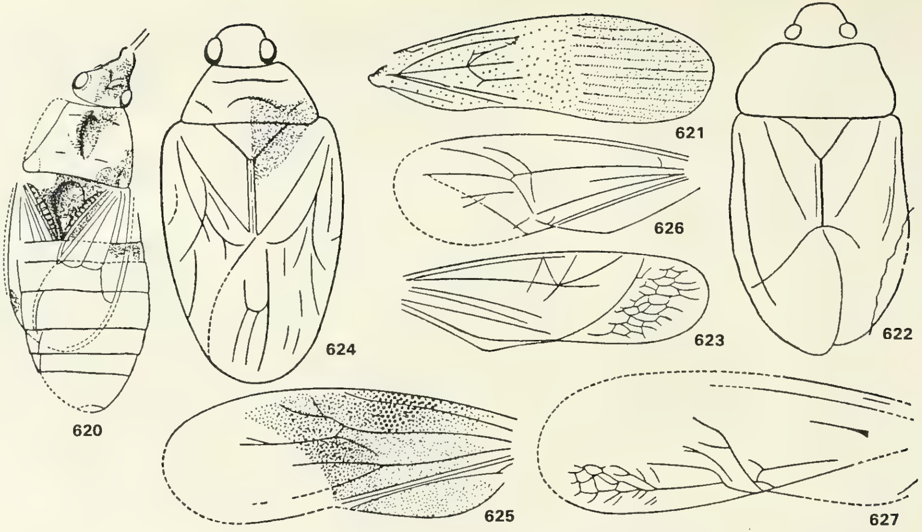
Forewings demarcated into clavus, corium and membrane; corium with distinct primary veins—SC, R, M and CuA; clavus narrow, long and angular; membrane demarcated by thick cross veins. Head free, elongated in front, broad; eyes small. Pronotum large and slightly trapezoidal with a shallow longitudinal impression; scutellum large, triangular, slightly elongated along length, with pear-shaped impression at middle. Length of forewing 9 mm (Fig. 620). Jurassic of Western Europe. Two genera: *Hadrocoris* Handlirsch, 1939; *Liasocoris* Wendt, 1940.

Family PACHYMERIDIDAE Handlirsch, 1906

Forewings narrowed basally, clavus narrow, without angular projection; corium hardly reaching halfway along forewing, indistinctly demarcated from membrane, spotted with a few distinct veins; membrane with 10 indistinct straight, parallel veins. Length of forewing 6 mm (Fig. 621). Jurassic of Western Europe. One genus: *Pachymeridium* Geinitz, 1880.

Family PROTOCORIDAE Handlirsch, 1906

Forewings with sharply demarcated corium, clavus and membrane; membrane
212 of moderate size; clavus short and broad; SC distinct; M and CuA present; membrane without veins. Head of moderate size, rounded in front with protruding eyes. Pronotum broad, slightly trapezoidal with weakly notched anterior margin; scutellum small, shaped like an isosceles triangle. Length of body 10 mm (Fig. 622). Jurassic of Western Europe. One genus: *Protocoris* Heer, 1865.



211 Figs. 620–627. Families Hadrocoridae, Pachymeridiidae, Protocoridae, Psychocoridae, Cuneocoridae, Sisyrocoridae and Diatilidae.

620. *Hadrocoris scutellaris* Handlirsch; general view, × 6. Lower Jurassic, Germany (Handlirsch, 1939). 621. *Pachymeridium dubium* Geinitz; forewing, × 9.9. Lower Jurassic, Germany (Handlirsch, 1906). 622. *Protocoris insignis* Heer; dorsal view, × 6.1. Lower Jurassic, Switzerland (Handlirsch, 1906). 623. *Psychocoris cuneifera* Handlirsch; tegmen, × 10.8. Lower Jurassic, Germany (Handlirsch, 1939). 624. *Cuneocoris scutellaris* Handlirsch; dorsal view, × 20.8. Lower Jurassic, Germany (Handlirsch, 1939). 625. *Sisyrocoris rudes* Handlirsch; tegmen, × 12.5. Lower Jurassic, Germany (Handlirsch, 1939). 626. *Diatilus debilis* Handlirsch; forewing, × 10.6. Lower Jurassic, Germany (Handlirsch, 1939). 627. *Aposicoria semideleta* Handlirsch; forewing, × 9.3. Lower Jurassic, Germany (Handlirsch, 1939).

Family PSYCHOCORIDAE Handlirsch, 1939

Forewings with sharply demarcated corium, clavus and membrane; embolium and cuneus indistinct; four longitudinal veins of corium terminate abruptly, not crossing over to membrane; membrane with irregular network of many veins; clavus angular, encloses scutellum of medium size. Length of forewing 5 mm (Fig. 623). Resembles representatives of Recent Miridae and Anthocoridae. Jurassic of Western Europe. One genus: *Psychocoris* Handlirsch, 1939.

Family CUNEOCORIDAE Handlirsch, 1939

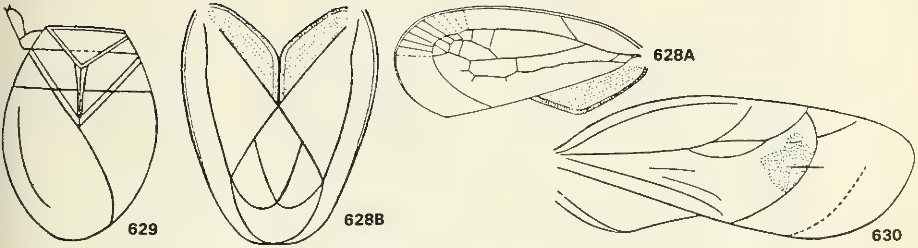
Forewings with large clavus and indistinctly demarcated corium and membrane; cuneus indistinct; membrane with five or six indistinct veins. Head of medium size with convex eyes. Pronotum broad; trapezoidal, width double the length; scutellum short, triangular, much narrower than pronotum. Small forms. Length of forewing 3 mm (Fig. 624). Jurassic of Western Europe. One genus: *Cuneocoris* Handlirsch, 1939.

Family SISYROCORIDAE Handlirsch, 1939

Forewings with large membrane, not sharply demarcated from corium, latter characterized by wartlike ornamentation and wrinkles; SC looks like a line demarcating embolium; R strong with small bifurcations (similar to cuneus) on border of membrane; M indistinct at base, connected with R and CuA at midpoint by cross vein; CuA branching halfway along forewing; clavus of medium size, angular. Length of forewing 5 mm (Fig. 625). Jurassic of Western Europe. Genus *Sisyrocoris* Handlirsch, 1939 to which Bode added the following 16 genera: *Acromocoris* Bode, 1953; *Adelocoris* Bode, 1953; *Corynecoris* Bode, 1953; *Dichaspis* Bode, 1953; *Emgerrophorus* Bode, 1953; *Ensphingocoris* Bode, 1953; *Entomecoris* Bode, 1953; *Euraspidium* Bode, 1953; *Eurynotis* Bode, 1953; *Ischnocoris* Bode, 1953; *Macropterocoris* Bode, 1953; *Mesomphalocoris* Bode, 1953; *Somatocoris* Bode, 1953; *Stophroschema* Bode, 1953; *Strobilocoris* Bode, 1953; *Trachycoris* Bode, 1953.

Family DIATILIDAE Handlirsch, 1939

Forewings with comparatively small membrane, demarcated from corium by a distinct line; corium not strongly opaque, without ornamentation; primary veins from corium extend onto membrane; SC distinct; R strong, with a series of branches connected to CuA by arcuate cross vein; M with only distal part preserves; clavus sharply delimited, one-half of length of forewing. Length of forewing 5–7 mm (Figs. 626, 627). Jurassic of Western Europe. Three genera: *Diatilus* Handlirsch, 1939; *Apsicoria* Handlirsch, 1939; *Cathalus* Handlirsch, 1939.



Figs. 628–630. Families Triassocoridae and Hypocimicidae.

628. *Triassocoris meyrsi* Tillyard; A—forewing, B—dorsal view, × 7.8. Upper Triassic, Australia (Tillyard, 1923). 629. *T. ovalis* Tillyard; body and forewing, × 7.6. Upper Triassic, Australia (Tillyard, 1923). 630. *Hypocimex membranaceus* Handlirsch; forewing, × 9.6. Lower Jurassic, Germany (Handlirsch, 1939).

Family TRIASSOCORIDAE Tillyard, 1922

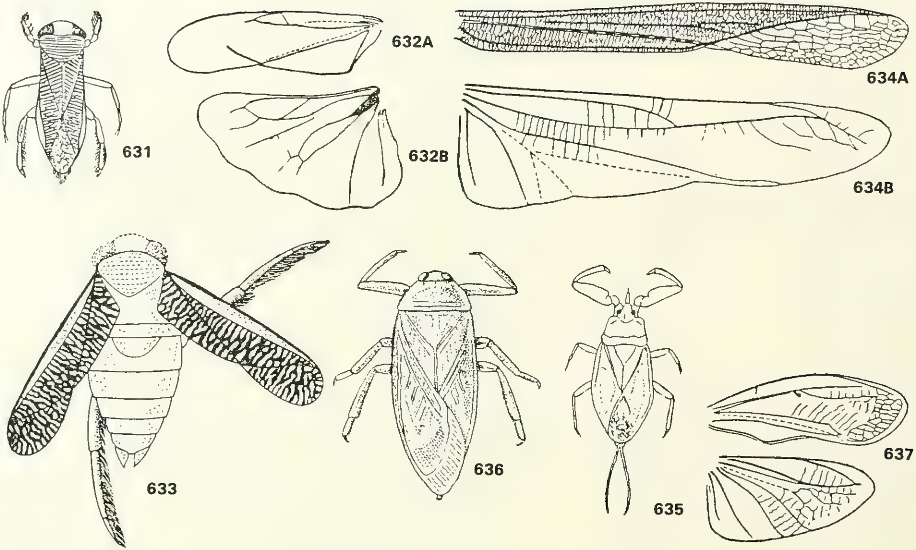
Forewings divided into clavus, corium and membrane; only vestiges of embolium visible; corium extending beyond midpoint of forewing demarcated
213 from narrow membrane by arcuate vein parallel to margin of wing; main stems of M and CuA distinct at base; in membrane, R and M have series of radial branches crossing over to arcuate marginal vein; clavus short, shifted toward base, projecting, reaches only to middle of CuP; distal parts of forewing overlapping. Scutellum triangular and twice as wide as long. Femur and tibia of forelegs short and broad. Length of forewing 4–5 mm (Figs. 628, 629). Ancestors of most Recent representatives of Hydrocorisae. Triassic of Australia. One genus: *Triassocoris* Tillyard, 1922.

Family HYPOCIMICIDAE Handlirsch, 1939

Forewings demarcated into corium, clavus and membrane; embolium indistinct, resembling cuneus; membrane divided by concentric and arcuate lines parallel to margin of wing; R preserved in corium, M and CuA leave it distally; clavus short, wide and angular; isolated veins present on membrane. Scutellum small. Length of forewing 6.5. mm (Fig. 630). Characters of this family resemble those of Triassocoridae; but, forewings more specialized and closer to Naucoridae; it differs from them both in the presence of a rudimentary cuneus that is very characteristic in the Geocorisae. Jurassic of Western Europe. One genus: *Hypocimex* Handlirsch, 1939.

Family CORIXIDAE Leach, 1815
[nom. transl. Kirby, 1837 (ex Corixida Leach, 1815)]

Forewings divided into clavus, corium, linear embolium and a membrane,



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Figs. 631–637. Families Corixidae, Nepidae and Belostomatidae.

631. *Corixa praeusta* Fieber; dorsal view, × 1.75. Recent, Europe (Jensen-Haarup, 1925). 632. *C. punctata* Illiger; A—forewing , B—hindwing, × 2.9. Recent, Europe (Handlirsch, 1925). 633. *C. rhenana* Statz; dorsal view, × 6.5. Paleogene, Germany (Statz; 1950). 634. *Renatra linearis* Linnaeus; A—forewing, B—hindwing, × 2.6. Recent (Handlirsch, 1925). 635. *Nepa cinerea* Linnaeus; dorsal view, × 1.4. Recent (Stichel, 1925). 636. *Mesobelostomum deperditum* (Germar); reconstruction, × 0.66. Upper Jurassic, Germany (Handlirsch, 1925). 637. *Limnogeton fieberi* Mayr; A—forewing, B—hindwing, × 1.5. Recent (Handlirsch, 1925).

without veins. Frons markedly bent backward; proboscis not segmented, or two-segmented, short and completely hidden by head capsule; antennae three-segmented, shorter than head, attached below eyes. Meso- and meta-thorax complex, latter with parapleurae; forelegs short; tarsi two-segmented, transformed into paddle (pala), in males beset with denticles which serve as 214 organs of sound production; midlegs slender; simple; hindlegs of swimming type, claws without appendages. Abdomen in males often asymmetrical (at bottom). Live in drains or slow-moving, rarely, fast-moving bodies of freshwater. Feed on aquatic vegetation. Length of body 2–16 mm (Figs. 631–633). Paleogene to Recent. Few genera in family, of which one genus is a fossil form from the Paleogene of Western Europe, the Neogene of North America and the Quaternary of Western Europe.

Family NEPIDAE Latreille, 1802. Water scorpions

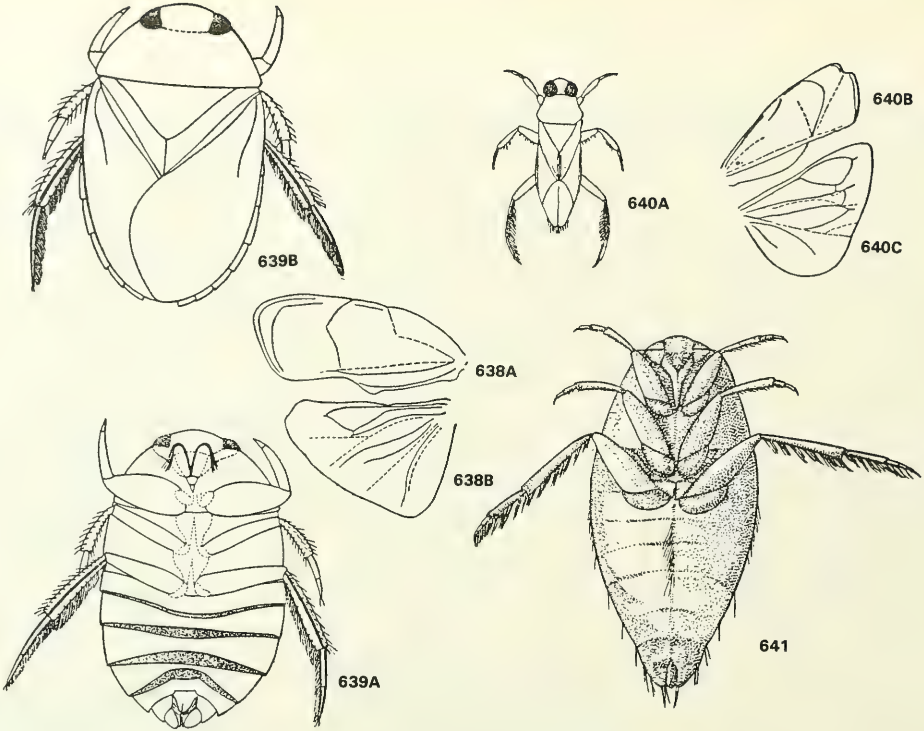
[nom. transl. Stephens, 1829 (ex Nepariae Latreille, 1802)]

Forewings demarcated into clavus, corium and membrane; embolium indistinct; membranal veins forming a network. Head shifted forward; ocelli absent; proboscis three-segmented, very short; antennae very short, shorter than head, three-segmented, with lateral processes, concealed and located under eyes. Fore coxae attached to anterior margin of prothorax or close to it; forelegs of prehensile type; middle and hindlegs of walking type; coxae movable. Body very much flattened, with long breathing tube. Tarsi of all legs one-segmented. Predators. Length of body 15–65 mm (Figs. 634, 635). Jurassic to Recent. Family with few genera; among known fossils *Mesonepa* Handlirsch, 1906 from the Upper Jurassic of Western Europe, one genus from the Paleogene of Europe (Baltic amber), the Paleogene and Neogene of Western Europe, and one genus from the Quaternary deposits of North America.

Family BELOSTOMATIDAE Leach, 1815

[nom. transl. Uhler, 1886 (ex Belostomida Leach, 1815)]

Forewings demarcated into clavus, corium and membrane; membrane with distally distinct veins forming a network, and a marginal border. Head non-projecting; ocelli absent; proboscis three-segmented, very short; antennae short, four-segmented, both middle segments often serrate. Meso- and metathorax fused; forecoxae project markedly; forelegs prehensile, hindlegs modified for swimming; tarsi of middle and hindlegs two-segmented, with two claws. Breathing tubes short, lancet-shaped, two-segmented, projecting from end of abdomen or concealed. Predators. Inhabit lower courses of rivers down to surf zone. Length of body 35–90 mm (Figs. 636, 637). Jurassic to Recent. Few genera in family, out of which *Mesobelostomum* Haase, 1820 from the Upper Jurassic of Western Europe, one genus from the Paleogene and Neogene of Western Europe and one genus from the Neogene of Western Europe are found as fossils.



Figs. 638–641. Family Naucoridae and Notonectidae.

638. *Iliocoris cimicoides* (Linnaeus); A—forewing, B—hindwing, × 7. Recent, Europe (Handlirsch, 1925). 639. *Naucoris rottensis* Statz; A—ventral view, B—dorsal view, × 20.8. Paleogene, Germany (Statz, 1950). 640. *Notonecta glauca* Linnaeus; A—dorsal view, × 1.6; B—forewing; C—hindwing, × 2.4. Recent (Handlirsch, 1925). 641. *Asionecta curtipes* J. Popov; ventral view, × 7.4. Upper Jurassic, Southern Kazakhstan (original figures).

Family NAUCORIDAE Fallen, 1814

[nom. transl. Samuelle, 1819 (ex Naucoridei Fallen, 1814)]

Forewings demarcated into clavus, corium and embolium; embolium without veins. Head transverse; eyes rudimentary; proboscis three-segmented; antennae shorter than head, four-segmented, simple, concealed. Forecoxae attached to anterior margin of prothorax; forelegs of prehensile type, hindlegs of swimming type; at least posterior tarsus two-segmented, with two claws. Body gently convex, without breathing tubes. Live in water. Predators. Length of body 10–30 mm (Figs. 638, 639). Jurassic to Recent. The genera known are *Palaeoheteroptera* Meunier, 1900 and *Nepidium* Westwood, 1854 from the Upper Jurassic of Western Europe, one genus from the Paleogene and Neogene of Western Europe and two from the Neogene of Western Europe and North America.

Family NOTONECTIDAE Leach, 1815

[nom. transl. Samuelle, 1819 (ex Notonectidae Leach, 1815)]

(Y.A. Popov)

Forewings demarcated into clavus, corium, embolium and membrane without veins, folding like a roof, notched along posterior margin. Four-segmented antennae, very short, attached under eyes, concealed. Proboscis short, reaching only up to forecoxae, four-segmented. Ocelli absent. Forelegs not raptorial, posterior legs of swimming type; forecoxae attached to posterior margin of prothorax, hindcoxae move in one plane; tarsi two-segmented, male foretarsi sometimes unsegmented. Abdomen without breathing tube. Live in stagnant or slow-moving water. Predators. Length of body 11–18 mm (Fig. 640A, B). Upper Jurassic to Recent.

Asionecta J. Popov gen. nov. Genotype—*A. curtipes* J. Popov sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Body oval-elongate. Femur conical, much thickened, slightly longer than tibia; trochanter large, rounded with elongated tip; tarsi two-segmented; first segment of tarsi of fore 215 and middle legs almost equal to second segment; first segment of hind tarsus almost equal to one-half of length of hind tibia. Sternum of eighth segment of abdomen consisting of two smooth plates. Length of body 9–9.5 mm (Fig. 641). One species. Upper Jurassic of Kazakhstan.

Besides this, *Notonectites* Handlirsch, 1906 from the Upper Jurassic of Germany, one genus from the Paleogene and Neogene of Western Europe and one from the Paleogene and Neogene and Quaternary of Western Europe and North America.

Family TINGIDAE Laporte, 1832. Lace bugs

[nom. transl. Fieber, 1861) (ex Tigidites Laporte, 1832)]

(E.E. Bekker-Migdisova)

Forewings covered with a network of cells over entire surface; clavus absent or fused with remaining part; no division of tegmen into corium and membrane. Head with cheek plates, not advancing forward; proboscis four-segmented, antennae four-segmented, longer than head, point of attachment visible on dorsal side. Pronotum pentagonal with long process that often covers scutellum; meso- and metathorax complete; each consisting of a single undivided sclerite; tarsus two-segmented, claws with appendages. Length of body 1.5–5 mm (Fig. 642). Jurassic to Recent. More than 160 species.

Tingiopsis Bekker-Migdisova, 1953. Genotype—*T. reticulata* Bekker-Migdisova, 1953; Upper Triassic, Central Asia (Madigen series, Madigen). Forewing covered with distinctly prominent network; distal part of forewing has rounded outline; SC absent; R and RS very long; cross vein r + rs present; M branches at distal one-fourth; also present rs + m. Length of forewing 5.5 mm (Fig. 643). One species. Lower Jurassic of Central Asia.

In addition, family includes two genera from the Paleogene of Europe (Baltic amber), one genus from the Paleogene of North America, two from the Paleogene and Neogene of Western Europe and North America and one from the Neogene of Western Europe and North America.

Family SALDIDAE Amyot and Serville, 1843. Littoral hoppers

[nom. transl. Costa, 1852 (ex Saldides Amyot et Serville, 1843)]
(Acanthiidae Stephens, 1829)

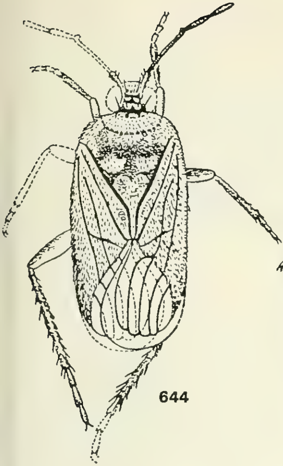
Forewings demarcated into clavus, corium and membrane; membrane with five or six longitudinal veins forming cells, but not reaching up to apex. Eyes very 217 large, convex, with a posterior indentation; two ocelli on prominences; antennae four-segmented, much longer than head; proboscis three-segmented, extending up to tip of mesothorax. Tarsus three-segmented; claws without appendages. Live along shores of rivers, streams, lakes and seas. Predators. Length of body 3–7 mm (Fig. 644). Paleogene to Recent. One genus from the Paleogene and one from the Paleogene and Quaternary of Western Europe.

Family DIPSOCORIDAE Dohrn, 1859

[Ceratocombidae Puton, 1869; Cryptostemmatidae Hedicke, 1935]

(Y.A. Popov)

Forewings demarcated into large clavus, corium and membrane; cuneus usually present. Head elongated or slightly slanting; eyes normally small; ocelli present; proboscis three-segmented; antennae four-segmented, first and second segments short and other two long and slender and covered with slender setae, third segment thickened at base. Thorax simple. Openings of odoriferous glands absent. Length of body 0.8–3 mm (Figs. 645, 646). Live on mosses, under fallen leaves, in anthills and along riverbanks. Neogene to Recent. Very few genera. One Recent genus from the Neogene of North America.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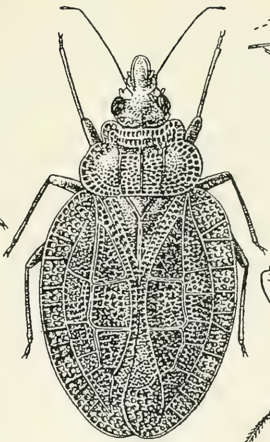
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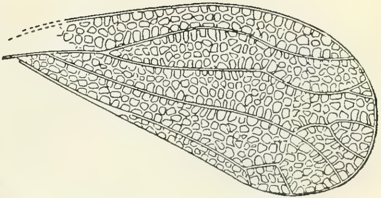
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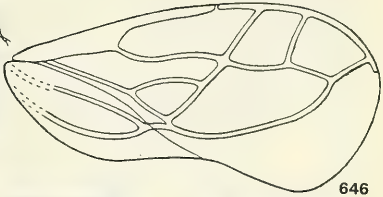
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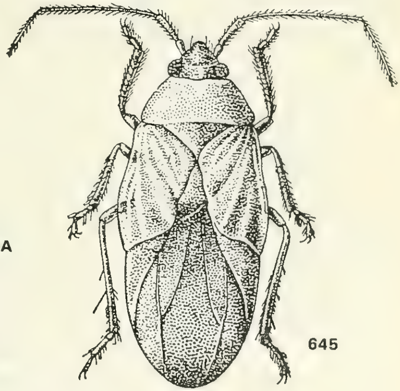
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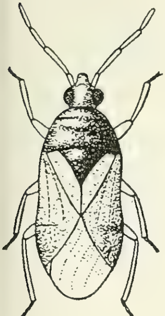
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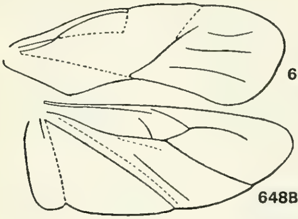
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648B

216 Figs. 642–648. Tingidae, Saldidae, Dipsocoridae and Anthocoridae.

642. *Phantoma baltica* Drake; dorsal view, × 16. Paleogene, Europe (Baltic amber) (Drake, 1950). 643. *Tingiopsis reticulata* Bekker-Migdisova; forewing, × 12.5. Lower Jurassic, Central Asia (Bekker-Migdisova, 1953). 644. *Oligosaldina aquatilis* Statz; dorsal view, × 8.5. Paleogene, Germany (Statz, 1950). 645. *Cryptostemma alienum* Herrich-Schaeffer; dorsal view, × 24.4. Recent (Kirichenko, 1951). 646. *Ceratocombus hurdi* Wygodzinsky; tegmen, × 60. Neogene (amber), Mexico (Wygodzinsky, 1959). 647. *Orius minutus* (Linnaeus); dorsal view, × 22. Recent (Handlirsch, 1925). 648. *Anthocoris silvestris* Linnaeus; A—forewing, B—hindwing, × 14. Recent (Handlirsch, 1925).

Family ANTHOCORIDAE Amyot and Serville, 1843

[nom. transl. Dallas, 1852 (ex Anthocorides Amyot et Serville, 1843)]

(E.E. Bekker-Migdisova)

Forewings sharply demarcated into clavus, corium, cuneus, embolium and membrane; membrane with very narrow, triangular cell* at base, situated along border of corium and not reaching apex. Head horizontal, shortened at anterior end; proboscis three-segmented; antennae four-segmented. Meso- and metathorax fused; tarsus three-segmented. Length of body 1.5–4 mm (Figs. 647, 648). Predators, many feed on aphids; some suck blood. Paleogene to Recent. About 70 species, one genus from Paleogene of Western Europe.

Family MIRIDAE Hahn, 1831. Plant bugs

(Capsidae Burmeister, 1835)

Forewings demarcated into clavus, corium, cuneus and membrane; membrane usually with one or two cells. Ocelli absent; proboscis four-segmented; antennae very much longer than head, four-segmented. Meso- and metathorax fused; hind coxae movable in one plane; tarsus three-segmented, claws with appendages. Posterior edge of each abdominal segment overlapping anterior part of following segment. Integument delicate, soft, poorly preserved. Large number of genera and species (Fig. 649). Jurassic to Recent. More than 600 species.

Miridoides Bekker-Migdisova, gen. nov. Genotype—*M. mesozoicus* Bekker-Migdisova, sp. nov; Upper Jurassic, Chimkent province (Malm, Karatau). Head sloping markedly and transverse, width between eyes less than width of posterior margin of pronotum. Antennae slender, shorter than length of body; first segment conical, reaching tip of head, second segment twice as long as first, remaining segments together only slightly longer than second; proboscis slender, reaching to middle coxae; eyes small, touching anterior margin of trapezoidal pronotum. Forewings reaching to end of abdomen, non-transparent, with anterior and posterior margins arcuately convex in basal region; CuP markedly depressed; only two veins on corium; membrane not transparent; cuneus little longer than width at base. Legs slender; tibiae straight; hind femurs not reaching end of abdomen, slightly longer and stouter than middle femora. Length of body about 5 mm (Fig. 650). One species. Upper Jurassic of Kazakhstan.

In addition, about 18 genera from the Paleogene of Western Europe and about 11 genera from the Neogene of North America.

Family NABIDAE Costa, 1852

[nom. transl. Dohrn, 1859 (ex Nabini Costa, 1852)]

Forewings demarcated into corium, clavus and membrane; embolium

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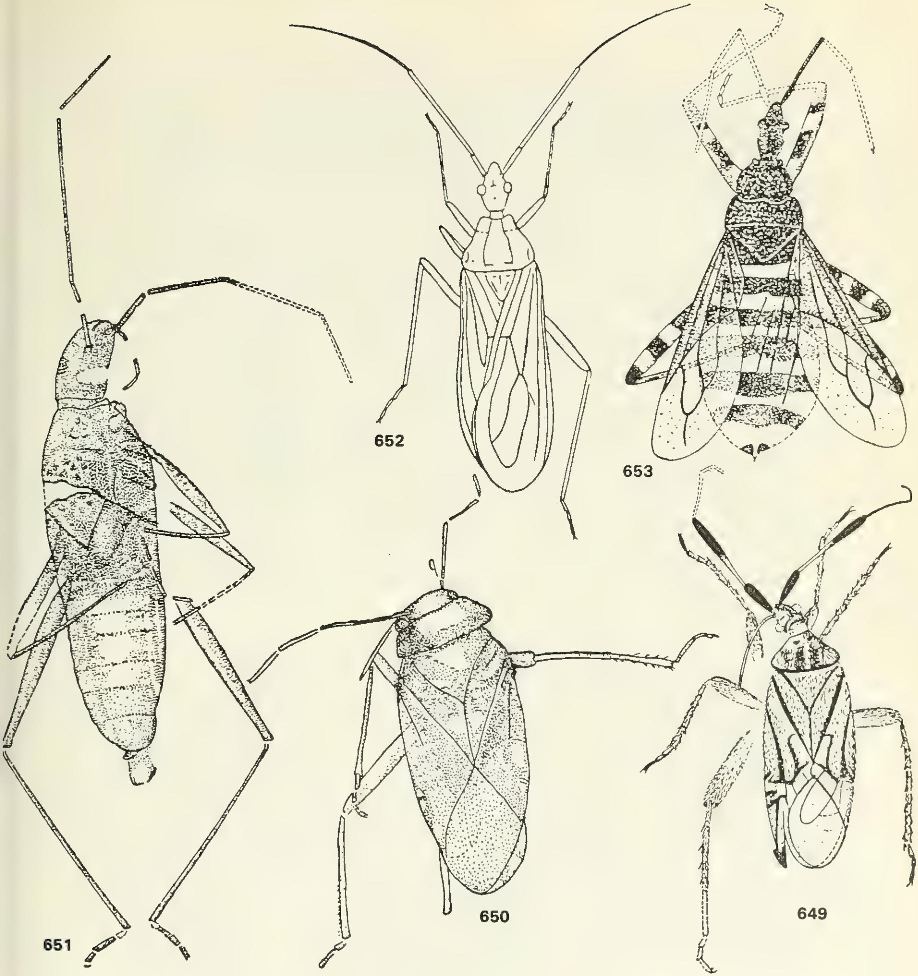
*Editor's note: Anthocorids do not have closed cells.



Figs. 649–653. Families Miridae, Nabidae and Reduviidae.

649. *Calocoris antennatus* Statz; general view from dorsal side, × 5.8. Paleogene, Germany (Statz, 1950). 650. *Miridoides mesozoicus* Bekker-Migdisova; general view, × 10.8. Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1963). 651. *Karanabis kiritshenkoi* Bekker-Migdisova; general view, Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1963). 652. *Platymeris insignis* (Germar); general view, × 5.6. Paleogène, Europe (Baltic amber) (Handlirsch, 1952). 653. *Rhinocoris michalki* Statz; general view, × 5. Paleogene, Germany (Statz, 1950).

occasionally present; three or four large cells in membrane, from which parallel veins run to apex of tegmen. Parietal region of head projects far in front of eyes, rounded at front; proboscis bent, four-segmented; first segment short; antennae usually four-segmented. Prothorax without sound-producing organ; meso- and metathorax complete; tarsus three-segmented, claws without appendages. Two 219 genital segments in female with a cleft in middle, enclosing ovipositor. Few genera. Length of body 5–10 mm. Jurassic to Recent.

Karanabis Bekker-Migdisova gen. nov. Genotype—*K. kiritshenkoi* Bekker-Migdisova, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Body elongated. Head moderately elongated, somewhat conical; antennae four-segmented, long, located in middle of preocular region; second segment of antenna somewhat more slender than first, third and fourth slender; first three segments almost equal in length, third segment longest. Proboscis fairly short, thin, distally bent. Pronotum conical, narrowing in front to form distinct neck, with posterior part arcuately bent, middle of disk flat; scutellum small; legs long; coxae of forelegs weakly elongated; forefemora of uniform width, without serrations, somewhat shorter than middle femurs; anterior tibiae equal to length of femora. Abdomen with distinct margin on ventral side, demarcated from central part by distinct depression. Forms of medium size. Length of body 5 mm (Fig. 651). One species. Upper Jurassic of Kazakhstan.

In addition, one genus from the Paleogene of Europe (Baltic amber), the Paleogene and Neogene of Western Europe, and one genus from the Neogene of Western Europe.

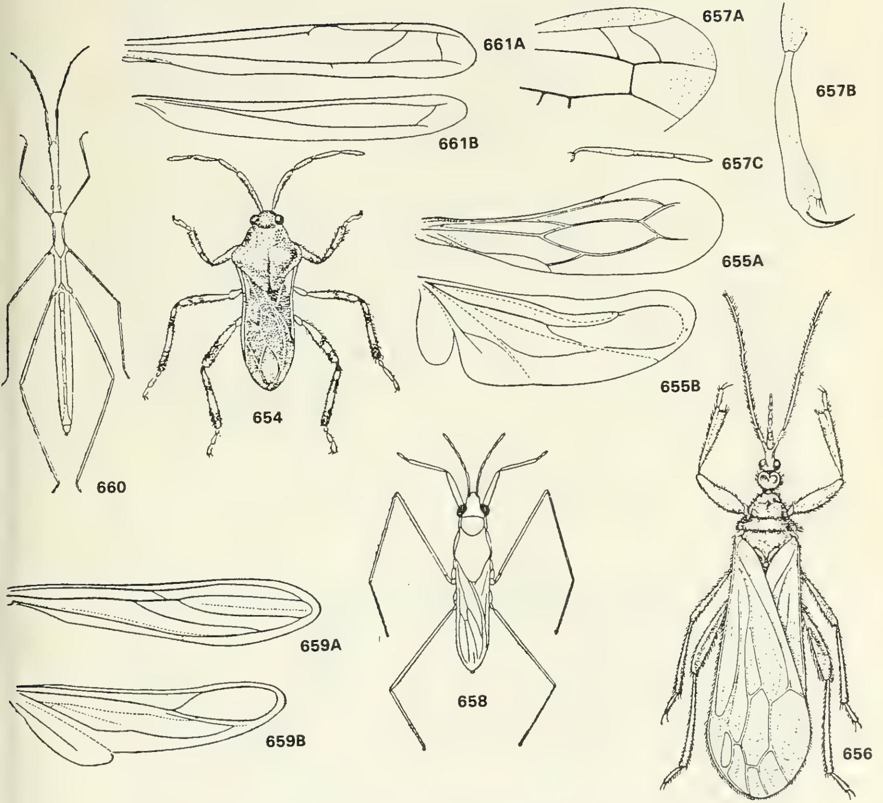
Family REDUVIIDAE Latreille, 1807. Assassin bugs

[nom. transl. Stephens, 1829 (ex Reduvini Latreille, 1807)]

Forewings demarcated into clavus, corium and membrane; membrane with two or three basal cells and two or three free veins. Proboscis bent, strong; antennae four-segmented, geniculate, sometimes with additional tapering segments at tip; ocelli on an elevation. Prothorax in the form of a trough, traversed by peculiar cross ribs that serve as a sound-producing organ; scutellum small or of medium size; meso- and metathorax complete; tarsus three-segmented, rarely two-segmented. Sometimes foretarsus one-segmented; claws without appendages. Mostly found in tropical countries, few live in the Palearctic. Exclusively predatory. Length of body 4 mm (Figs. 652, 653). Paleogene to Recent. More than 300 genera. In fossil form about five genera from the Paleogene of Europe (Baltic amber), two genera from the Paleogene of Western Europe and North America, about six genera from the Neogene of Western Europe and North America and one from the Quaternary deposits of Western Europe.

Family VELIIDAE Duglas and Scott, 1865. Ripple bugs

Clavus, corium and membrane fused in forewing. Head short, sloping and narrowing toward front; eyes touching anterior margin of pronotum; ocelli



Figs. 654–661. Family Veliidae, Henicocephalidae, Gerridae and Hyrometridae.

654. *Velia branchialis* Stal; dorsal view, × 6.4. Recent, North and South America (Blatchley, 1926). 655. *V. rivulorum* Fabricius; A—forewing, B—hindwing, × 3.6. Recent (Handlirsch, 1925). 656. *Henicocephalus formicinus* Uhler; dorsal view, × 2. Recent, North America (Beier, 1938). 657. *H. fossilis* Cockerell; A—distal part of forewing, × 2.5; B—foreleg; C—antenna. Burmese amber (Cockerell, 1916). 658. *Gerris argentata* Schummel; dorsal view, × 5. Recent, Europe (Beier, 1938). 659. *G. paludum* Fabricius; A—forewing, B—hindwing, × 7.9. Recent (Handlirsch, 1925). 660. *Hydrometra martini* Kirkaldy; dorsal view, × 5.3. Recent, North America (Blatchley, 1926). 661. *H. stagnorum* Linnaeus; A—forewing, B—hindwing, × 6. Recent (Handlirsch, 1925).

absent or indistinct; proboscis three-segmented; antennae considerably longer than head, four-segmented. Pronotum prolonged posteriorly to form a triangular process that covers scutellum; pro- and mesothorax of same length, complete; middle coxae attached almost equidistant from pro- and metathorax; hindlegs longer than forelegs, with stouter femurs; females with tarsi two- or three-segmented, claws attached in front of their apices. Live on surface of quick-flowing or stagnant water. Length of body 2–8 mm (Figs. 654, 655). Paleogene to Recent. One genus from the Paleogene of Western Europe and one from the Neogene of North America.

Family HENICOCEPHALIDAE Stal, 1865

[nom. transl. Berg, 1896 (ex Henicocephalida Stal, 1865)]

Forewing without demarcation into corium and membrane; veins close, not broken in middle, forming large cells at center of wing; clavus distinctly demarcated. Head long, distinctly demarcated from thorax; ocelli distinct; antennae four-segmented; proboscis three-segmented. Pleurae of meso- and metathorax indistinctly demarcated; prothorax with furrow for stridulation; tarsus of anterior legs one-segmented, hindlegs three-segmented, without arolia; foretibiae widened toward tip. Odoriferous glands absent. Length of body about 3.0 mm (Figs. 656, 657A, B). Predators. Paleogene to Recent. Two genera from the Paleogene of South Asia (Burmese amber).

Family GERRIDAE Leach, 1815. Water striders

[nom. transl. Dohrn, 1859 (ex Gerrida Leach, 1815)]

Corium, clavus and membrane fused in forewing. Head rarely longer than width; eyes at base of head, touching anterior margin of pronotum; two ocelli, sometimes indistinct; proboscis four-segmented; scutellum completely covered by backward triangular extension of pronotum; meso- and metathorax 220 complete; mesothorax very large; metathorax short; hind and specially middle legs considerably longer than forelegs; coxae of middle and hindlegs close; hindcoxae long, cylindrical, can be rotated, attached to sides of body and far apart; tarsus two-segmented; claws without appendages, attached at tip. Live on surface of water; some forms marine. Length of body 6–18 mm (Figs. 658, 659). Paleogene to Recent. One genus known from the Paleogene of Europe (Baltic amber) and one genus from the Paleogene, Neogene and Quaternary of Western Europe, Transbaikal and North America.

Family HYDROMETRIDAE Billberg, 1820. Stick-like water measurers

[nom. transl. Stephens, 1829 (ex Hydrometraedes Billberg, 1820)]

Forewings homogeneous with no demarcation into corium and membrane. Wingless forms or forms with rudiments of wings predominate. Head markedly elongated, widened at tip; eyes shifted away from anterior margin of pronotum;

221 ocelli absent; proboscis three-segmented, short. Scutellum absent or very small; meso- and metathorax complete; legs very slender, threadlike; tarsi three-segmented; claws at tip of tarsus, without appendages. Live on surfaces [of water] and along banks of water bodies. Length of body 9–25 mm (Figs. 660, 661). Paleogene to Recent. One genus known from the Paleogene of Europe (Baltic amber) and one from the Paleogene and Neogene of North America and the Neogene of Western Europe and North America.

Family ARADIDAE Br., 1835. Flat bugs

[nom. transl. Costa, 1852 (ex Aradiens Br., 1835)]

Forewings divided into clavus, corium and membrane; clavus narrows toward apex, sometimes does not reach up to apex of scutellum; membrane with few, 222 irregular anastomosing veins, rarely completely without veins. Head horizontal, with a long process extending between antennae; tubercles supporting antennae strongly developed, sharply pointed; proboscis four-segmented, first segment small. Meso- and metathorax complete; tarsus two-segmented, claws lack appendages. Body flat above and below. Live under bark of trees and on polyporales, suck fungal mycelia and juices of plants. Length of forewing 2–5 mm (Fig. 662). Paleogene to Recent. About 40 genera: two genera from the Paleogene of Europe (Baltic amber) and one genus from the Paleogene and Neogene of Western Europe and North America.

Family LYGAEIDAE Schilling, 1829

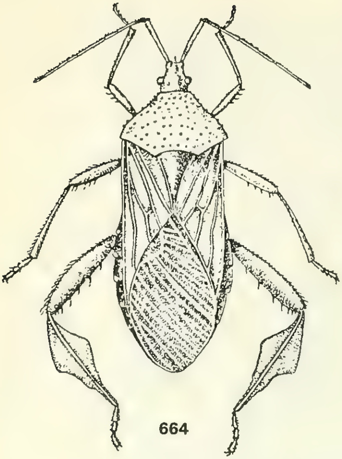
[nom. transl. Herrich-Schaeffer, 1835 (ex Lygaeides Schilling, 1829)]
(Myodochidae Kirkaldy, 1899)

Forewings demarcated into clavus, corium and membrane; membrane with five longitudinal veins. Often with short wings. Head without constriction in front of eyes; tubercles supporting antennae lateral in position; ocelli frequently present; proboscis four-segmented; antennae four-segmented, longer than head. Meso- and metathorax complete. Two genital segments divided by a longitudinal slit which conceals ovipositor. Tarsus three-segmented, with appendages. Herbivores and saprophages. Length of body about 2.5–20 mm (Fig. 663). More than 100 genera. Cretaceous to Recent. Known fossil forms include *Mesolygaeus* Ping, 1928, from the Cretaceous of China, two genera from the Paleogene of Europe (Baltic amber), about 12 genera from the Paleogene of Western Europe and North America, four genera from the Paleogene and Neogene of Western Europe and North America and about 30 genera from the Neogene of Western Europe and America.

Family COREIDAE Leach, 1815. Leaf-footed bugs

[nom. transl. Stephens, 1829 (ex Coreides Leach, 1815)]

Forewings demarcated into clavus, corium and membrane; clavus forms a



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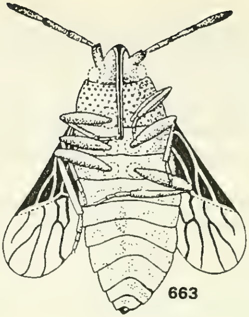

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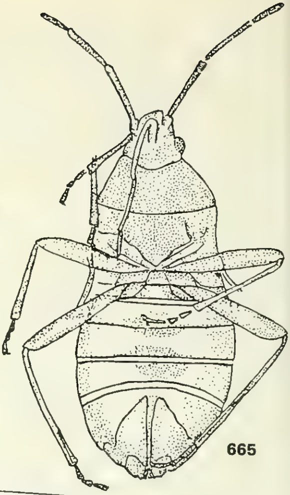

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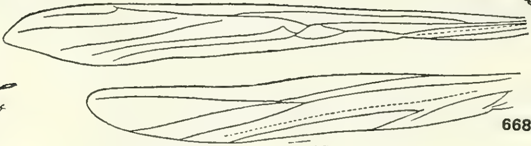

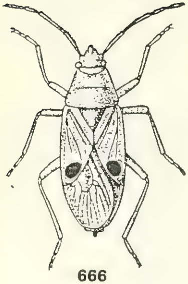

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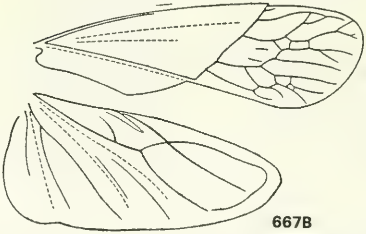

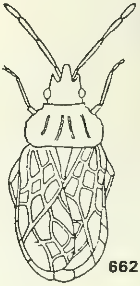

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221 Figs. 662–668. Families Aradidae, Lygaeidae, Coreidae, Pyrrhocoridae and Berytidae.

662. *Aradus superstes* Germar; dorsal view, × 10. Paleogene, Europe (Baltic amber) (Germar, 1856). 663. *Lygeosoma wagneri* Statz; ventral view, × 9.5. Paleogene, Germany (Statz, 1950). 664. *Acanthocephala fermorata* Fabricius; dorsal view, × 3. Recent. North America (Blatchley, 1926) 665. *Karatavocoris asiatica* Bekker-Migdisova; ventral view, × 8.2. Upper Jurassic, South Kazakhstan (Bekker-Migdisova, 1963). 666. *Odontopus migricornis* Stal; dorsal view, × 3.4. Recent, India (Beier, 1938). 667. *Largus rufipennis* Laporte; A – forewing, B – hindwing, × 5.8. Recent (Handlirsch, 1925). 668. *Neides tipularius* (Linnaeus); A—forewing, B—hindwing, × 9.2 Recent, Europe (Handlirsch, 1925).

common junction behind scutellum; membrane with numerous, sometimes connected, veins. Head does not form a shield and lacks transverse depression in front of eyes; ocelli present; proboscis four-segmented; antennae much longer than head, four-segmented, with point of attachment visible from dorsal side. Scutellum of moderate size, one-half length of abdomen; meso- and metathorax complete; tarsus three-segmented, pretarsus with appendages. Herbivores. Length of body 5 mm (Fig. 664). Upper Jurassic to Recent. About 200 genera.

Karatavocoris Bekker-Migdisova, gen. nov. Genotype—*K. asiatica* Bekker-Migdisova, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Surfaces of body, antennae and legs bare. Head much narrower than pronotum, short, width with set-in eyes slightly exceeding length; cheek plates not protruding in front; first segment of antenna short, not reaching to anterior margin of head; second and third segments not thick; second slightly longer than third; fourth segment elongate, egg-shaped, five-eights the length of second and five-sevenths the length of third segment; proboscis almost reaches coxae of middle legs. Pronotum with complete lateral borders; scutellum open, depressed at base; coxae of hindlegs separate, femur not armored, tibiae of hindlegs equal in length to hind femora, almost straight, not bent, or armed with spines. Abdomen elliptically rounded, not wide; sixth sternite of abdomen of female slit in two by longitudinal cleft. Length of body about 8 mm (Fig. 665). One species. Upper Jurassic of Kazakhstan.

Outside the USSR: eight genera from the Paleogene of Western Europe and North America, one genus from the Paleogene and Neogene of Western Europe, about 15 genera from the Neogene of Western Europe, North America and South America and one genus from the Neogene of North America and the Quaternary of Africa.

Family PYRRHOCORIDAE Amyot and Serville, 1843. Red bugs

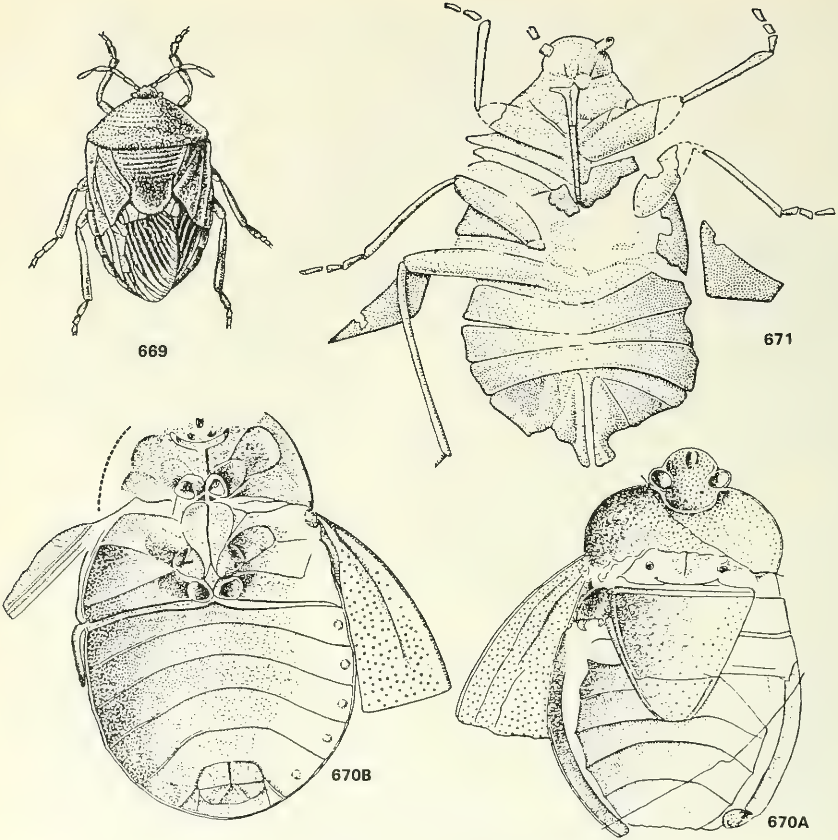
[nom. transl. Dohrn, 1859 (ex Pyrrhocorides Amyot et Serville, 1843)]

Forewings demarcated into clavus, corium and membrane; membrane with more than five veins, that are short and connected by cross veins or fused. Head with lateral tubercles that support antennae; proboscis four-segmented; antennae four-segmented, considerably longer than head; meso- and metathorax simple; tarsus three-segmented; pretarsus with appendages. Length of body 7–8 mm (Figs. 666, 667). Paleogene to Recent. About 50 genera, primarily tropical. Fossil forms include one genus from the Paleogene of Western Europe and one from the Neogene of North America.

223 Family BERYTIDAE Fieber, 1851. Stilt bugs

[nom. transl. Fieber, 1861 (ex Beritidea Fieber, 1851)]

Forewings demarcated into clavus, corium and membrane; membrane with four or five veins. Meso- and metathorax simple. Head with constriction; eyes shifted together toward base of head; ocelli present; proboscis four-segmented;



Figs. 669–671. Families Pentatomidae and Cydnidae, and Heteroptera incertae sedis.

669. *Aspongopus nubilis* Westwood; dorsal view, × 1.7. Recent, Africa (Schouteden, 1913). 670. *Cydnopsis vishneviensis* J. Popov; A—dorsal view, B—general view from ventral side, × 15.7. Neogene, North Caucasus (original drawing—Bekker-Migdisova). 671. *Lygenocoris prynadai* J. Popov; ventral view, × 17. Upper Jurassic, Southern Kazakhstan (Y. Popov, 1964).

antennae four-segmented, geniculate, much longer than head, with long first segment. Scutellum very small. Legs long; femur club-shaped apically; tarsus three-segmented; pretarsus with appendages. Length of body 6–12 mm (Fig. 668). Paleogene to Recent. One genus: *Berytinus* Menge*, 1856 from the Paleogene of Europe (Baltic amber).

Family PENTATOMIDAE Leach, 1815. Shield bugs

[nom. transl. Samuelle, 1819 (ex Pentatomidea Leach, 1815)]

Forewings demarcated into clavus, corium and membrane; clavus narrows toward apex, does not form a common junction behind scutellum, or this 224 junction very short; membrane with numerous veins. Head has form of shield, made up of clypeus and cheek plates; proboscis four-segmented; antennae five-segmented, much longer than head, on ventral side, base not visible from dorsal side. Meso- and metathorax complete; claws with appendages. Herbivores, rarely predators. Length of body 20 mm (Fig. 669). Paleogene to Recent. Numerous genera and species. In fossil form 10 genera from the Paleogene of Western Europe (Baltic amber) and North America, about 30 genera from the Neogene of Western Europe, Primorye province and North America and four genera from the Quaternary deposits of Western Europe and Trans-Caucasus.

Family CYDNIDAE Billberg, 1820

[nom. transl. Fieber, 1861 (ex Cydnidea Billberg, 1820)]
(Thyreocoridae Van Duzee, 1907)

(Y.A. Popov)

Forewings completely covering abdomen; corium almost triangular; membrane without veins. Second abdominal sternum completely or nearly completely covered by posterior margin of metathorax, only six tergites have visible abdominal rim. Tibia densely covered with spines; tarsus three-segmented. Length of body 3–20 mm (Fig. 670A, B). Live in soil at roots of plants. Paleogene to Recent. In fossil form two genera from the Paleogene of Western Europe and North America, about 10 genera from the Paleogene and Neogene of Western Europe and the North Caucasus, about five genera from the Neogene of Western Europe and North America and one genus from the Quaternary deposits of Trans-Caucasus.

Heteroptera Incertae sedis

(E.E. Bekker-Migdisova and Y.A. Popov)

Lygaenocoris J. Popov, 1961. Genotype—*L. prynadai* J. Popov, 1961; Upper Jurassic, Southern Kazakhstan (Karatau). Body elongate-oval. Head semicircular, short; proboscis reaching coxae of middle legs; thorax flat and broad; sides of metathorax posteriorly straight. Abdomen broad, somewhat

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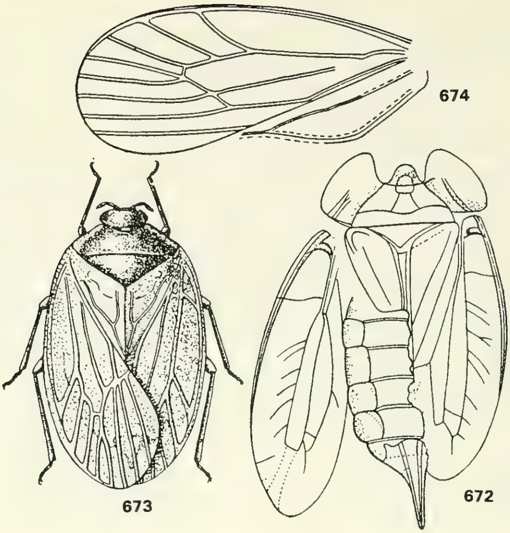
*Editor's note: Should be *Berytinus* Kirkaldy, 1900.



Figs. 672–674. Families Paraknightiidae and Actinoscytinidae.

672. *Paraknightia magnifica* Evans; general view, × 4.2. Upper Permian, Australia (Evans, 1943). 673. *Cicadocoris kuliki* Bekker-Migdisova; (reconstruction), × 9.6. Upper Triassic, Central Asia (Bekker-Migdisova, 1958). 674. *Olgamartynovia turamica* Bekker-Migdisova; forewing, × 18. Upper Triassic, Central Asia (Bekker-Migdisova, 1958).

shortened. Abdominal segments, except seventh, slightly narrow toward middle; sternite of seventh segment completely divided by sternal plate of eighth segment. Sternite of eighth segment very well developed, covers ninth segment. Length of body 5.6. mm (Fig. 671). Upper Jurassic of Southern Kazakhstan.

Family PARAKNIGHTIIDAE Evans, 1950

[Ipsviciidae (pars) Evans, 1953; non Ipsviciidae Tillyard, 1919]

(E.E. Bekker-Migdisova)

Forewing with a short, but wide embolium extending up to junction of R + M, without nodal furrow. Pronotum with well-developed paranotal expansions. In females ovipositor well developed (Fig. 672). Triassic of Australia. One genus: *Paraknightia* Evans, 1943.

Family ACTINOSCYTINIDAE Evans, 1956
(Cicadocoridae Bekker-Migdisova, 1958)

(E.E. Bekker-Migdisova)

Forewings leathery, without spotted ornamentation, fold back flat on dorsal side, meeting along a straight line, or distal part of one wing overlaps other, 225 posterior margin of anal area shifted upward; veins broad, often spread out, or absent at base; distal part of tegmen thinner, with closer veins, anterior margin thickened by broad, sclerotized C; R_1, R_2 and RS short, parallel and of equal length. Head small, narrower than anterior margin of pronotum, latter narrows toward head. Scutellum very large and triangular, with anterior margin equal to width of base of pronotum. Anal tube short. Upper Triassic to Lower Jurassic. Ten genera.

Cicadocoris Bekker-Migdisova, 1958. Genotype—*C. kuliki* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Forewing oval, with convex margin; M three-branched; M_{3+4} simple; base of CuA transformed into cross vein that with cross veins between M_{3+4}, CuA and bases of M_{3+4}, M_{1+2} and M_1 forms a complex arcuate line from apex of anal area to anterior margin of forewing. Length of forewing 4–6 mm (Fig. 673). Three species. Upper Triassic of Issyk-Kul province.

Olgamarlynovia Bekker-Migdisova, 1958. Genotype—*O. turanica* Bekker-Migdisova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian stage, Issyk-Kul). Tegmen oval; anterior margin convex; M three- or two-branched; M_{3+4} simple; cross vein $cua_1 + cua_2$ absent; CuA terminates on CuP. Length of forewing 3–5 mm (Fig. 674). Two species. Upper Trias of Issyk-Kul province.

Outside the USSR: *Archicercopis* Handlirsch, 1939; *Eocercopis* Handlirsch, 1939; *Cercoprisca* Handlirsch, 1939; *Cercopinus* Handlirsch, 1939; *Actynoscytina* Tillyard, 1926; *Heteroscytina* Evans, 1956; *Platyscytinella* Evans, 1956; *Triscytina* Evans, 1956.

In addition, the following genera belong to Heteroptera incertae sedis:

Shurabella Bekker-Migdisova, 1949. Genotype—*S. lepyroniopsis* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Forewings strongly sclerotized; anterior margin arcuately convex; venation absent except for R, present in form of furrow along entire length of tegmen, and CuP, in the form of a similar furrow that divides anal area. Scutellum small, triangular with drawn out, pointed apex. Length of forewing 3.5–4.9 mm (Fig. 675A, B). One species. Lower Jurassic of Central Asia.

Karataviella Bekker-Migdisova, 1949[1]. Genotype—*K. brachyptera* Bekker-Migdisova, 1949; Upper Jurassic, Chimkent province (Malm, Karatau). Forewing strongly sclerotized, lancet-shaped, not covering end of abdomen. Abdomen nine-segmented. Scutellum large, triangular, twice as wide as long,

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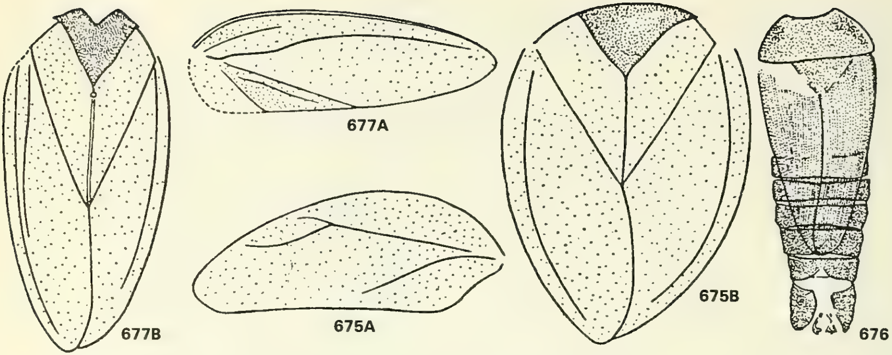
[1] According to recent data, genus *Karataviella* Bekker-Migdisova belongs to family Corixidae of aquatic Hemiptera (Yu.A. Popov).



Figs. 675–677. Heteroptera incertae sedis.

675. *Shurabella lepyroniopsis* Bekker-Migdisova; A—forewing, B – forewing and scutellum, × 17. Lower Jurassic, Central Asia (Bekker-Migdisova, 1949). 676. *Karataviella brachyptera* Bekker-Migdisova; dorsal view of forewing and parts of body, × 6.5. Upper Jurassic, Southern Kazakhstan (Bekker-Migdisova, 1949). 677. *Coleopteropsis dolickoptera* Bekker-Migdisova; A—forewing, B—forewing and scutellum, × 14. Lower Jurassic, Central Asia (Bekker-Migdisova, 1949).

with obtuse-angled apex; pro- and mesonotum broad, former twice as wide as it is long. Length of forewing 4.5–6.2 mm. Length of body 8–9 mm (Fig. 676). One species. Upper Jurassic of Kazakhstan.

226 *Coleopteropsis* Bekker-Migdisova, 1949. Genotype—*C. dolichoptera* Bekker-Migdisova, 1949; Lower Jurassic, Central Asia (Lower Lias, Schurab II). Forewings markedly sclerotized, with straight anterior margins; venation limited to R and CuP that are in form of longitudinal furrows. Scutellum longer than broad, with peculiar shape, many-sided, apex drawn out into a sharp point, anterior margin with triangular incision. Forewing 3.8–5 mm long (Fig. 677). One species. Lower Jurassic of Central Asia.

Outside the USSR: from the Upper Jurassic of Western Europe: *Scylacocoris* Handlirsch, 1906; *Hemipteron* Westwood, 1854; *Dimeropterum* Handlirsch, 1906; *Cimicidium* Westwood, 1854; *Galerucites* Oppenheim, 1888; *Anacoloptera* Handlirsch, 1906; *Ischyopteron* Oppenheim, 1888. Besides these genera and individual species from Upper Jurassic described of Western Europe as Cimicidae Westwood, 1854; Phillips, 1871; Brodie, 1845; Pentatomidae Brodie, 1845; Nepidae Westwood, 1854; ? *Cimex* Brodie, 1854; ? *Corita* Oppenheim, 1888; *Hydrometra* Brodie, 1845; *Velia* Brodie, 1845; *Kleidocerys* (= *Pachimerus*) Brodie, 1845; ? *Cimicidae priscus* Giebel, 1856; *Pachimerus zucholdi* Giebel, 1856; *Velia* ? *cormita* Weyenberg, 1879; *Protocorus ovalis* Heer, 1865; also about 10 genera from the Paleogene of Europe (Baltic amber) and the Paleogene of North America, and about 10 genera from the Neogene of North America.

SUPERORDER PSOCOPTEROIDEA. Booklice-like insects

(E.E'. Bekker-Migdisova and V.N. Vishnyakova)

Mouthparts of biting type, rarely of piercing type, or modified; usually with oral pump moved by thick muscles, point of attachment of these muscles reflected in markedly raised clypeus. Eyes small. Wings, if present, dissimilar, rarely almost similar; reduced or secondarily feather like (ptilopterous—with long hair-like fringe along margin) completely wingless individuals included; venation reduced; cross veins few. Permian to Recent. Phylogenetic affinities of superorder indicated with group of Lower Permian neopteran Archaescytinidae, close to booklice and Homoptera. Orders: Psocoptera, Perielytrodea, Anoplura, Mallophaga, Rhynchophthiraptera and Zoraptera; of these, first three known in fossil form. A representative of Anoplura (one species) is found in the Pleistocene deposits of Siberia.

The evolutionary history of Psocopteroidea is still not fully understood. Apparently, development of feeding (mycetophagy, saprophagy or parasitism) side by side with decrease in body size and shift toward cramped, covered living conditions (under bark, in soil, etc.) were major trends of evolution in this group. In some cases a 'communal' life style (as in Zoraptera), and parasitism on vertebrates developed.

Order PSOCOPTERA. Booklice

(Corrodentia, Copeognatha)

(E.E'. Bekker-Migdisova and V.N. Vishnyakova)

Two pairs of dissimilar, rarely similar, membranous wings, with thickened veins; sometimes wings markedly shortened or absent. SC disrupted, its distal part closes pterostigma, proximal part free or terminates on R; M and CuA fused at base or connected by short cross veins; CuP straight; anal area short. Head hypognathous, rarely prognathous; compound eyes developed; winged forms with three ocelli; posterior division of clypeus convex; labrum broad; mandibles of biting type; maxillae long, separate, lacinia like a scraper, galea soft. Legs of running type. Abdomen nine-segmented; ovipositor reduced. Frequently parthenogenetic. Feed on mycelium of fungi, Protococcal and Pleurococcal algae, lichens, different kinds of organic debris, rarely tissues of higher plants. Live in litter, under bark, on branches of trees and bushes, in cracks in stone walls, in nests and burrows of animals, in human dwellings and warehouses. Lower Permian to Recent. Three suborders: Permopsocida, Parapsocida, Eupsocida.

Suborder Permopsocida

227 Wings similar. In forewing SC long; pterostigma not sclerotized; RS two-branched; M with four branches; two anal veins. Head with flat clypeus. Tarsus five-segmented. Cerci present. Permian. Three families: Psocidiidae, Martynopsocidae, Permopsocidae.

Family PSOCIDIIDAE Tillyard, 1926

Forewing markedly elongated; SC long, arcuate, fused with R at base and distally; pterostigma not isolated. Two branches of RS, rarely three, often short; branches of M four or more; fork of CuA large, with width two or three times height; anal area short and narrow; two cross veins, r-rs and rs-m. Permian. Four genera.

Dichentomum Tillyard, 1926 (*Psocidium* Tillyard, 1926; *Chaetopsocidium* Tillyard, 1926; *Metapsocidium* Tillyard, 1926; *Pentapsocidium* Tillyard, 1926; *Permentomum* Tillyard, 1926 and *Parapsocidium* G. Zalessky, 1937). Genotype—*D. tinctum* Tillyard, 1926; Lower Permian, North America
228 (Kansas). Anterior margin of forewing straight; SC fused with R a little more basally than pterostigma; R_2, RS and M very long, diverge at basal one-fourth of wing; fork of RS with two short branches; one inter-radial cross vein r-rs present; branches of M number four. Length of forewing 4–5 mm (Figs. 678, 679). Seven species. Lower Permian of Urals and North America and Upper Permian of Arkhangelsk province.

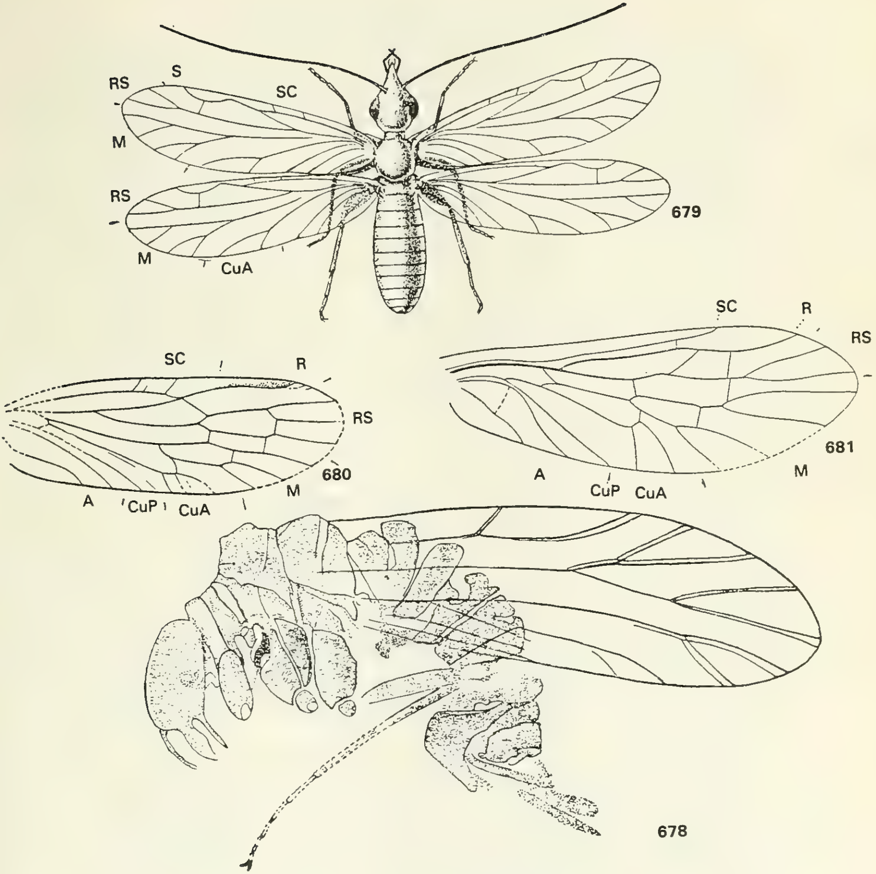
Outside the USSR: *Austropsocidium* Tillyard, 1935 and *Stenopsocidium* Tillyard, 1935. Because of poor preservation the systematic position of the genus *Megapsocidium* Tillyard, 1935, not clear.

Family MARTYNOPSOCIDAE Karny, 1930

(Dinopsocidae Martynov, 1928)

Forewing moderately broad, elongated; SC long, bent arcuately, united at base and distally with R; pterostigma not isolated; three long branches of RS; branches of M number three; stem of CuA long; fork of CuA small; anal area fairly wide and long; some cross veins form closed cells at distal part of wing. Upper Permian. One genus.

Martynopsocus Karny, 1930 (*Dinopsocus* Martynov, 1928; *Idelopsocus* M. Zalessky, 1929). Genotype—*Dinopsocus arcuatus* Martynov, 1928; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). In forewing, SC fused with R at midpoint of wing, has a row of short branches toward anterior margin; R straight, with slight bend in pterostigmal area; RS arises from R at basal one-third of the wing; its anterior branch and M_{3+4} branched. Length of forewing 11 mm (Fig. 680). Two species. Upper Permian of Arkhangelsk province and Urals.



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Figs. 678–681. Suborder Permopsocida.

678. *Dichentomum sojanense* Bekker-Migdisova; lateral view, × 11.5. Upper Permian, Arkhangelsk province (Bekker-Migdisova, 1961). 679. *D. tinctum* Tillyard; (reconstruction), × 10. Lower Permian, North America (Carpenter, 1933). 680. *Martynopsocus arcuatus* Martynov; forewing, × 5.5. Upper Permian, Arkhangelsk province (Martynov, 1928). 681. *Permopsocus congener* Tillyard; forewing, × 16. Lower Permian, North America (Tillyard, 1926).

Family PERMOPSOCIDAE Tillyard, 1926

Forewing moderately broad; SC long, straight and close to R; pterostigma isolated; branches of M number four; width of fork of CuA less than its height; anterior branch of CuA sharply bent; some cross veins seen between branches of R and M; cross vein m_{3+4}—cua always present (Fig. 681). Permian. Four genera.

Outside the USSR: *Progonopsocus* Tillyard, 1926; *Permopsocus* Tillyard, 1926 (*Ancylopsocus* Tillyard, 1926); *Lithopsocidium* Carpenter, 1932; *Orthopsocus* Carpenter, 1932.

Suborder Parapsocida

Winged or apterous. Wings dissimilar. Venation of forewings retains primitive features; anterior margin weakly costalized; costal area wide; veins straight, with long branches. Hindwings considerably shorter than forewings, with reduced venation; two anal veins, free or united at apex into a common stalk, or one anal vein terminating approximately at margin of wing. Head with convex clypeus. Tarsus usually three-segmented. Permian to Recent. 13 families: Surijocopsocidae, Lophioneuridae, Zygopsocidae, Pachytroctidae, Sphaeropsocidae, Liposcelidae, Amphientomidae, Lepidopsocidae, Empheriidae, Psyllipsocidae, Archipsyllidae, Archipsocidae, Psoquillidae; only last with no known fossil representatives.

Family SURIJOKOPSOCIDAE Bekker-Migdisova, 1961

Forewings broaden sharply at distal part, transparent; veins close; anterior margin straight and slightly thickened; SC long, straight, close to R + M, but weak; at base of wing distinct basal cell (B) bordered by thick segments of R + M, CuA (up to bend toward M), base of M (up to its sharp bend at right-angle) and cross vein m-cua; M with five short branches; anal area markedly narrow. Upper Permian. One genus.

Surijokopsocus Bekker-Migdisova, 1961. Genotype—*S. radtshenkoi* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). In forewing basal cell open, four-sided, with narrow base; costal area broadened at base, slightly thickened; RS parallel to R; M branches little more distally than midpoint of tegmen; M_5 independent; basal part of CuA forms small bend toward base of M, from which cross vein m-cua takes off; stalk of CuA very short; fork of CuA two or three times wider than high; anal area very narrow, as in specialized forms adapted for flight. Length of forewing about 9 mm (Fig. 682; Pl. XVI, Fig. 1). One species. Upper Permian of Kuznetsk basin.

Family LOPHIONEURIDAE* Tillyard, 1921

(Cyphoneuridae Carpenter, 1932; Zoropsocidae Tillyard, 1935)

Forewings transparent, gently narrowing at distal part, or lancet-shaped; SC free, short, terminates at C more basally than midpoint along wing, rarely, absent; R simple; RS markedly bent with long bifurcation; branches of M always
230 number two; CuA simple, more or less bent at distal part or with weak posterior branch, fused with CuP at base, or connected to it by a sloping vein (bend of CuA at base), or it is free and runs parallel to base of M and descends toward R + M; basal cell in many species isolated. Hindwings two-thirds length of forewings; SC absent; R_{1+2} almost straight. Pronotum small, cylindrical; mesonotum with well-developed sclerites; metanotum considerably weaker. Permian to Triassic. Ten genera.

Lophioneurodes Bekker-Migdisova, 1953. Genotype—*L. sarbalensis* Bekker-Migdisova, 1953; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala). Forewing narrow, long; fork of RS longer than that of M; CuA almost straight, retaining very weak base, connected with CuP; crossvein r + m–cua distinct, long, therefore it looks as if CuA has lost its base and branches off from R + M. Length of forewing 3 mm (Fig. 683). One species. Lower Permian. Kuznetsk basin.

Zoropsocus Tillyard, 1935. Genotype—*Z. delicatulus* Tillyard, 1935; Upper Permian, Australia. Forewing narrow, long, with rounded apex; pterostigma pointed; bifurcation of RS longer than that of M; CuA not fused with M, but connected to it by a more or less short cross vein, or in contact with its base, demarcating basal cell; anal area narrow, long, triangular in form. Length of forewing 1.8–3 mm (Fig. 684; Pl. XVI, Fig. 2). Four species. Upper Permian of Kuznetsk basin and Australia.

Surijokocypha Bekker-Migdisova, 1961. Genotype—*S. surijokovensis* Bekker-Migdisova, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Forewing at distal part asymmetrically broad; membrane thin; pterostigma at base; costal area narrow and long; R bent at base and runs parallel to anterior margin distally; fork of RS shorter than fork of M. Length of forewing 1.6–1.8 mm (Fig. 685). One species. Upper Permian of Kuznetsk basin.

Vitriala Bekker-Migdisova, 1961. Genotype—*V. nigriapex* Bekker-Migdisova, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing transparent, with wrinkled membrane; veins free; R bent at distal part toward anterior margin of wing; RS with a long fork; M almost straight without bifurcation; CuA slightly bent; anal area narrow. Length of forewing 3.5. mm (Fig. 686). One species. Lower Permian of Kuznetsk basin.

Psococicadellopsis Bekker-Migdisova, 1961. Genotype—*P. primitiva* Bekker-Migdisova, 1961; Upper Triassic, Issyk-Kul province (Rhaetian stage,

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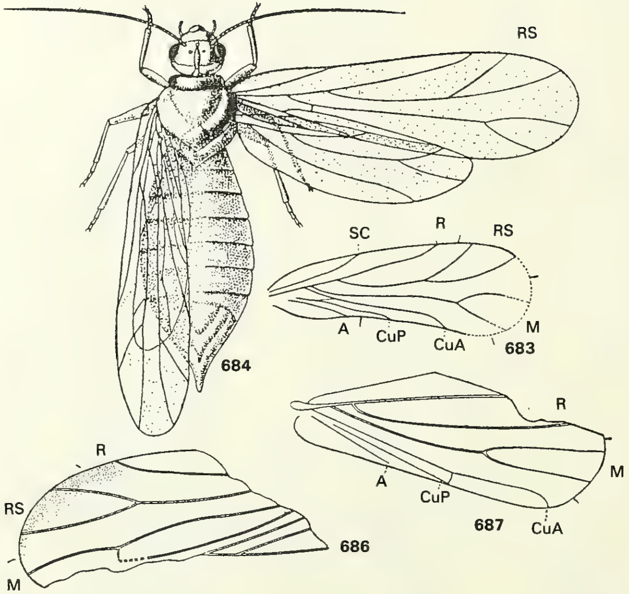
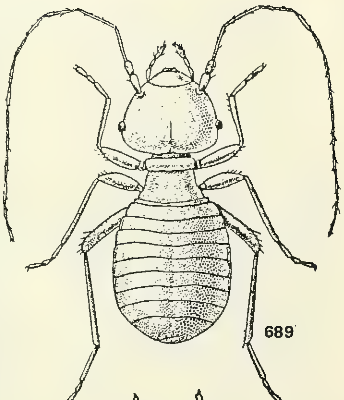
*Editor's note: In a 1981 paper Vishniakova showed these insects to be thrips.

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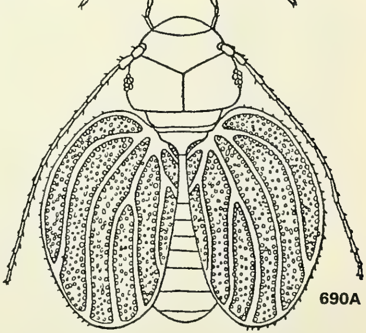
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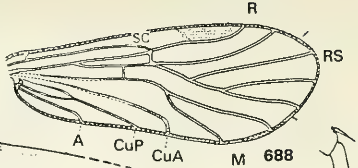

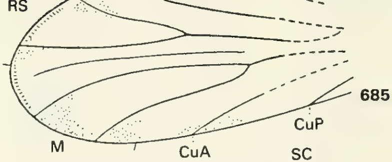

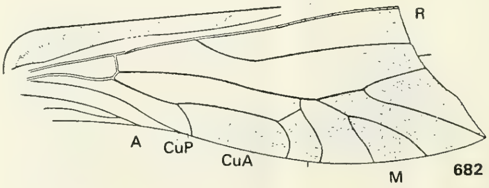

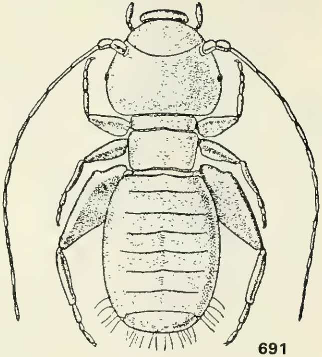

Figs. 682–691. Suborder Parapsocida.

682. *Surijokopsocus radtshenkoi* Bekker-Migdisova; forewing, × 10.7. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 683. *Lophioneurodes sarbalensis* Bekker-Migdisova; forewing, × 15. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1953). 684. *Zoropsocus tomiensis* Bekker-Migdisova; (reconstruction), × 20. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1953). 685. *Surijokocypha surijokovensis* Bekker-Migdisova; forewing, × 33.7. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 686. *Vitriala nigriapex* Bekker-Migdisova; forewing, × 15.2. Lower Permian, Kuznetsk basin (Bekker-Migdisova, 1961). 687. *Psococicadellopsis primitiva* Bekker-Migdisova; forewing, × 32. Upper Triassic, Central Asia (Bekker-Migdisova, 1961). 688. *Zygopsocus permianus* Tillyard; forewing, × 11.5. Upper Permian, Australia (Tillyard, 1935). 689. *Palaeotroctes succinicus* Hagen; dorsal view, × 7. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 690. *Sphaeropsocus kunowi* Hagen; A—dorsal view, × 62; B—tarsus of middle leg, × 300. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 691. *Liposcelis atavus* Enderlein; dorsal view, × 50. Paleogene, Europe (Baltic amber) (Enderlein, 1911).

Issyk-Kul). In forewing SC absent; R + M and R present as one straight markedly thickened vein; RS without bifurcation; M has a long bifurcation; CuA free at base, neither fused with nor connected by cross vein with M, bent at distal part, with indistinct posterior branch of fork; CuP weak. A distinct; anal area long. Length of forewing 1.8–2 mm (Fig. 687). One species. Upper Triassic of Issyk-Kul province.

Outside the USSR: *Cyphoneura* Carpenter, 1932; *Cyphoneurodes* Bekker-Migdisova, 1953; *Lophioneura* Tillyard, 1922; *Lophiocypha* Tillyard, 1935; *Austrocypha* Tillyard, 1935.

Family ZYGOPSOCIDAE Tillyard, 1935

Forewings membranous, with thick veins; SC long, fused with R at distal part; pterostigma weakly sclerotized; RS simple, fused with M at base of CuA; fork of CuA narrow and long; cross vein r-m present; CuP bent at distal part; two anal veins. Length of forewing 4.7 mm (Fig. 688). Upper Permian of Australia. One genus.

Family PACHYTROCTIDAE Enderlein, 1903

[nom. transl. Pearman, 1936 (ex Pachytroctinae Enderlein, 1903)]

Apterous or winged, with reduced venation; only two or three longitudinal veins preserved. Antennae 15-segmented. Tarsus three-segmented, femur thin. Body short and convex. Paleogene to Recent. Subfamilies: Pachytroctinae, Tapinellinae, latter not known in fossil form.

Subfamily Pachytroctinae Enderlein, 1905

Apterous forms.* Meso- and metathorax divided by suture. Integument ornamented. Length of body 0.6–1.4 mm (Fig. 689). Paleogene to Recent. Three genera, of which one from the Paleogene of Europe (Baltic amber).

Family SPHAEROPSOCIDAE Menon, 1942

Forewings shortened, elytra-like, hemispherical, ornamented. Hindwings reduced. Antennae 15-segmented. Tarsus three-segmented. Length of body 0.8 231 mm (Fig. 690). Paleogene to Recent. One Recent genus also from the Paleogene of Europe (Baltic amber).

Family LIPOSCELIDAE Enderlein, 1911

(Troctidae Kolbe, 1882)

Apterous forms*. Pronotum broad; meso- and metanotum fused. Antennae 15-segmented. Femurs of posterior legs stout. Body elliptical or egg-shaped,

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*Editor's note: Winged females are known for most of the genera.

dorsoventrally flattened. Tarsi three-segmented. Length of body 1–2 mm (Fig. 691). Paleogene to Recent. Three Recent genera, of which one is also known from the Paleogene of Europe (Baltic amber) and from Africa (copal).

Family AMPHIENTOMIDAE Enderlein, 1903

Forewings and body covered with scales, or forewings covered with microtrichia; SC more or less short; pterostigma not sclerotized; M bears three branches; fork of CuA short; posterior branches of CuA shorter than its stalk; anterior branch of CuA not connected with M by cross vein; two anal veins; A_1 comes into contact with CuP at apex; A_2 free; rarely, A_1 and A_2 fused distally. Segments of antennae number 13. Pronotum not visible from dorsal side, or poorly visible. Tarsus three-segmented. Paleogene to Recent. Three subfamilies: Amphientominae, Electrentominae, Tineomorphinae, last not known in fossil form.

Subfamily Amphientominae Enderlein, 1903

Forewings and body covered with scales which are truncated at end, or bear two denticles; SC straight; anal veins separate from one another, rarely close, but never fused to form one stalk. Pronotum not visible from dorsal side. Claws of tarsus with two teeth. Length of forewing 2–4 mm (Fig. 692). Paleogene to Recent. About 10 tropical genera in Recent fauna, of which only one genus is from the Paleogene of Europe (Baltic amber).

Subfamily Electrentominae Enderlein, 1911

Wings partly or completely covered with microtrichia; scales absent; SC forms short curve in forewing, with distal end terminating on R + M; ends of A_1 and A_2 fused. Pronotum very short, flat, rounded, only rarely visible from dorsal side. Claws of tarsus with one tooth-like projection. Length of forewing 2.2 mm (Fig. 693A, B). Two genera in the Paleogene of Europe (Baltic amber).

Family LEPIDOPSOCIDAE Enderlein, 1903
(Lepidillidae Ribaga, 1905)

Wings and body covered with hair-like setae or scales. In forewing SC long; branches of M number three; branches of M and CuA long; fork of CuA very long and narrow; CuA_2 two or three times longer than stem of CuA. One anal vein fused with CuP toward apex. Segments of antennae number from 21 to 47. Pronotum seen from above as a narrow belt. Tarsus three-segmented. Jurassic to Recent. Five subfamilies: Perientominae, Thylacinae, Asientominae, Echinopsocinae, Lepidopsocinae. Only last two found in Recent fauna*.

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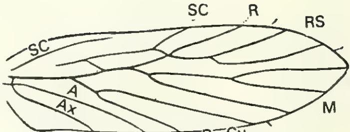
*Editor's note: Perientominae and Thylacinae also—as indicated under those subfamilies—in Recent fauna.



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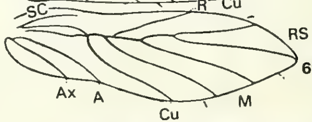

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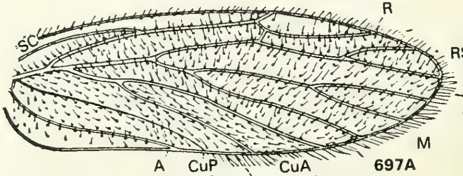

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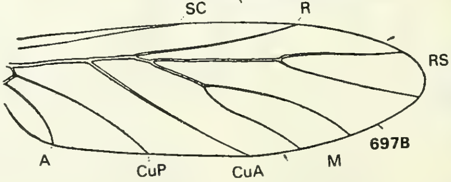

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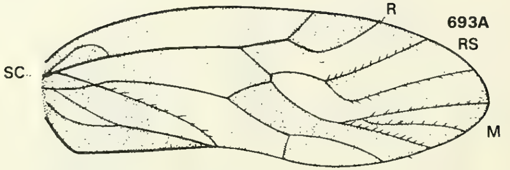

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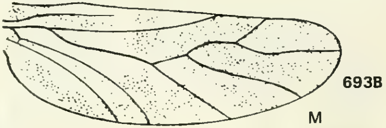

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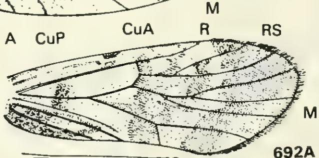

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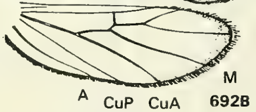

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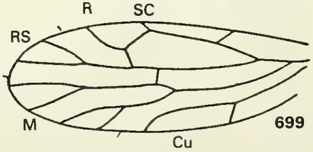

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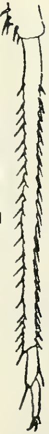

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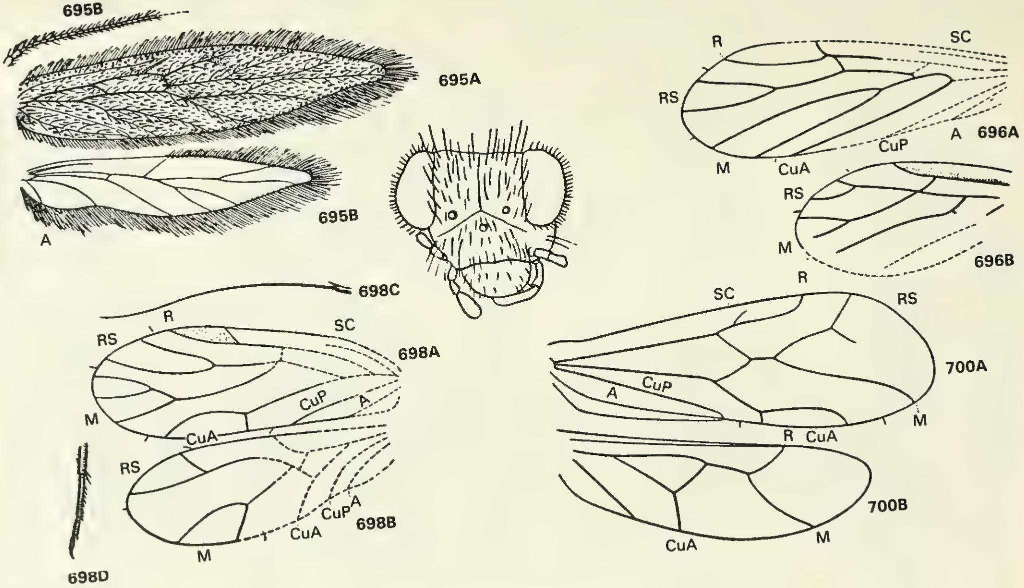

Figs. 692–700. Suborder Parapsocida.

692. *Amphientomum paradoxum* Pictet; A—forewing, B—hindwing, × 13.5. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 693. *Electrentomum klebsianum* Enderlein; A—forewing, B—hindwing, × 29, C—hindleg, × 150. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 694. *Perientomum ceylonicum* Enderlein; A—forewing, B—hindwing, × 20. Recent (Enderlein, 1906). 695. *Thylacella eversiana* Enderlein; A—forewing, B—hindwing, C—antenna, D—head, × 41.4. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 696. *Asientomum praecox* (Martynov); A—forewing, B—hindwing, × 26.2. Upper Jurassic, Southern Kazakhstan (Martynov, 1926). 697. *Trichempheria villosa* Hagen; A—forewing, B—hindwing, × 36, C—hindleg, × 100. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 698. *Psyllipsocus banksi* Cockerell; A—forewing, B—hindwing, C—antenna, × 30.5; D—tarsus, × 100. Burma, amber (Cockerell, 1916). 699. *Archipsylla turanica* Martynov; forewing, × 11.8. Upper Jurassic, Southern Kazakhstan (Martynov, 1926). 700. *Archipsocus puber* Hagen; A—forewing, B—hindwing, × 28.7. Paleogene, Europe (Baltic amber) (Enderlein, 1911).

Subfamily Perientominae Kolbe, 1884

[nom. transl. Enderlein, 1903 (ex Perientomini Kolbe, 1884)]

Wings and body covered with scales. Apices of both pairs of wings drawn out. Setae sometimes found along anterior margin of forewing. Two cross veins between R and M. Hindwing with a narrow closed cell between R + M and CuA; R_1 arises between branches of M. Length of forewing 2—3 mm (Fig. 694). Neogene to Recent. About 10 tropical genera in Recent fauna, of which two are also from copal of India and Africa.

Subfamily Thylacinae Enderlein, 1903

No scales on body or wings. Forewing sometimes has setae along margin. Apices of both pairs of wings sharply pointed. In forewing two r-m cross veins. Hindwing with narrow closed cell between M and CuA. Length of forewing 1.6 mm (Fig. 695A, B). Quaternary to Recent. Some tropical genera in Recent fauna, of which two are also from copal of Africa.

Subfamily Asientominae Martynov, 1926

[nom. transl. Bekker-Migdisova, 1961, hic (ex Asientomidae Martynov, 1926)]
(Lithentomidae Martynov, 1926; Lithopsocidae Karny, 1930)

232 Apex of both pairs of wings rounded. In forewing, distal part of SC partly fused with R; basal part of R straight, and distal part arcuate; weakly sclerotized pterostigma; RS with small fork; M with two branches; stalk of M short; CuA short, does not branch; anal area narrow and long. In hindwing RS and M form small forks; CuA simple. Jurassic. One genus.

Asientomum Martynov, 1926 (*Lithentomum* Martynov, 1926, nec. Scudder, 1867; *Lithopsocus* Karny, 1930). Genotype—*Lithentomum praecox* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). In forewing costal area narrow; R terminates at apex of wing; RS begins a little more basally than midpoint of wing, bent while cross veins r-rs and rs-m_{1+2} fan out; M branches more basally than midpoint of wing. In hindwing distal part of R indistinct; base of RS vertical; M fused with RS for some distance; CuA simple and straight. Length of forewing 2 mm (Fig. 696). One species. Upper Jurassic of Kazakhstan.

Family EMPHERIDAE Enderlein, 1911

Wings with hair-like setae. Apices of both pairs of wings more or less rounded. In forewing SC weakly convex, terminates on R; CuA two-branched. CuP and A not connected at apex. Antennae many segmented, with variable number of segments. Paleogene to Recent. Two subfamilies: Empheriinae and Tapinellinae*; latter not known in fossil form.

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*Editor's note: This subfamily was already dealt with under Pachytroctidae, pg. 324, where it is placed by most modern authors.

Subfamily Empheriinae Kolbe, 1884

[nom. transl. Enderlein, 1908 (ex Empheriidae Kolbe, 1884)]

Forewing with one cross vein, r-rs; fork of CuA long, narrow, with short stalk. In hindwing RS starts at midpoint between bases of M and CuA; bases of R, M and CuA fused. Length of forewing 2–4 mm (Fig. 697). Paleogene to Recent. Two* genera in Recent fauna: *Empheria* Hagen, 1856 and *Bebiosis* Enderlein, 1911, and one extinct genus from the Paleogene of Europe (Baltic amber).

Family PSYLLIPSOCIDAE Kolbe, 1884

[nom. transl. Enderlein, 1903 (ex Psyllipsocini Kolbe, 1884)]

Wings and body not covered with scales; M with two or three branches; SC long, disrupted at distal part, fused with R; CuP and A connected at apex or are close. 22 to 25 segments in antenna. Pronotum distinctly visible from above; meso- and metanotum distinctly separate; tarsus three-segmented. Length of forewing 2.5–5.5 mm (Fig. 698). Neogene to Recent. Four genera in Recent fauna, of which one Recent genus is also known from the Paleogene of South Asia (Burmese amber).

Family ARCHIPSYLLIDAE Handlirsch, 1925

Forewings more or less elongated; SC not free, fused basally with C and distally with R; R distally bent; borders distinct, broad pterostigma; RS long, with small fork, starts at base of wing; M bears four branches; CuA gently inclined; anal area reduced. Jurassic. One genus.

Archipsylla Handlirsch, 1907. Genotype—*A. primitiva* Handlirsch, 1967; Lower Jurassic, Germany. Forewing oval, elongated, with length three times width; distal free part of SC short; RS starts in basal one-fourth of the wing; R very long, runs obliquely, toward anterior margin of wing, angularly bent distally; M branches at midpoint of the wing; stem of CuA long, fork wide; CuA_2 short. Length of forewing 4–5 mm (Fig. 699). Two species from the Lower Jurassic of Western Europe and the Upper Jurassic of Kazakhstan.

234 Family ARCHIPSOCIDAE** Enderlein, 1903

[nom. transl. Pearman, 1936 (ex Archipsocinae Enderlein, 1903)]

Males apterous. Wing membrane of females covered with hair-like setae; venation poor. In forewing M fused with RS for some distance; fork of CuA independent and flat. In hindwing CuA does not branch. Antenna with 13 segments. Prothorax clearly seen from above; tarsus two-segmented, both in

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* Editor's note: Neither of these genera is in Recent fauna; only known from Baltic amber.

**Editor's note: This family is clearly close to the families, placed by these authors and others in Suborder Eupsocida and should be placed there.

nymphs and adult. Length of forewing 1.5–1.6 mm (Fig. 700). Paleogene to Recent. Three* Recent genera, of which one also from the Paleogene of Europe (Baltic amber).

Suborder Eupsocida

Wings dissimilar; hindwings shorter than forewings, with poor venation. Fork of CuA short; branches of CuA of unequal length; CuA_1 considerably longer than CuA_2; one anal vein. Antennae 13 segmented; tarsus two or three segmented. Paleogene to Recent. About 20 families**, of which only the following found in fossil form: Philotarsidae, Elipsocidae, Epipsocidae, Caeciliidae, Peripsocidae, Psocidae.

Family PHILOTARSIDAE Pearman, 1936

Both pairs of wings with hair-like setae. Anal margin of forewings covered with two rows of hair-like setae; R and M of both pairs of wings fused for some distance. Tarsi of adults three-segmented. Females with three pairs of gonapophyses. Length of forewing 1.5–3.5 mm (Fig. 701). Paleogene to Recent. Few Recent genera, of which one is also known from the Paleogene of Europe.

Family ELIPSOCIDAE Pearman, 1936

Margins of forewings and veins covered with hair-like setae. Hindwings not covered with hair-like setae, or only margin of wing between branches of RS covered with hair-like setae; R and M of forewings fused for some distance; R and M of hindwings connected by cross vein r-m. Tarsi of adults two or three segmented. Females with three pairs of gonapophyses. Length of forewing 1.8–3.7 mm (Fig. 702A, B). Paleogene to Recent. About five genera in Recent fauna, of which one also known from the Paleogene of Europe (Baltic amber).

Family EPIPSOCIDAE Pearman, 1936

Winged or apterous. If present, both pairs of wings, hairy. R and M of forewing connected by cross vein r-m. R and M of hindwing fused for some distance. Females with one or two pairs of gonapophyses. Paleogene to Recent. Three subfamilies: Epipsocinae, Neurostigminae, Gojinae; last two not known in fossil form.

Subfamily Epipsocinae Roesler, 1940

Anal vein of forewing without hair-like setae. Females apterous. Lacinia with eight to 10 apical teeth. Outer gonapophyses in females absent. Length of

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*Editor's note: Four Recent genera are now known.

**Editor's note: Found as fossils more recently: Trichopsocidae, Ectopsocidae, Myopsocidae, Ptiloneuridae.

forewing in male 5 mm (Fig. 703). Paleogene to Recent. One genus in Recent fauna, also from the Paleogene of Europe (Baltic amber).

Family CAECILIIDAE Kolbe, 1884

Wings hairy, occasionally shortened in females. R and M of both pairs of wings fused for some distance. Tarsus two-segmented. Outer gonapophyses of females reduced. Length of forewing 2–4 mm (Figs. 704, 705). Paleogene to Recent. Numerous genera in Recent fauna, of which four also known from the Paleogene of Europe (Baltic amber), two of these extinct.

Family PERIPSOCIDAE Kolbe, 1882

[nom. transl. Pearman, 1936 (ex Peripsocinae Kolbe, 1882)]

Wings occasionally shortened in females, without hair-like setae. R and M of forewings fused at one point or over some distance; CuA without branches. Tarsus two-segmented. Females with one to three pairs of gonapophyses. Length of forewing 2–4 mm (Fig. 706). Paleogene to Recent. Two genera, of which one known from the Paleogene of South Asia (Burmese copal).

Family PSOCIDAE Leach, 1815

[nom. transl. Stephens, 1836 (ex Psocida Leach, 1815)]

Wings sometimes shortened in females, hairless. R and M of forewings fused at one point or over some distance, or connected by cross vein r-m; CuA_1 in contact with M most of the way or connected by cross vein $m\text{-}cua_1$. Tarsus two-segmented. Three pairs of gonapophyses in female. Length of forewing 2–7 mm (Fig. 707). Paleogene to Recent. Numerous genera in Recent fauna, of which two are also from the Paleogene of Europe (Baltic amber).

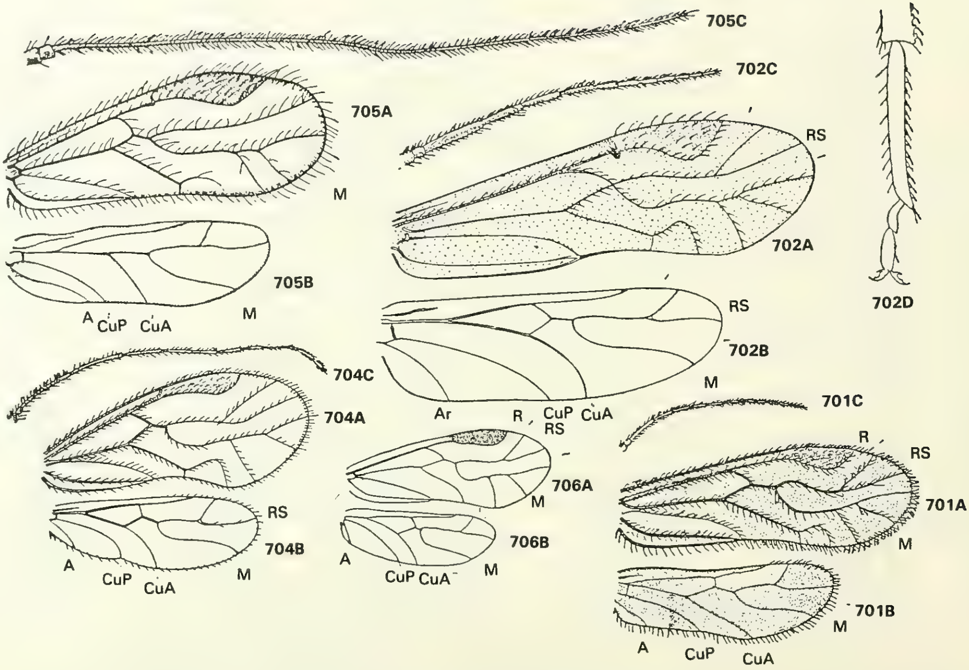
236 Psocoptera Incertae sedis

A few fossils belong to this order, which defy precise identification. The forms are: *Parapsocus* Scudder, 1890 from the Paleogene of Europe (Baltic amber) and from the Oligocene of North America; and *Lithentomum* Scudder, 1867 from the Oligocene of North America.

Order PERIELYTRODEA

(A.G. Sharov)

Wings lie along sides of body when at rest. Forewings oval, like tegmina: thick, with ornamentation in the form of small network; longitudinal veins in form of convex ribs forming constituent part of network; cross veins absent; costal area short, triangular; anal area located symmetrically to it, demarcated from rest of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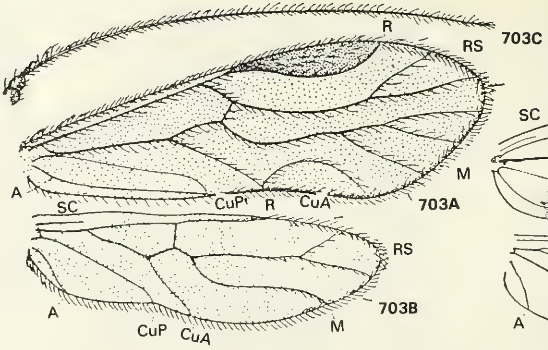

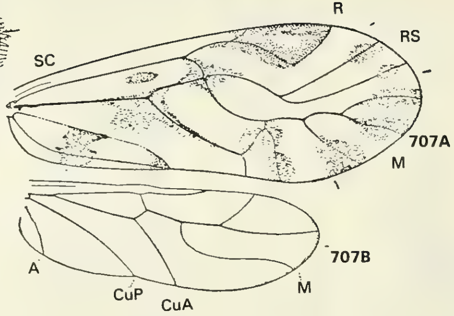

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Figs. 701–707. Suborder Eupsocida.

701. *Philotarsus antiquus* Kolbe; A—forewing, B—hindwing, × 25. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 702. *Elipsocus abnormis* Hagen; A—forewing, B—hindwing, C—antenna, × 38; D—hindtarsus, × 90. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 703. *Epipsocus ciliatus* Pictet and Hagen; A—forewing, B—hindwing, C—antenna, × 16.4. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 704. *Caecilius debilis* Pictet and Hagen; A—forewing, B—hindwing, C—antenna, × 16.4. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 705. *Palaeopsocus tener* Hagen; A—forewing, B—hindwing, C—antenna, × 41.8. Paleogene, Europe (Baltic amber) (Enderlein, 1911). 706. *Peripsocus phaeopterus* Stephens; A—forewing, B—hindwing, × 18.6. Recent (Enderlein, 1927). 707. *Psocus picteti* Enderlein; A—forewing, B—hindwing, × 24.2. Paleogene, Europe (Baltic amber) (Enderlein, 1911).

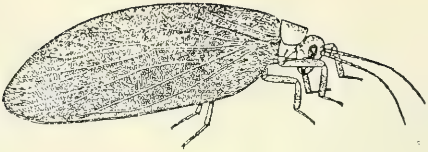

Fig. 708. Family Perielytridae.

Perielytron mirabile G. Zalessky (reconstruction). Lower Permian, Urals (original drawing).

wing by a deep furrow. Hindwings of roughly same size and shape as forewings, but thin and membranous, with a few veins.

Head hypognathous; mouth parts of chewing type; antennae 12–14 segmented, with diameter sharply diminishing in distal part; segments armed with short setae on apical part. Pronotum small, saddle-shaped; legs short; tibiae of fore- and hindlegs ornamented with ridges; tarsus three-segmented. Abdomen short and cylindrical; terga of abdomen without lateral expansions. Apparently with short cerci and short ovipositor. Permian. One family: Perielytridae.

Family PERIELYTRIDAE G. Zalessky, 1948

Forewing: SC sharply bent at distal part, oriented parallel to anterior margin of wing; R similarly bent posteriorly, with a few short branches; RS branches at distal one-third of wing, anal area with one vein, which does not branch. Permian. One genus.

Perielytron G. Zalessky, 1948. Genotype—*P. mirabile* G. Zalessky, 1948; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing: RS with two or three branches, which lose characteristics of veins in distal part and merge into ornamental network of wing; M with two or three branches which similarly are lost amid wing network. CuA pectinate, with short branches. Length of forewing 7–8 mm (Fig. 708; Pl. XVI, Fig. 3)[1]. One species. Lower Permian of Urals.

SUPERORDER THYSANOPTEROIDEA. Thrip-like insects

(O.M. Martynova)

Body distinctly elongate. Mouthparts of piercing and sucking type, with unusual structure. Head distinctly opisthognathous, long, with small eyes; antennae short, with few bead-like segments. Wings narrow, long, almost perfectly

[1] In 1959 Sharov discovered two new impressions of *Perielytron*, from which a more detailed reconstruction of this insect was possible than was given in Y. Zalessky's work (1948).

similar, fringed with long hair-like setae: feather-winged character well-expressed; venation reduced; not more than two longitudinal veins.

Phylogenetic relationship uncertain. The exceptionally peculiar structure of thrips, in fact, throws doubt on their affinity with Paraneoptera, to which they are nevertheless more closely related than to any other insects. Permian to Recent. Order: Thysanoptera.

237 Order THYSANOPTERA. Thrips

Small insects (0.5–5 mm long). Wings fold flat on back; many apterous forms. Cross veins not more than five; long hairs fringe margin of wing. Small anal lobe occasionally observed on hindwings. Head with compound eyes and often with three ocelli; antennae longer than head, 13 (sic) segmented; mouthparts of piercing and sucking type, asymmetrical. Legs of running type; tarsus one-or two-segmented; plate between claws transformed into a bladder-like vesicle (adaption for attachment). Abdomen with 10 segments.

Inhabit various plants, flowers, leaves, inflorescences and decayed plant remains. Suck sap of plants (some are harmful), rarely predators. Permian to Recent. Suborders: Terebrantia, Tubulifera.

Suborder Terebrantia. Egg-laying thrips*

Winged forms. Forewings longer than hindwings. Forewings with one or two longitudinal veins; membrane covered with microscopic hair-like setae. Last abdominal segment in females with ovipositor. Male with last segment broad, rounded. Permian to Recent. Families: Permothripidae, Liassothripidae, Aeolothripidae, Heterothripidae, Thripidae, and Merothripidae.

Family PERMOTHRIPIDAE Martynov, 1935

Wings when folded, longer than abdomen. Head somewhat elongated. Pronotum narrows toward front, short, less than one-half of length of pterothorax; legs short. Permian. One genus.

Permothrips Martynov, 1935. Genotype—*P. longipennis* Martynov, 1935; Lower Permian, Perm province (Kungurian stage, Chekarda). Head small, tetragonal; antennae short, thick. Femur slightly swollen; tibia thin, longer than femur. Length of body about 3 mm (Fig. 709). One species. Lower Permian of Urals.

Family LIASSOTHRIPIDAE Priesner, 1949

Head narrow; antennae fine, seven or eight-segmented. Forefemora markedly broad; tibiae thin. Jurassic. One genus.

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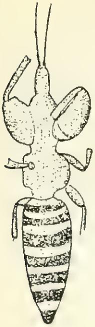
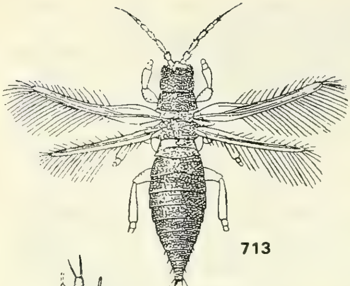
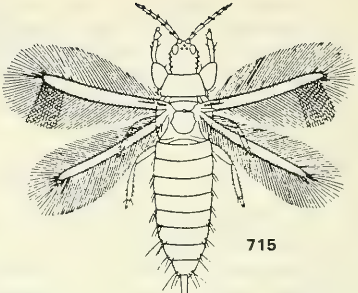
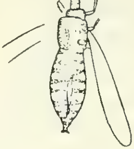
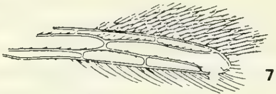
*Editor's note: A more correct common name would be 'thrips with ovipositors' since tubulifera also lay eggs.

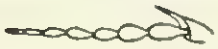












Figs. 709–715. Order Thysanoptera.

709. *Permothrips longipennis* Martynov; general view, × 8. Lower Permian, Urals (Martynov, 1935). 710. *Liassothrips crassipes* (Martynov); general view, × 18. Upper Jurassic, Southern Kazakhstan (Martynov, 1927). 711. *Archankothrips pugionifer* Priesner; A—forewing, B—antenna, × 50. Paleogene, Europe (Baltic amber) (Priesner, 1924). 712. *Protothrips speratus* Priesner; head and prothorax, × 40. Paleogene, Europe (Baltic amber) (Priesner, 1924). 713. *Heliothrips haemorrhoidalis* (Bouche); dorsal view, × 16.5. Recent, America (Russell, 1912). 714. *Praemerothrips hoodi* Priesner; antennae, × 135. Paleogene, Europe (Baltic amber) (Priesner, 1929). 715. *Phlaeothrips coriaceus* Haliday; dorsal view, × 20. Recent, Europe (Handlirsch, 1925).

Liassothrips Priesner, 1949. Genotype—*Mesothrips crassicornis**
238 Martynov, 1927; Upper Jurassic Chimkent province (Malm, Karatau). Wings not preserved. Abdomen narrows in basal and apical part. Length of body 2–2.5 mm (Fig. 710). One species. Upper Jurassic of Kazakhstan.

Family AEOLOTHRIPIDAE Haliday, 1836

Apex of forewing broadly rounded, with two longitudinal veins and three to five cross veins. Antennae nine-segmented. Ovipositor upturned (Fig. 711). Paleogene to Recent. Numerous genera in Recent fauna. Six genera from Paleogene of Europe (Baltic amber) and the Paleogene of Eastern America, of which four are extinct.

Family HETEROTHRIPIDAE Bagnall, 1912

Wings pointed. Forewings with two longitudinal veins; cross veins absent. Antennae nine, sometimes 10 segmented, third and fourth segments longer than

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*Editor's note: No species recorded as "*crassicornis*"; probably = *crassipes* Martynov, 1927.

the rest, conical. Ovipositor downturned. Second segment of anterior tarsus with claw-like appendage (Fig. 712). Paleogene to Recent. Few genera among Recent fauna, one extinct genus from the Paleogene of Europe (Baltic amber).

Family THRIPIDAE Stephens, 1829

Wings narrow and pointed; cross veins absent. Antennae six to eight segmented, last segment with spine-like hair. Ovipositor downturned (Fig. 713). Paleogene to Recent. Many genera among Recent fauna. Eight genera reported from the Paleogene of Europe, of which four are extinct.

Family MEROTHRIPIDAE Hood, 1912

Wings pointed, two longitudinal veins present, cross veins absent. Antennae prominent, eight-segmented, without pointed pencil at apex. Anterior and posterior femora markedly flattened. Ovipositor reduced (Fig. 714). Paleogene to Recent. One genus in Recent fauna and two genera from the Paleogene of Europe (Baltic amber), of which one is extinct.

Suborder Tubulifera. Thrips without ovipositors

Winged or apterous forms. Both pairs of wings of same length; marginal vein absent; longitudinal vein markedly reduced; no microtrichia on wing membrane. Last abdominal segment tube-like. Ovipositor absent. Paleogene to Recent. Family: Phloeothripidae.

Family PHLOEOTHRIPIDAE Haliday, 1836

Winged forms*. Antennae seven or eight segmented**. Maxillary palpus two-segmented. Middle coxae, directed sideways more than coxae of other legs. Last abdominal segment narrows to a tubular apex; width of the ninth segment slightly exceeds its length (Fig. 715). Paleogene to Recent. Many genera among Recent fauna. Seven genera from the Paleogene of Europe (Baltic amber) and the Paleogene of North America, of which five are extinct.

Paraneoptera Incertae sedis

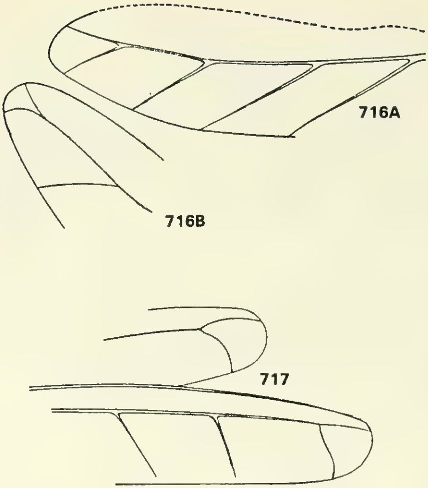
(E.E'. Bekker-Migdisova)

Family UNINERVIDAE Bekker-Migdisova, 1951

Wings almost similar, narrow, long, gradually taper, rounded; wing membrane very thin; one longitudinal vein in middle of wing, from which four posterior branches extend toward margin of wing. Size of wings small (2 to 3

*Editor's note: Apterous forms also known.

**Editor's note: Known to be 4–8-segmented.



239 Figs. 716–717. Paraneoptera incertae sedis.

716. *Uninervus zorapteroides* Bekker-Migdisova; A—forewing, B—hindwing, × 22. Upper Permian, Kuznetsk basin (Bekker-Migdisova, 1951). 717. *Mononeura angustipennis* Bekker-Migdisova; wings, × 24. Upper Triassic, Central Asia (Bekker-Migdisova, 1951).

mm). Structure of body not clear. Upper Permian to Upper Triassic. Two genera.

Uninervus Bekker-Migdisova, 1951. Genotype—*U. zorapteroides* Bekker-Migdisova, 1951; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Forewings lancet-shaped; anterior margin nearly straight; a longitudinal vein passes through middle of wing from which RS, M, CuA and CuP emerge at an angle; veins R and RS bifurcate, terminate on apex of wing.
239 Hindwings somewhat shorter than forewings, fork R-RS considerably short. Length of forewing about 3 mm (Fig. 716). One species. Upper Permian of Kuznetsk basin.

Mononeura Bekker-Migdisova, 1951. Genotype—*M. angustipiennis* Bekker-Migdisova, 1951; Upper Triassic, Issyk-Kul Province (Rhaetian, Issyk-Kul). Anterior margin of forewing convex in middle with straight C; central longitudinal vein raised toward anterior margin; M emerges from C almost at right angles; CuA oblique. Length of forewing 2–3 mm (Fig. 717). One species. Upper Triassic of Central Asia.

Cohort HOLOMETABOLA (OLIGONEOPTERA). Insects with complete metamorphosis or neoptera with reduced venation

(B.B. Rohdendorf)

Jugal area of wing very small, bears one simple non-branching vein. Venation and shape of wings vary widely: primarily different types of dissimilar wings, but many with almost similar wings. Mouthparts exhibit varied structure, mainly of biting type, usually modified in different groups into different types of sucking mouthparts. Characteristic post-embryonic development, with dormant stage, pupa, which does not feed and usually has poor movement. Early instars in form of larvae, which have distinctly different organization than adult insect organization: in their structure are observed larval adaptations to suit living conditions that are almost always different from those of adult forms. Lower Carboniferous to Recent. Four superorders: Coleopteroidea, Neuropteroidea, Mecopteroidea, Hymenopteroidea.

The first representative of the cohort (the scorpion fly *Metropator pusillus* Handlirsch), which was discovered in one of the most primitive faunal complexes of the Lower Carboniferous of North America, has been little studied so far and is known only from a poorly preserved wing impression. We first come across insects with complete metamorphosis in the Permian. These are the numerous and varied Mecoptera, Coleoptera and Neuroptera. Other Lower Permian representatives have been found of groups that attained noteworthy diversity of development only in the Upper Permian. The beginning of the Mesozoic marked the appearance of the Diptera in the Triassic and Hymenoptera in the Lower Jurassic. During the Jurassic, insects with complete metamorphosis exhibit maximum range of variation and occupy a dominant place among all the faunal complexes both in number of taxa and quantity of individuals. The phylogenetic relationships of this cohort with the others are not quite clear to this day. Relationships of individual superorders are currently outlined in a general way. Primitive mecopteroides like the Lower Permian Protomecoptera are distinctly related to Neuroptera and hence are believed to be probably derived from them. Ancestral forms of Neuroptera and Coleoptera are not distinct. Absence of data on primitive fauna and the profound differences among these superorders cast doubt on their affinity.

The relationship of Hymenoptera with other holometabolous insects, such as Neuroptera, is clearer. A direct relationship of Hymenoptera with the order Mecoptera has also been suggested, but this is ruled out by the absolutely different kind of specialization of flight mechanism (similar to early Diptera) and the anatomical peculiarities of Hymenoptera. On the whole, the evolution

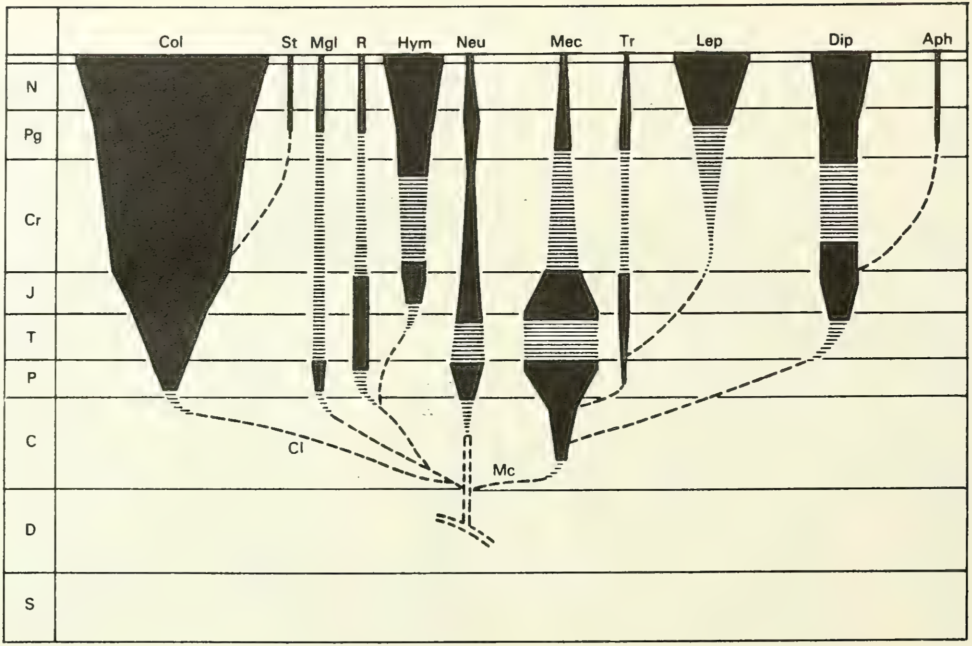


Fig. 718. Scheme of phylogenetic relationship among orders of insects showing complete metamorphosis (Holometabola).

The period of emergence, growth and distribution of the individual orders has been superimposed on a geochronological scale. Aph—Aphaniptera, Col—Coleoptera, Dip—Diptera, Hym—Hymenoptera, Lep—Lepidoptera, Mec—Mecoptera, Mgl—Megaloptera, Neu—Neuroptera, R—Raphidioptera, St—Strepsiptera, Tr—Trichoptera, Cl—Coleopteroidea, Me—Mecopteroidea (Rohdendorf et al., 1961).

of holometabolous insects was determined by perfection of ontogeny. During the process of complete metamorphosis the larvae thrive under conditions radically different from those of the adult forms. All these factors helped to perfect complete metamorphosis and gave these insects the edge in finding the best conditions for their peak development.

Figure 718 shows the phylogenetic relationships within cohort Holometabola.

SUPERORDER COLEOPTEROIDEA. Beetle-like insects

Sharp dissimilarity between two pairs of wings. Forewings transformed into thick covers (elytra) which do not beat during flight. Occasionally forewings almost completely reduced. Venation of forewings imperceptible in most cases, rarely seen as strong parallel veins with few branches. Hindwings 241 membranous with distinct venation, strongly costalized; form main organs of flight. Mouthparts of biting type with primitive structure modified showing reduction in various degrees. Larvae campodeiform, rarely eruciform, with prominent head, three pairs of legs and several spiracles. They live in soil, in bodies of water, in tissues of plants and decaying matter, and rarely, live independently on plants or as parasites on various animals. Lower Permian to Recent. Two orders: Coleoptera, Strepsiptera.

The phylogenetic relationships of the Coleopteroidea with other superorders are still not clear. The Coleoptera are the most isolated group among all holometabolous insects. They are characterized by a peculiar evolutionary trend—the appearance of an extreme form of protective covers formed by the transformed wings and the entire body. Similar adaptations are widely observed during the evolution of other cohorts of Neoptera, such as the Polyneoptera (Blattodea, Dermaptera and some others) and Paraneoptera (particularly Heteroptera). But, in the Holometabola protective wings are almost exclusively developed in Coleoptera. The appearance of protective wings in holometabolous insects indicates the extreme usefulness of this adaptation in the evolution of these insects, which are noted for their great variety and distribution. Present day Coleoptera are the most varied and most widely distributed order among all insects.

Order COLEOPTERA. Beetles

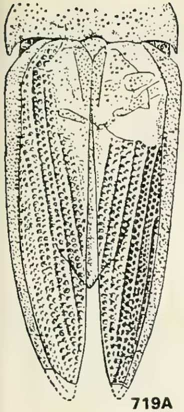
(B.B. Rohdendorf and A.G. Ponomarenko)

The thickened forewings come precisely in contact with each other at their anal margins, covering the metanotum, the upper surface of abdomen and the membranous hindwings. The mouthparts are of the biting type. The eyes usually are not large. The thoracic region is large; the prothorax with sharply isolated notum; the mesothorax is not large, and is fused with the metathorax to form a large sternal region. The abdomen consists of a varying number of segments and lacks long appendages. Their development involves complete metamorphosis. The larvae are well-defined, with a differentiated head and, usually, three pairs of thoracic legs; with cerci-like appendages, but no analogous processes at the end of the abdomen. The habitat and life history of the larvae vary. Feeding in beetles is very diverse: predation and parasitism, feeding on decomposing animal and plant matter, or primarily herbivorous. Characteristics used for differentiating the higher taxa such as families and superfamilies include the peculiarity of the venation of the hindwings, segmentation of the abdomen, structure of the legs, thoracic divisions and antennae, and the morphology of the developmental stages. The genera and species are characterized by structural details of the most variable parts of the body and organs. It should be noted that little use is made of the structure of the elytra in systematics. This poses problems when fossil Coleoptera are studied, since they are primarily represented by remnants of the elytra. Their phylogeny also is not clear, being exclusively based on comparative morphological studies so far unsupported by paleontological evidence. The Coleoptera probably appeared in the Carboniferous period from peculiar orthopteroids, which were ancestors of all holometabolous insects. These original forms, besides exhibiting complete metamorphosis, also possessed perfect protective coverings in the form of elytra. So far, transitional forms between orthopteroids and beetles have not been discovered.

The early Coleoptera appeared in the Lower Permian in Southern Siberia and the Urals and at the same time showed great variations. Such representatives comprise not fewer than six families—Tshekardocoleidae, Asiocoleidae, Kaltanocoleidae, Permarrhaphidae, Cupidae and Taldycupidae, of which the last three gave rise to the still richer Upper Permian fauna. The Lower Triassic Coleoptera attained maximum variety and gave rise to the richest known diversity among all insect orders. Research on the widely varied Mesozoic beetles (about 250 genera are known) is still very meager. The Coleoptera of the Tertiary period abound in species widely distributed in Recent families (about 60), and, similarly, most of their genera (over 650) also appeared then. Insufficient knowledge of the primitive Coleoptera precludes the systematic study of the families and higher categories of the Permian as well as most Mesozoic beetles. Hence the characteristics of superfamilies, series [sic] and suborders cannot be given for the coleopteran fossils described.

Family TSHEKARDOCOLEIDAE Rohdendorf, 1944

Elytron with well-developed venation, veins inclined; three radial veins—R, RS_1 and RS_2; SC short; two veins of M, one of Cu and three of A; between longitudinal veins many weaker cross veins, forming two rows of cells. Lower Permian. One genus.



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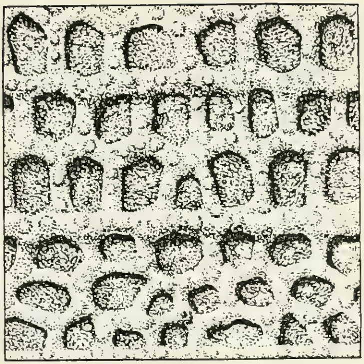

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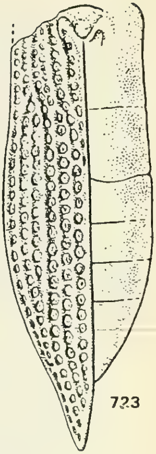

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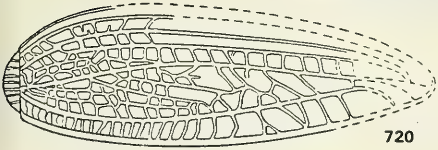

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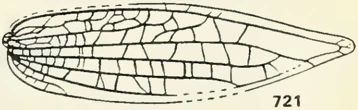

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Figs. 719–723. Families Tshekardocoleidae, Sojanocoleidae, Permarrhaphidae, Asiocoleidae and Kaltanocoleidae.

719. *Tshekardocoleus magnus* Rohdendorf; A—dorsal view, × 4.2; B—ornamentation of elytron, × 60. Lower Permian, Urals (Rohdendorf, 1944). 720. *Sojanocoleus reticulatus* Martynov; right elytron, × 5. Upper Permian, Arkhangelsk province (Martynov, 1932). 721. *Permarrhaphus venosus* Martynov; elytron, × 4.5. Upper Permian, Urals (Martynov, 1930). 722. *Asiocoleus novojilovi* Rohdendorf; elytron, × 11. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 723. *Kaltanocoleus pospelovi* Rohdendorf; elytron, × 16.5. Lower Permian, Kuznetsk basin (Rohdendorf, 1961).

Tshekardocoleus Rohdendorf, 1944. Genotype—*T. magnus* Rohdendorf, 1944; Lower Permian, Perm Province (Kungurian stage, Chekarda). A single row of cells between R and RS_1, and between RS_1 and RS_2, three rows of cells. Length of elytron 15 mm and width 2.5 mm (Fig. 719A, B). One species. Lower Permian of Urals.

Family SOJANOCOLEIDAE Martynov, 1932

Elytron with well-developed venation, consisting of firm longitudinal and cross veins: SC, two radial veins, stout trunk of M with short irregular branches, one Cu and one long A, running parallel up to apex. Upper Permian. One genus.

Sojanocoleus Martynov, 1932. Genotype—*S. reticulatus* Martynov, 1932; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Between 243 stems of R and M and also between M and Cu, irregular veins forming many rows of cells. Length of elytron about 12 mm and width 5 mm (Fig. 720). One species. Upper Permian of Arkhangelsk province.

Family PERMARRHAPHIDAE Martynov, 1930

Elytron with well-developed venation, consisting of irregular longitudinal and cross veins: two SC, short and long, two radials, one M, short Cu and two A, of which the second long one reaches tip of wing. Upper Permian. One genus.

Permarrhaphus Martynov, 1930. Genotype—*P. venosus* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Cross veins strong, but irregular; all veins dark, wing lacks ornamentation and is leathery. Length of elytron about 10 mm and width 3 mm (Fig. 721). One species. Upper Permian of Urals.

Besides the above-mentioned genus, the genus *Uralocoleus* G. Zalessky, 1947 probably belongs to this family. This genus from the Lower Permian of the Urals (Krutaya Katushka formations on the River Barde) has not been sufficiently studied.

Family ASIOCOLEIDAE Rohdendorf, 1961

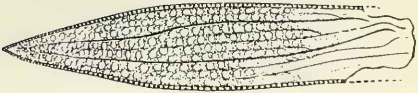
M and Cu fused at middle of elytron to form a distinct anastomosis resembling letter X; more than 10 longitudinal rows of angular cells present on elytron; R, M and Cu markedly convex; major segment of M and basal branches of RS tilted; A short but distinct. Lower Permian. One genus.

Asiocoleus Rohdendorf, 1961. Genotype—*A. novojilovi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Elytron with 12 rows of rounded cells; intervals between rows uniformly convex with a markedly tubercular surface; RS very weak, with four pectinately distributed branches at base; Cu sharply demarcated from M, almost parallel to anal margin; after anastomosing with M, Cu takes a sharp bend backward. Marginal rim of anterior and anal margins well developed. Length of elytron 7.4 mm, width 1.6 mm (Fig. 722). One species. Lower Permian of Kuznetsk basin.

Family KALTANOCOLEIDAE Rohdendorf, 1961

Elytron with distinctly branching, longitudinal veins forming six longitudinal rows of cells; all veins of approximately uniform thickness; radial stem consists

724A



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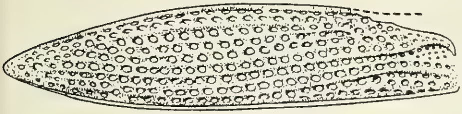

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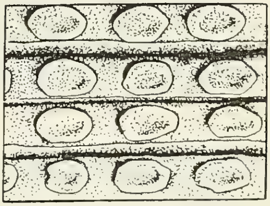

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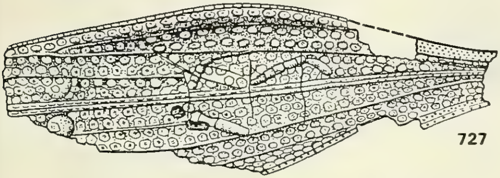

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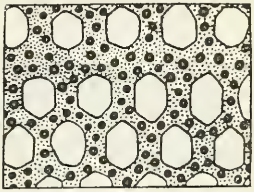

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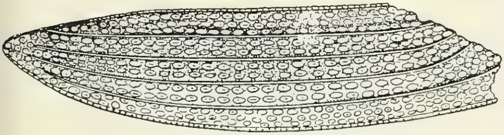

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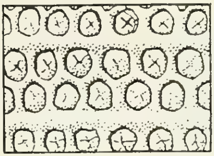

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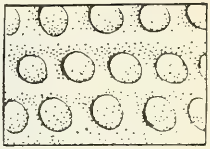

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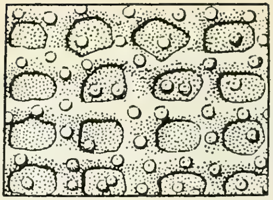
Figs. 724–729. Family Cupidae.

724. *Archicupes jacobsoni* Rohdendorf; A—elytron, × 15, B—ornamentation on elytron, × 60. Lower Permian, Kuznetsk basin (Rohdendorf, 1958). 725. *Eocupes lukjanovitshi* Rohdendorf; A—elytron, × 16.5, B—ornamentation on elytron, × 50. Lower Permian, Kuznetsk basin (Rohdendorf, 1958). 726. *Kaltanicupes richteri* Rohdendorf; A—elytron, × 120, B—ornamentation on elytron, × 70. Lower Permian, Kuznetsk basin (Rohdendorf, 1958). 727. *Palaeocupes kaltanicus* Rohdendorf; elytron, × 14.5. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 728. *Cytocupes angustus* Rohdendorf; elytron, × 17. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 729. *Protocupoides plavilstshikovi* Rohdendorf; A—elytron, × 15.8, B—ornamentation on elytron, × 80. Lower Permian, Kuznetsk basin (Rohdendorf, 1961).


730A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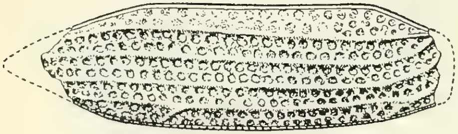
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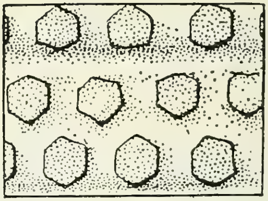
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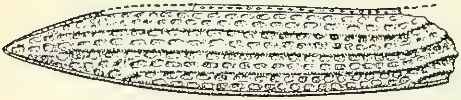
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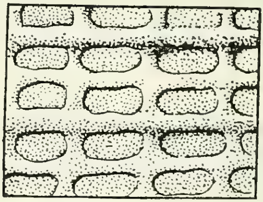
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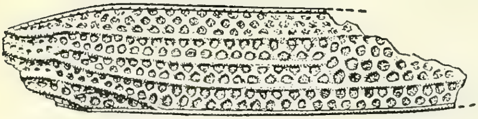
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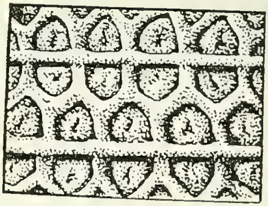
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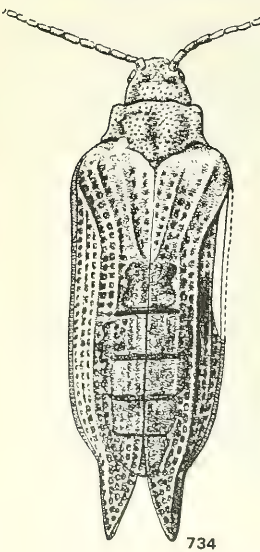
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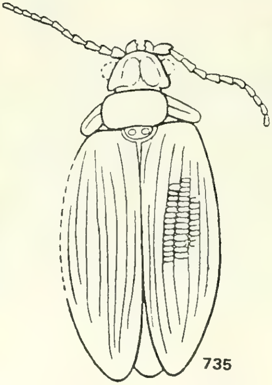
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of R which divides into two veins—RS_1 and RS_2; M and Cu simple, straight and fused for one-fourth of elytron into unpaired stem; A inclined, reaches end of basal one-third of anal margin of elytron. Simple rows of large cells between all veins. Abdomen shorter than elytra and has five visible sterna. Scutellum large. Lower Permian. One genus.

Kaltanocoleus Rohdendorf, 1961. Genotype—*K. pospelovi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Anterior margin of elytron with narrow, flat border; apices of elytra pointed and diverging; seven veins in all. Length of elytron 4.5–4.6 mm, width 0.78–0.85 mm (Fig. 723). One species. Lower Permian of Kuznetsk basin.

Family CUPIDAE Latreille, 1825

Longitudinal rows of large, prominent cells bordered by longitudinal, slender but strong rib-veins of variable thickness; between these stout rib-veins lie either two or three rows of cells. Permian to Recent. Seven Permian, one Jurassic and two Cenozoic genera. Two genera from the Paleogene of Europe (Baltic amber).

Archicupes Rohdendorf, 1961. Genotype—*A. jacobsoni* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Veins in posterior half of wing run obliquely toward anal margin; Cu runs for three-fifths of length of wing, whereas M runs all along apex of wing. Length of elytron 3.9–5.4 mm, width 0.75–1 mm (Fig. 724). Two species. Lower Permian of Kuznetsk basin.

Eocupes Rohdendorf, 1961. Genotype—*E. lukjanovitshi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). At base of elytron lies short common stem of R + M and base of Cu; eight rows of cells of almost regularly rounded form occur at center. Length of elytron 4.7 mm, width 1 mm (Fig. 725). One species. Lower Permian of Kuznetsk basin.

Kaltanicupes Rohdendorf, 1961. Genotype—*K. richteri* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Apex of elytron pointed and drawn out; veins neither oblique nor parallel; RS and M and in part Cu stronger than others; nine rows of cells. Length of elytron 5–6 mm, width 1.1 mm (Fig. 726). One species. Lower Permian of Kuznetsk basin.

Figs. 730–735. Family Cupidae.

730. *Protocupes martynovi* Rohdendorf; A—elytron, × 14.7. B—ornamentation on elytron, × 60. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 731. *Tomiocupes carinatus* Rohdendorf; A—elytron, × 22.5, B—ornamentation on elytron, × 80. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 732. *Tricupes acer* Rohdendorf; A—elytron, × 24.2, B—ornamentation on elytron, × 95. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 733. *Permocupoides skoki* Rohdendorf; A—elytron, × 15, B—ornamentation on elytron, × 60. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 734. *Permocupes sojanensis* Ponomarenko; general view, × 10. Upper Permian, Arkhangelsk province (original drawing). 735. *Mesocupes primitivus* Martynov; general view, × 7.5. Upper Jurassic, Southern Kazakhstan (Martynov, 1926).

Palaeocupes Rohdendorf, 1961. Genotype—*P. kaltanicus* Rohdendorf, 244 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Eight rows of large cells in middle of elytron; venation zigzag; R and M form a common stem at base of elytron and then branch; RS not isolated; M reaches apex of elytron; Cu stout and strong up to middle; primary veins zigzag; elytron convex with a prominent projection at midpoint of anterior margin and a slender apical area; surface of elytron tubercular. Length of elytron 5.2 mm, width 0.9 mm (Fig. 727). One species. Lower Permian of Kuznetsk basin.

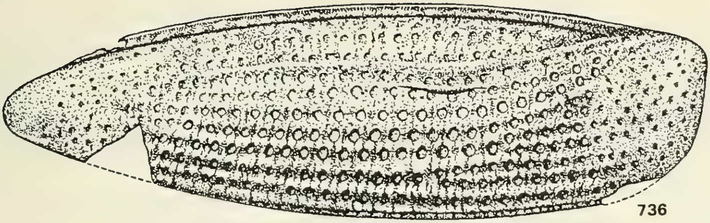
Cytocupes Rohdendorf, 1961. Genotype—*C. angustus* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Ten rows of 246 rounded-rectangular cells in middle of elytron; veins straight, but their main stems indistinct; veins M and Cu sharply defined at base of elytron; four convex veins seen in middle of elytron, of which RS and M particularly distinguished; elytron markedly convex; costal area slopes sharply to front; anterior margin projects weakly, without spines; apex of elytron pointed; surface of elytron smooth and shining. Length of elytron 5.1 mm, width 0.9 mm (Fig. 728). One species. Lower Permian of Kuznetsk basin.

Protocupoides Rohdendorf, 1961. Genotype—*P. plavilstshikovi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Elytra with four straight, strong veins (R, RS, M and Cu); A short, indistinct; 12 longitudinal rows of cells in middle of elytron; three rows of cells in costal and cubital areas; anterior margin convex; slight bend before apical one-third, apex of elytron fairly blunt; both anterior and anal margins of elytron exhibit coarse tubercles. Length of elytron segment 4.8 mm, width 1.1 mm (Fig. 729A, B). One species. Lower Permian of Kuznetsk basin.

Protocupes Rohdendorf, 1961. Genotype—*P. martynovi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Anterior margin of elytron with a narrow, but prominent border of rhomboid cells; eight or nine rows of cells in middle of elytron; veins R, RS, M and Cu straight, absolutely parallel, fringed by two rows of cells; intermediate longitudinal veins also parallel. Length of elytron 3.6–4.6 mm, width 0.65–0.90 mm (Fig. 730). Two species. Permian of Kuznetsk basin.

Tomiocupes Rohdendorf, 1961. Genotype—*T. carinatus* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Anterior rim of elytron poorly developed; 10 rows of cells in middle; veins R, RS, M and Cu bent arcuately, parallel, fringed by two rows of cells; intermediate longitudinal veins noticeably arranged in a zigzag fashion. Length of elytron 3 mm, width 0.8 mm (Fig. 731A, B). Two species. Upper Permian of Kuznetsk basin.

Tricupes Rohdendorf, 1961. Genotype—*T. acer* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Elytron narrow with three strong longitudinal veins in middle; all nine rows of angular cells bordered by very thin, straight intermediate longitudinal veins. Length of



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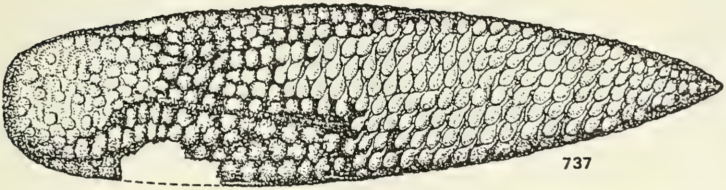

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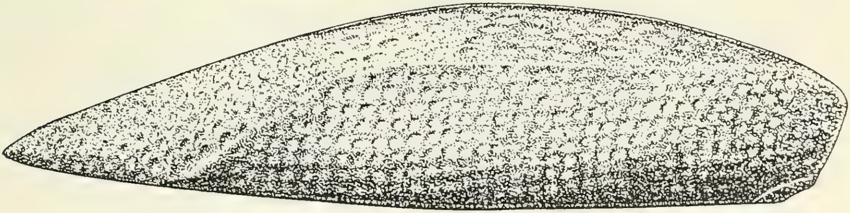

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Figs. 736–738, 740. Family Taldycupidae.

736. *Schizotaldycupes ananjevi* Rohdendorf; elytron, × 12.6. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 737. *Ichthyocupes tyzhnovi* Rohdendorf; elytron, × 26.5. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 738. *Carinicupes beckermigdisovae* Rohdendorf; elytron, × 24. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 740. *Tecticupes heckeri* Rohdendorf; elytron, × 25. Upper Permian, Kuznetsk basin (Rohdendorf, 1961).

elytron 3.1 mm, width 0.55 mm (Fig. 732A, B). One species. Upper Permian of Kuznetsk basin.

Permocupoides Martynov, 1933. Genotype—*P. distinctus* Martynov, 1933; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mts.). R, RS, M and Cu parallel, middle three veins particularly strong; intermediate veins zigzag, distinctly weaker than main veins. Length of elytron 5 mm; width more than 1 mm (Fig. 733A, B). Three species. Upper Permian of Pre-Urals and Kuznetsk basin.

Permocupes Martynov, 1933. Genotype—*P. semenovi* Martynov, 1933; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie mountain). All veins in middle part of elytron parallel; A_2, Cu and M strongest; intermediate veins straight, considerably weaker than main veins; anterior rim of elytron indistinct; eight rows of cells. Length of elytron 3.8 mm, width 0.9 mm (Fig. 734). Two species. Upper Permian of the Urals and Arkhangelsk province.

Mesocupes Martynov, 1926. Genotype—*M. primitivus* Martynov, 1926; Upper Jurassic, Kazakhstan. Not fewer than eight rows of cells; intermediate veins differ little from main veins, all straight; elytra wide, without distinct ornamentation. Length of body 7.5 mm and of elytron 5.6 mm. Width of elytron about 1.6 mm (Fig. 735). One species. Upper Jurassic of Kazakhstan.

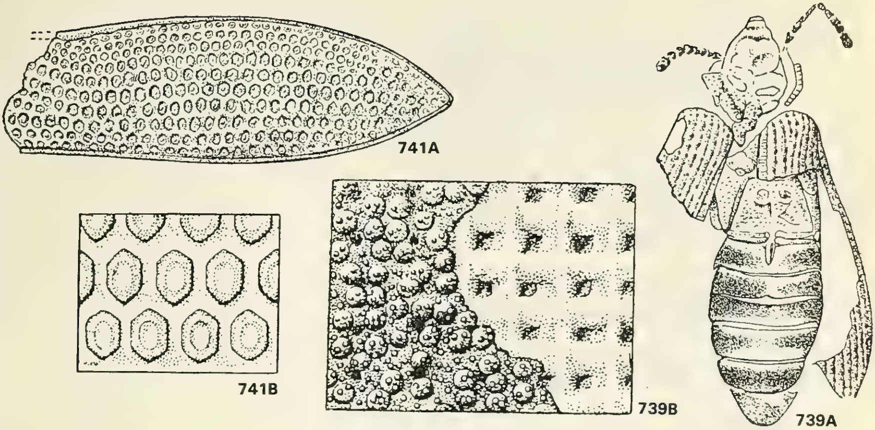
Family TALDYCUPIDAE Rohdendorf, 1961

Elytra without branching, sharply demarcated veins; seven to 10 parallel rows of cells separated by longitudinal and weaker transverse intervals; all longitudinal ribs similar; often elytron very dense and thick, due to which cells much reduced and clearly observed only on underside of elytron. Abdomen made up of six distinct sterna. Lower Permian to Triassic. 13 genera.

Schizotaldycupes Rohdendorf, 1961. Genotype—*S. ananjevi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Elytron with fairly clear, but not sharp, flat longitudinal rib in area of R_1; short furrow in radial area; 10 rounded-angular cells in middle of elytron; apex of elytron more rounded, with sparse extremely small cells; anterior margin with prominent, flat, epipleuron, smooth along edge and profusely pitted 247 elsewhere. Length of elytron 7.6 mm, width 2.3 mm (Fig. 736). One species. Lower Permian of Kuznetsk basin.

Ichthyocupes Rohdendorf, 1961. Genotype—*I. tyzhnovi* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Surface of elytron with dense tubercles and irregular cells, very shiny; venation weak; anterior margin almost straight for two-thirds of basal part; anal margin uniformly convex; apex of elytron gradually tapering, relatively pointed. Length of elytron 3.6 mm, width 0.9 mm (Fig. 727). One species. Lower Permian of Kuznetsk basin.

Carinicupes Rohdendorf, 1961. Genotype—*C. beckermigdisovae* Rohdendorf, 1961; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan).



248 Figs. 739–741. Family Taldycupidae.

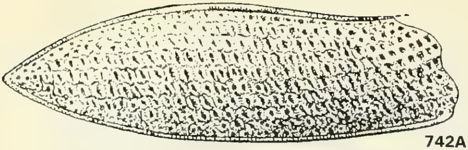
739. *Stegocupes fedotovi* Rohdendorf; A—general view, × 18, B—ornamentation of elytron, × 100. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 741. *Taldycupes khalfini* Rohdendorf; A—elytron, × 26, B—ornamentation of elytron, × 100. Upper Permian, Kuznetsk basin (Rohdendorf, 1961).

Elytron bears longitudinal rib-fold, inclined and distinct in apical section; 248 surface of elytron tubercular, with 12 longitudinal rows of large, rounded, shallow cells; anterior margin of elytron markedly and uniformly convex; anal margin almost straight. Length of elytron 4.75 mm, width 1.2 mm (Fig. 738). One species. Lower Permian of Kuznetsk basin.

Stegocupes Rohdendorf, 1961. Genotype—*S. fedotovi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Seven rows of cells in basal part of elytron; surface of elytron wrinkled, cells irregular. Six sterna on abdomen. Posterior coxae transverse, middle ones globular. Length of elytron 2.85–3.5 mm, width 0.65–0.7 mm. Overall length of insect 4 mm (Fig. 739). Two species. Upper Permian of Kuznetsk basin.

Tecticupes Rohdendorf, 1961. Genotype—*T. heckeri* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). 10 longitudinal rows of rounded cells; surface of elytron with broad granulation. Length of elytron 3–3.15 mm, width 0.65–0.85 mm (Fig. 740). Two species. Upper Permian of Kuznetsk basin.

Taldycupes Rohdendorf, 1961. Genotype—*T. khalfini* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). 10 rows of rounded cells. Surface of ribs smooth, without granulation or wrinkling. Length of elytron 2.6–3.6 mm, width 1–1.6 mm (Fig. 741A, B). Four species.



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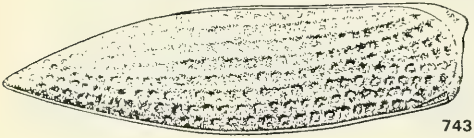

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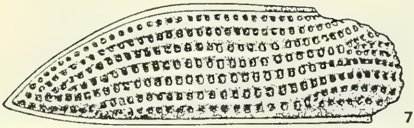

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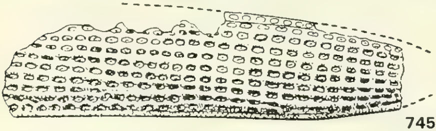

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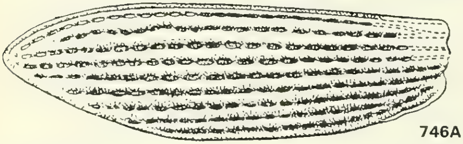

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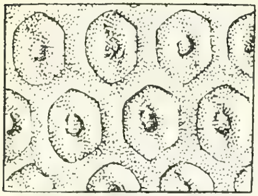

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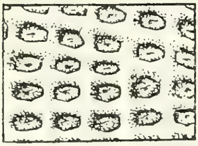

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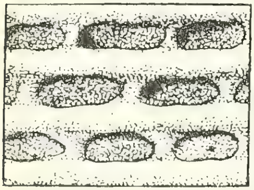

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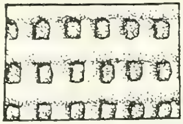

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Figs. 742–746. Family Taldycupidae.

742. *Taldycupidium bergi* Rohdendorf; A—elytron, × 38, B—ornamentation of elytron, × 200. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 743. *Cryptocupes rjabini* Rohdendorf; elytron, × 38. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 744. *Tychticupes radtshenkoi* Rohdendorf; A—elytron, × 27, B—ornamentation of elytron, × 70. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 745. *Tychtocupoides grjazevi* Rohdendorf; elytron, × 15, B—ornamentation of elytron, × 38. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 746. *Uskaticupes javorskyi* Rohdendorf; A—elytron, × 41.5, B—ornamentation of elytron, × 150. Upper Permian, Kuznetsk basin (Rohdendorf, 1961).

Upper Permian of Kuznetsk basin.

Taldycupidium Rohdendorf, 1961. Genotype—*T. bergi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). 10 rows of very small cells, indistinctly separated by flat intervals. Length of elytron 1.95–2.1 mm, width 0.72–0.74 mm (Fig. 742). One species. Upper Permian of Kuznetsk basin.

Cryptocupes Rohdendorf, 1961. Genotype—*C. rjabinini* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Elytron convex, smooth, with eight rows of large indistinct rounded cells, at the bottom of which lie medium-sized tubercles; anterior and anal margins of elytron moderately, almost uniformly convex; apex of elytron angular, fairly pointed, not extended. Length of elytron 1.9 mm, width 0.5 mm (Fig. 743). One species. Upper Permian of Kuznetsk basin.

Tychticupes Rohdendorf, 1961. Genotype—*T. radtschenkoi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Longitudinal rib-veins not prominent; seven or eight rows of longitudinal rounded or angular cells in center of elytron. Length of elytron 2.5–3.4 mm, width 0.6–0.8 mm (Fig. 744). Five species. Upper Permian of Kuznetsk basin.

Tychtocupoides Rohdendorf, 1961. Genotype—*T. grjazevi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Longitudinal rib-veins fairly prominent; seven longitudinal rows of cells in middle of elytron; cells quadrate or rectangular in outline; regularly spaced. Length of elytron 4.5 mm, width 1 mm (Fig. 745A, B). One species. Upper Permian of Kuznetsk basin.

Uskaticupes Rohdendorf, 1961. Genotype—*U. javorskyi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Ten rows of longitudinally rectangular cells; longitudinal rib-veins distinctly projecting throughout their length. Length of elytron 1.8 mm, width 0.5 mm (Fig. 746A, B). Two species. Upper Permian of Kuznetsk basin.

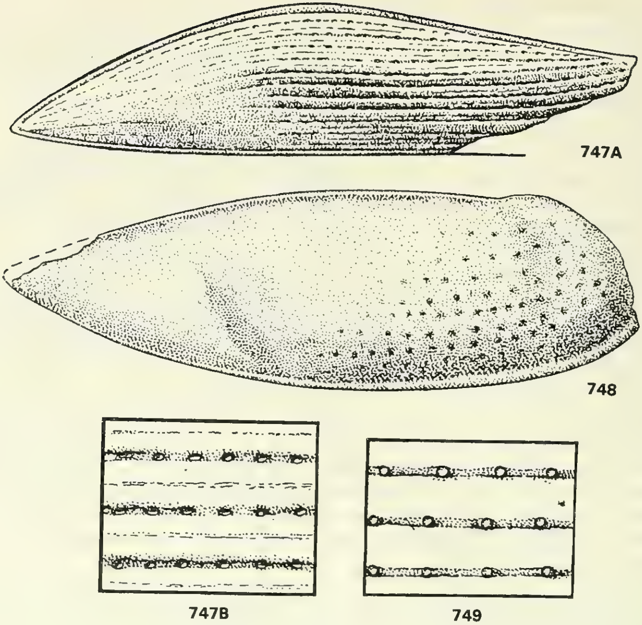
Outside the USSR: *Mesothrosis* Tillyard, 1916 (pars); *Simmondsia* Dunstan, 1924.

Family RHOMBOCOLEIDAE Rohdendorf, 1961

Two-fifth of basal half of elytron with longitudinal rows of small cells and 11-14 longitudinal ribs; however, apical part smooth. Upper Permian. Two genera.

Rhombocoleus Rohdendorf, 1961; Genotype—*R. andreae* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Twelve or 13 rows of very narrow cells form longitudinal furrows; humeral protuberance prominent. Length of elytron 5 mm, width 1.2 mm (Fig. 747A, B). One species. Upper Permian of Kuznetsk basin.

Erunakicupes Rohdendorf, 1961. Genotype—*E. kryshtofovichi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). 10 rows of cells appearing like deep punctures separated by 11



250 Figs. 747–749. Family Rhombocoleidae.

747. *Rhombocoleus andreae* Rohdendorf; A—elytron, × 25, B—ornamentation of elytron, × 108. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 748. *Erunakicupes kryshtofovichi* Rohdendorf; elytron, × 32.3. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 749. *E. schmalhauseni* Rohdendorf; ornamentation of elytron, × 132. Upper Permian, Kuznetsk basin (Rohdendorf, 1961).

longitudinal ribs; humeral protuberance less prominent. Length of elytron 1.75–3.75 mm, width 0.75–1.1 mm (Figs. 748, 749). Four species. Upper Permian of Kuznetsk basin.

Family SCHIZOCOLEIDAE Rohdendorf, 1961

A short longitudinal furrow stands out distinctly in area of RS on elytron, in the form of an abrupt depression; this furrow is usually deep and sharp, rarely indistinct; elytron with varied ornamentation: sometimes with fine transverse wrinkles, longitudinal rows of tubercles, spotted pits or slender ribs. Abdomen with five distinctly separated sterna, last one particularly large. Permian. Seven genera.

Rossocoleus Rohdendorf, 1961 (*Curculiopsis* Martynov, 1937, nec *Curculiopsis* Handlirsch, 1906). Genotype—*R. grandis* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Sureikovo I). Convex elytron with rows of prominent tubercles; furrow well expressed. Length of elytron 3.2–4.2 times of width; length 2.3–4.9 mm, width 0.7–1.35 mm (Fig. 750). Seven species. Upper and Lower Permian of Kuznetsk basin and Urals.

Schizocoleus Rohdendorf, 1961. Genotype—*S. kuznetskiensis* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo II). Anterior margin of elytron weakly convex, and parallel in basal two-thirds, becoming pointed only at apex; surface finely, irregularly wrinkled; furrow distinct, humeral protuberance indistinct. Length of elytron 7.2 mm, width 2 mm (Fig. 751A, B). One species. Upper Permian of Kuznetsk basin.

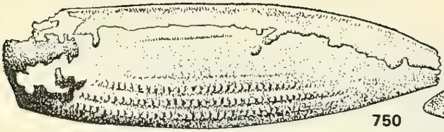
Schizocupes Rohdendorf, 1961. Genotype—*S. obrutshevi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Zelenyi Lug). Markedly convex elytron with prominent humeral protuberance; elytron 2.9 times longer than wide; furrow short, but distinct; up to 10 indistinct longitudinal rows of smaller pits at base; surface of elytron wrinkled. Length of elytron 3.2 mm, width 1.1 mm (Fig. 752A, B). One species. Upper Permian of Kuznetsk basin.

Karakanocoleus Rohdendorf, 1961. Genotype—*K. lebedevi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Elytron very convex, with rounded humeral protuberance, elongated, 3.3–3.7 times longer than wide; furrow of variable form; longitudinal rows of delicate dots or ribs observed in various locations. Length of elytron 2.6–4.6 mm, width 0.8–1.35 mm (Fig. 753). Six species. Upper Permian of Kuznetsk basin and Australia.

Karakanocoleodes Rohdendorf, 1961. Genotype—*K. latissimus* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Elytron weakly convex, with markedly projecting humeral protuberance, broad, only 2.75 times longer than wide; furrow in large depression; rows of very small transverse depressions and convex longitudinal ribs seen in posterior part of elytron. Length of elytron 4.4 mm, width 1.6 mm (Fig. 754). One species. Upper Permian of Kuznetsk basin.

Uskatocoleus Rohdendorf, 1961. Genotype—*U. zalesskyi* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II).
253 Elytron moderately convex, narrows sharply toward apex; surface almost smooth, only slightly wrinkled; humeral protuberance prominent. Length of elytron 2.25–4.6 mm, width 0.75–1.3 mm (Fig. 755). 13 species. Upper Permian of Kuznetsk basin.

Aenigmocoleus Rohdendorf, 1961. Genotype—*A. borissiaki* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolava II). Base of elytron converges markedly, with sharply projecting humeral protuberance. Anterior margin almost straight, anal margin strongly convex; apex of elytron fairly pointed; slitlike furrow short, distinct; elytron barely convex, apparently thin, with surface densely covered with small tubercles. Length of elytron 4.8 mm, width 1.2 mm (Fig. 756). One species. Upper Permian of Kuznetsk basin.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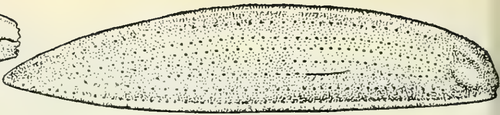
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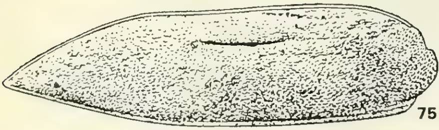
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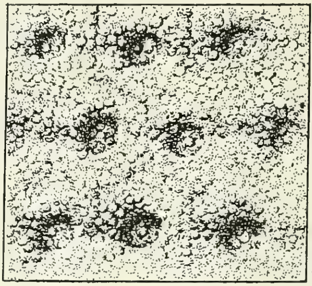
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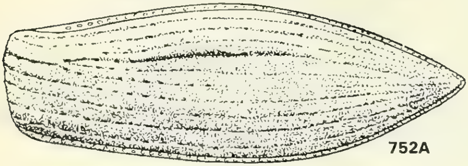
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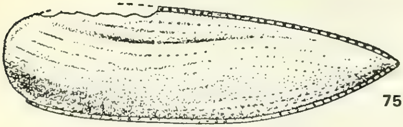
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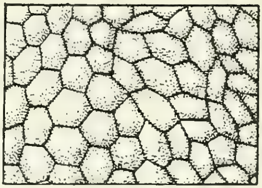
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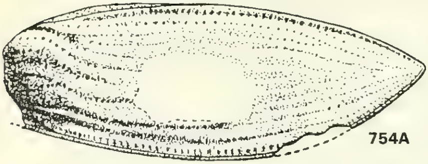
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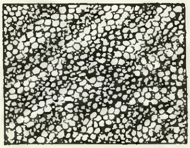
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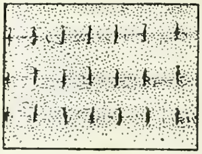
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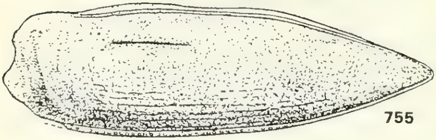
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Figs. 750–756. Family Schizocoleidae.

750. *Rossocoleus avus* Rohdendorf; elytron, × 16. Lower Permian, Kuznetsk basin (Rohdendorf, 1961). 751. *Schizocoleus kuznetskiensis* Rohdendorf; A—elytron, × 10, B—ornamentation of elytron, × 40, C—ornamentation of elytron, × 160. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 752. *Schizocupes obrutshevi* Rohdendorf; A—elytron, × 24, B—ornamentation of elytron, × 150. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 753. *Karakanocoleus lebedevi* Rohdendorf, elytron, × 25. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 754. *Karakanocoleodes latissimus* Rohdendorf, A—elytron, × 16.5, B—ornamentation of elytron, × 50. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 755. *Uskatocoleus zalesskyi* Rohdendorf; elytron, × 23. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 756. *Aenigmocoleus borissiaki* Rohdendorf; elytron, × 16. Upper Permian, Kuznetsk basin (Rohdendorf, 1961).

Family PERMOSYNIDAE Tillyard, 1924

Elytron without noticeable venation, with smooth or finely wrinkled surface, usually with parallel furrows, sometimes with indistinct depressions; radial furrow 'cleft' absent on elytron. Abdomen with four to five sterna. Upper Permian-Triassic. About 15 genera.

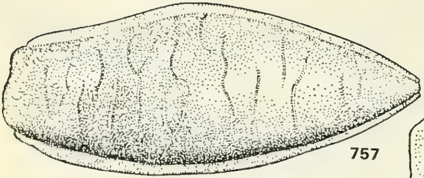
Palademosyne Rohdendorf, 1961. Genotype—*P. martynovae* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Elytron moderately convex, with blunt base noticeably narrower than its maximum width; anterior margin distinctly convex, irregularly bent in front of base; anterior area very gently and uniformly sloping forward; anal margin regular, arcuately convex with broad, flat welt; apex of elytron convex, acute-angled; basal part stands out and is flatter; ornamentation in form of fine tuberculation; longitudinal markings absent. Length of elytron 2.2 mm, width 0.88 mm (Fig. 757). One species. Upper Permian of Kuznetsk basin.

Stegosyne Rohdendorf, 1961. Genotype—*S. rugosa* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Ilinian series, Chistaya Griva). Elytron moderately convex, broad, with blunt base insignificantly narrower than its maximum width. Anterior margin markedly convex with prominently projecting area halfway along elytron; anterior area very weakly depressed; anal margin uniformly convex, with a not particularly narrow welt; apex of elytron moderately convex, angular, pointed; surface covered with coarse, irregular tubercles; longitudinal ornamentation indistinct; elytron with strong luster. Length of elytron 1.8 mm, width 0.82 mm (Fig. 758). One species. Upper Permian of Kuznetsk basin.

Tychtocoleus Rohdendorf, 1961. Genotype—*T. neuburgae* Rohdendorf, 1961; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Elytron markedly convex, base not particularly broad, somewhat pointed; anterior margin slightly convex; anterior area markedly depressed being almost vertical at base of elytron; anal margin uniformly though slightly convex, with convex welt; nine parallel, broad, slightly convex ribs separating 10 fine, deep furrows bearing small pits; surface of elytron uneven, with facets clearly seen with oblique illumination. Length of elytron 1.8–1.82 mm, width 0.52–0.55 mm (Fig. 759). One species. Upper Permian of Kuznetsk basin.

Ademosyne Handlirsch, 1906. Genotype—*A. major* Handlirsch, 1961; Triassic, Australia. Humeral protuberance prominent; seven to 10 distinct furrows bearing distinct, but small pits; ratio of width to length 1 : 1.9–3.5; no rib in front of sutured margin. Length of elytron 1.5–6.2 mm, width 0.55–3 mm (Fig. 760). Sixteen species. Upper Permian, Kuznetsk basin and Triassic of Australia.

Ademosynoides Dunstan, 1924. Genotype—*Ademosyne minor* Handlirsch, 1906; Triassic, Australia. Humeral protuberance well developed; eight to 10 furrows without spots or pits; ratio of length of elytron to width 1 : 2;4–3; costal margin without border; no rib in front of sutured margin.



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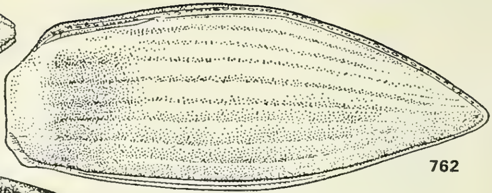

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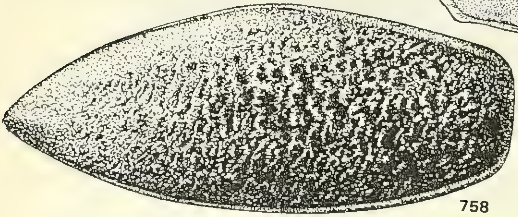

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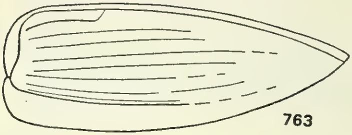

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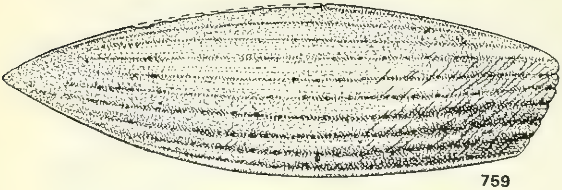

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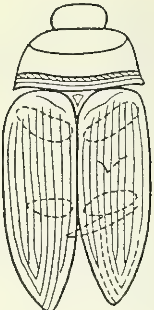

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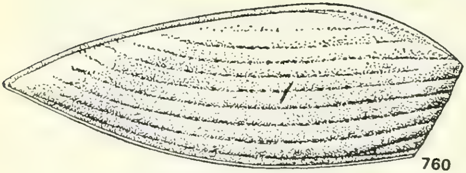

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Figs. 757–763. Family Permosynidae.

757. *Palademosyne martynovae* Rohdendorf; elytron, × 25. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 758. *Stegosyne rugosa* Rohdendorf; elytron, × 38. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 759. *Tychtocoleus neuburgae* Rohdendorf; elytron, × 42. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 760. *Ademosyne sibirica* Rohdendorf; elytron, × 50. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 761. *Ademosynoides asiaticus* Martynov; elytron, × 11. Triassic, Kuznetsk basin (Martynova, 1936). 762. *Polysitum kuznetskiense* Rohdendorf; elytron, × 37. Upper Permian, Kuznetsk basin (Rohdendorf, 1961). 763. *Permocrossos elongatus* Martynov; elytron, × 10. Upper Permian, Arkhangelsk province (Martynov, 1932).

Length of elytron 2–8.5 mm, width 0.8–2.9 mm (Fig. 761). Eight species. Triassic of Kuznetsk basin (Babii Kamen) and Australia.

Polysitum Dunstan, 1924. Genotype—*P. punctatum* Dunstan, 1924; Triassic, Australia. Humeral protuberance well developed; furrows not much in evidence: only rudiments observed, particularly on anterior half; surface of elytron wrinkled; costal margin with narrow border. Length of elytron 1.7–6.9 mm, width 0.75–2.7 mm (Fig. 762). Three species. Upper Permian of Kuznetsk basin and Triassic of Australia.

Permocrossos Martynov, 1932. Genotype—*P. elongatus* Martynov, 1932; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Very broad
254 costal border forming humeral widening; humeral protuberance prominent; furrows without pits or spots. Length of elytron 5.4 mm, width 2 mm (Fig. 763). One species. Upper Permian of Arkhangelsk province.

Outside the USSR: *Permosyne* Tillyard, 1924; *Platycrossos* Dunstan, 1924; *Tryoniopsis* Dunstan, 1924; *Ulomites* Tillyard, 1916; *Reeveana* Dunstan, 1924; *Grammositum* Dunstan, 1924; *Shepherdia* Dunstan, 1924.

Family CARABIDAE Latreille, 1825. Ground beetles

Large or medium sized insects. Elytron relatively flat with longitudinal rows of tubercles or pits; number of pitted furrows ranges from nine to 32. Diagnosis from structure of elytron difficult. Upper Jurassic to Recent. One of the large families of the Recent fauna, also rich in representatives from Tertiary faunal complexes (more than 50 genera).

Carabopteron Martynov, 1926. Genotype—*C. punctatolineatum* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Four main longitudinal ribs with tubercles and four secondary riblets between main ribs; sometimes ribs smooth. Length of elytron 17.5–21 mm, width 6.5–6.8 mm (Fig. 764). Two species. Upper Jurassic of Kazakhstan.

Besides the numerous Tertiary genera a few Jurassic genera such as *Procalosoma* Meunier, 1895, *Nebrioides* Handlirsch, 1906 and many others belong to this family.

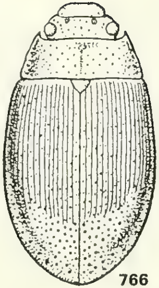
Family CICINDELIDAE Latreille, 1802. Tiger beetles

Beetles of large or medium size, with long running legs, broad head with large mandibles and projecting eyes. Elytron smooth. Paleogene to Recent. Three genera.

255 Family COPTOCLAVIDAE Ponomarenko, 1961

Large aquatic beetles. Body smooth. Middle and posterior legs of swimming type, flat, with broad segments, but without swimming bristles. Larvae with swimming legs and biting mandibles. Upper Jurassic. One genus.

Coptoclava Ping, 1928. Genotype—*C. longipida* Ping, 1928; Upper Jurassic, China (Laiyan). Beetle: not large; mandibles of biting type; pronotum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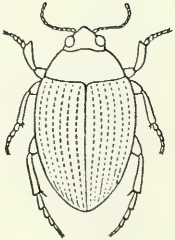
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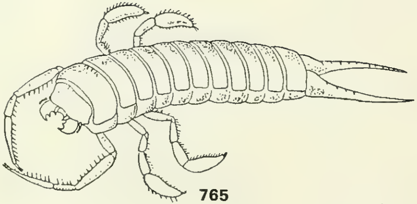
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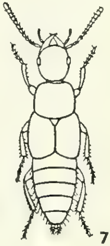
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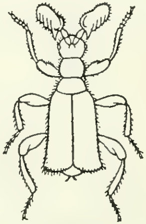
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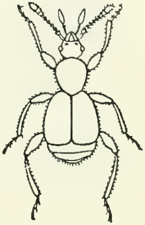
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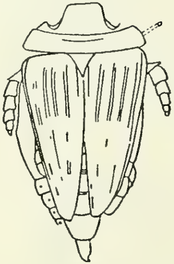
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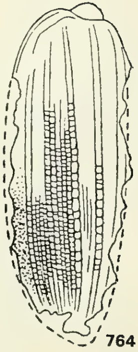
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Figs. 764–771. Families Carabidae, Coptoclavidae, Dytiscidae, Haliplidae, Palaeogyrinidae, Paussidae, Staphylinidae and Pselaphidae.

764. *Carabopteron punctatolineatum* Martynov; elytron, × 3.4. Upper Jurassic, South Kazakhstan (Martynov, 1926). 765. *Coptoclava longipoda* Ping; larva (reconstruction), × 1.5. Upper Jurassic, Eastern Siberia (Ponomarenko, 1961). 766. *Dytiscus lapponicus* Gyllenhal; dorsal view, × 1.5. Quaternary and Recent, West Ukraine (Lomniki, 1894). 767. *Haliplus* sp.; dorsal view, × 9. Recent (Yakobson, 1915). 768. *Palaeogyrinus strigatus* Schlechtendal; dorsal view, × 10. Paleogene, Germany (Hatch, 1928). 769. *Paussus* sp.; dorsal view, × 7. Recent (Yakobson, 1915). 770. *Philonthus* sp.; dorsal view, × 16. Recent (Yakobson, 1915). 771. *Bythinus* sp.; dorsal view, × 16. Recent (Yakobson, 1915).

as long as it is broad; abdomen with six sterna. Middle and posterior tibiae and tarsi very broad, length of body 34–41 mm. Larva: mandible; three-toothed, forelegs raptorial; middle and hindlegs broad, adapted for swimming; length 10–35 mm (Fig. 765). One species. Upper Jurassic of East Asia (Transbaikal, Mongolia and China).

Family DYTISCIDAE Latreille, 1825. Predaceous diving beetles

Large or medium sized. Elytra smooth or with numerous furrows. Body flat. Posterior legs of swimming type. Jurassic to Recent. About 2,300 species of Recent fauna belonging to 90 genera, of which about 50 are also represented in Tertiary fauna (Fig. 766). The Mesozoic fauna have not yet been sufficiently studied.

Family HALIPLIDAE Aube, 1836

Small, with short convex body and very large posterior coxae and swimming hairs on legs. Aquatic beetles (Fig. 767). Neogene to Recent. About 130 species in Recent fauna belonging to three genera. One species of the genus *Haliplus* Latreille, 1825 is from the Upper Miocene of Western Europe.

Family PALAEOGYRINIDAE Schlechtendal, 1894

Aquatic beetles. Mesothorax transverse. Middle and hindlegs flat, of swimming type; segments of tarsus not transverse. Upper Oligocene of Europe. One genus.

Palaeogyrinus Schlechtendal, 1894. Genotype—*P. strigatus* Schlechtendal, 1894; Upper Oligocene, Western Europe (Rott). Pronotum markedly transverse. Abdomen with six sterna. Elytron with nine furrows, segments of tibia and basal segment of tarsus of almost equal length and breadth (Fig. 768). One species. Upper Oligocene of Western Europe.

Family GYRINIDAE Latreille, 1810. Whirligig beetles

Small or medium sized beetles with flat body, swimming middle and hindlegs, much enlarged mesothorax, divided eyes and short antennae. Jurassic to Recent. More than 500 species under nine genera present in Recent fauna; four genera in Tertiary fauna. Species from the Jurassic known, but as yet insufficiently studied.

Family PAUSSIDAE Latreille, 1807

Small beetles, with much enlarged and stout antennae. Live in anthills (Fig. 769). Paleogene to Recent. About 350 species of Recent fauna relegated to nearly 30 genera. Eight genera found in the Paleogene of Europe (Baltic amber).

Family STAPHYLINIDAE Latreille, 1802. Rove beetles

Small, rarely medium sized beetles, with reduced elytra, considerably shorter than long, flexible abdomen (Fig. 770). Paleogene to Recent. One of the major families of the Recent fauna including more than 20,000 species and approximately 900 genera; 42 genera in the Tertiary fauna.

Family PSELAPHIDAE Latreille, 1802

Small beetles, with short elytra and short, inflated body, usually an elongated head and large maxillary palps (Fig. 771). Paleogene to Recent. More than 4,000 species and 500 genera in Recent fauna; 23 genera in the Paleogene of Europe (Baltic amber).

Family SCYDMAENIDAE Leach, 1815

Small beetles, living in anthills, with separated, elongated posterior coxae, long elytra and antennae (Fig. 772). Paleogene to Recent. About 1,300 species and 60 genera represented in the Recent fauna; 11 genera in the Paleogene of Europe (Baltic amber).

Family SILPHIDAE Latreille, 1807. Carrion beetles

Beetles of various sizes, with club-shaped antennae, hindcoxae not separated, 256 and forecoxae long, projecting (Fig. 773). Paleogene to Recent. More than 200 species and 200 genera in the Recent fauna; eight genera in the Tertiary fauna.

Family PTILIIDAE Heer, 1844

Exceptionally small beetles (0.25–1.4 mm) with short body, large head and, usually, feathery wings (Fig. 774). Paleogene to Recent. About 350 species and 30 genera in the Recent fauna; also found in the Paleogene of Europe (Baltic amber).

Family SCAPHIDIIDAE Latreille, 1806

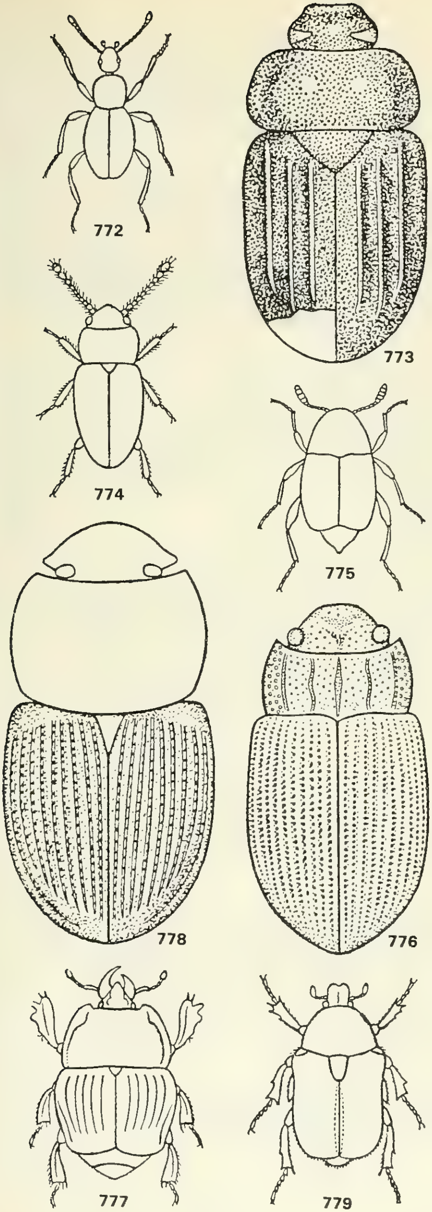
Small, strongly inflated beetles, with long elytra projecting anterior, and separated middle and posterior coxae (Fig. 775). Paleogene to Recent. More than 550 species and 20 genera in the Recent fauna; three genera in the Tertiary fauna.

Family HYDROPHILIDAE Latreille, 1802. Water scavenger beetles

Small or medium sized, rarely large, with club-shaped, inflated, short antennae directed to the front of head. Pronotum broad; elytra long, usually not a little shortened. Legs often bear swimming hairs or broad tarsi (Fig. 776). Paleogene to Recent. More than 1,700 species and 130 genera found in the Recent fauna; 15 genera in the Tertiary fauna.

Family HISTERIDAE Gyllenhal, 1808. Hister beetles

Small, rarely of medium size, with distinctly short, blunt body both posteriorly and anteriorly rarely elongate; with widely-placed coxae; elytra not covering end



Figs. 772–779. Families Scydamaenidae, Silphidae, Ptiliidae, Scaphidiidae, Hydrophilidae, Histeridae, Scarabaeidae.

772. *Scydamaenus* sp.; dorsal view, × 12. Recent (Yakobson, 1915). 773. *Blitophaga vetusta* Lomnicki; dorsal view, × 5. Quaternary; West Ukraine (Lomnicki, 1894). 774. *Ptenidium* sp.; dorsal view, × 28.1. Recent (Yakobson, 1915). 775. *Scaphidium* sp.; dorsal view, × 4.5. Recent (Yakobson, 1915). 776. *Helophorus polonicus* Lomnicki; dorsal view, × 15.5. Quaternary, West Ukraine (Lomnicki, 1894). 777. *Hister* sp.; dorsal view, × 5. Recent (Yakobson, 1915). 778. *Aphodicus rhinocerontis* Lomnicki; dorsal view, × 6.5. Quaternary, West Ukraine (Lomnicki, 1894). 779. *Cetonia aurata* Linnaeus; dorsal view, × 1.5. Recent (Yakobson, 1915).

of abdomen (Fig. 777). Paleogene to Recent. More than 3,000 species and 130 genera in Recent fauna; genus *Hister* Linnaeus, also reported from Tertiary fauna.

257 Family SCARABAEIDAE Latreille, 1802. Lamellicorn beetles

Medium sized, sometimes large beetles with varied structure. Antennal club made up of flat leaflike segments. Body usually blunt with clinging or digging legs; normally well-developed wings and large head and thoracic divisions (Figs. 778, 779). Paleogene to Recent. More than 20,000 species and 1,600 genera in Recent fauna; 31 genera in Tertiary fauna. *Proteroscarabeus* Grabau, 1921 reported from the Upper Jurassic.

Family LUCANIDAE Latreille, 1802. Stag beetles

Large, rarely of medium size, with club-shaped, lamellar antennae and large mandibles, sometimes attaining large dimensions in males (Fig. 780). Paleogene to Recent. About 900 primarily tropical species known belonging to 80 genera; four genera reported from the Tertiary fauna.

Family DASCILLIDAE Guerin, 1823

Medium-sized beetles, with mandibles protruding in front, threadlike or weakly serrated antennae, broad pronotum, close coxae and broadly segmented tarsi. Jurassic to Recent. About 400 species and 40 genera reported from the Recent fauna; two genera from the Tertiary fauna and one from the Jurassic.

Mesodascilla Martynov, 1926. Genotype—*M. jacobsoni* Martynov, 1926; Upper Jurassic, Kazakhstan (Malm, Karatau). Head free. Antennae little longer than head and pronotum, stout and serrated. Length of body about 12 mm (Fig. 781). One species.

Family HELODIDAE Leconte, 1862

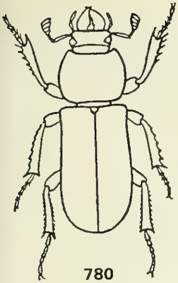
Small convex beetles, with short oval body, perpendicular head, threadlike antennae, short legs and five segmented tarsi (Fig. 782). Paleogene to Recent. About 650 species and 20 genera known from the Recent fauna; two genera from the Tertiary fauna.

258 Family PSEPHENIDAE Lacordaire, 1854

Small, flat, elongated beetles with projecting head, long and weakly serrated antennae, strong legs, swollen femur and five segmented tarsi. Neogene to Recent. About 20 species belonging to a few genera; a relict group in the Recent fauna linked to mountain streams, represented also in the Miocene fauna of North America.

Family BYRRHIDAE Latreille, 1806

Small, rarely medium-sized, short-oval, sharply inflated Coleoptera with small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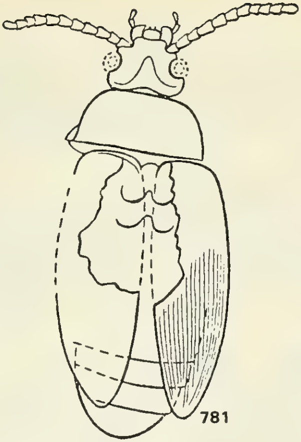
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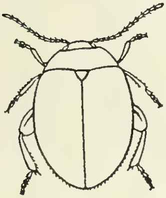
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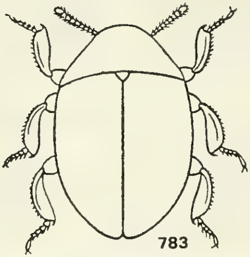
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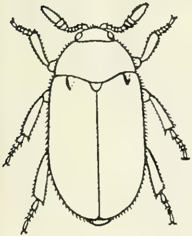
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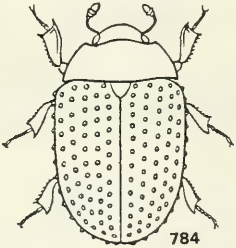
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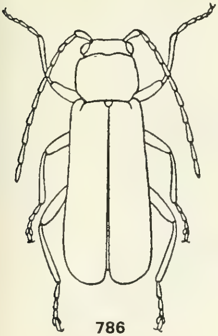
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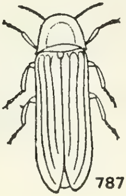
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Figs. 780–787. Families Lucanidae, Dascillidae, Helodidae, Byrrhidae, Nosodendridae Dermestidae, Canthariididae, Lampyridae.

780. *Platycerus caraboides* Linnaeus; dorsal view, × 2.7. Recent (Yakobson, 1815). 781. *Mesodascilla jacobsoni* Martynov; dorsal view, × 5.4. Upper Jurassic, South Kazakhstan (Martynov, 1926). 782. *Scirtes hemisphaericus* Linnaeus; dorsal view, × 8. Recent (Yakobson, 1915). 783. *Byrrhus* sp.; dorsal view, × 5.7. Recent (Yakobson, 1915). 784. *Nosodendron fasciculare* Olivier; dorsal view, × 8.5. Recent (Yakobson, 1915). 785. *Attagenus pellio* (Linnaeus); dorsal view, × 4.8. Recent (Yakobson, 1915). 786. *Cantharis* sp.; dorsal view, × 3.7. Recent (Yakobson, 1915). 787. *Lampyrus noctiluca* Linnaeus; dorsal view, × 3. Recent (Yakobson, 1915).

head deeply withdrawn toward prothorax; antennae capitate. Legs short, strong with four or five segmented tarsi (Fig. 783). Paleogene to Recent. About 450 species and 30 genera known in the Recent fauna; two genera from the Tertiary fauna.

Family NOSODENDRIDAE Erichson, 1846

Fairly small, short-oval, markedly inflated beetles with weakly projecting head, capitate antennae, sharply transverse forecoxae, very large metanotum and short legs with five-segmented tarsi (Fig.784). Paleogene to Recent. Forty species belonging to two genera from the Recent fauna; two genera from the Tertiary fauna.

Family DERMESTIDAE Latreille, 1802. Skin beetles

Not particularly small to medium sized, moderately elongate or short-oval beetles, without luster, with downwardly projecting head, capitate antennae; legs short with slightly separated anterior and middle, and closely placed hindcoxae, and five segmented tarsi (Fig. 785). Paleogene to Recent. About 700 species and 40 genera from the Recent fauna; three genera from the Tertiary fauna.

Family CANTHARIDIDAE Heyden, Reitter and Weise, 1883. Soldier beetles, soft-bodied beetles

Medium sized, rarely small or large, gently convex, elongate beetles, with distinct prothorax; abdomen with seven to eight sterna; legs weak (Fig. 786). Paleogene to Recent. About 1,300 species in Recent fauna; six genera from the Tertiary fauna.

Family LAMPYRIDAE Leach, 1817. Fire flies

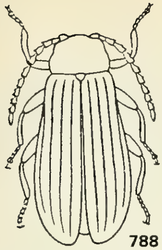
Medium sized, elongate and nonconvex, with head covered by overhanging pronotum, bearing serrate antennae; long elytra in males, bearing epipleura; legs with inflated femora and five segmented tarsi. Females wormlike (Fig. 787). Paleogene to Recent. About 18,000 species and 60 genera from the Recent fauna; two genera from the Tertiary fauna.

Family LYCIDAE Lacordaire, 1857

Medium or large sized, moderately elongate, flat, with small head covered by pronotum; often with serrate antennae; large flat elytra with reticulate venation; legs with broad femurs and large trochanter (Fig. 788). Paleogene to Recent. More than 2,800, primarily tropical species, belonging to 53 genera; one genus reported from the Paleogene of Europe (Baltic amber).

Family MELYRIDAE Newmann, 1834. Soft-winged flower beetles

Fairly small and moderately elongate beetles, with large head directed forward,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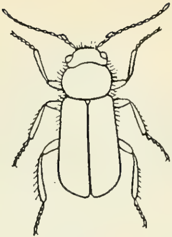
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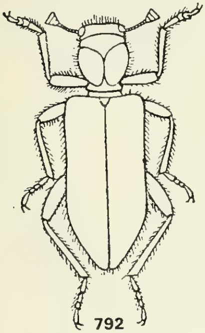
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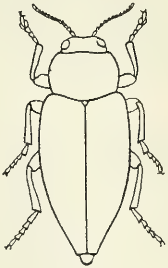
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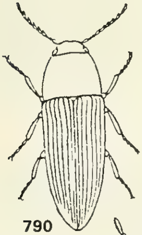
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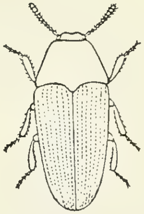
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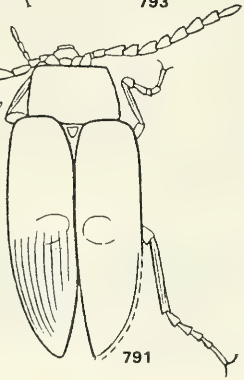
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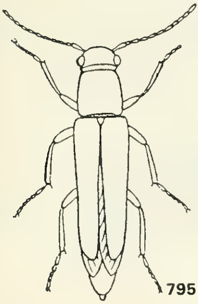
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Figs. 788–795. Families Lycidae, Melyridae, Cleridae, Elateridae, Melasidae, Throscidae, Buprestidae, Lymexylidae.

788. *Lycostomus* sp.; dorsal view, × 2.2. Recent (Yakobson, 1915). 789. *Malachius bipustulatus* Linnaeus; dorsal view, × 4.8. Recent (Yakobson, 1915). 790. *Eucnemis capucina* Ahrens; dorsal view, × 5.7. Recent (Yakobson, 1915). 791. *Tersus crassicornis* Martynov; dorsal view, × 4.6. Upper Jurassic, Kazakhstan (Martynov, 1926). 792. *Trichodes* sp.; dorsal view, × 3.2. Recent (Yakobson, 1915). 793. *Throscus dermestoides* Linnaeus; dorsal view, × 9.8. Recent (Yakobson, 1915). 794. *Buprestis* sp.; dorsal view; × 2.7. Recent (Yakobson, 1915). 795. *Lymexylon navale* linnaeus; dorsal view, × 3.7. Recent (Yakobson, 1915).

with capitate antennae; pronotum distinctly separate; elytra flat; abdomen sometimes short, with six or seven sterna; tarsi five-segmented, foretarsi occasionally four-segmented (Fig. 789). Paleogene to Recent. More than 1,800 species in the Recent fauna; three genera from the Tertiary fauna.

Family CLERIDAE Latreille, 1802. Checkered beetles

Small or medium sized, elongate and fairly convex with head directed forward, antennae serrate or capitate, prothorax separate; legs strong, often long, with five-segmented tarsi; abdomen with five or six sterna (Fig. 790). Paleogene to Recent. About 2,500 species and 200 genera from the Recent fauna; five genera from the Tertiary fauna—primarily from the Paleogene of Europe (Baltic amber).

Family ELATERIDAE Leach, 1815. Click beetles

Medium or large sized beetles, with elongated body, somewhat elongated head 259 and broad, flat prothorax; mesothorax relatively mobile; antennae threadlike, often serrate or pectinate, located in front of eyes, and below margin of frons. Jurassic to Recent. Extensively distributed. More than 7,000 species belonging to 350 genera from the Recent fauna; about 80 species belonging to nearly 20 genera from the Tertiary fauna; a few little-studied genera from the Upper Jurassic of Western Europe; one genus from the Upper Jurassic of Kazakhstan.

Tersus Martynov, 1926. Genotype—*T. crassicorneis* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Pronotum broader than long, transverse; elytron with traces of furrows; tibiae slender longitudinally ribbed. Length of body 12.25 mm. Length of pronotum 2.15 mm (Fig. 791). One species. Upper Jurassic of Kazakhstan.

Family MELASIDAE Leach, 1817

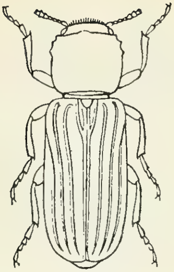
Small or medium sized beetles resembling click beetles; antennae located between eyes, threadlike or pinnate, close at base (Fig. 792). Paleogene to Recent. About 1,100 species belonging to 150 genera from the Recent fauna; three genera from the Tertiary fauna.

Family THROSCIDAE Lacordaire, 1857

Small, stout beetles with markedly inflated head, often capitate antennae and fairly broad body across base of elytra (Fig. 793). Paleogene to Recent. About 200 species belonging to several genera found in the Recent fauna; one genus from the Paleogene of Europe (Baltic amber).

Family BUPRESTIDAE Leach, 1815. Metallic wood borers

Medium sized beetles, often large, rarely small, usually with elongate body and head; threadlike or serrate antennae; closely fused, immobile thoracic region;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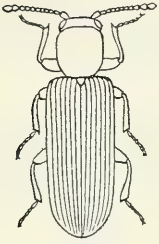
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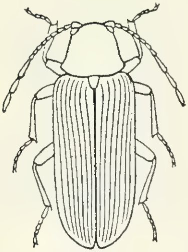
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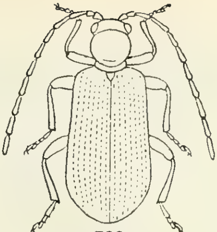
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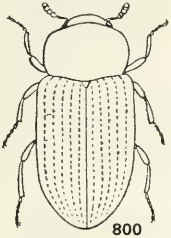
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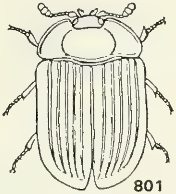
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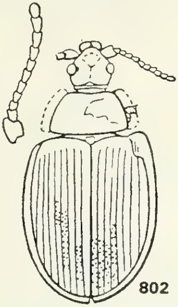
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Figs. 796–802. Families Bostrychidae, Lyctidae, Anobiidae, Ptinidae, Cisidae, Ostomatidae.

796. *Apate* sp.; dorsal view, × 2.2. Recent (Yakobson, 1915). 797. *Lyctus* sp.; dorsal view, × 1.5. Recent (Yakobson, 1915). 798. *Anobium rufipes* Fabricius; dorsal view, × 8.5. Recent (Yakobson, 1915). 799. *Ptinus* sp.; dorsal view, × 9.2. Recent (Yakobson, 1915). 800. *Cisboleti* Scopoli; dorsal view, × 11.5. Recent (Yakobson, 1915). 801. *Ostoma ferrugineum* Linnaeus; dorsal view, × 3.5. Recent (Yakobson, 1915). 802. *Lithostoma expansum* Martynov; dorsal view, × 7.5. Upper Jurassic, Kazakhstan (Martynov, 1926).

legs short and strong; elytra convex (Fig. 794). Paleogene to Recent. Extensively distributed, primarily a tropical family; more than 12,000 species and 400 genera in the Recent fauna; 17 genera from the Tertiary fauna.

260 Family LYMEXYLIDAE Leach, 1917. Ship-timber beetles

Medium sized beetles with cylindrical form; elongate, with large head and eyes, threadlike or serrate antennae and narrow or shortened, diverging elytra (Fig. 795). Paleogene to Recent. About 40 species under five genera in the Recent fauna, of which three genera are also known in the Tertiary fauna.

Family BOSTRYCHIDAE Latreille, 1802

Medium sized, cylindrical beetles, not necessarily long; with markedly convex pronotum overhanging head, capitate antennae; elytra posteriorly truncated (Fig. 796). Neogene to Recent. About 350 species and 50 genera in the Recent fauna; species of two genera in the Tertiary fauna.

Family LYCTIDAE Billbergh, 1820

Small beetles with elongate body, projecting head, narrow pronotum not overhanging head, slender antennae with indistinct club, long non-truncated elytra (Fig. 797). Paleogene to Recent. About 60 species under three genera in the Recent fauna; one genus in the Paleogene of Europe (Baltic amber).

Family ANOBIIDAE Shuck, 1840. Death watch beetles

Small and moderately elongate beetles, with prominently convex prothorax not overhanging head and directed downward; antennae often capitate; legs weak; elytra not shortened (Fig. 798). Paleogene to Recent. More than 1,200 species under 90 genera in the Recent fauna; five genera in the Tertiary fauna.

Family PTINIDAE Latreille, 1802. Spider beetles

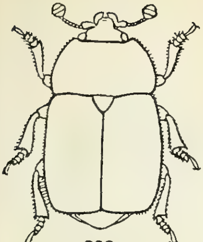
Small, beetles, very close to previous family of Coleoptera, with threadlike antennae and prothoracic region sharply tapering posteriorly; legs strong, not particularly short (Fig. 799). Paleogene to Recent. About 500 species and 40 genera occur in the Recent fauna; one genus in the Tertiary fauna.

Family CISIDAE Leach, 1819

Small and moderately elongate beetles, with broad pronotum directed down
261 over head; antennae capitate; elytra not shortened; epipleura wide; legs weak; tarsi four segmented (Fig. 800). Paleogene to Recent. Nearly 350 species and 25 genera from the Recent fauna; two genera from the Tertiary fauna.

Family OSTOMATIDAE Reitter, 1882

Small, rarely medium sized, with head projecting forward, weakly capitate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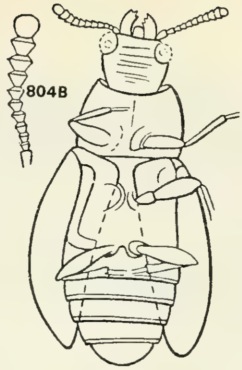
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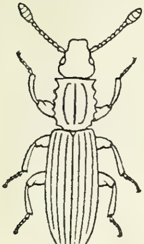
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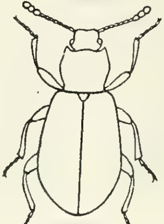
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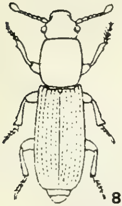
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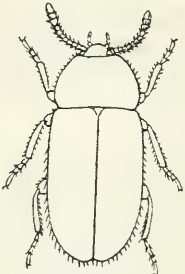
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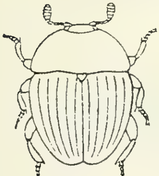
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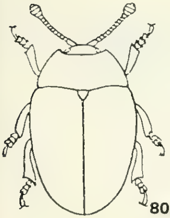
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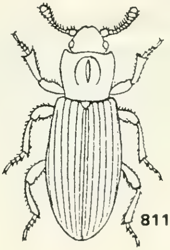
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Figs. 803–811. Families Nitidulidae, Rhizophagidae, Cucujidae, Phalacridae, Erotylidae, Lathridiidae, Mycetophagidae, Colydiidae.

803. *Nitidula bipunctata* Linnaeus; dorsal view, × 8.2. Recent (Yakobson, 1915). 804. *Nitidulina eclavata* Martynov; A—general view, × 1.5; B—antenna, × 2.8. Upper Jurassic, South Kazakhstan (Martynov, 1926). 805. *Rhizophagus bipustulatus* Fabricius; dorsal view, × 11. Recent (Yakobson, 1915). 806. *Silvanus* sp.; dorsal view, × 12. Recent (Yakobson, 1915). 807. *Phalacrus* sp.; dorsal view, × 8. Recent (Yakobson, 1915). 808. *Tritoma* sp.; dorsal view, × 7.5 Recent (Yakobson, 1915). 809. *Lathridius* sp.; dorsal view, × 16.5. Recent (Yakobson, 1915). 810. *Triphyllus bicolor* Fabricius; dorsal view, × 10. Recent (Yakobson, 1915). 811. *Bothrideres* sp.; dorsal view, × 6.3. Recent (Yakobson, 1915).

antennae, transversely disposed forecoxae; body usually flat and broad, with broad, marginal expansions along elytra and pronotum; legs weak, with very short first segment of tarsus (Fig. 801). Jurassic to Recent. More than 600 species and 50 genera in the Recent fauna; three genera in the Tertiary fauna; single genus from the Jurassic.

Lithostoma Martynov, 1926. Genotype—*L. expansum* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Antennae with very weakly developed terminal bulge; anterior margin of pronotum uniform, without any expansion; elytra without convex longitudinal ribs. Length of body about 6 mm (Fig. 802). One species. Upper Jurassic of Kazakhstan.

Family NITIDULIDAE Latreille, 1802

Small, fairly convex, moderately elongate or with short body; head directed forward, with capitate antennae; legs strong, but short; tarsi broad, five-segmented; elytra often shortened (Fig. 803). Jurassic to Recent. More than 2,400 species and 160 genera in the Recent fauna; 20 genera in the Tertiary fauna and one genus in the Jurassic.

Nitidulina Martynov, 1926. Genotype—*N. eclavata* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Antennae short with a faintly visible bulge at tip; pronotum one and one-half times as broad as it is long. Length of body 4.9 mm (Fig. 804). One species. Upper Jurassic of Kazakhstan.

262 Family RHIZOPHAGIDAE Redtenbacher, 1845

Small and elongate beetles with large head directed forward, antennae moderately inflated at apices; legs strong; pronotum elongated; elytra long, but not covering end of abdomen (Fig. 805). Paleogene to Recent. More than 40 species and three genera in the Recent fauna, of which one is also known from the Paleogene of Europe (Baltic amber).

Family CUCUJIDAE Latreille, 1802

Small, rarely of medium size, elongate and flat beetles, with large head projecting in front; antennae elongate, capitate or threadlike. Sockets of middle coxae not closed behind; elytra long with longitudinal ribs or tubercles, also seen on pronotum (Fig. 806). Paleogene to Recent. More than 1,300 species and 100 genera known in the Recent fauna; five genera in the Tertiary fauna.

Family PHALACRIDAE Leach, 1815

Small, very short, markedly convex beetles, with elongated head, capitate antennae; smooth elytra sometimes bearing slender furrows, covering entire abdomen; legs short (Fig. 807). Paleogene to Recent. More than 500 species and 50 genera in the Recent fauna; two genera in the Tertiary fauna.

Family EROTYLIDAE Latreille, 1802

Small or medium-sized, rarely large beetles, with small elongated head, capitate antennae, broad pronotum, widely spaced globular coxae, with closed coxal sockets; legs short, strong; elytra long (Fig. 808). Paleogene to Recent. About 3,800 species and 230 genera in the Recent fauna; seven genera in the Tertiary fauna.

Family LATHRIDIIDAE Redtenbacher, 1845

Small or very small, elongate beetles with projecting head, capitate antennae; narrow prothorax, often with clear ornamentation; elytra long, often with longitudinal ribs (Fig. 809). Paleogene to Recent. About 550 species and 30 genera in the Recent fauna; two genera in the Paleogene of Europe (Baltic amber) and Oligocene of Western Europe.

Family MYCETOPHAGIDAE Leach, 1815

Small or medium sized, oval beetles, with small head withdrawn toward prothorax and weakly capitate antennae; pronotum broad; elytra long; legs relatively slender, with four-segmented tarsi (in males three segments!) (Fig. 810). Paleogene to Recent. About 200 species and 20 genera from the Recent fauna; one genus from the Lower Oligocene of Western Europe.

Family COLYDIIDAE Erichson, 1845

Small or of medium sized and markedly convex or flat beetles with well-developed ornamentation in the form of tubercles and ribs; large projecting head, capitate antennae; long elytra with ribs and pits; legs fairly strong, with four-segmented tarsi (Fig. 811). Paleogene to Recent. About 1,400 species and 100 genera from the Recent fauna; four genera from the Paleogene of Europe (Baltic amber).

Family ENDOMYCHIDAE Leach, 1810

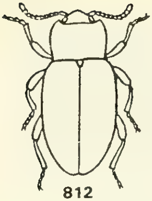
Small, oval and moderately convex beetles, with small elongated head and capitate antennae; legs short with simple claws on four- (or three-) segmented tarsi (Fig. 812). Paleogene to Recent. About 1,000 species and 90 genera in the Recent fauna; three genera in the Paleogene of Europe (Baltic amber).

Family COCCINELLIDAE Latreille, 1807

Small, rarely medium sized, short, oval, sometimes almost rounded, markedly convex beetles. Head not large, with capitate antennae; legs short, broad at base or with toothed claws on three-segmented or, rarely four-segmented tarsi (Fig. 813). Live on plants. Paleogene to Recent. About 3,400 species and 240 genera in the Recent fauna; seven in the Tertiary fauna.

Family OEDEMERIDAE Latreille, 1810

Medium sized or small and elongate beetles, with head extending and projecting



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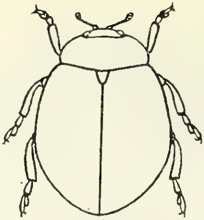

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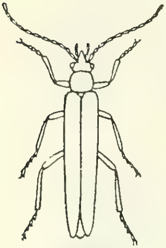

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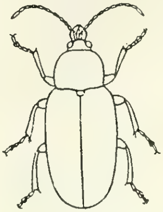

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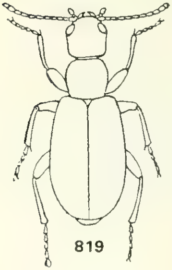

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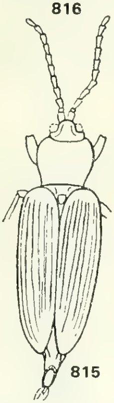

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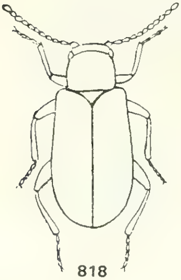

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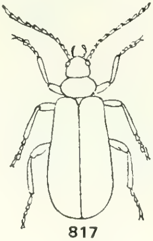

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Figs. 812–819. Families Endomychidae, Coccinellidae, Oedemeridae, Pythidae, Pyrochroidae, Aderidae, Anthicidae.

812. *Lycoperdina succincta* Linnaeus; dorsal view, × 6.5. Recent (Yakobson, 1915). 813. *Coccinella* sp.; dorsal view, × 6. Recent (Yakobson, 1915). 814. *Oedemera lurida* Marsham; dorsal view, × 6. Recent (Yakobson, 1915). 815. *Necromera baeckmani* Martynov; dorsal view, × 5.2. Upper Jurassic, Kazakhstan (Martynov, 1925). 816. *Mycterus curculionoides* Illiger; dorsal view, × 3.5. Recent (Yakobson, 1915). 817. *Pyrochroa coccinea* Linnaeus; dorsal view, × 1.9. Recent (Yakobson, 1915). 818. *Aderus* sp.; dorsal view, × 12. Recent (Yakobson, 1915). 819. *Anthicus* sp.; dorsal view, × 12.5. Recent (Yakobson, 1915).

anteriorly; eyes large; antennae long and slender; pronotum narrow. Elytra long, often with divergent apices; coxae large, protruding; middle and foretarsi 263 five-segmented, hindtarsi four-segmented (Fig. 814). Jurassic to Recent. About 800 species and 70 genera in the Recent fauna; one genus in the Jurassic and one in the Paleogene of Europe (Baltic amber).

Necromera Martynov, 1926. Genotype—*N. baeckmani* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Pronotum broad in anterior half, noticeably narrower than both elytra, which bear indistinct bands; antennae two to five times longer than pronotum. Length of body 7.75 mm (Fig. 815). Upper Jurassic of Kazakhstan. One species.

Family PYTHIDAE Solsky, 1834

Small or medium sized and moderately elongate beetles with small projecting head and slender, rarely serrate or weakly capitate antennae; tarsi as described under previous family (Fig. 816). Paleogene to Recent. About 300 species and 46 genera known in the Recent fauna; three genera in the Tertiary fauna.

Family PYROCHROIDAE Latreille, 1807

Fairly small or medium sized with head projecting and tapering toward base, pinnate or serrate, rarely threadlike, antennae; pronotum small, broader than head, but narrower than elytra, which widen toward posterior extremity and completely cover abdomen; legs slender, long with large coxae, five-segmented fore- and middle tarsi and four-segmented hindtarsi (Fig. 817). Paleogene to Recent. About 150 species and 14 genera from the Recent fauna; one genus from the Paleogene to Europe (Baltic amber).

Family ADERIDAE Auct

Small or very small, moderately elongate and convex beetles, with head directed downward, withdrawn toward prothorax; eyes large, narrow; antennae slender, beaded, weakly capitate; pronotum narrower than long, smooth elytra; fore- and middle coxae protrude; tarsi with markedly shortened penultimate segment, five- or four-segmented (Fig. 818). Paleogene to Recent. About 650 species and 10 genera in the Recent fauna; two genera in the Paleogene of Europe (Baltic amber).

264 Family ANTHICIDAE Latreille, 1825

Small beetles of moderate build, with projecting, large head, distinctly separate from prothorax, bearing beaded antennae; pronotum distinctly narrowing posteriorly, separated from elytra; coxae protruding; tarsi five- and four-segmented (Fig. 819). Paleogene to Recent. About 2,200 species and 40 genera in the Recent fauna; two genera in the Paleogene to Europe (Baltic amber) and in the Oligocene of Western Europe.

Family MORDELLIDAE Latreille, 1802

Small or medium sized beetles, noticeably laterally compressed with body tapering posteriorly; head small, directed downward with threadlike or serrate antennae; broad pronotum of same width as elytra; elytra convergent, not covering entire abdomen; abdomen with five or six sterna; hindtarsi longer than tibiae (Fig. 820). Paleogene to Recent. About 1,000 species and 24 genera in the Recent fauna; two genera in the Paleogene of Europe (Baltic amber) and the Miocene of Sicily.

Family PRAEMORDELLIDAE Sceguleva-Barovskaja, 1929

[nom. transl. Rohdendorf, hic (ex Praemordellinae Scegoleva-Barovskaja, 1929)]

Beetles of medium size, laterally compressed, with distinctly pointed abdomen bearing seven sterna; elytra not covering end of abdomen; hindtarsi shorter than tibiae. Allied to beetles of family Mordellidae, distinguished by large number of free sterna of abdomen and short posterior tarsi. Jurassic. One genus.

Praemordella Scegoleva-Barovskaja, 1929. Genotype—*P. martynovi* Scegolevy-Barovskaja, 1919; Upper Jurassic, Chimkent province (Malm, Karatau). Tibia with one broad spur. Segments of tarsi approximately of same size. Length of body 7.3 mm (Fig. 821). One species. Upper Jurassic of Kazakhstan.

265

Family SCRAPTIIDAE Mulsant, 1856

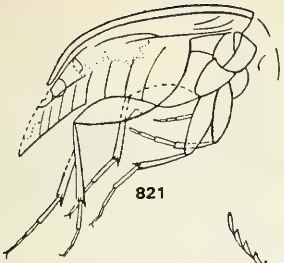
Small beetles, with elongate body and large head directed downward or forward; antennae threadlike; pronotum short, hardly narrower than width of elytron; elytra longer, covering abdomen completely (Fig. 822). Paleogene to Recent. About 125 species and 10 genera in the Recent fauna; one genus in the Tertiary fauna.

Family SERROPALPIDAE Latreille, 1829

Beetles of small or medium size, oval or elongate, with small head directed downward bearing threadlike or moderately capitate antennae; pronotum broad; legs slender, with two spurs and five- and four-segmented tarsi (Fig. 823). Paleogene to Recent. About 430 species and 90 genera in Recent fauna; three genera in the Paleogene of Europe (Baltic amber).

Family MELOIDAE Gyllenhal, 1810. Blister beetles

Beetles of medium or fairly large size, with head distinctly separated from thorax; antennae moderately long, of varied structural types; prothorax small, narrower than elytra; legs strong, tenacious (Fig. 824). Paleogene to Recent. About 2,300 species and 90 genera from the Recent fauna; five genera from the Tertiary fauna.



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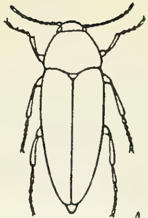

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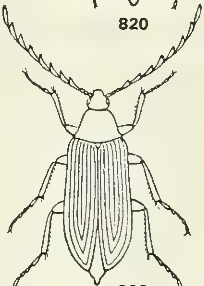

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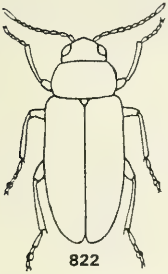

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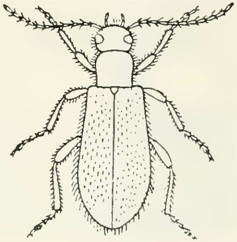

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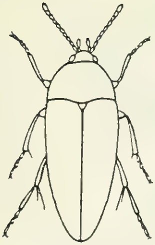

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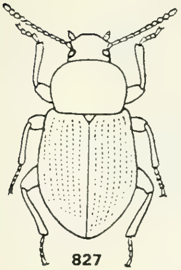

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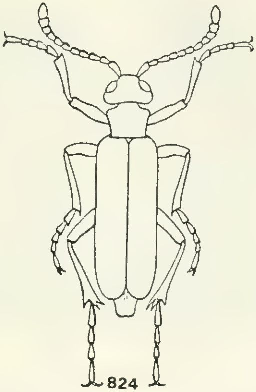

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Figs. 820–827. Families Mordellidae, Praemordellidae, Scraptiidae, Serropalpidae, Meloidae, Lagriidae, Alleculidae, Tenebrionidae.

820. *Anaspis* sp.; dorsal view, × 7. Recent (Yakobson, 1915). 821. *Praemordella martynovi* Scegoleva-Barovskaja; lateral view, × 6.6. Upper Jurassic, Kazakhstan (Scegoleva-Barovskaja, 1929). 822. *Scraptia* sp.; dorsal view, × 14. Recent (Yakobson, 1915). 823. *Orchesis micans* Panzer; dorsal view, × 6.6. Recent (Yakobson, 1915). 824. *Lytta* sp.; dorsal view, × 1.9. Recent (Yakobson, 1915). 825. *Lagria hirta* Linnaeus; dorsal view, × 3.4. Recent (Yakobson, 1915). 826. *Pseudocistella cerambycoides* Linnaeus; dorsal view, × 4.8. Recent (Yakobson, 1915). 827. *Helops* sp.; dorsal view, × 3.4. Recent (Yakobson, 1915).

Family RHIPIPHORIDAE Costa, 1850

Beetles of medium size, elongate, with convex ventral surface of body; head small, directed downward and backward; pronotum broad; elytra usually shortened. Paleogene to Recent. About 350 species and 30 genera from the Recent fauna; three genera in the Tertiary fauna.

Family LAGRIIDAE Latreille, 1825

Beetles of small or medium size, with moderately elongate body and free projecting head with threadlike or weakly capitate antennae; pronotum small, almost cylindrical, considerably narrower than elytra, which cover abdomen completely and widen posteriorly; legs long, tarsi five- and four-segmented (Fig. 825). Paleogene to Recent. About 650 species and 60 genera from the Recent fauna; one genus from the Paleogene of Europe (Baltic amber).

Family ALLECULIDAE Mulsant, 1856

Beetles of medium or small size, with small protruding head, considerably narrower than pronotum, bearing threadlike and more or less serrate antennae; pronotum broad posteriorly; elytra usually cover entire abdomen; legs long; tarsi five and four-segmented (Fig. 826). Paleogene to Recent. About 1,400 species and 120 genera from the Recent fauna; five genera from the Tertiary fauna.

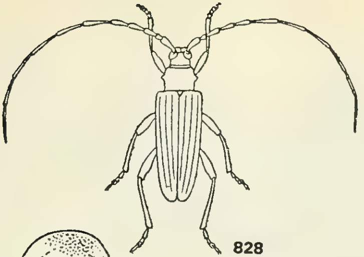
Family TENEBRIONIDAE Latreille, 1802. Darkling beetles

Beetles of medium or large size, rarely small. Head bears broad frontal plate, in form of shield, covering base of antennae; antennae threadlike, beaded or weakly capitate; middle and posterior coxae more or less closely placed; elytra cover entire abdomen; legs strong and long; tarsi five- and four-segmented (Fig. 827). Paleogene to Recent. More than 14,000 species in the Recent fauna; 15 genera in the Tertiary fauna.

Family CERAMBYCIDAE Latreille, 1802. Long-horned beetles

Beetles of medium or large size, with an elongate body. Head moderately large with very long, threadlike or beaded antennae; elytra usually long, sometimes with distinct traces of venation; legs strong; tarsi with greatly reduced fourth segment, because of which they appear to be four-segmented (Fig. 828). Jurassic to Recent. Very abundant in the Recent fauna, with more than 17,000 species and nearly 2,400 genera of which 31 are known from the Tertiary fauna and one from the Jurassic.

Parandrexis Martynov, 1926. Genotype—*P. parvala* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Head large, transverse with mandibles directed forward and upward, equal to or exceeding head; antennae long, threadlike; legs fairly short. Length of body 4.5–5.5 mm, of antennae 3.5–5.2 mm (Fig. 829). One species. Upper Jurassic of Kazakhstan.



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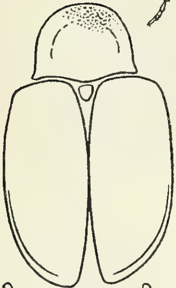

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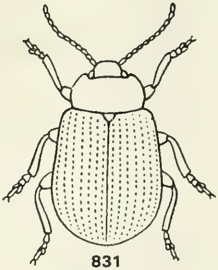

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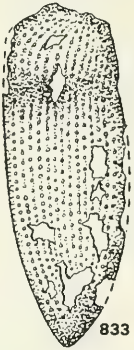

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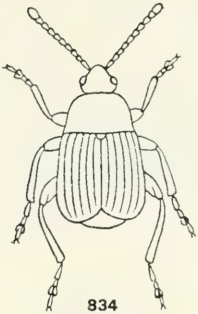

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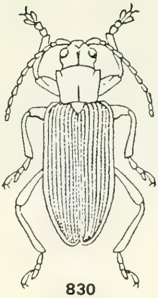

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Figs. 828–834. Families Cerambycidae, Chrysomelidae, Bruchidae.

828. *Cerambyx cerdo* Linnaeus; dorsal view, × 0.7. Recent (Yakobson, 1915). 829. *Parandrexis parvula* Martynov; ventral view, × 5.5. Upper Jurassic, Kazakhstan. 830. *Donacia* sp.; dorsal view, × 3.5. Recent (Yakobson, 1915). 831. *Chrysomela* sp.; dorsal view, × 3.2. Recent (Yakobson, 1915). 832. *Meseumolpites jurassicus* (Martynov); dorsal view, × 13.3. Upper Jurassic, Kazakhstan (Martynov, 1926). 833. *Mesosagrites multipunctatus* Martynov; elytron, × 5.2. Lower Jurassic, Western Siberia (Martynov, 1935). 834. *Bruchus rufipes* Herbst; dorsal view, × 7.7. Recent (Yakobson, 1915).

Family CHRYSOMELIDAE Latreille, 1802. Leaf beetles

Beetles of small and medium size, usually oval or short-oval, rarely elongate, usually markedly convex, with small head, often markedly withdrawn into 266 prothorax; antennae beaded, rarely weakly serrate or capitate; pronotum always narrower than elytra, which usually cover entire abdomen; legs short, of clinging type; tarsi apparently four-segmented (Figs. 830, 831). Jurassic to Recent. Very large family in the Recent fauna with more than 24,000 species and 1,200 genera; about 30 genera known in the Tertiary fauna and two in the Jurassic.

Meseumolpites Ponomarenko, nom. nov. (*Eumolpites* Martynov, 1926, nec *Eumolpites* Heer, 1865, syn. nov.). Genotype—*Eumolpites jurassicus* Martynov, 1926; Upper Jurassic, Kazakhstan (Malm, Karatau). Head not visible from above; pronotum rounded in front, with pointed posterior—lateral angles and broad marginal belt covered by pits and depressions; elytra broader than pronotum. Length of body 10.6 mm, of elytron 7.75 mm (Fig. 832). One species. Upper Jurassic of Kazakhstan.

Mesosagrites Martynov, 1935. Genotype—*M. multipunctatus* Martynov, 1935; Lower Jurassic, Chelyabinsk province (Lower Liassic, Sykhomesovo). Basal one-third of elytron, distinctly convex; 14 rows of pitlike depressions on elytron; between rows of pits fine transverse wrinkles. Length of elytron 11.5 mm, width 4 mm (Fig. 833). One species. Lower Jurassic of West Siberia.

Family BRUCHIDAE Latreille, 1802. Seed weevils

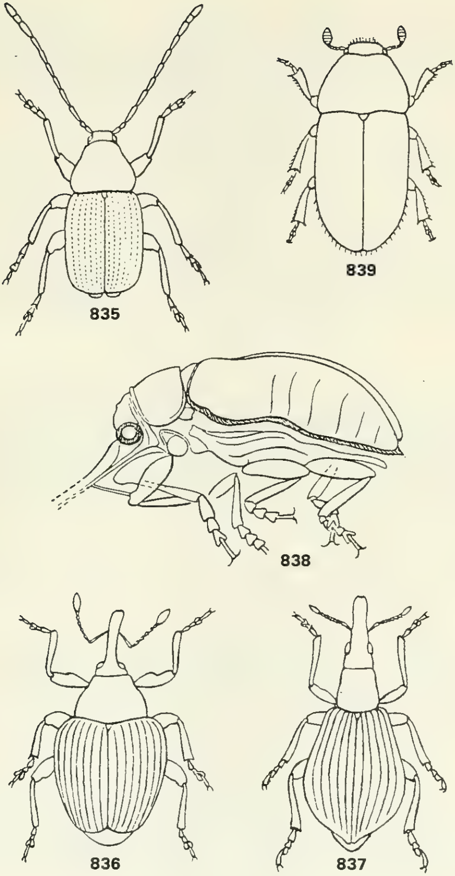
Beetles of small, rarely medium size with short, markedly convex body. Head pointed in front and depressed below; antennae filiform, serrate or weakly capitate; pronotum broad at back, of same width as elytra, which are shortened and do not cover end of abdomen; legs long, strong with apparently four-segmented tarsi (Fig. 834). Paleogene to Recent. About 900 species and 13 genera from the Recent fauna; four genera from the Tertiary fauna.

Family ANTHRIBIDAE Billbergh, 1820

Beetles of very small, rarely medium size, moderately elongate with small, short head directed downward and distinctly protruding mandibles; antennae long, without pedicel, clavate; pronotum broad posteriorly; elytra somewhat shortened (Fig. 835). Paleogene to Recent. About 2,200 species and 280 genera from the Recent fauna; 11 genera from the Tertiary fauna.

Family CURCULIONIDAE Latreille, 1802. Weevils

Beetles of small, rarely medium or large size, with head produced into more or less elongated rostrum; geniculate antennae with distinctly demarcated pedicel (Figs. 836, 837). Jurassic to Recent. Largest family of Coleoptera with more than 40,000 species and several thousand genera in the Recent fauna; more than 130 genera from the Tertiary fauna and one genus from the Jurassic of Kazakhstan.



267 Figs. 835–839. Families Anthribidae, Curculionidae, Ipidae.

835. *Anthribus albinus* Linnaeus; dorsal view, × 3. Recent (Yakobson, 1915). 836. *Ceutorhynchus* sp.; dorsal view, × 9.3. Recent (Yakobson, 1915). 837. *Apion* sp.; dorsal view, × 9. Recent (Yakobson, 1915). 838. *Archeorrhynchus tenuicornis* Martynov; lateral view, × 8. Upper Jurassic, South Kazakhstan (Martynov, 1926). 839. *Hulesinus fraxini* Panzer; dorsal view, × 12.5. Recent (Yakobson, 1915).

Archaeorrhynchus Martynov, 1926. Genotype—*A. tenuicorne* Martynov, 1926; Upper Jurassic, Chimkent province (Malm, Karatau). Rostrum straight, at least double the length of head; basal segment of antenna with furrows; pronotum short; elytra long; femur inflated. Length of body 6.2 mm (Fig. 838). One species. Upper Jurassic of Kazakhstan.

Family IPIDAE Heyden, Reitter and Weise, 1833. Bark beetles

Beetles of small or very small size, with short, cylindrical body, blunt at posterior end. Head large, markedly drawn into pronotum, directed downward; antennae capitate, short; legs short but strong; elytra long, with peculiar notches or denticles on posterior side, bordering large depression at end of body ('declivity' of bark beetles) (Fig. 839). Paleogene to Recent. About 2,000 species and 130 genera in the Recent fauna; five genera in the Tertiary fauna.

* * *

Numerous Mesozoic genera of Coleoptera have not been included in the present summary. Their affinity with the known families cannot be determined for lack of good descriptions and diagrams. An introduction to these forms is provided by Handlirsch (1906, 1938). Thirty-six genera have been described from the Cretaceous. Also, many remains of Coleoptera have not been given scientific names.

268 Order STREPSIPTERA. Twisted-winged insects

(O.I. Martynova)

Small (1.5–4 mm) insects, with pronounced sexual dimorphism. Males winged; forewings rudimentary, transformed into short, narrow bent plates; hindwings well developed, broad, fold back like a fan when at rest; veins longitudinal; few. Large, compound eyes present; ocelli absent; mouthparts reduced; antennae four- to seven-segmented, third segment always with lateral growth. Pro- and mesothorax very small; metathorax well developed, with tergum covering base of abdomen; tarsus two to five segmented. Abdomen with 10 segments.

Females resemble larvae, without wings, often also without legs and other appendages. In the great majority of species females sedentary, remain within body of host insect in which they lived as larvae, Endoparasites of various orders of insects. Paleogene to Recent. Seven families in the Recent fauna, of which only one is known in fossil form—Mengeidae.

Family MENGEIDAE Pierce, 1908

Antennae in males seven-segmented; tarsi five-segmented with two claws (Fig. 840). Paleogene to Recent. One species belongs to the Paleogene of Europe (Baltic amber).

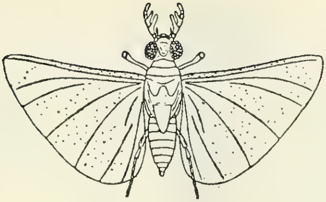


Fig. 840. Order Strepsiptera.

Mengea tertiaria (Menge); dorsal view, × 9. Paleogene, Europe (Baltic amber) (Menge, 1866).

Coleopteroidea Incertae sedis

(B.B. Rohdendorf)

Family PROTOCOLEIDAE Tillyard, 1924

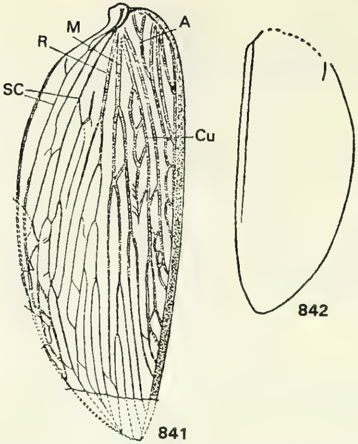
Anterior wings in the form of broad, but rather flat elytra, with relatively complex venation, consisting of many, generally parallel veins, or with indistinct venation, consisting of single marginal (? costal) vein. Structure of hindwing and body not known. Length of elytron 8–15 mm. Upper Permian. Two genera.

Protocoleus Tillyard, 1924. Genotype—*P. mitchelli* Tillyard, 1924; Upper Permian, Australia (Belmont). Anterior (?) margin of elytron markedly convex and delicate; venation consists of several weakly branching longitudinal veins, almost without cross veins; almost all systems of veins distinguishable (SC, R, M, Cu and A); anal (?) margin almost straight, much thickened. Length of wing about 15 mm (Fig. 841). One species. Upper Permian of Australia.

Arctocoleus Martynov, 1933. Genotype—*A. ivensis* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Venation indistinct; anal (?) margin straight, thickened. Length of elytron 9–10 mm, width about 4 mm (Fig. 842). One species. Upper Permian of Arkhangelsk province.

269 SUPERORDER NEUROPTEROIDEA

Wings elongate, normally similar, very rarely hindwings shorter than forewings; venation very rich, with repeated branching of veins of almost all systems; rarely venation poor; distinct dissimilarity (dipterous Coniopterygidae) also found. Mouth parts of biting type; occasionally, in nonfeeding winged insects, mouth parts weak, not sufficiently developed. Larvae campodeiform, with strong, large jaws; predators attacking other insects and acarids, inhabiting dry land, rarely found in bodies of water. Venation of primitive Neuropteroidea is highly reminiscent of pattern seen in some Blattopteroidea. Probably Neuropteroids evolved from some such group of Blattopteroids. Their evolution was



Figs. 841–842. Coleopteroidea Incertae sedis.

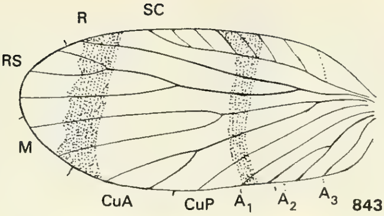
841. *Protocoleus mitchelli* Tillyard; elytron, × 5 (with usual symbols to designate various veins). Upper Permian, Australia (Tillyard, 1924). 842. *Arctocoleus ivensis* Martynov; elytron, × 2.2. Upper Permian, Arkhangelsk province (Martynov, 1933).

accompanied by expansion and perfection of predatory habit in the larvae and the development in them of external digestion. Recent fauna include a large number of relict forms. Upper Carboniferous to Recent. Order: Megaloptera, Raphidioptera and Neuroptera.

Order MEGALOPTERA. Alder flies

(O.M. Martynova)

Insects of medium or large size, with two pairs of broad, similar wings covered with small hairlike setae. Venation functional, but not perfect. Forewing: costal area broad; anal margin convex; SC terminates at costa or is fused with R, in latter case numerous branches of SC cross over to R; branches of RS range from three to nine; M with two simple branches or additional bifurcations. CuA with bifurcation; CuP simple; three anal veins; often an additional bifurcation on A_2; pterostigma absent. Longitudinal veins do not form short bifurcations along wing margin; wings assume roof-like position at rest. Head prognathous, flat, with numerous segmented, threadlike antennae; compound eyes widely spaced; mouth parts of biting type. Thoracic segments almost similar; segments of tarsi five; fourth segment short, two-lobed, abdomen 10 segmented, with



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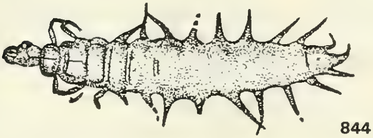


844

270 Figs. 843–844. Order Megaloptera.

843. *Permosialis bifasciata* Martynov; forewing, × 6. Upper Permian, Arkhangelsk province (original drawing). 844. *Permosialis* sp.; larva, × 2.5. Permian, Southern Urals (Sharov, 1953).

short cerci at end. In female, ovipositor absent. Adults do not eat, are nocturnal, living close to standing or slowly moving bodies of water with muddy bottom; survive for a few days. Eggs deposited on above-water parts of plants.

Larvae aquatic, predatoy, live for two years, at first in water, later buried in silt, with seven to nine pairs of tracheal gills. At first tracheal gills not segmented, but segmentation appears later. In Recent fauna rarely bear relict characters. Permian to Recent. Families: Permosialidae, Sialidae and Corydalidae; Sialidae not known as fossils.

Family PERMOSIALIDAE Martynov, 1928

SC terminates at costa in middle of anterior margin of wing or a little more proximally; branches of SC six to 10, of RS, two to four; branches of M simple; CuA and M fused or connected by a cross vein at base of wing for a short distance; CuA with simple bifurcation; one of anal veins, more often A_2, with
270 bifurcations; cross veins rare or practically absent; occasionally wing markings in form of transverse bands present. Permian. One genus.

Permosialis Martynov, 1928. Genotype—*P. paucinervis* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). SC parallel to C; R has no branches; RS starts at end of basal quarter of wing. Length of wings 10–18 mm. Larva: head prognathous with large mandibles. Tarsi of legs single-segmented with two claws. Nine pairs of segmental tracheal gills. Length of larva 25 mm (Figs. 843, 844). Sixteen species. Permian of Arkhangelsk province, Urals, Kuznetsk basin.

Family CORYDALIDAE Leach, 1815

[nom. transl. Burmeister, 1838 (ex Corydalida Leach, 1815)]

Forewing: SC long, fused with R; SC with 16–17 branches, R with two on three branches; RS starts more distally than midpoint of basal half of wing; M not fused with CuA at base; branches of M either simple or with bifurcations; all anal veins with bifurcations; many cross veins; quite large "mirrors" on wings. Length of wings varies from 30 to 62 mm. Paleogene to Recent. About 20 genera in Recent fauna distributed mainly in tropical and subtropical regions of both hemispheres, of which one genus is from the Paleogene of Europe (Baltic amber).

Outside the USSR: One extinct genus from Colorado.

Order RAPHIDIOPTERA. Snake flies

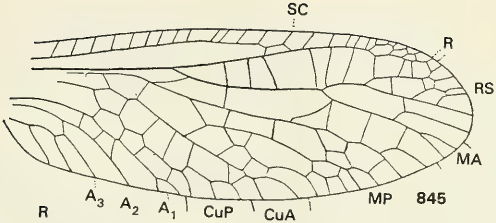
(O.M. Martynova)

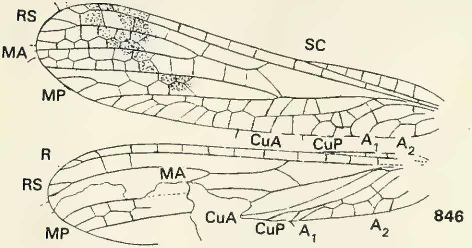
Two pairs of almost similar wings. Forewing with broad costal area; SC terminates roughly midway along wing (except in family Sojanoraphidiidae); branches of SC vary from six to 13; RS with small number of branches; RS and MA fused for some distance at base. In hindwings, free base of MA long, resembles cross vein; Cu branches at basal one-fourth of wing; CuA many-branched; CuP simple; two or three anal veins; cross veins form rows of characteristic cells; a colored pterostigma always present. Thoracic segments not uniformly developed; prothorax in Permian representatives shorter than meso- and metathorax; in Mesozoic and Recent forms, prothorax longer than others. Head flat, prognathous, part lying behind eyes elongated; mouthparts of biting type; eyes not large; ocelli occasionally present. Females with long ovipositor. Adults and larvae predators. Larva campodeiform, lives in cracks in bark of coniferous trees, forest litter and mosses. Upper Carboniferous to Recent. Families: Fatjanopteridae, Letopalopteridae, Sojanoraphidiidae, Mesoraphidiidae, Raphidiidae and Inocelliidae.

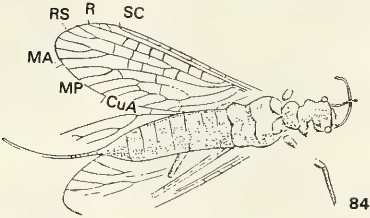
Family FATJANOPTERIDAE O. Martynova, 1961

Forewing: anterior margin uniformly convex; SC bent forward, running almost parallel to anterior margin of wing to a point a little more distal than midway along wing; costal area narrower than the fairly wide subcostal area; RS begins more proximally than midway along wing; up to 12 cells in radial area more distal than beginning of RS; free base of MA slanting, long, begins more
271 proximally than bifurcation of MP; CuA not fused with M; pterostigma absent. Wing large: ratio of length to width 2.8. Upper Carboniferous. One genus.

Fatjanoptera O. Martynova, 1961. Genotype—*F. mnemonica* O. Martynova, 1961; Upper Carboniferous, Tungus Basin (Burguklinian series, Fatyanikha). 15 or 16 branches on SC, up to eight branches on R; width of subcostal area maximum at level of origin of RS; three anal veins, all of them







270 Figs. 845–847. Order Raphidioptera; families Fatjanopteridae, Letopalopteridae, Sojanoraphidiidae.

845. *Fatjanoptera mnemonica* O. Martynova; forewing, × 3. Upper Carboniferous, Tungus basin (Martynova, 1961). 846. *Letopaloptera albardiana* O. Martynova; forewing and hindwing, × 7.5. Upper Permian, Arkhangelsk province (Martynova, 1961). 847. *Sojanoraphidia rossica* O. Martynova; dorsal view, × 7.5. Upper Permian, Arkhangelsk province (Martynova, 1952).

bifurcate. Length of forewing 23–25 mm (Fig. 845). One species. Upper Carboniferous of Tungus Basin.

Family LETOPALOPTERIDAE O. Martynova, 1961

Forewing: anterior margin weakly convex at base of wing; SC short, straight, ends a little more distad than middle of proximal half of wing; costal area somewhat broader than subcostal area, little narrower than radial area, distad to origin of RS, with uniform width throughout; RS starts slightly more proximally than middle of length of wing; free base of MA inclined and long, takes off from M in front of many branched MP, more proximally than beginning of RS; CuA long, does not come in contact with M; pterostigma absent. Wing narrow and long: length four times more than width. Prothorax longer than head. Legs very long. Upper Permian. One genus.

Letopaloptera O. Martynova, 1961. Genotype—*L. albardiana* O. Martynova, 1961; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). SC with five or six branches; about eight branches on R; RS_{1+2}, MA, MP and MP_2 absolutely straight, with zigzaging branches, resembling intercalary veins; Cu branches more proximally than midpoint of basal half of wing; CuA runs parallel to anal margin of wing; two anal veins. Length of wing 10 mm (Fig. 846). Two species. Upper Jurassic of Arkhangelsk province.

Family SOJANORAPHIDIIDAE O. Martynova, 1952

Forewing: anterior margin straight. SC long, straight, terminating halfway along distal half of wing; costal and subcostal areas of same width; RS starts more proximally than midpoint of basal half of wing; up to eight cells in radial area; MA short, leaves M more distally than beginning of RS; CuA not fused with M; pterostigma absent. Wing short and narrow: ratio of length to width 3 : 1. Prothorax shorter than head. Upper Permian. One genus

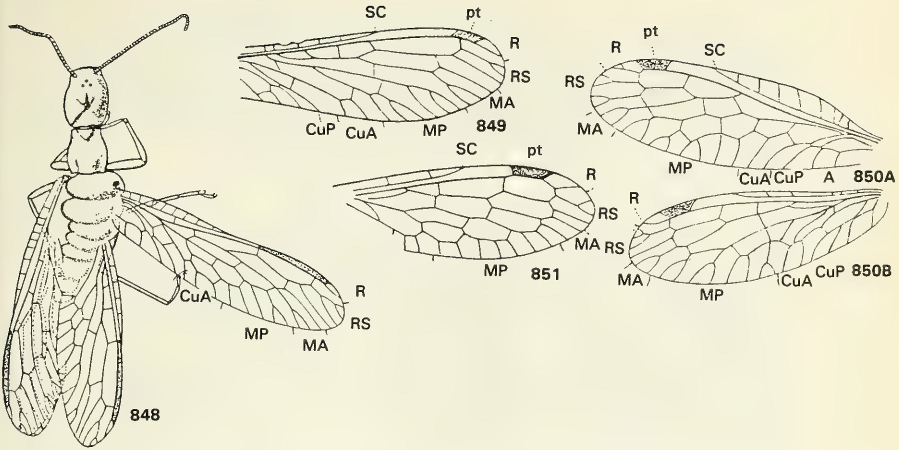
Sojanoraphidia O. Martynova, 1952. Genotype—*S. rossica* O. Martynova, 1952; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). SC with
272 six branches and R with two or three, not all branches zigzag; Cu branches off almost at base of wing; anal veins two, simple. Length of wing 5 mm (Fig. 847). One species. Upper Permian of Arkhangelsk province.

Family MESORAPHIDIIDAE Martynov, 1925

Forewing: anterior margin gently convex; costal area almost equal to subcostal; SC straight, ends halfway along wing, or more distally; RS starts considerably more proximally than middle of wing; three cells in radial area; free base of MA leaves M a little more proximally than bifurcation of MP; CuA comes into contact with M at one point; pterostigma long, does not intersect cross veins. In hindwing free base of MA long, as in wing of Recent genus *Raphidia*. Prothorax shorter than head, but of same length as mesothorax. Jurassic. Two genera.

Mesoraphidia Martynov, 1925. Genotype—*M. grandis* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Pterostigma large— one-third of length of wing; basal border of pterostigma and cross vein r-rs placed at same level. Length of forewings 5.5–16 mm (Fig. 848). Seven species. Jurassic of Kazakhstan and Western Europe.

Proraphidia O. Martynova, 1947. Genotype—*P. turkestanica* O. Martynova, 1947; Upper Jurassic, Chimkent province (Malm, Karatau). Pterostigma small, with basal border located more distally than cross vein r-rs



271 Figs. 848–851. Order Raphidioptera; families Mesoraphidiidae, Raphidiidae, Inocelliidae.

848. *Mesoraphidia pterostigmalis* O. Martynova; dorsal view, × 3.5. Upper Jurassic, Southern Kazakhstan (Martynova, 1947). 849. *Proraphidia turkestanica* O. Martynova; forewing, × 6. Upper Jurassic, South Kazakhstan (Martynova, 1947). 850. *Raphidia ophiopsis* Linnaeus; A—forewing, B—hindwing, × 6. Recent Europe (original drawing). 851. *Fibla exusta* (Cockerell and Custer); hindwing, × 5. Neogene, Colorado (Carpenter, 1936).

and midpoint of apical half of wing. Length of wing 11–12 mm (Fig. 849). One species. Upper Jurassic of Kazakhstan[1].

Family RAPHIDIIDAE Latreille, 1810

[nom. transl. Stephens, 1836 (ex Raphidiinae Latreille, 1810)]

Forewing: anterior margin of wing convex; SC straight, ends at distal half of wing; costal area wider than subcostal; SC* starts almost halfway along wing; three cells in radial area; MA takes off not from M, but from anterior branch of MP, i.e., its base is shifted distally; CuA fused with M for some distance; with pterostigma bordered and intersected by cross veins; length of wing 2.8—3.2, more often 2.8 times of width. Two short anal veins. Prothorax of same length as, or shorter than head, both longer than mesothorax; head oval with three ocelli. Neogene to Recent. Two genera in the Recent fauna, of which one is also found in the Tertiary fauna.

[1] Family Baisopteridae O. Martynova, 1961, with one genus and two species is known from the Upper Jurassic of Trans-Baikal. It differs from Mesoraphidiidae in the large number of cells in the radial area. (The description appeared after this book went to press.)

* Misprint in the original. Should read RS—General Editor.

Raphidia Linnaeus, 1735. Genotype—*R. ophiopsis* Linnaeus, 1735 (*Subilla* Navas, 1916; *Alena* Navas, 1915; *Lesna* Navas, *Erma* Navas, 1918); Recent, Western Europe. In hindwings free base of MA long; proximal border of pterostigma lies at level of middle of pterostigmal cell. Length of wings 7.5–12 mm (Fig. 850). About 20 species found in the Recent fauna of Europe and one in North America. Eight species from the Miocene of North America. Miocene to Recent.

Family INOCELLIIDAE Navas, 1916

Differs from previous family in nature of pterostigma, which is not bordered and intersected by cross veins. Prothorax longer than pterothorax, but shorter than or of same length as head; head not tapered toward base. Paleogene to Recent. Two genera in the Recent fauna, of which one also found in the Tertiary fauna.

Fibla Navas, 1915 (*Burcha* Navas, 1915). Genotype—*F. hesperica* Navas, 1915 (*Inocellia maclachlani* Navas nec Albarda, 1908); Recent, Portugal. In hindwing free base of MA long. Length of wing 9–14 mm (Fig. 851). Paleogene to Recent. One species in the Recent fauna and two species from the Paleogene of Europe (Baltic amber) and North America.

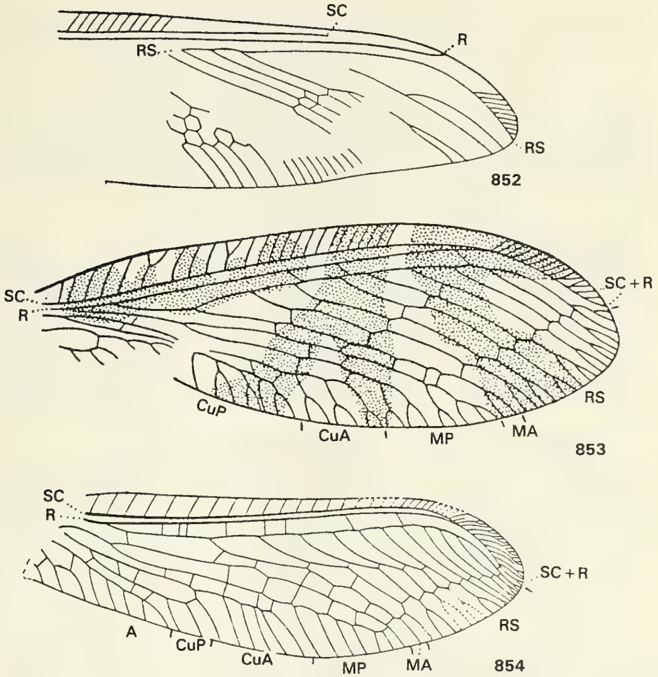
Order NEUROPTERA. Net-winged insects

(O.M. Martynova)

Two pairs of almost similar wings except Nemopteridae; venation rich (reduced only in family Coniopterygidae); additional distal bifurcations observed on longitudinal veins; often many branches of SC cross over to R; branches of RS pectinately disposed; anterior branch of M in Mesozoic and Recent forms
273 usually fused for short distance (except Chrysopidae) with R or RS. Head hypognathous, with biting mouthparts; eyes compound; usually with three ocelli on forehead, which are sometimes absent; antennae of moderate length, filiform, occasionally thickened at end. Thorax primitive; legs of running type, with five-segmented tarsus. In female no ovipositor (except *Dilar*). Larvae campodeiform, predatory with elongated mandibles. Neuroptera, known from the Lower Permian as a fully-formed order, obviously appeared in a more ancient geological period. The overall resemblance in the venation of the wings of Neuroptera and the most primitive and archaic scorpion flies suggests that this order was ancestral to all orders of the mecopteroid complex. Permian to Recent. Four superfamilies: Myrmeleontidea, Polystoechotidea, Hemerobiidea, Coniopterygidea.

SUPERFAMILY MYRMELEONTIDEA

Wings long (up to 80 mm), comparatively narrow; distal parts of SC and R fused; anterior branch of M fused with R; M and CuA almost parallel; MP single



Figs. 852–854. Superfamily Myrmeleontidea.

852. *Solenoptilon martynovi* O. Martynova; forewing, × 3.2. Upper Jurassic, Kazakhstan (Martynova; 1949). 853. *Sogjuta speciosa*, O. Martynova; forewing, × 7.7. Upper Triassic, Central Asia (Martynova, 1958). 854. *Chrysoleonites ocellatus* Martynov; forewing, × 5. Upper Jurassic; South Kazakhstan (Martynova, 1949).

or two-branched; proximal branch of CuA thicker than other branches; CuP short. Jurassic to Recent. Five families: Solenoptilidae, Nymphitidae, Myrmeleonidae, Ascalaphidae, Nemopteridae.

Family SOLENOPTILIDAE Handlirsch, 1908

R short in forewing, without curve extending parallel to apical margin of wing, with rows of simple, inclined branches. Jurassic. One genus.

Solenoptilon Handlirsch, 1908. Genotype—*S. abiakochi* Geinitz, 1888;
274 Lower Jurassic, Western Europe (Upper Lias, Germany). Anterior margin of

apical part of wing strongly bent towards posterior side; posterior margin with shallow notch; cross veins irregularly distributed. Length of wing 33–40 mm (Fig. 852). Two species. Jurassic of Kazakhstan and Western Europe.

Family NYMPHITIDAE Handlirsch, 1908

SC and R coverage and eventually merge; SC + R curves smoothly; RS long, leaves R basally, branches almost halfway along the wing; MP with two branches; proximal branch of CuA does not differ much from other branches; MP and CuA never converge. Jurassic to Recent. Three genera in the Recent fauna of Australia and New Guinea and six genera as fossils.

Sogjuta O. Martynova, 1958. Genotype—*S. speciosa* O. Martynova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). In forewing radial area wider than subcostal, but narrower than costal area; costal area in apical part of same width as in middle of wing; some branches of SC with additional bifurcations; branches of RS eight, straight; basal branch of RS takes off from a point more proximal than halfway along wing; two steplike series of cross veins. Length of wing 12 mm (Fig. 853). One species. Upper Triassic of Issyk-Kul province.

Chrysoleonites Martynov, 1925. Genotype—*C. ocellatus* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). In forewings radial area twice as wide as subcostal and almost as wide as costal area; costal area in apical part wider than in middle of wing; two steplike rows of cross veins. Length of wing 15–17 mm (Fig. 854). One species. Upper Jurassic of Kazakhstan.

Outside the USSR: *Epigambria* Handlirsch, 1939; *Mesonymphes* Carpenter, 1929; *Nymphites* Haase, 1890; *Sialium* Westwood, 1854.

Family MYRMELEONIDAE Burmeister, 1839. Ant lions

SC and R gradually converge until they fuse; SC + R with smooth curve; branches of SC simple; SC + R with bifurcations; MP simple, somewhat close to CuA; proximal branch of CuA not sharply marked; antennae, much shorter than wings, widen at end. Ocelli absent. Larva with broad body, quadrate head and long mandibles. Paleogene to Recent. Large family: about 1,200 species belonging to numerous genera in the Recent fauna; two genera from the Paleogene of Europe (Baltic amber) and Western Europe.

Family ASCALAPHIDAE Lefroy, 1842

[nom. transl. Schenider, 1845 (ex Ascalaphides Lefroy, 1842)]

SC and R run parallel, bend sharply before fusing finally; SC + R straight, R with a break; branches of SC simple in region of pterostigma; SC + R with bifurcation and cross veins; MP simple; proximal branch of CuA stands out sharply. Antennae widen at end, longer than wings or slightly shorter in larger forms. Larvae resemble larvae of ant lions. Neogene to Recent. Large family: three subfamilies and numerous genera; most abundant in tropics; one genus from the Neogene of France.

Family NEMOPTERIDAE Hagen, 1866

Hindwings elongated, ribbon-like. In forewings SC and R gradually converge; SC + R bend smoothly; branches of SC simple, usually located in distal part; RS branches more distally than midpoint of wing; MP and CuA near each other. Head prolonged into a rostrum; antennae small, shorter than or equal to length of wings, without widening at end. Neogene to Recent. About 25 genera in the Recent fauna, with about 100 tropical and subtropical species, of which two genera are also from the Miocene of North America.

SUPERFAMILY POLYSTOECHOTIDEA

Length of forewings almost double their width. In forewings SC fused with R; MA simple, many-branched and fused with RS in Recent and Mesozoic forms, free in Paleozoic forms; MP divided into two main branches; CuA and CuP long, with short branches turning posteriorly; three anal veins; many cross veins, often forming steplike series. Permian to Recent. Families: Permithonidae, Archeosmylidae, Osmylitidae, Mesopolystoechotidae, Osmylidae; last family not known as fossils.

275 Family PERMITHONIDAE Tillyard, 1922

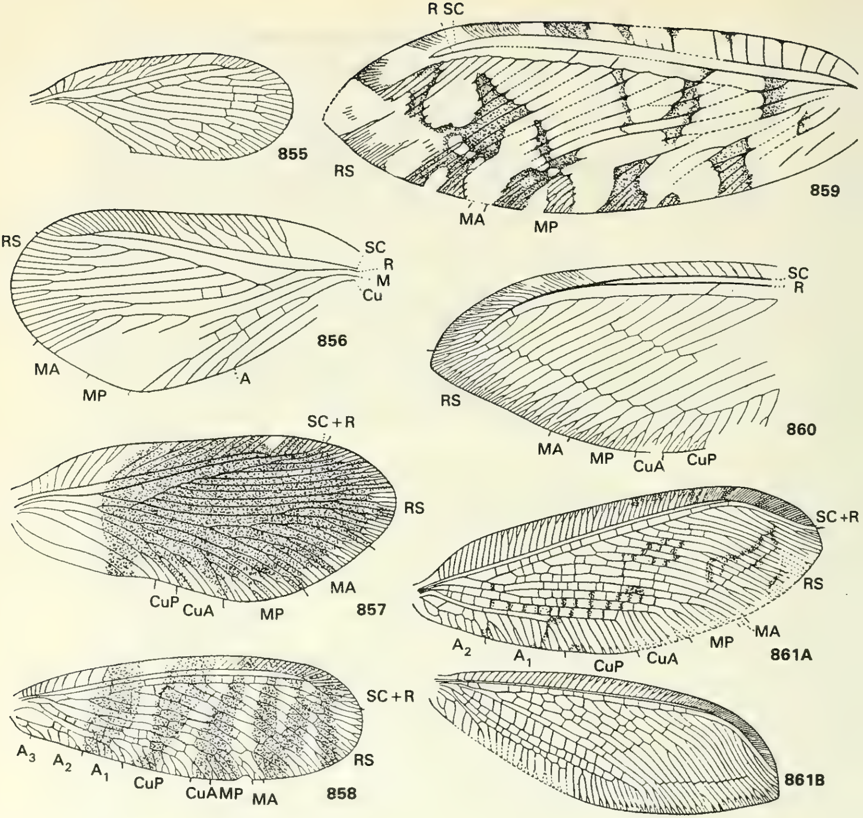
(Permegalomidae O. Martynova, 1952; Permopsychopsidae Riek, 1953)

In forewings radial area wider than subcostal; SC fused with R almost halfway along distal half of wing; M branches about halfway along basal half of wing; MA many-branched, free; CuP simple or with short branches; cross veins do not form regular rows. Permian. Seven genera.

Permegalomus Martynov, 1930. Genotype—*P. regulariis* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Mountains). Apex of forewing rounded; anal margin straight; branches of SC in distal half of wing without bifurcations; M branches more proximally than point of origin of RS and more distally than point of branching of Cu. Length of wing 10 mm (Fig. 855). Two species. Upper Permian of the Urals and Arkhangelsk province.

Eopsychops Martynov, 1933. Genotype—*E. sojanensis* Martynov, 1933;
276 Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Apex of forewing rounded; anterior margin concave distal to midpoint of wing; anal margin bent at an angle at level of concavity of anterior margin. Branches of SC in distal half simple; length of stem of MP exceeds half of the length of MA; cross vein connects MA with proximal branch of RS. Length of wing 13 mm (Fig. 856). Two species. Upper Permian of Arkhangelsk province and Kuznetsk basin.

Permithonopsis Martynov, 1933. Genotype—*P. ivensis* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Apex of forewing distinct; anal margin without sharp, distinct angle; all branches of SC with bifurcations; M branches at level of origin of RS; stem of MP half of length of stem of MA or even shorter. Length of forewing 10–16 mm (Fig. 857). 12



Figs. 855–861. Superfamily Polystoechotidae.

855. *Permegalomus maculipennis* Martynov; forewing, × 4.5. Upper Permian, Arkhangelsk province (Martynov, 1952). 856. *Eopsychops sojanensis* Martynov; forewing, × 4.6. Upper Permian, Arkhangelsk province (Martynova, 1952). 857. *Permithonopsis obscura* O. Martynova; forewing, × 5. Upper Permian, Arkhangelsk province (Martynova, 1952). 858. *Petrushevskia borisi* O. Martynova; forewing, × 4. Upper Trias, Central Asia (Martynova, 1958). 859. *Kirgisellodes ornatus* (Martynov); forewing, × 4.6. Upper Jurassic, South Kazakhstan (original drawing). 860. *Mesopolystoechus apicalis* Martynov; hindwing, × 4. Lower Jurassic, Central Asia (Martynova, 1949). 861. *Lithosmylus columbianus* (Cockerell); A—forewing, B—hindwing, × 2.5; Neogene, North America (Carpenter, 1935)

species. Upper Permian of Arkhangelsk province and Kuznetsk basin.

Outside the USSR: *Permithone* Tillyard, 1922; *Permorapisma* Tillyard, 1926; *Permosmylus* Tillyard, 1926; and *Permopsychops* Tillyard, 1926.

Family Archeomylidae Riek, 1952 is close to Permithonidae, as revealed by the characters of its only genus *Archeomylus* Riek, 1953 from the Permian and Triassic of Australia.

Family OSMYLITIDAE O. Martynova, 1949

In forewings costal and radial areas narrow, nearly of same width; SC and R fused considerably more distad than midpoint of apical half of wing; M branches considerably more proximally than midpoint of basal half of wing; MA simple, fused with RS; MP with two simple branches; CuA with short bifurcation; row of short pectinately disposed branches characterizes CuP and A_1 and sometimes A_2. Upper Triassic to Upper Jurassic. Five genera.

Petrushevskia O. Martynova, 1958. Genotype—*P. borisi* O. Martynova, 1958; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Apex of forewing rounded, not distinct; RS with nine to 11 branches; distal end of CuP smooth; cross veins of radial area straight, with designs in the form of cross bands. Length of forewing 16 mm (Fig. 858). One species. Upper Triassic of Issyk-Kul province.

Kirgisellodes Martynov, 1925. Genotype—*Kirgisella ornata* Martynov, 1925; Jurassic, Chimkent province (Malm, Karatau). Apex of forewing slightly marked; SC and R join without gradually converging; branches of SC at distal part of costal area, four times more than in basal part. RS with 19 branches; bifurcations of RS long; cross veins of radial area inclined; dark spots seen on wing. Length of forewing 20 mm (Fig. 859). One species. Upper Jurassic of Kazakhstan.

Outside the USSR: *Osmylites* Haase, 1890; *Tetanoption* Bode, 1953; and *Mesomylina* Bode, 1953.

Family MESOPOLYSTOECHOTIDAE O. Martynova, 1949

Apex of forewing acute; SC and R gradually converge and fuse more proximally than midpoint of distal half of wing; branches of RS without long bifurcations; MA simple, fused with RS; MP with two simple branches; rows of short pectinately placed branches on CuA; few cross veins in radial area; two steplike series of cross veins, distal series ends at branches of CuA. Jurassic. One genus.

Mesopolystoechus Martynov, 1937. Genotype—*M. apicalis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab I). Forewing with small bifurcations on branches of C + R; terminal bifurcations observed on SC; branches of RS, M and CuA of same type; distal series of cross veins parallel to anal margin of wing, forming a border. Length of forewing about 25 mm (Fig. 860). One species. Lower Jurassic of Central Asia.

Family OSMYLIDAE Leach, 1815

[nom. transl. Brauer, 1851 (ex Osmylida Leach, 1815)]

SC and R fused distal to apical half of forewing; short bifurcations on all branches of main veins; two series of cross veins, distal series ends at branches of MP; numerous cross veins in radial area and basal half of wing; ocelli present. Triassic to Recent. Recent tropical and subtropical fauna include 20 genera belonging to six subfamilies, of which following three: Osmylinae, Protosmylinae and Kempyninae—known from Tertiary deposits, last two from outside the USSR.

Subfamily Osmylinae Kruger, 1913

In forewing distal series of cross veins consists of 19 veins extending from SC + R to MP (Fig. 861). Paleogene to Recent. One genus in Recent fauna and in the Paleogene of Europe (Baltic amber).

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SUPERFAMILY HEMEROBIIDEA

(Psychopsidoidea O. Martynova, 1952)

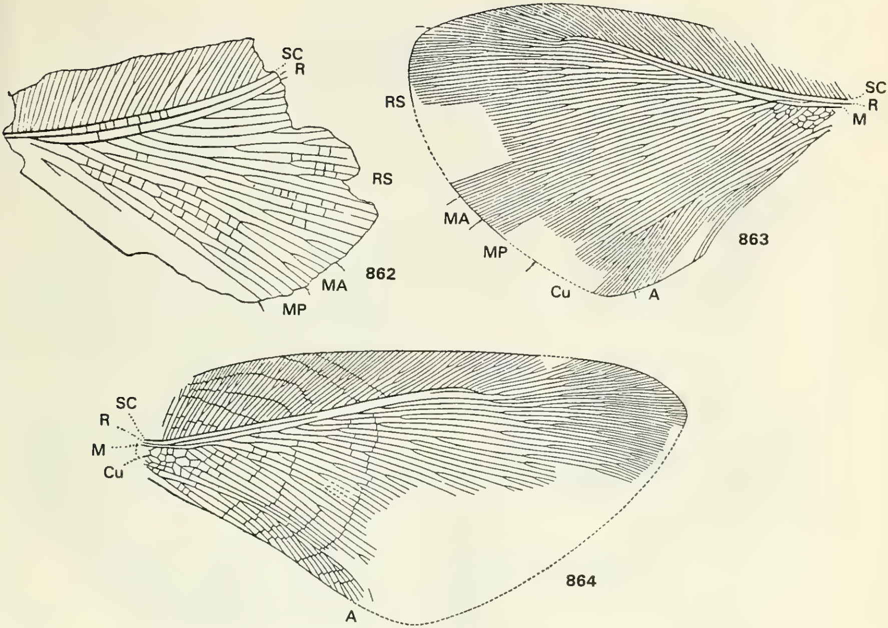
Wings comparatively wide, length up to double the width; SC not fused with R distally; SC, R and RS close (except Chrysopidae and Mesochrysopidae), run parallel; subcostal and radial areas together narrower than costal area (except Chrysopidae). In Mesozoic and Recent forms MA fused with R or RS for some distance, whereas in Paleozoic forms MA free. Permian to Recent. Families: Psychopidae, Kalligrammatidae, Brongniartiellidae, Palaemerobiidae, Sialidopseidae, Hemerobiidae, Sisyridae, Berothidae, Mesochrysopidae, Chrysopidae, Prohemerobiidae, Proberothidae, Osmylopsychopidae; last three found only outside the USSR.

Family PSYCHOPIDAE Handlirsch, 1906

[nom. transl. Handlirsch, 1908 (ex Psychopsinae Handlirsch, 1906)]

Wings large, triangular. In forewings costal area three times wider than subcostal and raidal areas together; humeral vein short, bent toward base of wing; distal parts of SC, R and RS connected by cross veins which are as thick as the longitudinal veins they connect, distal connections thinnest; cubital-anal area forms a border along anal margin of wing analogous to costal area; MA fused with RS; cross veins distributed at random along border or form regular rows. Hindwing narrower than forewing. Jurassic to Recent. Eight genera in the Recent fauna of Australia, South Africa and South Asia; nine genera as fossils.

Angaropsychops O. Martynova, 1949. Genotype—*A. turgensis* O. Martynova, 1949; Upper Jurassic, Chita province (Transbaikal, Turgino-Vitim series, Byrka). SC, R and RS curved backward; MP divides almost at base to form series of long bifurcations; cubital area half the width of costal area, many cross veins, arranged in disorderly fashion. Length of forewing 40 mm (Fig. 862). One species. Upper Jurassic of Transbaikal.



Figs. 862–864. Family Psychopidae.

862. *Angaropsychops turgensis* O. Martynova; forewing, × 2. Upper Jurassic, Transbaikal (Martynova, 1949). 863. *Embaneura vachrameevi* G. Zalessky; forewing, × 1.5. Upper Cretaceous, West Kazakhstan (original drawing from photograph of holotype). 864. *Grammopsychops lebedevi* O. Martynova; forewing, × 2. Upper Cretaceous, Krasnoyar district (Martynova, 1954).

278 *Embaneura* G. Zalessky, 1953. Genotype—*E. vachrameevi* G. Zalessky, 1953; Upper Cretaceous, Aktiobinian province (Senoman, Emba). SC, R and RS slightly bent backward; costal and cubital areas almost of same width; cross veins almost absent. Wing dark with three round light colored spots*. Length of forewing about 50 mm (Fig. 863). One species. Upper Cretaceous of West Kazakhstan.

Grammopsychops O. Martynova, 1954. Genotype—*G. lebedevi* O. Martynova, 1954; Upper Cretaceous, Krasnoyar district (Suchkovian series, River Kem). SC, R and RS do not bend backward; five pectinately placed

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*This description does not agree with Fig. 863.—General Editor.

branches of M up to the point where it branches into MA and MP; MA fused with RS; cubital area slightly narrower than costal area; cross veins form a few concentrically placed series intersecting costal and anal areas. Length of forewing 44 mm (Fig. 864). One species. Upper Cretaceous of East Siberia.

Outside the USSR: *Apeirophlebia* Handlirsch, 1908; *Liassopsychops* Bode, 1953; *Archepsychops* Tillyard, 1919; *Triassopsychops* Tillyard, 1922; *Protopsychopsis* Tillyard, 1917 and one from Baltic amber and Miocene of North America.

Family KALLIGRAMMATIDAE Handlirsch, 1906

Wings large (80–120 mm in length). Hindwings narrower than forewings; costal area twice as wide as subcostal and radial areas put together, or as wide; with strong cross vein sc-r; similarity between costal area and anal margin of wing exists, but to a small degree; MP many-branched; posterior branch of MP forms a series of branches directed anteriorly; large number of cross veins cover entire wing. Upper Jurassic. Three genera.

Kalligramma Walter, 1904. Genotype—*K. haeckeli* Walter, 1904; Upper 279 Jurassic, Western Europe (Malm, Zolengofen). In forewing costal area one and one-half times as wide as subcostal and radial areas put together; RS with 8–12 branches; annular two-colored spot at base of distal half of wing. Length of forewing 90–120 mm (Fig. 865). Two species. Upper Jurassic of Karatau and Western Europe.

Kalligrammula Handlirsch, 1919. Genotype—*K. senkenbergiana* Handlirsch, 1919; Upper Jurassic, Western Europe (Malm, Zolengofen). Costal area almost as wide as subcostal and radial areas combined; RS with five to eight branches; no spots on wing. Length of forewing 70–80 mm (Fig. 866). Two species. Upper Jurassic of Kazakhstan and Western Europe.

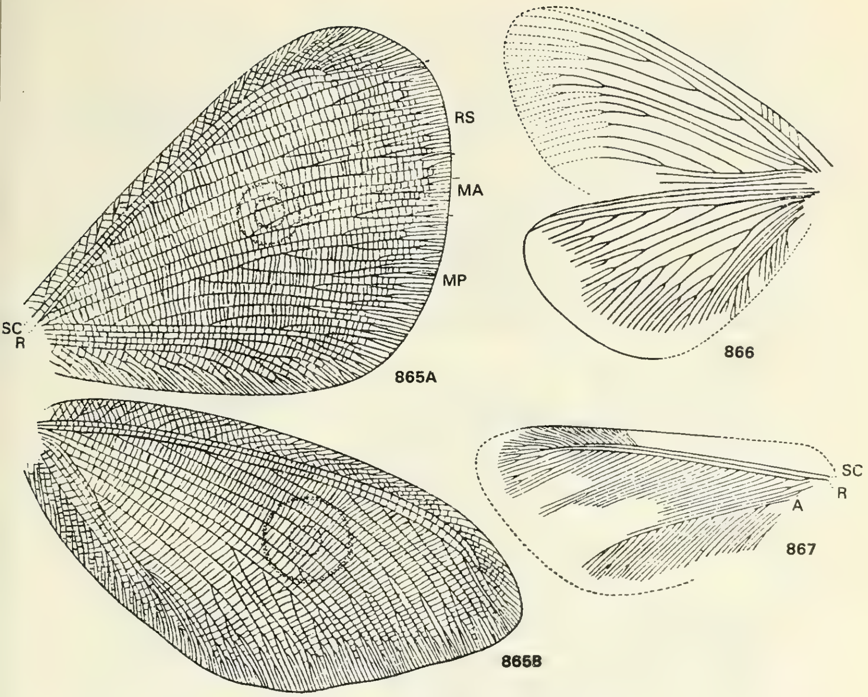
Outside the USSR: *Meioneurites* Handlirsch, 1908.

Family BRONGNIARITELLIDAE O. Martynova, 1949

Wings triangular; cross veins sc-r and r-rs absent in distal part of wing; RS with 16 to 26 branches; MP branches at base of wing; CuA and CuP with many branches; cross veins absent. Jurassic. Six genera.

Epactinophlebia Martynov, 1927. Genotype—*E. karabasica* Martynov, 1927; Upper Jurassic, Chimkent province (Malm, Karatau). Costal area almost one and half times as wide as combined subcostal and radial areas; RS with 27 branches; MP with two main branches; branches of CuA and CuP disposed pectinately; cubital area twice as wide as costal area. Length of forewing 21.5 mm (Fig. 867). One genus. Upper Jurassic of Karatau.

Outside the USSR: *Actinophlebia* Handlirsch, 1908; *Brongniartiella* Meunier, 1897; *Mesopsychopsis* Handlirsch, 1908; *Pterinoblattina* Scudder, 1885; *Paractinophlebia* Handlirsch, 1908.



278 Figs. 865–867. Families Kalligrammatidae, Brongniartiellidae.

865. *Kalligramma haeckeli* Walter; A—forewing, B—hindwing, × 0.6. Upper Jurassic, Germany (Handlirsch, 1908). 866. *Kalligrammula senkenbergiana* Handlirsch; wings, × 0.75. Upper Jurassic, Germany (Handlirsch, 1919). 867. *Epactinophlebia karabasica* Martynov; forewing, × 3. Upper Jurassic, South Kazakhstan (Martynov, 1927).

Family PALAEMEROBIIDAE Martynov, 1928

Wings small (8–12 mm), oval. Apex of forewing rounded; anterior margin convex; costal area narrow at base and at apex; at least four branches seen on RS; both branches of M free; MA not fused with RS; MA and MP branch into two major branches, MA more distally than MP; CuA branches twice; CuP weak, with short bifurcation; three anal veins, occasionally with bifurcations; longitudinal veins form bifurcations at various distances from wing margin; six or seven cross veins seen in radial area; cross veins between all longitudinal veins distributed at random. Permian. Three genera.

Palaemerobius Martynov, 1928. Genotype—*P. proavitus* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). In anterior wing SC ends half-way along distal half; five or six branches of SC pass to R; costal area one-fifth of width of whole wing; RS with five to six branches; M branches at level of origin of RS; MA branches distal to midpoint of wing. Length of forewing 8–8.5 mm (Fig. 868). Three species. Permian of Arkhangelsk province, Urals and Kuznetsk basin.

Tychtobius O. Martynova, 1958. Genotype—*T. brevicostatus* O. Martynova, 1958; Upper Permian, Kuznetsk basin (Erunakovian Series, Sokolova II). In forewing SC ends a little distad to midpoint of wing; width of costal area 1.8 times of entire width of wing; 10 branches of SC (some with bifurcations) transferred to R; RS with six branches; MA branches halfway along wing and MP a little more proximally; anal veins have bifurcations. Length of forewing 10.75 mm (Fig. 869). One species. Permian of Kuznetsk basin.

Bianchia O. Martynova, 1952. Genotype—*B. spectabilis* O. Martynova, 1952; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). In forewing SC ends distal to midpoint of distal half of wing; one branch of SC transferred to R; RS with six branches; MA branches halfway along wing; stem of MP almost one-third length of stem of MA. Length of forewing 11 mm (Fig. 870). One species. Upper Permian of Arkhangelsk province.

Family SIALIDOPSEIDAE M. Zalessky, 1926

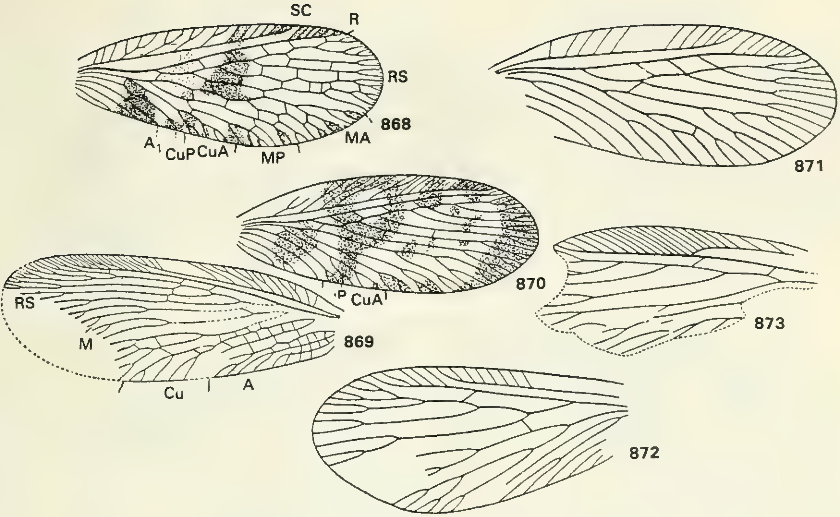
(Permosisyridae Martynov, 1933)

Wings oval (length: 7.6–13 mm). In forewing apex rounded; anterior margin weakly convex; costal area narrower at base and at tip of wing; SC ends proximal to midpoint of apical half of wing; some simple branches of SC transferred to R; RS with four branches; longitudinal branches form bifurcations at various distances from wing margin; with slanting cross veins in radial area; few cross veins distributed along wing. Permian. Four genera.

280 *Sialidopsis* M. Zalessky, 1926. Genotype—*S. kargalensis* M. Zalessky, 1926; Upper Permian, Orenburg province (Kargala). In forewing SC ends at proximal three-fourths of wing; M branches at level of midpoint of stem of RS. Length of forewing 10.5–12.5 mm (Fig. 871). Three species. Upper Permian of Urals and Arkhangelsk province.

Permosisyra Martynov, 1933. Genotype—*P. latipennis* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). In forewing SC ends at the middle of proximal three-fourths of wing; M branches proximal to midpoint of stem of RS; CuA with simple bifurcation. Length of forewing 7.5–10.5 mm (Fig. 872). Two species. Upper Permian of Arkhangelsk province.

Parasisyra G. Zalessky, 1933. Genotype—*P. kargalica* G. Zalessky, 1933; Upper Permian, Orenburg province (Kargala). In forewing SC short; ten branches of SC transferred to R; two cross veins in radial area. Length of



Figs. 868–873. Families Palaemerobiidae, Sialidopseidae.

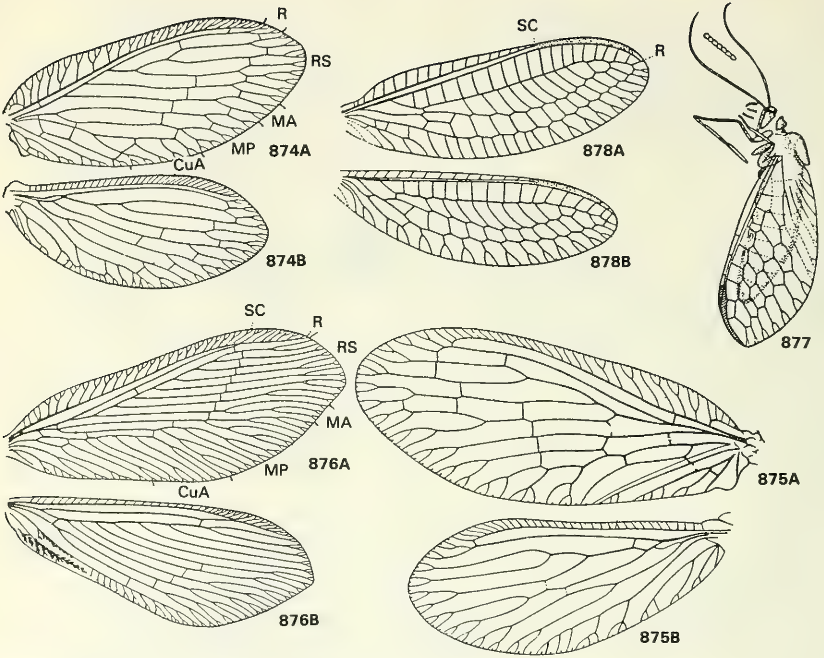
868. *Palaemerobius proavitus* Martynov; forewing, × 6.5; Upper Permian, Urals (Martynov, 1928). 869. *Tychtobius brevicostatus* O. Martynova; forewing, × 6. Upper Permian, Kuznetsk basin (Martynova, 1958). 870. *Boanchia spectabilis* O. Martynova; forewing, × 5. Upper Permian, Arkhangelsk province (Martynova, 1952). 871. *Sialidopsis sojanensis* O. Martynova; forewing, × 6. Upper Permian, Arkhangelsk province (Martynova, 1952). 872. *Permosisyra latipennis* Martynov; forewing, × 7.2. Upper Permian, Arkhangelsk province (Martynov, 1933). 873. *Parasisyra kargalica* G. Zalessky; forewing, × 7. Upper Permian, Southern Urals (G. Zalessky, 1933).

forewing about 10 mm (Fig. 873). One species. Permian of Urals.

Family HEMEROBIIDAE Latreille, 1802

[nom. transl. Westwood, 1840 (ex Hemerobini Latreille, 1802)]

Length of wings 3–15 mm, most often 8–10 mm. In forewing humeral vein long, bent toward basal region of wing; SC long; two to four branches of SC transferred to R; M branches at base of wing; MA and two to four proximal branches of RS (sometimes all branches of RS, as in *Drepanopteryx*) fused with R at base and take off from there; MP divided into two long branches at base; CuA with pectinate row of branches on posterior side; CuP simple (except in large forms). Three anal veins; cross veins form two steplike series (Fig. 874). Paleogene to Recent. About 25 widely distributed genera in the Recent fauna; four genera in the Paleogene of Europe (Baltic amber), Western Europe and North America.



281 Figs. 874–878. Superfamily Hemerobiidea.

874. *Hemerobius humuli* Linnaeus; A—forewing, B—hindwing, × 7. Recent, Europe (Comstock, 1918). 875. *Sisyra flavicornis** Linnaeus; A—forewing, B—hindwing, × 10. Recent, Europe (original drawing). 876. *Spermophorella* sp.; A—forewing, B—hindwing, × 3. Recent, Caucasus (original drawing). 877. *Mesypochrysa latipennis* Martynov; general view, × 8. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 878. *Palaeochrysa striata* Scudder; A—forewing, B—hindwing, × 3.5. Neogene, North America (Carpenter, 1935).

Family SISYRIDAE Handlirsch, 1906

Length of forewings 5—6 mm. In forewings base of costal area narrow; humeral vein short; in distal part of wing cross vein sc-r short; MA fused with R at base,
281 departs from RS; MP divides into two branches near origin of MA; at base of MA lies cross vein ma-mp_1; CuA with branches; CuP simple; cross veins few, not in rows (Figs. 875). Paleogene to Recent. Five genera (about 30 widely

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* Editor's note: No such species. Linnaeus never described a *Sisyra*, nor a *flavicornis* in Neuroptera. Nor is there any *flavicornis* in Sisyridae!!

distributed species), of which one genus is also from the Paleogene of Europe (Baltic amber).

Family BEROTHIDAE Handlirsch, 1906

[nom. transl. Handlirsch, 1908 (ex Berothinae Handlirsch, 1906)]

In forewing humeral vein short; SC short, ends at midpoint of distal half of wing; five or six branches of SC transferred to R; M, MA and MP fused with R at base; MA takes off from RS and MP from R; branches of RS not fused with R; CuA with branches; CuP with long bifurcation; rows of scales on wings (Fig. 876). Paleogene to Recent. 10 tropical and subtropical genera in Recent fauna. One genus from the Paleogene of Europe (Baltic amber).

Family MESOCHRYSOPIDAE Handlirsch, 1908

Every vein of wing terminates in a simple short fork; in forewing SC short, ending at beginning of apical margin of wing; R reaches apex of wing and is bent backward; cross veins in radial area, touching corresponding number of branches of RS; M branches at level of beginning of RS, both branches end at anal margin of wing; Cu branches more distally than M; cross veins form two longitudinal series. Upper Jurassic. Two genera.

Mesypochrysa Martynov, 1927. Genotype—*M. latipennis* Martynov, 1929; Upper Jurassic, Chimkent province (Malm, Karatau). In forewing SC ends in 282 region of pterostigma, often intersected by predominant branches; RS with seven branches. Length of forewing 12 mm (Fig. 877). One genus. Upper Jurassic of Kazakhstan.

Outside the USSR: *Mesochrysopa* Handlirsch, 1906.

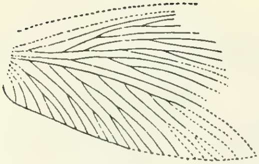
Family CHRYSOPIDAE Hagen, 1866

In forewing SC and R curved, following contour of apical margin of wing, but do not reach apex; radial area wider than costal and subcostal areas together; each cross vein in radial area corresponds to branch of RS; M fused with R at base; MP forms a loop, fuses with MA; MP + MA fuse with branches of RS, do not reach margin of wing; A_1 and A_2 with wide forks; A_3 short, simple; two longitudinal series of cross veins (Fig. 878). Paleogene to Recent. 40 widely distributed genera in the Recent fauna; four in the Paleogene of Europe (Baltic amber) and North America.

Hemerobiidea Incertae sedis

Archedilaropsis Martynov, 1935 (Fig. 879); Upper Trias–Lower Jurassic, Eastern slope, Urals; *Dilarites* Martynov, 1925 (Fig. 880); Upper Jurassic, Karatau; *Eopsychopsis* Martynov, 1928 (Fig. 881); Lower Permian, Tikhie Mountains.

Outside the USSR: Jurassic of Western Europe—*Archegetes* Handlirsch,



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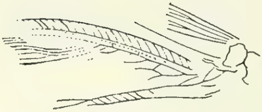

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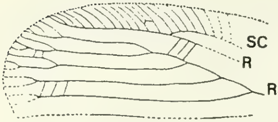

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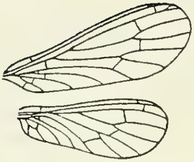

Fig. 882. Superfamily Coniopterygidea.

Semidalis aleurodiformis Stephens; wings, × 15. Recent, Europe (Handlirsch, 1925).

Figs. 879–881. Hemerobiidea incertae sedis.

879. *Archedilaropsis furcata* Martynov; fragment of wing, × 3.2. Neogene, Western Siberia (Martynov, 1935). 880. *Dilarites incertus* Martynov; fragment, × 3.5. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 881. *Eopsychopsis permiana* Martynov; fragment of forewing, × 9. Upper Permian, Urals.

1906; *Creagroptera* Handlirsch, 1906; *Dicranoptila* Handlirsch, 1906; *Gigantotermes* Haase, 1890; *Ineptiae* Handlirsch, 1906; *Loxophleps* Handlirsch, 1939; *Megapolystoechus* Tillyard; *Mellamnous* Handlirsch, 1939; *Melaneimon* Handlirsch, 1939; *Mesoleon* Handlirsch, 1906; *Osmylopsis* Handlirsch, 1906; *Palparites* Handlirsch, 1906; *Pseudomyrmeleon* Handlirsch, 1906; Cretaceous of China—*Mesohemerobius* Ping, 1928.

SUPERFAMILY CONIOPTERYGIDEA

Very small insects, 3–10 mm in size. Wings covered with white spots; venation poor, without additional forks; hindwings narrower and shorter than forewings. Jurassic to Recent. One family: Coniopterygidae.

Family CONIOPTERYGIDAE Burmeister, 1839

SC ends at apical part of wing, not united with R; RS simple or with one bifurcation; M and Cu with two simple branches (Fig. 882). Paleogene to Recent. About 20 widely distributed genera in the Recent fauna; four genera in the Paleogene of Europe (Baltic amber) and Western Europe.

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SUPERORDER MECOPTEROIDEA

(B.B. Rohdendorf)

Wings always membranous, of uniform consistency, occasionally similar, more often forewings larger than hindwings, latter sometimes considerably shorter or absent altogether: dipterous condition encountered in many groups. Venation poor, cross veins usually few. Mouthparts basically of biting type: often transformed into suctorial or piercing proboscis with peculiar structure. Larvae eruciform, usually with hypognathous head; thoracic legs short, rarely long, sometimes with prolegs on abdomen, or legs altogether absent. Live under extremely diverse conditions: in soil, in water, in decaying matter, in plant tissues, as parasites in bodies of animals or freely on plants. Perfection in metamorphosis (adaptability of growth stages), feeding (changes in mouthparts) and locomotion (development of specialized flight mechanism)—all these adaptations have determined origin and evolution of Mecopteroidea, the most varied recent superorder of winged insects. Lower Carboniferous to Recent. Orders: Mecoptera, Trichoptera, Lepidoptera, Diptera, Aphaniptera.

Order MECOPTERA. Scorpion flies

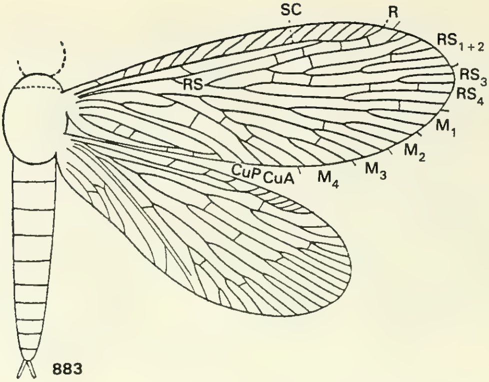
(O.M. Martynova)

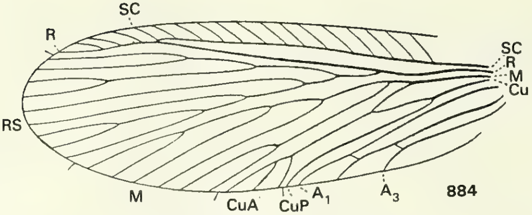
Two pairs of almost similar wings. In suborder Paratrichoptera diminution of hindwings noticed. RS and M dichotomously branched into four main branches; RS with four to 12 branches and M with four to eight; Cu branches into two at base of wing; CuA forked; CuP always simple; usually three anal veins reaching upto anal margin of wing; three or four ''specula'' in constant positions.

Head hypognathous, with chewing mouth parts, elongated in form of a beak (except in suborder Paratrichoptera), antennae filiform, do not exceed length of wing; large compound eyes, three ocelli; prothorax little shorter than meso- and metathorax; legs similar, cursorial; tarsus five-segmented with two claws on last segment (in Bittacidae only one claw). Abdomen a little longer than wings, with ninth genital segment raised and well-developed gonopods; in suborder Eumecoptera from the Mesozoic, sixth, seventh and eighth segments elongate. Females with short three-segmented cerci. Larvae eruciform, live in decaying stumps of trees and in moist forest litter. Adults and larvae feed on decaying organic remains, pollen grains, eggs of Lepidoptera and, rarely, newly dead insects. Members of family Bittacidae are predators. Suborder
284 Protomecoptera ancestral to Trichoptera–Lepidoptera; suborder Paratrichoptera ancestral to Hymenoptera, Diptera and Aphaniptera (Martynova, 1959). Lower Carboniferous to Recent. Suborders: Protomecoptera, Eumecoptera, Paratrichoptera.

Suborder Protomecoptera

Six large branches of SC in both pairs of wings. CuA with bifurcation. Permian to Recent. Three families in the Recent fauna of America and Australia. Extinct families: Platychoristidae, Kaltanidae, Cycloristidae, Cyclopteridae, Tomiochoristidae, Permomeropidae, Archipanorpidae; last two found outside the USSR.





283 Figs. 883–884. Family Platychoristidae.

883. *Platychorista venosa* Tillyard; (reconstruction), × 11.7. Lower Permian, North America (Carpenter, 1980). 884. *Marimerobius splendens* G. Zalessky; forewing; × 7. Lower Permian, Urals (original drawing from photograph of holotype).

Family PLATYCHORISTIDAE Carpenter, 1930
(Protomeropidae Tillyard, 1926)

In forewing anterior margin weakly convex; tip of SC connected with R by a strong, inclined vein, giving impression of fusion with R; pterostigma absent; SC with 12 large branches; RS starts proximal to midpoint of basal half of wing; RS with nine to 12 branches; RS_{1+2} twice as long as RS_{3+4} or more; eight or nine branches on M; distal parts of anal veins connected by inclined cross veins; ends of anal veins distal to connecting cross veins and thinner, so that they resemble anal veins of forewings of Trichoptera, but they differ from the latter in absence of non-crossing veins in wide post-costal area. Length of forewing 5.6–10 mm (Fig. 883). Lower Permian of Urals and North America. Two genera.

Marimerobius G. Zalessky, 1946. Genotype—*M. splendens* G. Zalessky, 1946; Lower Permian, Perm province (Kungurian stage, Chekarda). RS starts somewhat proximal to midpoint of basal half of wing; RS_{1+2} more than twice the length of RS_{3+4}; M_{1+2} shorter than M_{3+4}, latter with a simple fork; ends of anal veins do not resemble cross veins. Length of forewing 10 mm (Fig. 884). One species. Lower Permian of Urals.

Outside the USSR: *Platychorista* Tillyard, 1926.

Family KALTANIDAE O. Martynova, 1958

Anterior margin of forewing weakly convex; tip of SC connected with R by a straight cross vein, does not appear fused with R; pterostigma absent; SC with six to 12 branches; RS starts at midpoint of basal half of wing or more proximally, it has seven to 10 branches; R_{1+2} somewhat longer than R_{3+4}, but more often they are of same length; six to nine branches of M; distal parts of anal veins not connected by cross veins; sometimes there are tubercles on longitudinal 285 veins. Permian. Three genera.

Altajopanorpa O. Martynova, 1948 (*Kaltana* O. Martynova, 1958). Genotype—*A. kaltanica* O. Martynova, 1948; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Branches of SC not more than nine, usually six or seven; six branches of M, with bifurcations on M_1 and M_2; M_{1+2} branches more distally than where RS branches and is longer than M_{3+4}; longitudinal veins covered with tubercles. Length of forewings 5.7–8 mm (Fig. 885). 10 species from the Lower Permian and one from the Upper Permian of Kuznetsk basin.

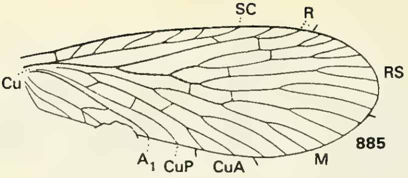
Pinnachorista O. Martynova, 1958. Genotype—*P. sarbalensis* O. Martynova, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala). Branches of SC not fewer than 10; branches of M more than six; tubercles present on 10 longitudinal veins in forms from the Lower Permian. Length of forewings 5.25–19 mm (Fig. 886). Eight species from the Lower Permian and one from the Upper Permian of Kuznetsk basin.

Megachorista O. Martynova, 1958. Genotype—*M. khalfini* O. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Kemerovian province). Nine branches of SC; six branches of M; forks on M_1 and M_4; M_{1+2} branches more proximally than where RS branches and is shorter than M_{3+4}; tubercles present on longitudinal veins. Length of forewing 13–13.5 mm. (Fig. 887). One species. Upper Permian of Kuznetsk basin.

Family CYCLORISTIDAE O. Martynova, 1958

Anterior margin of forewing markedly convex; costal area one and half times wider than subcostal area; pterostigma present; seven branches of SC; R weakly bent; RS with eight branches and M with six; with tubercles on longitudinal veins. Permian. One genus.

Cyclorista O. Martynova, 1958. Genotype—*C. convexicosta* O. Martynova, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan).



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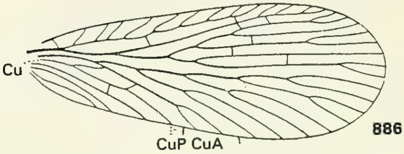

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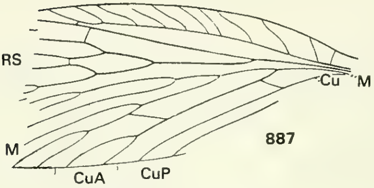

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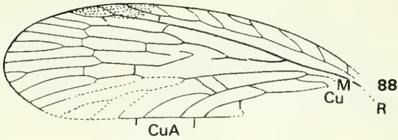

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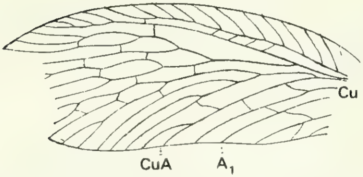

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Figs. 885–889. Family Kaltanidae [Cycloristidae, Cyclopteridae].

885. *Altajopanorpa pilosa* (O. Martynova); forewing, × 10. Lower Permian, Kuznetsk basin (Martynova, 1958). 886. *Pinnachorista sarbalensis* O. Martynova; forewing, × 10. Lower Permian, Kuznetsk basin (Martynova, 1958). 887. *Megachorista khalfini* O. Martynova; forewing, × 6. Upper Permian, Kuznetsk basin (Martynova, 1958). 888. *Cyclorista convexicosta* O. Martynova; forewing, × 8.6. Lower Permian, Kuznetsk Basin (Martynova, 1958). 889. *Cycloptera autumnalis* O. Martynova; forewing, × 4. Upper Permian, Kuznetsk basin (Martynova, 1958).

Additional bifurcations and M_1 and M_3; CuA branches proximal to branching of M. Length of forewing 7 mm (Fig. 888).

Family CYCLOPTERIDAE O. Martynova, 1958

Anterior margin of forewing markedly convex; costal area more than twice as wide as the subcostal area. Pterostigma present. 12 or 13 branches of SC. R bent toward posterior side at base of wing, distal to this it is arcuately bent towards anterior side, and runs almost parallel to anterior margin of wing; RS with nine branches, M with eight; tubercles on longitudinal veins absent. Premian. One genus.

Cycloptera O. Martynova, 1958. Genotype—*C. autumnalis* O. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Sureikovo). SC and R curved forward; M_3 simple; CuA and M_4 branch at same level; two series of cross veins arranged in a steplike way. Length of forewing 14.5–15 mm (Fig. 889). One species. Upper Permian of Kuznetsk basin.

Family TOMIOCHORISTIDAE O. Martynova, 1958

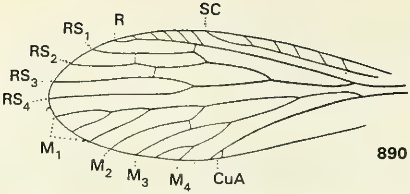
Anterior margin of forewing weakly convex; pterostigma absent; SC with about 10 branches and RS with four; M with four to seven; tubercles present on longitudinal veins. Lower Permian. Two genera.

Tomiochorista O. Martynova, 1958. Genotype—*T. nubila* O. Martynova, 1958. Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). In forewings
280 costal and subcostal areas of same width; stem of RS slightly longer than R_{1+2} and R_{3+4} if not of same length; no free base of M_5; M with more than four branches. Length of forewing 4.47–5.1 mm (Fig. 890). Five species. Lower Permian of Kuznetsk basin.

Kaltanochorista O. Martynova, 1958. Genotype—*K. grjasevi* O. Martynova, 1958; Permian, Kuznetsk basin (Kuznetsk series, Kaltan). In forewing costal area twice as broad as subcostal area; RS shorter than RS_{1+2} and R_{3+4}; R_{1+2} longer than its own bifurcation; free base of M_5 noticeable; four branches of M. Length of forewing 8 mm (Fig. 891). One species. Lower Permian of Kuznetsk basin.

Family PERMOMEROPIDAE Riek, 1953

Anterior margin of forewing almost straight; SC short, slightly longer than half of length of wing, with seven or eight branches; posterior margin of pterostigma bordered by R; RS with 10 branches and M with eight; M_{1+2} branches halfway along apical half of wing; bifurcations of branches of RS and M very short, almost equal in length (Fig. 892). Upper Permian. Australia. Two genera: *Permomerope* Tillyard, 1926; *Aphryganoneura* Tillyard, 1926.



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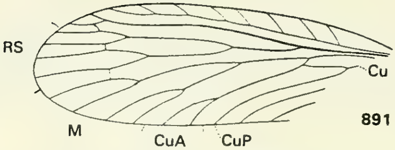

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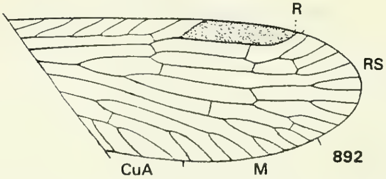

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285 Figs. 890–892. Families Tomiochoristidae, Permomeropidae.

890. *Tomiochorista nubila* O. Martynova; forewing, × 12.5. Lower Permian, Kuznetsk basin (Martynova, 1958). 891. *Kaltanochorista grjasevi* O. Martynova; forewing, × 7.5. Lower Permian, Kuznetsk basin (Martynova, 1958). 892. *Permomerope australis* Tillyard; forewing, × 6.8. Upper Permian, Australia (Tillyard, 1926).

Suborder Eumecoptera

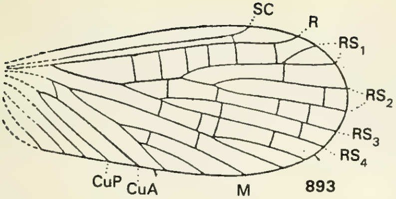
(Paramecoptera)

In forewing not more than three branches of SC; R bent at base and at distal part, except in Metropatridae; four to 10 branches of RS and four to eight of M; CuA without bifurcation. Lower Carboniferous to Recent. Five families in the Recent fauna. Following families found as fossils: Metropatridae, Permopanorpidae, Permochoristidae, Anormochoristidae, Tychtopsychidae, Permocentropidae, Orthophlebiidae, Neorthophlebiidae, Panorpidae, Bittacidae, Nannochoristidae, Choristidae; last four are Recent.

Outside the USSR: Metropatridae, Anormochoristidae, Nannochoristidae, Choristidae.

Family METROPATRIDAE Handlirsch, 1906

Forewing differs from that of all other families of suborder in its almost straight



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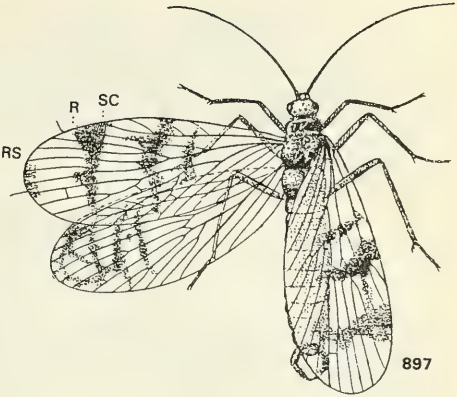

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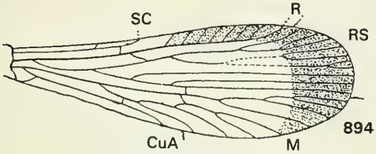

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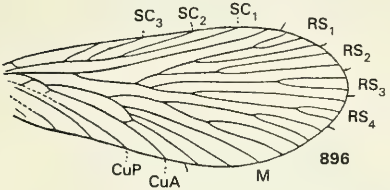

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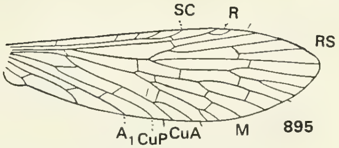

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Figs. 893–897. Families Metropatridae [Permopanorpidae], Permochristidae.

893. *Metropator pusillus* Handlirsch; forewing, × 7. Lower Carboniferous, North America (Tillyard, 1926). 894. *Permopanorpa angustata* Martynov; forewing, × 6. Upper Permian, Arkhangelsk province (Martynov, 1948). 895. *Belmontia mitsheli* Tillyard; forewing, × 2.7. Upper Permian, Australia (Tillyard, 1919). 896. *Sylvopanorpa carpenteri* Martynov; forewing, × 6. Lower Permian, Urals (Martynov, 1940). 897. *Agetochorista tillyardi* Martynov; (reconstruction), × 5.3. Lower Permian, Urals (Martynov, 1940).

SC and R and in its radial area, which is wider than costal and subcostal areas put together; bifurcations present on RS_1, RS_2 and M_4; RS branches considerably more proximally than halfway along wing; anal area short, ends at basal one-fourth of wing. Many cross veins arranged without any regularity. Length of forewing 8.9 mm (Fig. 893). Top layers of Lower Carboniferous. One genus, *Metropator* Handlirsch, 1906 from North America.

Family PERMOPANORPIDAE Tillyard, 1926

Forewing narrow, length exceeding width by 3.5 times or more; SC short, not longer than one-half of wing length; pterostigma present. R with three to eight branches and RS with many, which branch off in turn; M with six or seven branches; M_5 inclined, long; cross veins few. Permian to Triassic. Three genera.

Permopanorpa Tillyard, 1926. Genotype—*P. formosa* Tillyard, 1926; Lower Permian, North America (Kansas). RS_{1+2} branches off halfway along the wing and is longer than RS_{3+4}; bifurcations on M_1 and M_3 occasionally split into two; crossveins in radial area and between branches of M. Length of forewing 4–11 mm (Fig. 894). Six species. Upper Permian of Arkhangelsk province and Lower Permian of North America.

Outside the USSR: *Neopermopanorpa* Riek, 1955; and *Xenopanorpa* Riek, 1955.

Family PERMOCHORISTIDAE Tillyard, 1917

(Mesopanorpidae Tillyard, 1918; Belmontiidae Tillyard, 1919; Mesochoristidae Tillyard, 1925; Agetopanorpidae Carpenter, 1930; Idelopanorpidae M. Zalessky, 1929; Xenochoristidae Riek, 1953)

Forewing: length of wing exceeds its width more than threefold; SC long, ends more distally than halfway along wing; R without branches or with one branch; RS with four to 10 branches, all of which branch in turn; branches of M usually not more than six (except in *Sylvopanorpa*); M_5 inclined; few crossveins (Fig. 895). Permian to Jurassic. Subfamilies: Protochoristinae and Permochoristinae.

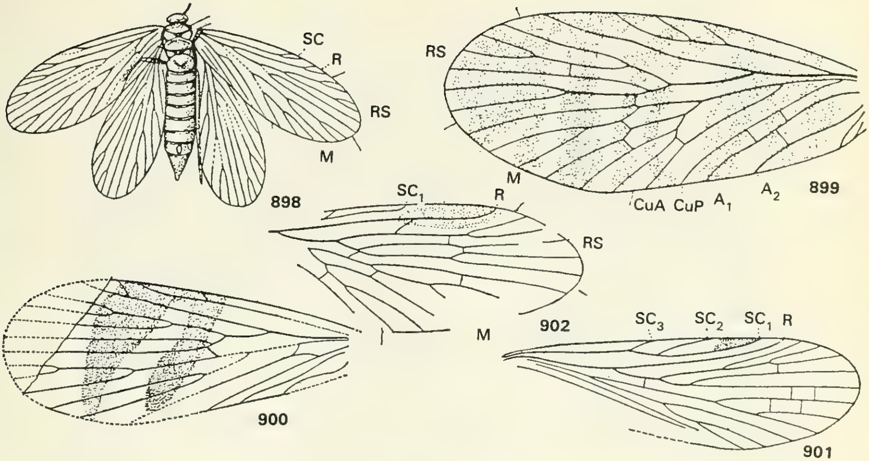
Subfamily Protochoristinae O. Martynova, subfam. nov.

Branches of RS more than four; M with six branches. Permian. Twelve genera.

Sylvopanorpa Martynov, 1940. Genotype—*S. carpenteri* Martynov, 1940; Lower Permian, Perm province (Kungurian stage, Chekarda). Forewing: costal area twice as wide as subcostal; three gently sloping long branches of SC starting proximal to origin of RS; length of SC_2 and SC_3 almost four times of width of costal area; RS with 10 branches; RS_{1+2} and RS_{3+4} shorter than stem of RS; branching proximal to middle of length of wing; A_1 ends at midpoint of basal half of wing. Length of forewing 10.5 mm (Fig. 896). One species. Lower Permian of Urals.

Agetochorista Martynov, 1933 (*Neoageta* Riek, 1953; *Agetochoristella* Riek, 1953). Genotype—*A. ornata* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: costal area 1.5–2 times of width of subcostal area; length of gently sloping SC_2 2–2.5 times of width of costal area; RS with five branches; additional bifurcations found on RS_4, M_2 and M_4; RS_{1+2} branches more distally than halfway along wing and is longer than RS_{3+4}. Length of forewing 4.2–14 mm (Fig. 897). 15 species. Lower Permian of Urals and Kuznetsk basin; Upper Permian of Arkhangelsk province, Kuznetsk province and Australia.

Kamopanorpa Martynov, 1928. Genotype—*K. lata* Martynov, 1928; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). RS_{1+2} branches halfway along wing, and RS_{3+4} more proximally; additional bifurcations observed on RS_1, RS_2, M_1 and M_3. Length of forewing 4.8–5.5 mm (Fig. 898). Three species.



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Figs. 898–902. Family Permochoristidae.

898. *Kamopanorpa rotundipennis* Martynov; general view, × 6.3. Upper Permian; Arkhangelsk region (Martynov; 1933). 899. *Oochorista gunderseni* Martynov; forewing, × 6.0. Upper Permian, Arkhangelsk region (Martynov, 1933). 900. *Parachorista uralensis* Martynov; forewing, × 11.0. Lower Permian, Urals (Martynov, 1940). 901. *Protopanorpoides elongata* (Martynov); forewing, × 6.8. Upper Permian, Arkhangelsk region (Martynov, 1933). 902. *Stigmorista captiosa* O. Martynova; forewing, × 10.0. Upper Permian, Kuznetsk basin (Martynova, 1958).

Lower Permian of Urals and Upper Permian of Arkhangelsk province and Urals.

Oochorista Martynov, 1933. Genotype—*O. gunderseni* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). Forewing: costal and subcostal areas of same length; length of SC_2 2.5 times of width of costal area; R_{1+2} longer than R_{3+4}. Both branch more distally than halfway along wing; additional bifurcations seen on R_2, R_4, M_2 and M_4; with dark transverse bands. Length of forewing 12.2 mm (Fig. 899). One species. Upper Permian of Arkhangelsk province.

Parachorista Tillyard, 1926 (*Phipoides* Riek, 1953). Genotype—*Parachorista pincombeae* Tillyard, 1926; Upper Permian, Australia. Forewing: costal area narrower than subcostal area; SC with one short branch; R with short bifurcation; additional bifurcations seen on R_1, M_1 and M_4; with transverse bands. Length of forewing 5–14 mm (Fig. 900). Six species. Lower Permian of Urals, Upper Permian of Arkhangelsk province and Australia.

Protopanorpoides O. Martynova, gen. nov. Genotype—*Protopanorpa elongata* Martynova, 1933; Upper Permian, Arkhangelsk province (Kazanian

stage, Soyana). Forewing: SC curved; costal area narrower than subcostal up to beginning of SC_3 but in region of SC_2 is twice as wide; length of SC three times of width of costal area at its narrowest; additional bifurcations on R_2, M_2 and
288 M_3; M branches proximal to beginning of RS. Length of forewing 9 mm (Fig. 901). One species. Upper Permian of Arkhangelsk province.

Stigmorista O. Martynova, 1958. Genotype—*S. captiosa* O. Martynova, 1958; Upper Permian, Kuznetsk basin (Ilinian series, Suriekovo). Forewing: anterior margin straight; costal and subcostal area narrow, of same width; SC_2 and SC_3 short; RS_{1+2} significantly longer than RS_{3+4}; additional bifurcations on RS_4, M_2 and M_4; presence of large leaflike pterostigma with its posterior margin in radial area close to RS_1 distinguishes this genus from other genera of this subfamily. Length of forewing 7 mm (Fig. 902). One species. Upper Permian of Kuznetsk basin.

Outside the USSR: *Protochorista* Tillyard, 1926; *Agetopanorpa* Carpenter, 1930; *Protopanorpa* Tillyard, 1926; *Belmontia* Tillyard, 1919; and *Parabelmontia* Tillyard, 1922.

Subfamily Permochoristinae O. Martynova, subfam. nov.

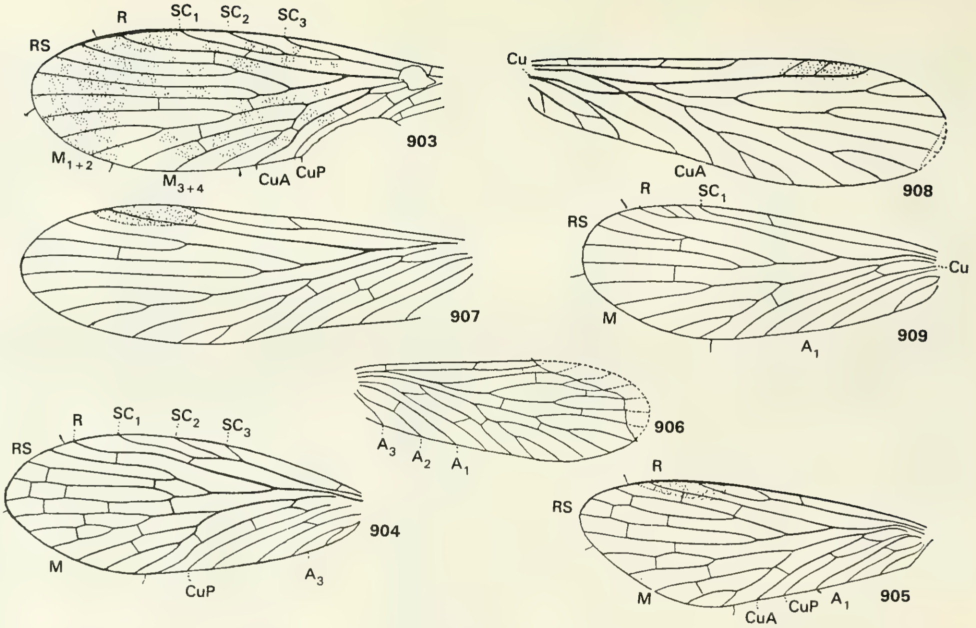
RS with four branches and M with four to six. Permian through Jurassic. Nine genera.

Petromantis Handlirsch, 1904 (*Idelopanorpa* M. Zalessky, 1929; *Martynoviella* Handlirsch, 1937). Genotype—*P. rossica* Handlirsch, 1904; Upper Permian, Tatar ASSR (Kazanian stage, Tikhie Gory). Forewing: wide costal area more distal than base of SC_3; SC_2 and SC_3 long; length of gently sloping SC_2 3.5–4 times of width of costal area at its narrowest part; RS_{1+2} and RS_{3+4} short, equal or almost equal in length, one-third to one-fourth of length of their own bifurcations. Length of forewing 4.5–12.5 mm (Fig. 903). Nineteen species. Lower Permian of Kuznetsk basin; Upper Permian of Arkhangelsk province, Urals and Kuznetsk basin.

Asiachorista O. Martynova, 1958. Genotype—*A. neuburgae* O. Martynova, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). Forewing: costal area distal to base of SC_2, whose length is 3–5 times of width of costal area at its narrowest; SC_3 short, resembles a somewhat slanting cross vein; RS_{1+2} and RS_{3+4} short, equal or almost equal in length, one-third to one-fourth of length of their own bifurcations. Length of forewings 5–10 mm (Fig. 904). Nine species from the Lower Permian and four species from the Upper Permian of Kuznetsk basin.

Callietheira O. Martynova, 1958. Genotype—*C. khalfini* O. Martynova, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Kaltan). This differs from *Asiachorista* in the more sharply distinct apex of wing and branches of RS terminating distally with curvature toward anterior margin. Length of forewing 7.5–9.5 mm (Fig. 905). Three species. Lower Permian of Kuznetsk basin.

289 *Petrochorista* Martynov, 1930 (*Neopteromantis* Riek, 1953). Genotype—*P. elegantula* Martynov, 1930; Upper Permian, Tatar ASSR (Kazanian stage,



Figs. 903–909. Family Permochoristidae.

903. *Petromantis kaltanica* O. Martynova; anterior wing, × 8.5. Lower Permian, Kuznetsk basin (Martynova, 1961). 904. *Asiachorista neuburgae* O. Martynova; forewing, × 6.7. Lower Permian, Kuznetsk basin (Martynova; 1958). 905. *Callietheira khalfini* O. Martynova; forewing, × 8. Lower Permian, Kuznetsk basin (Martynova, 1958). 906. *Petrochorista elegantula* Martynova; forewing, × 8. Upper Permian, Urals (Martynova, 1930). 907. *Mesochorista oblonga* O. Martynova; forewing, × 12.3. Upper Permian, Kuznetsk basin (Martynova, 1961). 908. *Lithopanorpa pusilla* (Tillyard); forewing, × 18. Lower Permian, North America (Carpenter, 1930). 909. *Liassochorista asiatica* O. Martynova; forewing, × 10. Upper Triassic, Central Asia (Martynova, 1948).

Tikhie Gory). Forewing: costal area narrow, not wider than subcostal; SC long with short branches; not more than one branch on R; RS_{1+2} and RS_{3+4} almost equal in length, approximately of same length as their bifurcations and longer than RS; they branch more distally than halfway along wing. Length of forewing 3.6–10 mm (Fig. 906). Eighteen species. Lower Permian of Kuznetsk basin; Upper Permian of Arkhangelsk province, Urals, Kuznetsk basin and Australia.

Mesochorista Tillyard, 1916 (*Permochorista* Tillyard, 1918; *Caenoptilon* G. Zalessky, 1933; *Prochoristella* Riek, 1953). Genotype—*Mesochorista proavita* Tillyard, 1916; Triassic, Australia (Queensland). Costal area narrow, but wider than subcostal area; SC long with short branches; RS_{1+2} considerably longer than RS_{3+4}; RS_{3+4} always shorter than stem of RS and much shorter than its own bifurcation. Length of forewing 3.3–11 mm (Fig. 907). Forty-eight species. Lower Permian of Urals and Kuznetsk basin; Upper Permian of Arkhangelsk province, Urals, Kuznetsk basin and Australia; Triassic of Australia.

Lithopanorpa Carpenter, 1930. Genotype—*Protopanorpa pusilla* Tillyard, 1926; Lower Permian, North America (Kansas). Wings small and narrow; costal area narrow; SC short, ends halfway along wing; R with two or three branches; RS branches halfway along wing; RS shorter than RS_{3+4}; RS_{1+2} slightly longer than RS_{3+4}, considerably longer than its short bifurcation. Length of forewing 4–5 mm (Fig. 908). Two species. Lower Permian of North America; Upper Permian of Kuznetsk basin.

Liassochorista Tillyard, 1933. Genotype—*L. anglicana* Tillyard, 1933; Lower Lias, England. This differs from *Mesochorista* in presence of two or three branches on R and long SC. Length of forewing 5–7.5 mm (Fig. 909). Upper Triassic of Issyk-Kul province; Lower Jurassic of Western Europe.

Outside the USSR: *Mesopanorpodes* Tillyard, 1918.

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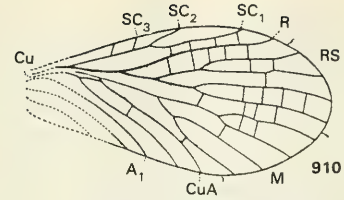
Family TYCHTOPSYCHIDAE O. Martynova, 1958

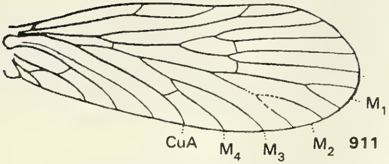
Forewing wide, with length more than double width; base narrow, about one-third width of wing; anterior margin of forewing convex; apex markedly rounded; SC ends distal to middle of wing; R markedly curved; RS and M with four branches. Upper Permian. One genus.

Tychtopsyche O. Martynova, 1958. Genotype—*T. beljanini* O. Martynova, 1958; Upper Permian, Kuznetsk basin (Erunakovian series, Sokolova II). Up to beginning of SC_2 costal area narrower than subcostal but widens distal to SC_2; SC_2 longer than the short SC_3; RS short, equal in length to RS_{3+4}; RS_{1+2} slightly longer than RS_{3+4}; many cross veins. Length of forewing 6.2 mm (Fig. 910). One species. Upper Permian of Kuznetsk basin.

Family PERMOCENTROPIDAE Martynov, 1933

Anterior margin of forewing convex, curved and bent; length of wing two to eight times width; SC ends at midpoint of wing, is curved parallel to anterior





Figs. 910–911. Families Tychtopsychidae, Permocentropidae.

910. *Tychtopsyche beljanini* O. Martynova; forewing, × 10. Upper Permian, Kuznetsk basin (Martynova, 1958). 911. *Permocentropus philopotamoides* Martynov; forewing, × 10. Upper Permian, Arkhangelsk province (Martynov, 1933).

margin and has one short branch; R with one branch; RS branches halfway along wing, longer than RS_{1+2} and RS_{3+4}; RS with four branches; additional bifurcations on M_1 and M_2. Upper Permian. One genus.

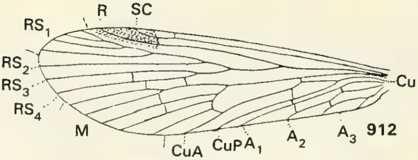
Permocentropus Martynov, 1933. Genotype—*P. philopotamoides* Martynov, 1933; Upper Permian, Arkhangelsk province (Kazanian stage, Soyana). RS_{1+2} shorter than RS_{3+4}, both about one-half of length of their own bifurcations. Length of forewing 6.3 mm (Fig. 911). One species. Upper Permian of Arkhangelsk province.

Family NANNOCHORISTIDAE Tillyard, 1917

Forewing: branches of RS three; RS_{1+2} does not branch; M and CuA fused together for some distance. In the Recent fauna of Australia two genera with five species. Upper Permian of Australia. Two genera: *Nannochoristella* Riek, 1953 and *Neochoristella* Riek, 1953.

Family ORTHOPHLEBIIDAE Handlirsch, 1906

Forewing: length more than three times width; SC has one branch at most; R simple; RS with five to nine branches; additional branches distributed pectinately on RS_1; RS_{1+2} branches proximal to distal end of SC; additional bifurcation on M_4; M_5 short, almost straight. Evolution of Orthophlebiidae involved tapering of wings and reduction of venation. Probably the present-day Panorpidae developed from this family. Triassic through Neogene. Three genera.



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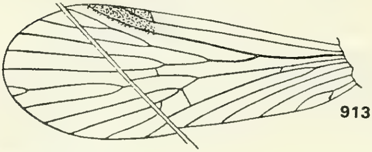

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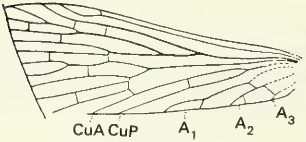

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Figs. 912–914. Family Orthophlebiidae.

912. *Orthophlebia liassica* (Mantell); forewing, × 4. Lower Jurassic, England (Tillyard, 1938). 913. *Protorthophlebia latipennis* Tillyard; forewing, × 7.3. Lower Jurassic, England (Tillyard, 1933). 914. *Mesopanorpa hartungi* Brauer, Redtenbacher and Ganglbauer; forewing × 5.5. Lower Jurassic, Irkutsk province (Martynov, 1927).

291 *Orthophlebia* Westwood, 1843 (*Orthophlebioides* Handlirsch, 1906; *Orthophlebiites* Handlirsch, 1939; *Synorthophlebia* Handlirsch, 1939, pars; *Dinopanorpa* Cockerell, 1924; *Neoparachorista* Riek, 1955, pars). Genotype—*Panorpa liassica* Mantell, 1844; Lower Jurassic, Western Europe (Lower Lias, England). RS_{1+2} and RS_{3+4} branch almost at same level; RS_1 has more than three branches. Length of forewing 7–35 mm (Fig. 912). Twenty-nine species. Upper Triassic of Issyk-Kul province and Australia; Jurassic of Kazakhstan, Central Asia and Western Europe; Miocene of Eastern Siberia (Kudya).

Protorthophlebia Tillyard, 1933 (*Choristopanorpa* Riek, 1950; *Neoparachorista* Riek, 1955, pars). Genotype—*P. latipennis* Tillyard, 1933; Lower Jurassic, Western Europe (Lower Lias, England). RS_{1+2} and RS_{3+4} branch almost at same level; RS_1 has two branches. Length of forewing 7.5–12 mm (Fig. 913). Five species. Upper Triassic of Issyk-Kul province and Australia; Lower Jurassic of England.

Mesopanorpa Handlirsch, 1906 (*Synorthophlebia* Handlirsch, 1939, pars; *Neoparchorista* Riek, 1955, pars). Genotype—*Panorpa hartungi* Brauer, Redtenbacher and Ganglbauer, 1889; Lower Jurassic, Irkutsk province

(Cheremkhovian series, Ust-Ballei). RS_{1+2} twice as long as RS_{3+4}; RS has three branches or more. Length of forewing 7–31 mm (Fig. 914). Twenty-three species. Upper Triassic of Issyk-Kul province and Australia; Jurassic of Western Europe, Kazakhstan, Central Asia and East Siberia.

Family PANORPIDAE M. Leay, 1821

[nom. transl. Stephens, 1835 (ex Panorpina M. Leay, 1821)]

Forewing: length four times width; SC has one short branch; R has no branches; five to seven branches of RS; additional branches distributed pectinately on RS_1; RS_{1+2} branches at same level as distal termination of SC; M four-branched, without additional bifurcations; M_5 short, straight (Fig. 915). Paleogene to Recent. Five genera and about 150 species in Recent fauna. Four genera as fossils in the Paleogene of Europe (Baltic amber) and Australia; of these two are also Recent.[1]

Family NEORTHOPHLEBIIDAE Handlirsch, 1921

Forewing: length four times width; SC short, without branches; R has one branch; distal end of R not curved in form of dipper; four branches on RS; R_{1+2} twice as long as R_{3+4}; additional bifurcations on M_4; two anal veins; longitudinal veins in distal half of wing do not zigzag. Neorthophlebiidae was ancestral to Bittacidae, in which wings became more specialized.

Neorthophlebia Handlirsch, 1908 (*Mesobittacus* Handlirsch, 1939). Genotype—*Orthophlebia megapolitana* Geinitz, 1884; Lower Jurassic, Western Europe (Upper Liassic, Germany). Pterostigma weakly chitinized, not large in size; before fusing, M and CuA diverge proximal to beginning of RS; SC not shorter than one-half of length of wing. Length of forewing 6–32 mm (Fig. 916). Fourteen species. Upper Triassic of Issyk-Kul province; Lower Jurassic of Central Asia and Western Europe.

Bittacopanorpa G. Zalessky, 1935. Genotype—*B. javorskii* G. Zalessky, 1935; Triassic, Kuznetsk basin (Maltsevian series, Babio Kamen). This differs from *Neorthophlebia* in the short SC not reaching halfway along wing and in M and CuA diverging distal to beginning of RS. Length of forewing about 11 mm. One species. Triassic of Kuznetsk basin.

Protobittacus Tillyard, 1933 (*Archebittacus* Riek, 1955). Genotype—*P. liassicus* Tillyard, 1933; Lower Jurassic, England. This differs from *Neorthophlebia* in its flat, wide pterostigma going up to R_{1+2} and presence of strong cross-vein rs-m and bifurcation of M_4 without stalk. Length of forewing 15.7 mm (Fig. 917). Four species. Triassic of Australia; Lower Jurassic of England.

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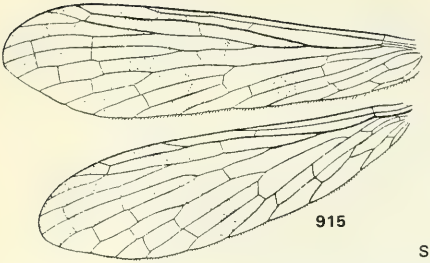
[1] According to Prof. Carpenter the genera *Holcorpa* Scudd, 1878 and *Panorpodes* McL., 1875 should be separated into special families.



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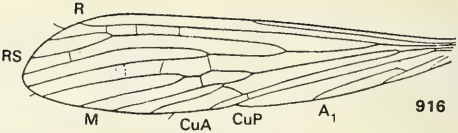

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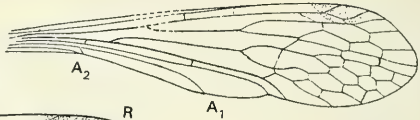

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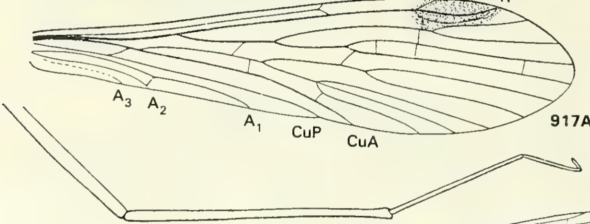

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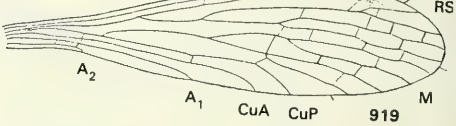

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291 Figs. 915–919. Families Panorpidae, Neorthophlebiidae, Bittacidae.

915. *Panorpa sibirica* Esb.—P.; wings, Recent. 916. *Neorthophlebia robusta* Martynov; forewing, × 3. Lower Jurassic, Central Asia (Martynov, 1937). 917. *Protobittacus liassicus* Tillyard: A—forewing, × 6, B—hindwing, × 14. Lower Jurassic, England (Tillyard, 1933). 918. *Probittacus avitus* Martynov, forewing, × 4. Upper Jurassic, Southern Kazakhstan (Martynov, 1927). 919. *Bittacus succinus* Carpenter; forewing, × 4.5. Paleogene, Europe (Baltic amber) (Carpenter, 1954).

Outside the USSR: *Auxobittacus* Bode, 1953 (*Protobittacus* ?); *Haplobittacus* Bode, 1953; *Metaxibittacus* Bode, 1953 (*Neorthophlebia*?); *Pleobittacus* Bode, 1953 (*Neorthophlebia*?); *Polydicrobittacus* Bode, 1953.

Family BITTACIDAE Enderlein, 1910

Differs from Neorthophlebiidae in having in forewing a dipper-like curve on distal end of R, connected with RS by one or two cross-veins, zigzagging of longitudinal veins in distal half of wing and absence of additional branches of M. Jurassic to Recent. In the Recent fauna about 60 species, related to six genera.

Many species distributed in the Southern Hemisphere. Four genera known as fossils.

Probittacus Martynov, 1927. Genotype—*P. avitus* Martynov, 1927; Upper Jurassic, Chimkent province (Malm, Karatau). R_{3+4} branches at level of midpoint of $R_{1+2;}$ M_4 with bifurcation; one cross-vein r-rs_{1+2} located proximal to pterostigma. Length of forewing 16.5 mm (Fig. 918). One species. Upper Jurassic of Kazakhstan and Eastern Europe (Baltic amber).

Outside the USSR: *Protobittacus** Tillyard, 1933; *Paleobittacus* Carpenter, 1929; and *Bittacus* Latreille, 1805 (Fig. 919).

Suborder Paratrichoptera

Distinguished from other suborders by its perfectly straight R at base, closer placing of CuA and CuP and presence of only one or two anal veins.

Head small, rounded, not drawn into a beak; antennae not longer than wings. Legs almost similar; tarsi five-segmented. Probably from this suborder two progressive orders—Diptera and Hymenoptera—arose following evolutionary paths of further costalization of forewings and reduction of hindwings (Martynova, 1959). Upper Permian to Jurassic. Families: Permotipulidae, Pseudopolycentropidae, Pseudodipteridae, Choristopsychidae, Mesopsychidae,Permotanyderidae, Dobbertiniidae; last two found outside the USSR.

Family PERMOTIPULIDAE Tillyard, 1937

(Rubinjohniidae O. Martynova, 1948)

Small forms. Similar wings have narrow costal area and narrow base; length of wing three times of its width; SC ends halfway along wing; three or four branches of RS; M branches considerably proximal to branching of RS; CuA and CuP very close together. One or two anal veins. Upper Permian. Two genera.

Permotipula Tillyard, 1929. Genotype—*P. patricia* Tillyard, 1929; Upper Permian, Australia. Hindwing: R_{1+2} has no bifurcation; two anal veins. Length of wing 4.8–5 mm (Fig. 920). Two species. Upper Permian of Kuznetsk basin and Australia.

Outside the USSR: *Robinjohnia* O. Martynova, 1948.

Family PSEUDOPOLYCENTROPIDAE Handlirsch, 1921

Hindwing considerably shorter than forewing (about three-fourths of its length); shape of forewing triangular; apex rounded, broadest at level of end of 293 M_4 (tornus); venation of both wings very similar; radial area at level where RS branches twice as wide as costal area; SC very short, ending at basal one-fourth of wing; R_{1+2} twice as long as R_{3+4}; M_2 with bifurcations; RS and M branch at almost same level; two anal veins. Jurassic. One genus.

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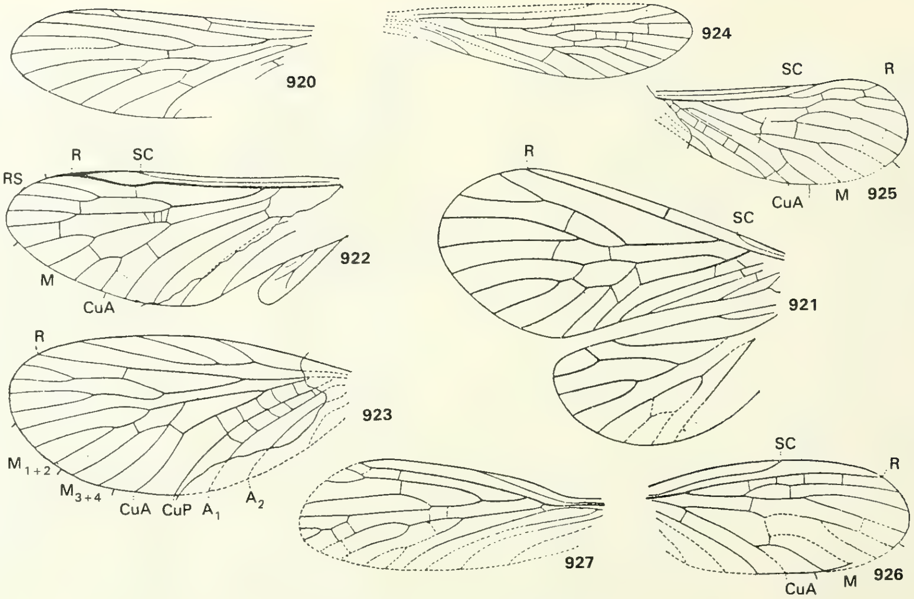
*Editor's note: This genus is also listed under preceding family, Neorthophlebiidae.



Figs. 920–927. Suborder Paratrichoptera.

920. *Permotipula borealis* O. Martynova; hindwing, × 10. Upper Permian, Kuznetsk basin (Martynova, 1961). 921. *Pseudopolycentropus latipennis* Martynov; wings, × 7.5. Upper Jurassic, Southern Kazakhstan (Martynov, 1927). 922. *Pseudodiptera gallica* Laurentiaux and Grauvogel; wings, × 5.7. Triassic, France (Martynova, 1959). 923. *Choristopsyche tenuinervis* Martynov; forewing, × 6.3. Lower Jurassic, Central Asia (Martynov, 1937). 924. *Sogdopsyche elongata* Martynov; forewing, × 3.6. Lower Jurassic, Central Asia (Martynov, 1937). 925. *Ferganopsyche rotundata* Martynov; hindwing, × 6.5. Lower Jurassic, Central Asia (Martynov, 1937). 926. *Ptychopteropsis mirabilis* Martynov; hindwing, × 4. Lower Jurassic, Central Asia (Martynov, 1937). 927. *Turanopsyche venosa* Martynov; hindwing, × 4.5. Lower Jurassic, Central Asia (Martynov, 1937).

Pseudopolycentropus Handlirsch, 1906. Genotype—*Phryganidium perlaeformis* Geinitz, 1884; Lower Jurassic, Western Europe. Three branches of M in hindwing. Length of forewing 6–8 mm (Fig. 921). Four species. Jurassic of Kazakhstan and Western Europe.

Family PSEUDODIPTERIDAE O. Martynova, 1961

Hindwings much reduced (less than one-half of length of forewings), with modified, reduced venation; forewings triangular, widest in region proximal to distal termination of CuA; apex of forewing narrow; SC ends distal to middle of wing, at three-fourths of length; R_{1+2} slightly shorter than R_{3+4}; bifurcations of RS and M short (Fig. 922). Triassic of France. One genus—*Pseudodiptera* Laurentiaux and Grauvogel, 1953[1].

Family CHORISTOPSYCHIDAE Martynov, 1937

Hindwings not known; forewings oval, wide, length being double of width; anterior margin convex; SC long, ending at distal one-fourth of wing, with two long branches; costal area at level of branch of RS wider than subcostal area, same width as radial area; R_{1+2} somewhat longer than R_{3+4}; M branches a little
294 more proximally than RS; five branches of M; bifurcations of M considerably longer than their stem. Lower Jurassic. One genus.

Choristopsyche Martynov, 1937. Genotype—*C. tenuinervis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). R_{1+2} longer than its bifurcation; R_{3+4} slightly shorter than its bifurcation; additional bifurcation on M_2. Length of forewing 9.5 mm (Fig. 923). One species. Lower Jurassic of Central Asia.

Family MESOPSYCHIDAE Tillyard, 1917

Wings long and narrow; anterior margin of forewing straight; SC shortened, but ends more distally than midway along wing; R_{1+2} considerably longer than R_{3+4} and its bifurcation; RS and M branch at same level; four branches of M; $M_{1+2}$and M_{3+4} shorter than their bifurcations. Upper Triassic to Lower Jurassic. Four genera.

Sogdopsyche Martynov, 1937. Genotype—*S. elongata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Length of forewing four times of width; R_{1+2} twice as long as its bifurcation and three times as long as R_{3+4}; R_{1+2} runs parallel to R; M and R_{3+4} branch at same level. Length of forewing 13–18 mm (Fig. 924). Two species. Lower Jurassic of Central Asia.

Outside the USSR: *Mesopsyche* Tillyard, 1917 (*Aristopsyche* Tillyard, 1919); *Neuropsyche* Tillyard, 1919; and *Triassopsyche* Tillyard, 1917.

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[1] One more genus of this family, *Ijapsyche* Kolosn and O. Mart., 1961 is found in the Upper Jurassic of Transbaikal.

Paratrichoptera Incertae sedis

Ferganopsyche Martynov, 1937. Genotype—*F. rotundata* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Hindwing: anterior margin curved at distal part; SC ends halfway along wing; R with long bifurcation, curved at distal part; R_{1+2} curved parallel to R, longer than its bifurcation and R_{3+4}; M branches more distally than RS, with four branches. Length of hindwing 7 mm (Fig. 925). One species. Lower Jurassic of Central Asia.

Ptychopteropsis Martynov, 1937. Genotype—*P. mirabilis* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Hindwing: wing oval in form; anterior margin uniformly convex; R slightly pushed to front; RS_{1+2} has no bifurcation; RS_{3+4} shorter than its bifurcation; M branches distal to branching of RS into four branches. Length of hindwing 11 mm (Fig. 926). Lower Jurassic of Central Asia.

Turanopsyche Martynov, 1937. Genotype—*T. venosa* Martynov, 1937; Lower Jurassic, Central Asia (Lower Lias, Shurab II). Hindwing: anterior margin straight; SC short, ends where RS branches; R_{1+2} almost four times as long as its bifurcation and almost as long as bifurcation of R_{3+4}; M branches into four distal to where RS branches; with additional bifurcations between R_4 and M_1. Length of hindwing 12 mm (Fig. 927). One species. Lower Jurassic of Central Asia.

Order TRICHOPTERA. Caddis flies

(O.M. Martynova)

Two pairs of wings covered with hairlike setae. Forewing: SC usually simple or with one short branch (in primitive forms more branches); RS and M divided dichotomously, giving rise to two bifurcations (primitive forms with additional bifurcations); CuA with a fork, but CuP simple; distal ends of CuP and A_1 converge and fuse; A_2 ends on A_1 and A_3 on A_2, forming enclosed cells and postcostal area. Hindwings usually have an anojugal fan; anal veins end freely; cross veins few. Always with two ''mirrors'' on wings: one at base of bifurcation of R_{3+4} and the other at distal part of thyridial cell (tc, medial area).

Head hypognathous; mouthparts of masticating type, but do not function; well-developed maxillary palps and a hypopharynx adapted to lick viscous fluids; antennae setaceous, many-segmented; compound eyes large; some families with three ocelli. Prothorax narrow, densely covered with hairlike setae; meso- and metathorax large; legs of running type; tarsus five-segmented; tibiae with spurs.

Larvae campodeiform or eruciform, six-legged, without prolegs on middle segments of abdomen; with a pair of anal legs provided with hooks on last abdominal segment; usually live in temporary cases built from threads produced by silk glands and covered by vegetative or mineral particles; inhabit stagnant or running water of certain kinds. Their varied diet consists of vegetative matter or 295 detritus; rarely predators; pupa usually aquatic. Order Lepidoptera evolved from Trichoptera probably living on vegetation. Permian to Recent. Suborders: Permotrichoptera, Annulipalpia, Integripalpia.

Suborder Permotrichoptera

Forewing: six branches on RS and M; distal parts of CuP and A_1 close, terminate at anal margin of wing proximal to its central part. Permian. Family: Microptysmatidae.

Family MICROPTYSMATIDAE O. Martynov, 1958

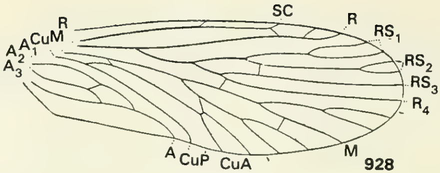
Forewing: SC convex in front, runs almost parallel to anterior margin of wing, connected at its end with R by a cross vein; additional bifurcations seen on RS_1, RS_2 and M_1 and M_3; RS leaves R almost halfway along basal half of wing; postcostal area twice as wide as costal area. Permian. Two genera.

Microptysma O. Martynova, 1958. Genotype—*M. sibiricum* O. Martynov, 1958; Lower Permian, Kuznetsk basin (Kuznetsk series, Sarbala II). Apex of forewing blunt; wing widest roughly halfway along length; M_4 fused with anterior branch of CuA, its base resembles slanting cross vein in Recent caddis flies; discoidal and medial cells closed by cross veins. Length of wing 4 mm (Fig. 928). One species. Lower Permian of Kuznetsk basin.

Microptysmodes O. Martynova, 1958. Genotype—*M. uralicus* O. Martynova, 1958; found in Permian of Tatar ASSR (Kazan stage, Tikhiya Mountains). Forewing has pointed tip; wing widest distal to middle part; M does not coalesce with anterior branch of CuA; radial and medial cells open. Length of forewing 5 mm (Fig. 929). One species. Upper Permian, Trans-Urals.

Suborder Annulipalpia

Forewing: usually all five apical forks present, only in forms with reduced venation are forks fewer (*Agapetus*, Hydroptilidae); first apical fork usually stalklike, if present (e.g. RS_{1+2}, branches distal to cross vein, enclosing discoidal cell); anastomosis not seen. Hindwings shorter than forewings; anojugal fan usually not large (except Macronematinae). Last segment of maxillary palp annulated or pointed. Larvae campodeiform, usually do not build a case, primarily inhabiting running water. In certain features representatives of this suborder resemble order Mecoptera. Upper Permian to Recent. Thirteen families: Cladochoristidae, Prorhyacophilidae, Prosepididontidae, Necrotaulidae, Rhyacophilidae, Glossosomatidae, Hydroptilidae, Philopotamidae, Stenopsychidae, Psychomyidae, Ecnomidae, Polycentropodidae, Hydropsychidae; first four known only as fossils, outside the USSR.



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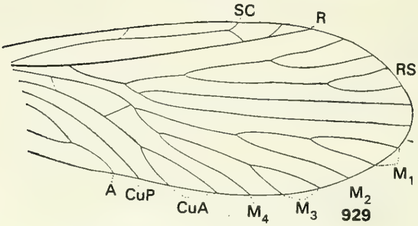

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Figs. 928–929. Suborder Permotrichoptera.

928. *Microptysma sibiricum* O. Martynova; forewing, × 11. Lower Permian, Kuznetsk basin (Martynova, 1958). 929. *Microptysmodes uralicus* O. Martynova; forewing, × 12. Upper Permian, Urals (Martynova, 1958).

Family CLADOCHORISTIDAE Riek, 1953

Forewing: anterior margin convex; six or seven branches of SC; additional branches on R; RS branches into four halfway along wing, R_{1+2} and R_{3+4} short, of same length; discoidal cell closed; M and CuA divided proximal to branching of RS; M_{1+2} shorter than its bifurcation; medial cell open; common end of anal veins halfway along wing. Length of forewing 12 mm. Upper Permian and 296 Triassic of Australia. Two monotypic genera (*Cladochorista* Tillyard, 1926, *Cladochoristella* Tillyard, 1955).

Family PRORHACOPHILIDAE Riek, 1955

Forewing: anterior margin of wing straight; SC has three branches; no additional branches on R; RS branches halfway along wing; R_{1+2} considerably shorter than the long R_{3+4}; discoidal cell open; M_{1+2} and M_{3+4} longer than their bifurcations; medial cell open; common end of anal veins end halfway along wing. Length of forewing 5 mm. Upper Triassic of Australia. One genus.

297 Family PROSEPIDIDONTIDAE Handlirsch, 1939

Forewing: anterior margin convex; costal area wide; SC short, has two branches; R has no additional branches; RS three-branched, branches considerably distal to halfway along wing; discoidal cell open; M and CuA branch proximal to beginning of RS and midpoint of wing; M divides wing plate into narrow anterior and wider posterior parts; fork of M_{1+2} very short; medial cell open; common end of anal veins proximal to middle of wing. Length of wing 10 mm. One genus. Lower Jurassic of Germany.

Family NECROTAULIDAE Handlirsch, 1906
(Liassophilidae Tillyard, 1933)

Usually small forms predominate with long forewings (3.5–6 mm), resembling Recent family Rhyacophilidae, but they differing from latter in the more proximal branching of RS, M, CuA and termination of common end of anal veins. Length of forewing 3.5–9 mm, only in *Liassophila* length 21 mm (Fig. 930). Triassic and Jurassic of Western Europe. Eleven genera: *Epididontus* Handlirsch, 1939; *Liadotaulius* Handlirsch, 1939; *Mesotrichopteridium* Handlirsch, 1906; *Metarchitaulius* Handlirsch, 1939; *Metatrichopteridium* Handlirsch, 1939; *Necrotaulius* Handlirsch, 1906; *Necrotauliodes* Handlirsch, 1939; *Parataulius* Handlirsch, 1939; *Palaeotaulius* Handlirsch, 1906; *Liassophila* Tillyard, 1933; *Pseudoorthophlebia* Handlirsch, 1906.

Family RHYACOPHILIDAE Stephens, 1936

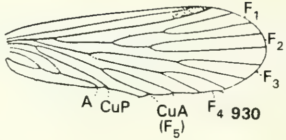
Medium or small sized forms, rarely large. Distal part of forewing elongate-triangular; hairs sparse, fringes absent; dc short and open; M and RS branch at same level, almost halfway along wing or a little proximally; bifurcations of M_{3+4} (fourth apical) of same length as stem or somewhat longer. Hindwings somewhat shorter than forewings; no anojugal fan. Antennae longer than wings. First two segments of maxillary palps short and thick, third longer and thicker, and fifth not annulated, pointed at tip. Spurs 3.4.4. Larvae free, live in streams. Pupae concealed in cases constructed from sand and gravel and anchored to substrate (Fig. 931). Tertiary to Recent. *Rhyacophila* Pictet, 1834, a Recent genus, also known from the Paleogene of Europe (Baltic amber).

Family GLOSSOSOMATIDAE Wallengren, 1891

Discoidal cell closed, medial cell open; RS branches proximal to middle of wing, both of its branches fork at same level; M divides distal to RS; forks of M_{3+4} (fourth apical) shorter than its stem. Larvae live in temporary cases. Spurs 2.4.4. Length of forewing 3–3.75 mm (Fig. 932). Paleogene to Recent. Two genera from the Paleogene of Europe (Baltic amber).

Family HYDROPTILIDAE Stephens, 1836

Very small forms, length of forewing 2.6–3.7 mm; wings narrow, similar, pointed at apex, densely covered with long hairlike setae; with fringe, whose length in hindwing, exceeds width of wing; veins rarely visible, venation



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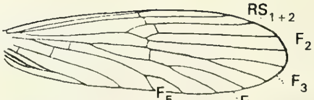

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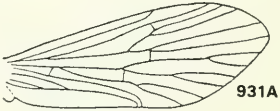
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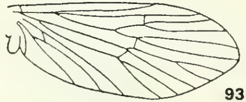
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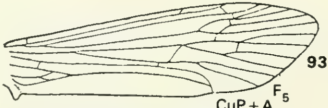

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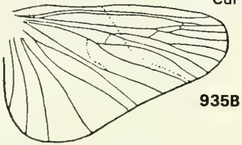
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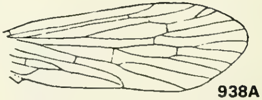
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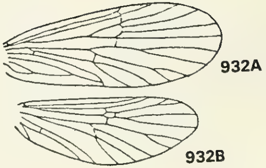

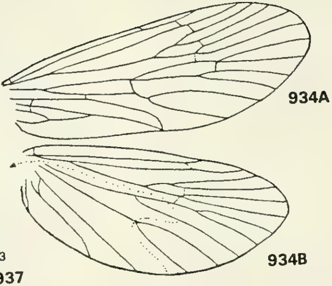

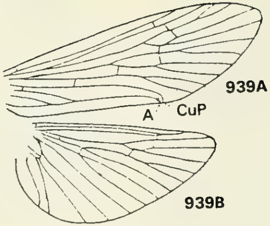

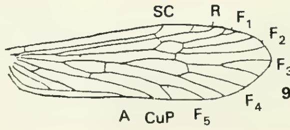

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Figs. 930–939. Suborder Annulipalpia.

930. *Necrotaulius furcatus* (Giebel); forewing, × 7.5. Lower Triassic, England (Tillyard, 1917). 931. *Rhyacophila profusa* Ulmer; A—forewing, B—hindwing, × 10. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 932. *Electragapetus scitulus* Ulmer; A—forewing, B—hindwing, × 10. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 933. *Electrotrichia subtilis* Ulmer; A—forewing, B—hindwing, × 22. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 934. *Electracanthinus klebsi* Ulmer; A—forewing, B—hindwing, × 8.6. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 935. *Stenopsyche imitata* Ulmer; A—forewing, B—hindwing, × 3. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 936. *Lype sericea* (Pictet); A—forewing, B—hindwing, × 17. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 937. *Ecnomus continentalis* Ulmer; forewing, × 7. Recent. Australia (Mosely, 1953). 938. *Neureclipsis geniculata* Ulmer; A—forewing, B—hindwing, × 8. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 939. *Potamyia nitida* Ulmer; A—forewing, B—hindwing, × 5.3. Paleogene, Europe (Baltic amber) (Ulmer, 1912).

reduced; often first apical fork long; in most cases RS_2 without base, fused with RS_{3+4}; true discoidal cell absent; medial cell open; M branches distal to RS, sometimes much more so; fourth and fifth apical bifurcations absent. Formula for spurs varies. Larvae without cases in early stages; in last (fifth) instar, they construct temporary cases from secretion of their silk glands, sometimes covered with algae or sand; inhabit mostly streams (Fig. 933). Paleogene to Recent. Many genera, about 150 species in the Recent fauna; three genera from Baltic amber.

Family PHILOPOTAMIDAE Stephens, 1836

Forewings elongated, oval in shape; discoidal and medial cells closed; thyridial cell shorter than bifurcations of CuA, equal to or shorter than medial cell; RS branches roughly halfway along wing, M more proximally; discoidal vein short; first apical bifurcation sessile or stalked; CuP and common end of anal veins terminates at same point, hence distance between ends of posterior branches of CuA and CuP greater than that between other veins; postcostal area wider than 298 costal. Antennae stout, but not long, with short segments; ocelli present; first segment of maxillary palp short, second longer and provided with setae, fourth equal to second in length and third longer, fifth annulated and equal in length to third and fourth put together. Spurs 2.4.4. Larvae build long tubes and inhabit mountain streams with cold water (Fig. 934). Paleogene to Recent. Eight genera in Recent fauna and three from the Paleogene of Europe (Baltic amber) and North America, of which one is extinct.

Family STENOPSYCHIDAE Martynov, 1924

Large forms, length of forewing 20 mm or more; discoidal cell closed and short—one-third or one-fourth of length of stem of RS; first apical fork (RS_{1+2}) shorter than third (RS_{3+4}). The medial cell closed, longer than discoidal and shorter than thyridial; postcostal area wide and long, its width exceeds that of costal area several times and it terminates considerably distal to middle of wing; anal cells short. Hindwings with anojugal fan. Antennae markedly longer than wings, serrated; fifth segment of maxillary palpi annulated, longer than remaining segments put together. Spurs 3.4.4. Larvae with very long head, live in mountain streams with pebble beds, build simple retreats in the form of tubes; microphages (Fig. 935). Paleogene to Recent. Three genera belong to Recent fauna, of which one is also found in Baltic amber.

Family PSYCHOMYIDAE Kolenati, 1859

Small forms, length of forewing 3–8 mm. Forewing: R with no branches; anterior apical bifurcation absent (RS_{1+2} simple); M branches proximal to middle of wing; discoidal cell about one-fourth of stem of RS, closed, half of medial cell; thyridial cell equal to or, often, shorter than medial, ends proximal to beginning of latter or where the latter begins; M_5* slightly longer than free base of CuA; bifurcation of CuA short and wide; postcostal area narrow, narrower than costal area. Hindwings shorter and narrower than forewings. Antennae shorter than wings; second segment of maxillary palpi longer than short first one; fifth segment annulated, equal in length to third and fourth put together. Spurs 2.4.4. Larvae are microphages, live in different types of water bodies (Fig. 936). Paleogene to Recent. Few genera in the Recent fauna, of which one, from the Baltic amber, is found also in fossil record.

Family ECNOMIDAE Ulmer, 1903

[nom. transl. Lepneva, 1956 (ex Ecnominae Ulmer, 1903)]

Small forms. Forewings: SC short; R with a branch; first apical bifurcation (RS_{1+2} branches off) stalked; M branches proximal to middle of wing. Discoidal cell one-third to one-fourth of stem of RS closed, one-third of medial cell; thyridial cell almost equal in length to medial cell, ends proximal to or where the latter starts; M_5* markedly longer than free base of CuA; bifurcation of CuA short; postcostal area narrow. First and second segments of maxillary palpi equal to or slightly shorter than third; fifth segment annulated, equal in length to next three segments put together. Spurs 3.4.4. Larvae predatory, live in retreats of primitive psychomyid type (Fig. 937). Paleogene to Recent. Three genera in Recent fauna, one extinct genus in the Paleogene of Europe (Baltic amber).

Family POLYCENTROPODIDAE Ulmer, 1903

[nom. transl. Ulmer, 1906 (ex Polycentropinae, 1903)]

Small forms. Length of forewing 3–8 mm. Forewing: R without branches; RS_{1+2} with a stalked fork or simple; discoidal cell equal in length to stem of RS and medial cell; thyridial cell longer than medial and discoidal cells, ends where medial cell starts; M_5* considerably longer than free base of CuA; bifurcation of CuA long and wide; postcostal area wider than costal area. Hindwings shorter than forewings, widened slightly in anojugal area. Antennae shorter or slightly longer than wings; first two segments of maxillary palpi very short, fifth segment annulated and longer than all the rest put together. Spurs 3.4.4. Larvae live usually in running, rarely in stagnant water; predators; constructing nets for trapping their prey (Fig. 938). Paleogene to Recent. In the Recent fauna 14 genera; seven genera known in fossil records from the Paleogene of Europe (Baltic amber), of which two are extinct.

Family HYDROPSYCHIDAE Curtis, 1835

Length of forewing 6–10 mm, forewings elongate, slanting truncated towards anal margin from apical part; SC long; R without branches; all five apical bifurcations present, first, third and fifth ones almost always stalked; discoidal

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*Editor's note: Original text uses M_5, this is unquestionably an error for F_5, or fork 5 (see figures 936 or 937); M_5 not present in Trichoptera.

cell small, one-half to one-third of length of RS, closed; medial cell somewhat 299 longer than discoidal, also closed; thyridial cell long, almost equal in length to stem of RS, sometimes longer still, terminating distal to beginning of medial cell; postcostal area slightly wider than costal area, terminates distal to midpoint of wing. Hindwings shorter and wider than forewings; anojugal area hardly enlarged; fourth apical bifurcation absent. Antennae thin, occasionally longer than wings; maxillary palpi: first segment short, second long, third and fourth shorter than second and widened on inner surface, fifth equal to the rest in length and annulated. Spurs 2.4.4. Larvae live in running water, including large, powerful rivers, constructing small nets with regular honeycomb pattern, attached to hard substratum (Fig. 939). Paleogene to Recent. Two subfamilies from the Recent fauna of which one, Hydropsychinae, with four genera (one extinct), is known from the Paleogene of Europe (Baltic amber).

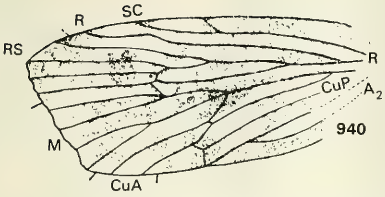
Suborder Integripalpia

Forewing: fourth apical bifurcation often absent, i.e., M_{3+4} does not branch, other bifurcations sometimes lacking; first apical bifurcation usually sessile, except in family Leptoceridae; anastomosis prominent; discoidal cell always closed. Hindwings shorter than forewings; anojugal fan present. Last segment of maxillary palpi complete, not pointed. Larvae eruciform or campodeiform, live primarily in stagnant and slow-moving bodies of water; resemble larvae of Lepidoptera. Cretaceous to Recent. Families: Kalophryganeidae, Phryganeidae, Limnophilidae, Leptoceridae, Calamoceridae, Odontoceratidae, Molannidae, Sericostomatidae; first one extinct and known only from outside the USSR.

Family PHRYGANEIDAE Burmeister, 1839

Large forms: length of forewing up to 30 mm; forewings usually wide and oval; costal area wider than postcostal area; distal end of R curved; fourth apical bifurcation absent in males; discoidal cell long, as long as stem of RS or longer; first apical bifurcation leaves almost from middle of discoidal cell, i.e., RS_{1+2} branches markedly proximal to RS_{3+4}; second and third apical forks present; anal veins on postcostal area arranged like wavy lines. Antennae thick, of same length as or shorter than wings; ocelli present; segments of maxillary palpi number four in males and five in females. Spurs 2.4.4. Cretaceous to Recent. 12 genera in the Recent fauna, mainly in the Northern Hemisphere; three genera known in fossil record.

Phryganea Linnaeus, 1940. Genotype—*P. grandis* Linnaeus,1740; Recent, Europe. Forewings parabolically truncated from behind; R curved at level of 300 end of discoidal cell; RS branches proximal to middle of wing; M branches almost in middle; discoidal cell long and narrow, short in hindwings. Larvae thrive in stagnant water, build cylindrical cases from small spirally placed plant



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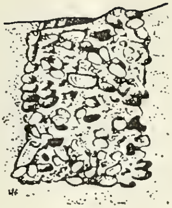

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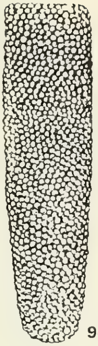

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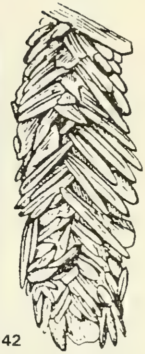

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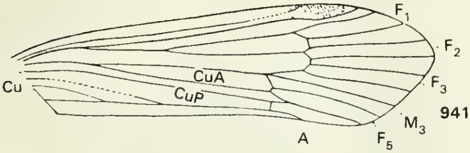

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Figs. 940–944. Families Phryganeidae, Limnophilidae.

940. *Phryganea lavrushini* Cockerell; forewing, male, × 3.5. Neogene, Primorye province (original drawing). 941. *Limnophilus kaspievi* (O. Martynova); forewing, × 5.9. Neogene, North Caucasus (original drawing). 942. *Limnophilus* sp.; larval cases from shells of *Spaniodontella*. Neogene, North Caucasus (original drawing). 943. *Limnophilidae*? Larval cases from shells of Ostracoda. Upper Jurassic, Transbaikal (Rele, 1909). 944. *Indusia sequoia* Cockerell. Larval cases made from needles of conifer *Sequoia lansdorffi*, × 3. Neogene, Primorye province (original drawing).

remains. Length of forewing 9–22 mm (Fig. 940). Cretaceous to Recent. 11 species from the Paleogene of Europe (Baltic amber) and the Neogene of Kazakhstan and East Siberia; besides these, many cases of larvae from the Cretaceous of Czechoslovakia and Tertiary deposits of Europe and Asia.

Family LIMNOPHILIDAE Kolenati, 1848

[nom. transl. Kolenati, 1859 (ex Limnophiloidea Kolenati, 1848)]

Medium or large sized forms. Forewings truncated in apical part along anterior margin, distinguished from other families by short apical part, which is less than one-half of length of the rest of wing; distal end of R curved; RS branches proximal to midpoint and M much more distally; discoidal cell as long as, shorter, or longer than, stem of RS and much shorter than thyridial cell; first apical bifurcation sessile, fourth one not so; cross vein m_3-cua slanting. Antennae almost as long as wings; ocelli present; maxillary palpi with three segments in males and four in females. Spurs 0.3.4, 1.3.4. Larvae live in different kinds of water, mostly stagnant, build cases out of particles of vegetation or detritus as well as fine sand. Neogene to Recent. In the Recent fauna six subfamilies, more than 680 species in the Northern Hemisphere, over 30 species in South America and one species in Australia. Only Limnophilinae known in fossil record.

Subfamily Limnophilinae Ulmer, 1903

In forewings SC terminates directly on costal margin, not on cross vein c-r, as in species of subfamily Apataniinae. Spurs 1.3.4, 0.3.4. (Figs. 941–944). Neogene to Recent. In the Recent fauna about 60 genera; six genera occur as fossils, of which three are extinct. Wings of Limnophilinae relating to three genera known from the Miocene of Western Europe, North Caucasus, East Siberia and North America. Cases of larvae relating to three genera known from Western Europe, North Caucasus (*Pectinariopsis* Andrusov, 1916), East Siberia and North America.

Family LEPTOCERIDAE Leach, 1815

Forewings long and narrow: length four times of width; distal end of R straight; RS branches proximal to M; discoidal cell almost as long as RS; medial cell absent; discoidal and thyridial cells end almost at same level; first stalk and fifth apical bifurcation always present; second and third apical bifurcations absent; cross vein cua-cup straight. Antennae very thin and two or three times as long as wings; ocelli absent; maxillary palpi five-segmented, plumose covered with long hair. Larvae live in both stagnant and running water, build their cases out of sand, rarely out of detritus or particles of vegetation. Paleogene to Recent. About 30 widely distributed genera in the Recent fauna. Subfamilies: Triplectidinae and Leptocerinae.

Subfamily Triplectidinae Ulmer, 1906

In hindwing discoidal cell closed; apical bifurcations—first, second and third—present. Length of forewing 8–12 mm (Fig. 945). Paleogene to Recent. One genus of the Recent fauna found in the Paleogene of Europe (Baltic amber).

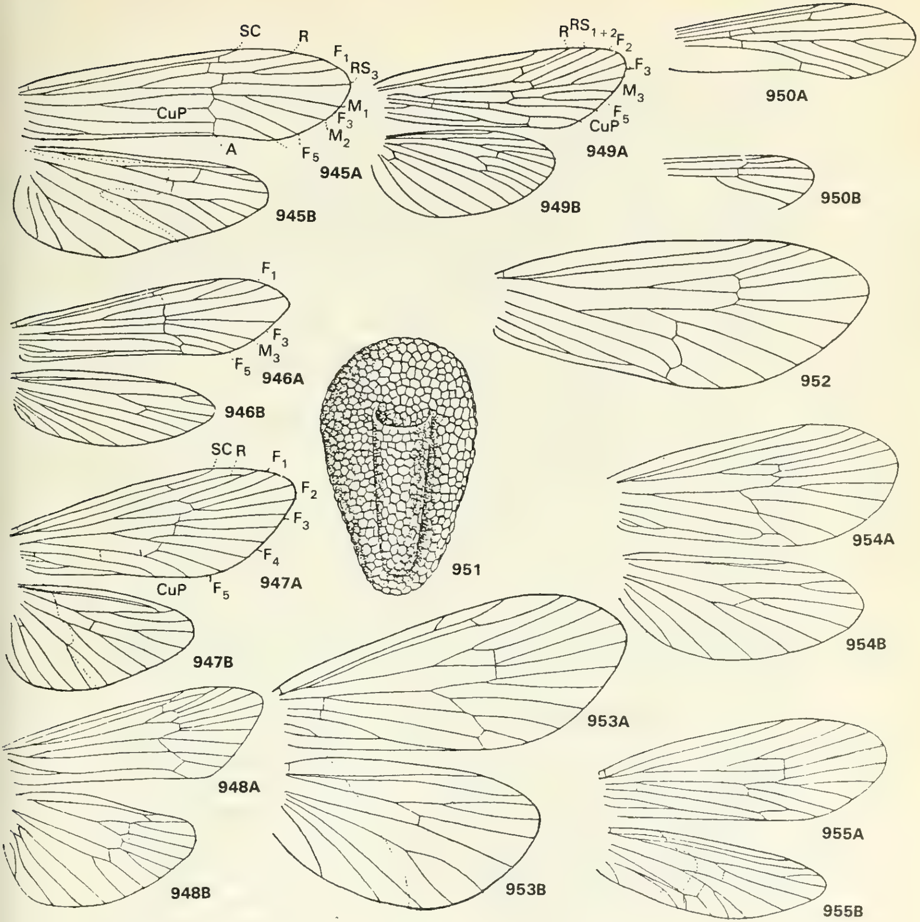
Subfamily Leprocerinae Ulmer, 1903

Discoidal cell open in hindwings; apical bifurcations—first and fifth—present. Length of forewing 4–7 mm (Fig. 946). Paleogene to Recent. Two genera in the Recent fauna found in the Paleogene of Europe (Baltic amber).

Family CALAMOCERATIDAE Ulmer, 1905

[nom. transl. Ulmer, 1906 (ex Calamoceratinae Ulmer, 1905)]

Length of forewing in fossil species 10–13 mm. In forewings distal end of R curved, ends at RS_1, short of margin of wing; RS branches distal to point of branching of M; discoidal cell almost as long as RS; thyridial cell ends distal to medial cell; five apical bifurcations, fifth one occasionally stalked; antennae almost three times as long as wings; ocelli absent; maxillary palpi five-segmented, thick, pilose. Spurs 2.4.4. Larvae live in stagnant water in cases constructed from large particles of vegetation (Fig. 947). Neogene to Recent.



Figs. 945–955. Suborder Integripalpia.

945. *Triplectides rudis* Ulmer; A—forewing, B—hindwing, × 5. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 946. *Erotesis aequalis* Ulmer; A—forewing, B—hindwing, × 9. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 947. *Ganonema regulare* Ulmer; A—forewing, B—hindwing, × 4. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 948. *Electroserum pedestre* Ulmer; A—forewing, B—hindwing, × 5. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 949. *Molanodes dubia* Ulmer; A—forewing, B—hindwing, × 4. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 950. *Molanna angustata* Ulmer; A—forewing, B—hindwing, × 7.5. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 951. *M. angustata* Ulmer; larval case, × 1.5. Recent, Europe (Bavlosky and Lepneva, 1948). 952. *Goera gracilicornis* Ulmer; forewing, × 8. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 953. *Brachycentrus labialis* Hagen; A—forewing, B—hindwing, × 10. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 954. *Archaeocrunoecia tunicornis* Ulmer; A—forewing, B—hindwing, × 12. Paleogene, Europe (Baltic amber) (Ulmer, 1912). 955. *Helicopsyche typica* Ulmer; A—forewing, B—hindwing, × 12. Paleogene, Europe (Baltic amber) (Ulmer, 1912).

Seven genera in the Recent fauna of Asia and America, of which two are found also in the Paleogene of Europe (Baltic amber).

301 Family ODONTOCERIDAE Wallengren, 1891

Length of forewing in fossil species 7–12 mm. Forewing: R straight, ends at RS_1, short of wing margin of apex; SC_1, R and RS_1 connected by cross veins; RS and M branch almost at same level; discoidal cell longer than RS; thyridial cell
302 at least twice as long as discoidal cell; medial cell absent; first apical bifurcation sessile, fourth one absent in males. Antennae twice as long as wings, serrate; ocelli absent; maxillary palpi long, five-segmented, hairy. Spurs 2.4.4. (Fig. 948). Paleogene to Recent. In the Recent fauna eight genera (about 25 species); three genera known from the Paleogene of Europe (Baltic amber).

Family MOLANNIDAE Wallengren, 1891

Length of forewing of fossil species 7–14 mm. Forewings narrow, rounded at apex, roll up into a tube in position of rest; SC and R straight, parallel; venation in different genera and species distorted in different ways; discoidal and medial cells absent. Hindwings shorter and wider than forewings. Antennae stout, of same length as wings or shorter; ocelli absent; maxillary palpi five-segmented, pilose. Spurs 2.4.4. Larvae live in lakes or estuaries of rivers; larval cases made from sand, and look like shields with tubes underneath (Figs. 949–951). Paleogene to Recent. Two genera in the Recent fauna (Europe, North America, Japan and India); two genera known from the Paleogene of Europe (Baltic amber—imago) and the Miocene of the European USSR (larval cases).

Family SERICOSTOMATIDAE Stephens, 1836

Wings comparatively wide and short, with length 2.5–3 times of width; covered with dense hairlike setae, often with folds and scales. Forewing: R almost straight, ends at C; RS branches somewhat proximal to end of M, a little distal to the middle of wing; discoidal cell almost as long as RS; first apical bifurcation sessile, sometimes taking off from middle of discoidal cell; fourth apical bifurcation absent; cross vein cua_2-cup short, slanting. Antennae almost as long as wings and densely covered with hairlike setae; ocelli absent. Maxillary palpi of varied construction. Larvae usually inhabit fast-moving water, rarely stagnant water. Paleogene to Recent. Four subfamilies: Goerinae, Brachycentrinae, Lepidostomatinae, Sericostomatinae; latter not known in fossil record.

Subfamily Goerinae Ulmer, 1903

Fore- and hindwings of males with four apical bifurcations (1, 2, 3 and 5). In hindwing discoidal cell open. Antennae not longer than forewing, with thickly pilose basal segment twice as long as head; maxillary palpi three-segmented in males and five-segmented in females, last segment long, pilose, bent upward. Length of forewing 5—9 mm (Fig. 952). Paleogene to Recent. Three genera of the Recent fauna also found in the Paleogene of Europe (Baltic amber).

Subfamily Brachycentrinae Ulmer, 1903

Forewing of males with four apical bifurcations (1, 2, 3 and 5) in hindwing with two. In hindwing discoidal cell open. Maxillary palpi of males three-segmented, bent upward. Spurs 2.3.3. Length of forewing 6—9 mm (Fig. 953). Paleogene to Recent. One genus of the Recent fauna found in the Paleogene of Europe (Baltic amber).

Subfamily Lepidostomatinae Ulmer, 1903

In forewings four apical bifurcations: 1, 2, 3 and 5, and in hindwings three: 1, 2, and 5; discoidal cell in hindwings open. Antennae of same length as forewings, with first segment long, occasionally longer than head, pilose, sometimes with scales; maxillary palpi in males three-segmented. Spurs 2.4.4. Length of forewing 4.5–8 mm (Fig. 954). Paleogene to Recent. Six extinct genera from the Paleogene of Europe (Baltic amber).

Family HELICOPSYCHIDAE Ulmer, 1912

[nom. transl. Kimmins, 1952 (ex Helicopsychinae Ulmer, 1912)]

Both fore- and hindwings with three apical forks: 1, 4 and 5. Sometimes in hindwings a fourth fork emerges; discoidal cell open. Antennae not longer than wings, with basal segment as long as head; maxillary palpi three or four-segmented. Spurs 2.2.4. Length of forewings 4–6 mm (Fig. 955). Paleogene to Recent. Three genera from Paleogene of Europe (Baltic amber), of which one is found in the Recent fauna.

Besides these, another eight genera of indistinct systematic position known from the Paleogene of Europe (Baltic amber).

303 Order LEPIDOPTERA. Butterflies and moths

(A.S. Danilevsky and O.M. Martynova)

Insects of varied size with two pairs of well-developed wings covered with colored scales (modified setae); SC short, often with one branch; RS with three or four branches; in primitive forms RS dichotomously divided; in advanced forms branches of RS on a single stalk; three or four branches on M (triassic suborder with five); often M and Cu fused at base, forming large cell; CuA with bifurcation; CuP simple; one to three anal veins; A_2 forms a short loop, fused with A_1 at distal part; A_3 reduced to short free vein or absent.

Head hypognathous, mouth parts of sucking type or atrophied in non-feeding adults; eyes large, convex; usually two ocelli; antennae moderately long, of varied form, setaceous, pectinate or clavate. Prothorax shorter than meso- and metathorax; legs long, cursorial, sometimes forelegs reduced. Abdomen shorter than wings, 10-segmented. Larvae eruciform—caterpillars; head large; mouth parts of biting type; three pairs of thoracic and five pairs of abdominal legs; herbivorous. Free type of pupa known only in primitive Micropterygidae. Paleogene to Recent. Suborders: Jugata and Frenata.

Suborder Jugata. Homoneurous Lepidoptera

Venation of fore- and hindwings similar; SC and R sometimes fused at base; in both wings RS with three or four branches; M with three branches. A_1 short, terminates proximal to middle of wing; Mandibles more or less developed; proboscis reduced. Paleogene to Recent. Seven families found in the Recent fauna of which two, Micropterygidae and Eriocraniidae, known also from the Paleogene.

Family MICROPTERYGIDAE Cotes, 1889. Primitive mandibulate moths

[nom. transl. Comstok, 1893 (ex Micropteryginae Cotes, 1889)]

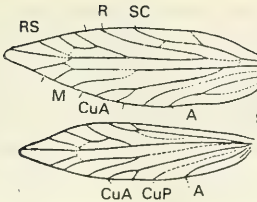
Very small insects—do not measure more than 12 mm; wings lanceolate with pointed apex; costal area broad; SC branched; RS with four branches; bifurcations on RS free; discoidal cell closed. Mandibles present. Larvae with long antennae; with legs on all abdominal segments (like Mecoptera). Maxillae with lacinia; pupa exarate (Fig. 956). Paleogene to Recent. Seven widely-distributed genera found in the Recent fauna, of which one also known in the Oligocene of Europe (Baltic amber) and the Miocene of South Asia (Burmese amber).

Family ERIOCRANIIDAE Rebel, 1901. Primitive moths

Differ from Micropterygidae in the more distal origin of RS, (halfway along wing). Mandibles absent. Larvae with short antennae; without legs. Maxillae with rudimentary lacinia; pupa exarate (Fig. 957). Paleogene to Recent. Three genera known in the Recent fauna; one extinct genus from the Paleogene of Europe (Baltic amber).

304 Suborder Frenata. Heteroneurous Lepidoptera

Venation of fore- and hindwings different. One simple R in hindwing; RS present; common stem of M usually reduced; M with three branches; A_1 ends halfway along wing or slightly more distally. Mandibles reduced. Proboscis developed or secondarily reduced. Paleogene to Recent. A very large number of species of Lepidoptera of the Recent fauna belong to this suborder. Infraorders: Microfrenata, Macrofrenata.



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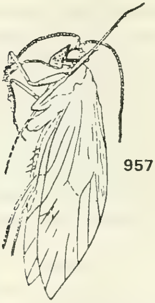

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Figs. 956–957. Suborder Jugata.

956. *Micropteryx* sp.; left wings. Recent (Handlirsch, 1925). 957. *Electrocrania immenisipalpa* Kuznezov; general view, × 12. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941).

Infraorder Microfrenata

Mostly small or very small Lepidoptera. Hindwings often fringed; length of fringe usually exceeds width of wing; base of M often developed; medial cell common; one or two anal veins. Larvae in most cases live concealed. Abdominal legs with crochets; with only primary setae. Paleogene to Recent. In the Recent fauna four superfamilies known from Tertiary times: Tineidea, Tortricidea, Gelechiidea, Pyralidea.

SUPERFAMILY TINEIDEA

Common stem of M present or vestigial. Head covered with protruding hairlike scales; maxillary palpi developed (except in family Psychidae); distal segment of labial palpi blunt. Larvae usually in cases or webbed galleries. Pupa with spines on terga, exserted from cocoon. Paleogene to Recent. About 20 families known in the Recent fauna, of which four known from Tertiary times: Incurvariidae, Adelidae, Tineidae, Psychidae.

Family INCURVARIIDAE Spuler, 1910 Stem miners or metallic moths

Differs from other families by presence of microtrichia on wing membrane in addition to scales. All veins present; radial and medial cells well outlined. Proboscis weakly developed, non-feeding; maxillary palpi longer than labial palpi. Paleogene to Recent. Two genera in the Recent fauna (about 70 species in northern temperate zone), of which one also from the Paleogene of Europe (Baltic amber).

Family ADELIDAE Spuler, 1910

[nom. transl. Meyrick, 1912 (ex Adelinae Spuler, 1910)]

Venation does not differ from that of Incurvariidae, but no microtrichia on wing membrane. Wings always with metallic luster. Unlike other families, members of this family have long, slender antennae (twice as long as wing); without basal pecten; parietal region without hairlike setae; proboscis well developed; maxillary palpi shorter than labial palpi. Paleogene to Recent. Few genera in the Recent fauna (about 200 widely distributed forest species), of which one also known from the Paleogene of Europe (Baltic amber).

Family TINEIDAE Linnaeus, 1758. True moths

[nom. transl. Leach, 1819 (ex Tineae Linnaeus, 1758)]

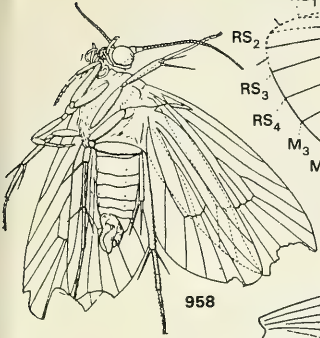
No microtrichia on wing membrane; fringe long, longer than half of wing width; usually wings lanceolate. Head covered by short bristle or hairlike setae; antennae as long as wings; basal segment of antennae enlarged, often with pecten; maxillary palpi slender, five-segmented or absent; labial palpi short (Fig. 958). Detritofages, living on lichens and fungi. Paleogene to Recent. In the Recent fauna majority of genera and about 1,800 species found in abundance in tropics; twelve genera in fossil record; Paleogene of Western Europe (Baltic amber) and the Neogene of North America.

Family PSYCHIDAE Boisduval, 1929. Bagworm moths

Microtrichia absent on wing membrane; wings broad; fringe of hindwing short. In forewings A_1 and A_2 fused for a short distance and then diverge to form a fork. Proboscis absent; maxillary and labial palpi usually absent. Females usually lack wings, often without legs. Larvae in cases. Neogene to Recent. Family not large, mainly confined to tropics (about 400 families in the Recent fauna). Larval cases from the Miocene of Western Europe.

SUPERFAMILY TORTRICIDEA. Leaf roller moths

Hindwings as broad as or broader than forewings, with free SC; M vestigial or well developed (Cossidae). Head covered with contiguous scales; maxillary palpi 305 absent or vestigial; distal segment of maxillary palpi short, cylindrical or blunt.



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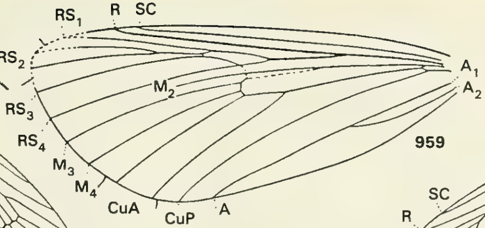

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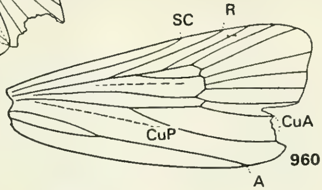

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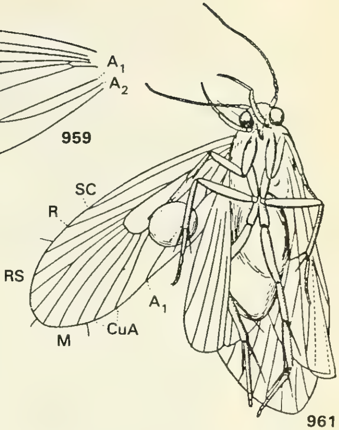

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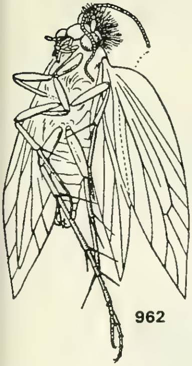

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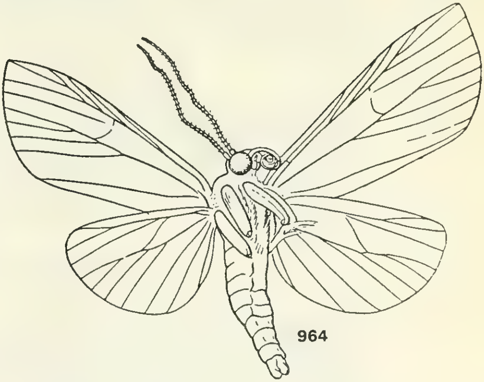

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Figs. 958–964. Suborder Frenata—Microfrenata.

958. *Palaeoscardiites mordvilkoi* Kusnetzov; general view, × 8. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941). 959. *Xyleutites miocenicus* Kozhantshikov; forewing, × 4. Paleogene, North Caucasus (original drawing from holotype). 960. *Prolyonetia cockerelli* Kusnetzov; forewing, × 19. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941). 961. *Glesseumeyrickia henrickseni* Kusnetzov; general view, × 9. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941). 962. *Symmocites rohdendorfii* Kusnetzov; general view, × 8.7. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941). 963. *Electresia zalesskii* Kusnetzov; general view, × 13. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941). 964. *Glendotricha olgae* Kusnetzov; general view, × 8.5. Paleogene, Europe (Baltic amber) (Kuznetsov, 1941).

Larvae usually live concealed in rolled-up leaves or inside plant tissues. Pupa with two rows of spines on each tergum. Paleogene to Recent. Three families in the Recent fauna, of which two also in fossil record: Cossidae and Tortricidae.

Family COSSIDAE Leach, 1815. Carpenter moths

[nom. transl. Walker, 1855 (ex Cossida Leach, 1815)]

Wings fairly broad, with rounded apex; base of M present, with three branches;
306 medial cell well developed; apex of radial cell located distal to medial cross-vein; additional bifurcations seen on one branch of RS; CuP distinct, forms a Y-shaped figure. Length of forewing 15–80 mm (Fig. 959). Neogene to Recent. About 20 genera known in the Recent fauna. One extinct genus from the Miocene of the Caucasus.

Family TORTRICIDAE Linnaeus, 1758. Leaf rollers

[nom. transl. Stephens, 1829 (ex Tortrices Linnaeus, 1758)]

Apices of radial and medial cells located at same level. Usually no additional bifurcations on branches of RS; CuP absent or vestigial in distal part of wing, no Y-shaped figure visible. Paleogene to Recent. Four subfamilies found in the Recent fauna, of which two also known from the Paleogene: Eucosminae and Phaloniinae.

Subfamily Eucosminae Durrent, 1918

In forewings CuA branches at level of three-fourths the length of medio-cubical cell; hindwings with comb of hair-like setae on CuA; base of CuA preserved (Fig. 960). Paleogene to Recent. Recent fauna of this widespread subfamily includes more than 10 genera; one extinct genus from the Paleogene of Europe (Baltic amber).

Subfamily Phaloniinae Rebel, 1901

[nom. transl. Rebel, 1935 (ex Phaloniidae Rebel, 1901)]

In forewings CuA branches close to distal corner of medio-cubital cell, at level of distal one-fourth of its length; CuP absent. Paleogene to Recent. About 10 genera in the Recent fauna of the Northern Hemisphere with a small number of species; one extinct genus from the Paleogene of Europe (Baltic amber).

SUPERFAMILY GELECHIIDEA

Venation close to that of Tortricidea. Head with contiguous scales, smooth; labial palpi lanceolate, with long, pointed distal segment. Larvae live in various types of shelters, sometimes they are miners. Pupae lack spines on terga, do not push themselves out from cocoon. Paleogene to Recent. Four families in the Recent fauna: Hyponomeutidae, Oecophoridae, Gelechiidae, Lyonetiidae.

Family HYPONOMEUTIDAE * Stainton, 1854. Small ermine moths

Wings narrow and lanceolate, particularly hind ones; pterostigma often present on forewings; RS arises close to R and then diverges, forming an angle; all branches of RS arise from apex of radial cell; R_4 starts from apical margin of wing; CuP present. Head smooth or with unevenly distributed scales; basal segments of antennae enlarged, sometimes thickened; proboscis usually well developed; maxillary palpi reduced. Paleogene to Recent. Most genera belong to the Recent fauna (about 800 species); three extinct genera from the Paleogene of Europe (Baltic amber).

Family OECOPHORIDAE Cootes, 1889

[nom. transl. Meyrick, 1895 (ex Oecophorinae Cotes, 1889)]

In forewings R_3 and R_4 on a long stalk or fused; common stem of M absent; radio-cubital cell broad. Posterior wings broad oval or somewhat lanceolate, differ from those of Gelechiidae in absence of notch along apical margin; SC free; R and M almost parallel. Head covered with appressed or loose scales; basal segment of antenna with pecten, proboscis invariably present; maxillary palpi short, four-segmented; labial palpi long, curved (Fig. 961). Paleogene to Recent. Many genera in the Recent fauna (about 3,000 species), half of which are Australian; four genera from the Paleogene of Europe (Baltic amber).

Family LYONETIIDAE Stainton, 1854

Very small insects. Wings narrow, lanceolate—particularly hind-ones; venation much reduced; M almost absent; CuP clearly visible. Proboscis very short; maxillary palpi geniculate, often reduced (Fig. 962). Paleogene to Recent. Few genera in the Recent fauna (about 900 widely-distributed species); one extinct genus from the Paleogene of Europe (Baltic amber).

Family GELECHIIDAE Stainton, 1854. Notch-winged moths

Wings more or less broad, of varied forms; in forewings radial cell not present; R_3 and R_4 on stem or fused; R_4 ends in front of apex; common stem of M vestigial; CuP often reduced; SC connected with R by cross vein. Hindwings
307 often trapezoid with a notch below apex along apical margin. Head smooth; basal segment of antennae with pecten; proboscis well developed. Maxillary palpi straight or absent; labial palpi long, curved upwards (Fig. 963). Paleogene to Recent. In the Recent fauna large number of widely distributed genera (about 4,000 species), two extinct genera from the Paleogene of Europe (Baltic amber).

SUPERFAMILY PYRALIDIDEA. Snout moths

Forewings with typical radial and medial cells, i.e., base of M completely reduced. Hindwings usually broader than forewings; SC and R fused at base and diverge at apex of the cells, rarely unite to form a single vein. Maxillary palpi well

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*Editor's note: Current spelling Yponomeutidae.

developed; labial palpi variable. Paleogene to Recent. Five families in the Recent fauna, of which only one family, Pyralididae, is known from Tertiary times.

Family PYRALIDIDAE Linnaeus, 1758. Snout moths

[nom. transl. Leach, 1819 (ex Pyralides Linnaeus, 1758)]

Wings triangular; in forewings R_2, R_3 and R_4 stalked; CuP absent or vestigial; A_1 long; A_2 absent. (Fig. 964). Paleogene to Recent. In the Recent fauna more than 300 genera (about 10,000 species predominantly Indo-Australian or Neotropical); two extinct genera from the Paleogene of Europe (Baltic amber) and the Neogene of North America.

Infraorder Macrofrenata

Mostly of large or medium size; posterior wings more or less broad, with short fringe; common stem of M reduced; medial cell absent; one or two anal veins. Larvae usually live exposed; abdominal legs with linear row of crochets. Paleogene to Recent. Seven superfamilies in the Recent fauna, of which three—Rhopalocera, Sphingodea and Noctuidea—known from Tertiary times; first two occur outside the USSR.

SUPERFAMILY NOCTUIDEA. Noctuidlike moths

In forewings bases of M_2 and M_3 close; CuP reduced. In hindwings RS not connected with R. Paleogene to Recent. In the Recent fauna six families of which Amatidae, Noctuidae and Arctiidae known from Tertiary times; last two from outside the USSR.

Family AMATIDAE Janese, 1917

(Syntomidae H. Schafer, 1847)

Medium sized moths with cryptic coloration; hindwings always smaller than forewings; branches of RS stalked beyond limits of cell in forewings. In hindwings SC + R absent, being fused with RS; branches of M appear to leave anterior branch of CuA and form a 'comb'; M with three branches. Ocelli reduced; proboscis and labial palpi well developed (Fig. 965). Paleogene to Recent. Most genera belong to the Recent fauna; one extinct genus from the Paleogene of Kazakhstan.

Order DIPTERA. Two-winged insects

(B.B. Rohdendorf)

One fore pair of wings. Anterior margin straight; SC without branches or with one short anterior branch resembling a cross vein; CuA and CuP simple, always very close, placed in form of a compact fold. Hindwings transformed into club-shaped structures called halteres. Proboscis of piercing and sucking type.

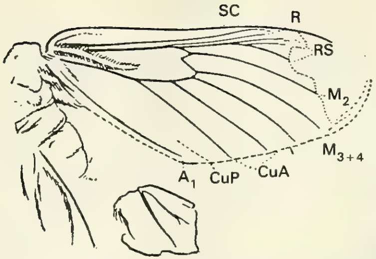


Fig. 965. Suborder Frenata—Macrofrenata.

Oligamatites martynovi Kusnetzov; forewing, × 1.3. Paleogene, East Kazakhstan (Kuznetsov, 1928).

Mesothorax very large, pro- and metathorax small; tarsus almost always five-segmented. Larvae without legs, often with an ill-defined head, live hidden in soil, freshwater, tissues of plants and animals. Winged phase intimately linked 308 with larval habitat, flowering plants or vertebrates. Food highly varied. Phylogeny still not understood fully (Fig. 966). Triassic to Recent. At the end of the Triassic both suborders, the primitive ancestral Archidiptera, and the Eudiptera, had attained development; the former already had a few groups of representatives and the latter was yet to attain wide development.

Suborder Archidiptera

Wings not very large, not more than 4 mm long, with numerous crossveins in almost all areas. Venation costalized; longitudinal veins not of equal thickness; C, R, CuA strong while RS, M, CuP and A thin. Mesozoic. Superfamilies: Dictyodipteridea, Hyperpolyneuridea, Dyspolyneuridea.

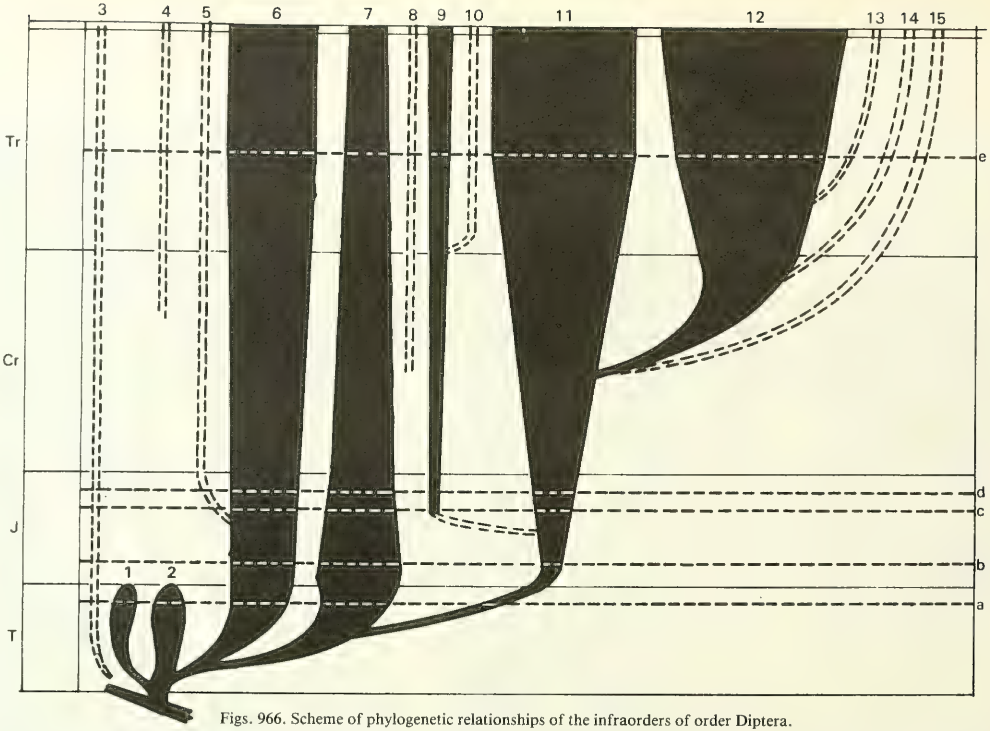
SUPERFAMILY DICTYODIPTERIDEA

Basal division of radial stem with shallow wavelike bend, without phragma or break; CuA well developed; anal area has well-developed crossveins. Triassic. One family.

Family DICTYODIPTERIDAE Rohdendorf, 1961

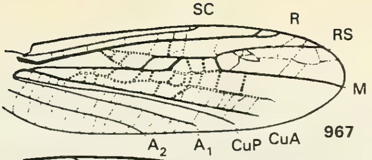
Anterior margin of wing straight in basal half; C, SC and R partly run parallel 309 and close; RS and M have a few thin branches; Cu roughly halfway along wing. Triassic. Four genera.

Dictyodiptera Rohdendorf, 1961. Genotype—*D. multinervis* Rohdendorf, 1961; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Crossveins lie between CuA and CuP; both veins of A almost parallel. Wing narrow, three



Figs. 966. Scheme of phylogenetic relationships of the infraorders of order Diptera.

Infraorders of Diptera, time of appearance and extinction, parental groups and related variants (shown by a broad band) are superimposed on geochronological scale. Broken lines show time of existence of best-understood past faunal complexes. Faunal complexes: a—Upper Triassic from Central Asia, b—Lower Jurassic from Western Europe, c—Upper Jurassic from Kazakhstan (Karatau), d—Upper Jurassic from Western Europe; e—Paleogene from Baltic amber. Infraorders of Diptera: 1—Diplopolyneuromorpha, 2—Dictyodipteromorpha, 3—Nymphomyiomorpha, 4—Deuterophlebiomorpha, 5—Blephariceromorpha, 6—Tipulomorpha, 7—Bibionomorpha, 8—Musidoromorpha, 9—Phoromorpha, 10—Termitoxenimorpha, 11—Asilomorpha, 12—Myiomorpha, 13—Braulomorpha, 14—Nycteribiomorpha, 15—Streblomorpha (Rohdendorf et al., 1961). Note: Phoromorpha is wrongly shown taking off from Asilomorpha in the Jurassic. In fact it branched from parental Miomorpha in the Cretaceous.



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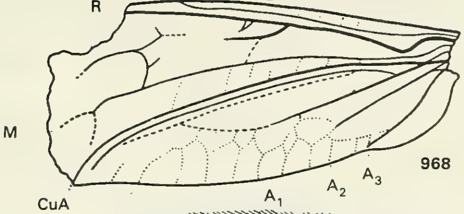

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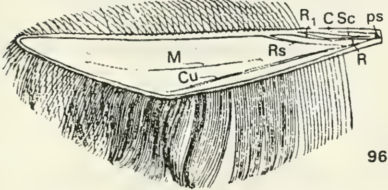

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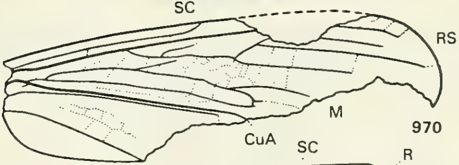

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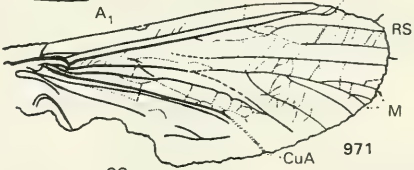

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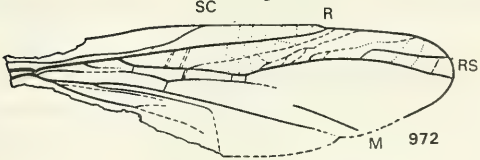

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Figs. 967–972. Suborder Archidiptera.

967. *Dictyodiptera multinervis* Rohdendorf; wing, × 21. Upper Triassic, Central Asia (Rohdendorf, 1961). 968. *Paradictyoptera trianalis* Rohdendorf; wing, × 25. Upper Triassic, Central Asia (Rohdendorf, 1961). 969. *Nymphomyia alba* Tokunaga; wing, × 20. Recent (Tokunaga, 1935). 970. *Dipterodictya tipuloides* Rohdendorf; wing, × 17. Upper Triassic, Central Asia (Rohdendorf, 1961). 971. *Hyperpolyneura phryganeoides* Rohdendorf; wing, × 24. Upper Triassic, Central Asia (Rohdendorf, 1961). 972. *Dyspolyneura longipennis* Rohdendorf; wing, × 20. Upper Triassic, Central Asia (Rohdendorf, 1961).

times as long as wide. Length of wing 2.8 mm (Fig. 967). One species. Upper Triassic of Issyk-Kul province.

Paradictyodiptera Rohdendorf, 1961. Genotype—*P. trianalis* Rohdendorf, 1961; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). No crossveins between CuA and CuP; A has three thin veins which are not parallel; with crossveins between C and SC. Wing narrow about 3.5 mm (Fig. 968). One species. Upper Triassic of Issyk-Kul province.

Dipterodictya Rohdendorf, 1961. Genotype—*D. tipuloides* Rohdendorf, 1961; Upper Trias, Issyk-Kul province (Rhaetian, Issyk-Kul). No crossveins between CuA and CuP; MP isolated in form of parallel vein in front of CuA, not connected with last crossveins. Wing narrow, three times as long as it is wide. Length about 3.5. mm (Fig. 970). One species. Triassic of Issyk-Kul region.

SUPERFAMILY HYPERPOLYNEURIDEA

Basal division of radial stem with sharp bend, forming a rudimentary phragma. Wing broad, with strong anterior cubital vein. Anal area of wing free of crossveins. Triassic. One family.

Family HYPERPOLYNEURIDAE Rohdendorf, 1961

Anterior margin of wing straight in basal half of wing; RS and R run close and parallel; RS has at least three branches and M at least six, running toward anal margin. Length of wing about 3 mm. Triassic. One genus.

Hyperpolyneura Rohdendorf, 1961. Genotype—*H. phryganeoides* Rohdendorf, 1961; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Crossveins seen between MP and the strong CuA; MP united with posterior branch of MA; SC very close to R near apex; A distally fused to form a closed cell. Wing approximately 2.5 times as long as wide. Length of wing 2.8 mm (Fig. 971). One species. Upper Triassic of Issyk-Kul province.

SUPERFAMILY DYSPOLYNEURIDEA

Basal division of radial vein with a break and phragma. Wing narrow, with a slightly thickened cubital vein. Anal area has no crossveins. Triassic. One family.

310 Family DYSPOLYNEURIDAE Rohdendorf, 1961

MP, sharply separated from MA, branches off CuA, connected with MA by a strong crossvein; RS in form of a strong stem, sends branches forward; Cu less than one-half of wing length; few strong radio-medial crossveins present. Triassic. One genus.

Dyspolyneura Rohdendorf, 1961. Genotype—*D. longipennis* Rohdendorf, 1961; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC thin,

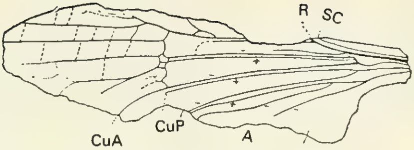

Fig. 973. Infraorder Diplopolyneuromorpha.

Diplopolyneura mirabilis Rohdendorf; wing, × 17. Upper Triassic, Central Asia (Rohdendorf, 1961).

terminates on C; crossveins between C and R.* At least five branches of RS terminate on anterior margin; basal half of MP runs strikingly close and parallel to CuA, which is bent backward at its end. Length of wing (3 mm) almost four times of width (Fig. 972). One species. Upper Triassic of Issyk-Kul province.

Suborder Eudiptera

Wings taper toward base; distinct radio-medial crossveins and a few intermedial veins always present; other crossveins, if any, distributed irregularly. Sizes vary widely: from 0.5 to 50 mm. Triassic to Recent. Fossil representatives known from infraorders Diplopolyneuromorpha, Tipulomorpha, Bibionomorpha, Asilomorpha, Phoromorpha, Musidoromorpha and Myiomorpha; the seven other known infraorders found until now only in Recent fauna.

Infraorder Diplopolyneuromorpha

Wing consists of two separate divisions: distal, with numerous cells and parallel veins, and proximal, with longitudinal veins running closely in pairs and no crossveins. Triassic. Family: Diplopolyneuridae.

Family DIPLOPOLYNEURIDAE Rohdendorf, 1961

R and SC only one-third of wing, close together like MA and MP, CuA and CuP, A_1 and A_2. Distal part of wing has at least four veins. A_2 has two branches. Triassic. One genus.

Diplopolyneura Rohdendorf, 1961. Genotype—*D. mirabilis* Rohdendorf, 1961; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). R, MA, CuA and C strong and markedly different from other veins; anal area of wing large; basal stem of M and CuA thin. Length of wing about 4.5 mm (Fig. 973). One species. Upper Triassic of Issyk-Kul province.

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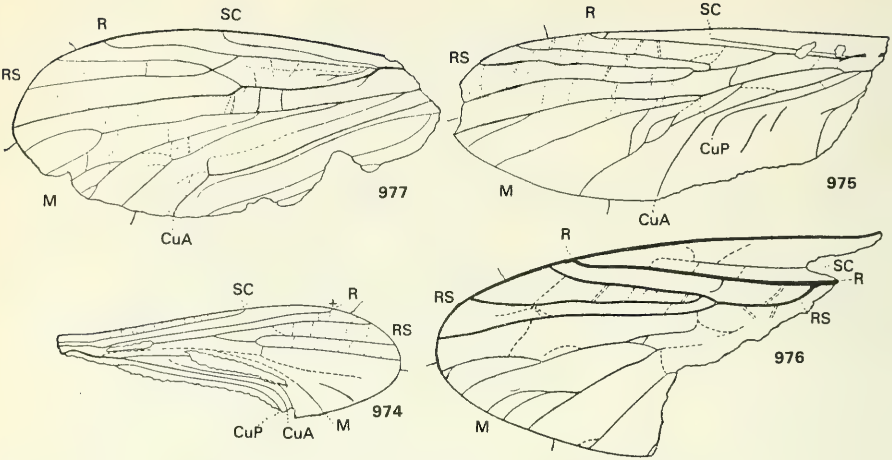
*According to Fig. 972 it should be 'between RS and R' and not 'C and R' as mentioned here—General Editor.



311 Figs. 974–977. Superfamilies Tipulodictyidea, Eopolyneuridea.

974. *Tipulodictya minima* Rohdendorf; wing, × 23. Upper Triassic, Central Asia (original drawing). 975. *Eopolyneura tenuinervis* Rohdendorf; wing, × 23. Upper Triassic, Central Asia (original drawing). 976. *Pareopolyneura costalis* Rohdendorf; wing, × 20. Upper Triassic, Central Asia (original drawing). 977. *Musidormomina crassinervis* Rohdendorf; wing, × 22. Upper Triassic, Central Asia (original drawing).

Infraorder Tipulomorpha

RS with parallel branches, which usually end on apical margin of wing. Wing elongate, with small apical division. Antennae always with similar segments. Development takes place mainly in water. Thirteen superfamilies: Tipulodictyidea, Eopolyneuridea, Tipulidea, Eoptychopteridea, Tanyderophryneidea, Dixidea, Culicidea, Psychodidea, Chironomidea, Rhaetomyiidea, Mesophantasmatidea, Thaumaleidea and Pachyneuridea; representatives of last two known until now only in Recent fauna.

SUPERFAMILY TIPULODICTYIDEA

Posterior branch of M close to CuA and forms a complex fold with CuA and CuP at midpoint of wing. RS has three parallel branches; with weak crossveins in costal area and between radial branches. Triassic. One family.

Family TIPULODICTYIDAE Rohdendorf, fam. nov.

Base of R with shallow, wavelike, furrow, without phragma. SC terminates on

C slightly beyond midpoint of wing; M weak. Triassic. One genus.

311 *Tipulodictya* Rohdendorf, gen. nov. Genotype—*T. minima* Rohdendorf, sp. nov; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Radiomedial crossvein distal to end of SC; at least 10 weak crossveins in costal area. Length of wing about 2.5 mm (Fig. 974). One species. Upper Triassic of Issyk-Kul province.

SUPERFAMILY EOPOLYNEURIDEA

M and SC markedly weaker than radial; branches of RS close, distributed in center of wing; weak crossveins between branches of RS and M. Triassic. Families: Eopolyneuridae and Musidoromimidae.

Family EOPOLYNEURIDAE Rohdendorf, fam. nov.

Costal-subcostal area very wide at base of wing, tapers uniformly toward apex; SC not connected with C; basal division of RS considerably shorter than its distal division with branches; MP not present. Triassic. Two genera.

Eopolyneura Rohdendorf, gen. nov. Genotype—*E. tenuinervis* Rohdendorf, sp. nov; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Crossveins absent between SC and R; end of anterior branch of RS closer to middle branch of RS than to R. Length of wing about 3 mm (Fig. 975). One species. Upper Triassic of Issyk-Kul province.

Pareopolyneura Rohdendorf, 1961. Genotype—*P. costalis* Rohdendorf, 1961; Upper Trias, Issyk-Kul region (Rhaetian, Issyk-Kul). Crossveins between SC and R; end of anterior branch of RS approaches R. Length of wing slightly more than 3 mm (Fig. 976). One species. Trias of Issyk-Kul region.

Family MUSIDOROMIMIDAE Rohdendorf, fam. nov.

Costal-subcostal area of uniform width, does not taper; SC thin, distinctly connected with C; basal stem of RS long, almost equal to its anterior branch; MP in form of thin vein, parallel to CuA. Triassic. One genus.

Musidoromima Rohdendorf, gen. nov. Genotype—*M. crassinervis* Rohdendorf, sp. nov; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). CuA with distinct process proximal to apex; with strong crossvein looking like base of distal branch of R. Length of wing about 3 mm (Fig. 977). One species. Upper Triassic of Issyk-Kul.

312 SUPERFAMILY TIPULIDEA

Veins of all main systems of equal thickness; branches of radial veins not close; intermedial cells small or absent; SC always long, more than one-half of wing. Legs of slender type. Larvae live primarily in water. Triassic to Recent. Eight families.

Family ARCHITIPULIDAE Handlirsch, 1906

Base of wing slightly narrowing; branches of RS and M, crossvein rm run close, located distal to center of wing; SC terminates on margin of wing. Small forms, rarely of medium size, not more than 9 mm. Triassic. Seven genera.

Dictyotipula Rohdendorf, gen. nov. Genotype—*D. densa* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). A_1 and A_2 run close to form a compact fold; costal and subcostal areas with very weak, but noticeable crossveins. Length of wing about 3 mm (Fig. 978). One species. Upper Triassic of Issyk-Kul province.

Diplarchitipula Rohdendorf, gen. nov. Genotype—*D. multimedialis* 313 Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). MP in form of thin fold behind MA; A irregular; M at least with five branches. Length of wing about 4 mm (Fig. 979). One species. Upper Triassic of Issyk-Kul province.

Architipula Handlirsch, 1906. Genotype—*A. seebachiana* Handlirsch, 1906; Lower Jurassic, Germany. M with four branches, anterior branches on a common stalk; no separate MP; one radio-medial crossvein. Length of wing ranges from 3 to 9 mm (Fig. 980). About 30 species. Upper Triassic of Issyk-Kul province; Jurassic of Kazakhstan and Western Europe.

Outside the USSR: *Eotipula* Handlirsch, 1906; *Protipula* Handlirsch, 1906; *Mesotipula* Handlirsch, 1939; and *Liassotipula* Tillyard, 1925.

Family EOLIMNOBIIDAE Rohdendorf, fam. nov.

Base of wing converges slightly; crossvein rm at midpoint of wing; SC terminates on C; intermedial crossveins absent; three prominent veins of A. Wings of medium size. Jurassic. One genus.

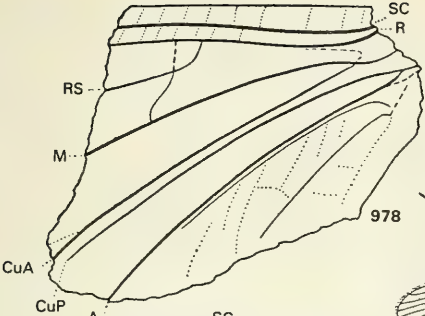
Eolimnobia Handlirsch, 1906. Genotype—*E. geinitzi* Handlirsch, 1906; Lower Jurassic, Germany. Wing 3.2 times as long (10.5 mm) as wide. C about two-thirds of length of wing (Fig. 981). One species. Lower Jurassic of Germany.

Family TRICHOCERIDAE Edwards, 1928

Base of wing converges sharply; bifurcations of M and crossvein rm considerably distal to midpoint of wing; intermedial crossveins isolate cell. A_2 shortened (Fig. 982). Larvae with a distinct head capsule, live in water. Wings of medium size. Paleogene to Recent. Four genera, of which one known from the Paleogene of Europe (Baltic amber).

Family LIMONIIDAE Hendel, 1936

Base of wing narrow; SC connected with C; bifurcation of M, crossveins rm and mcu close, distal to midpoint of wing; A_2 long (Fig. 983). Head capsule of larvae not distinct; larvae usually small, rarely of medium size, found in water



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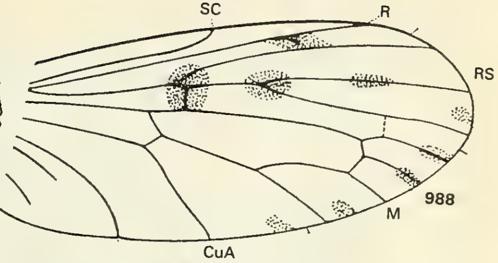

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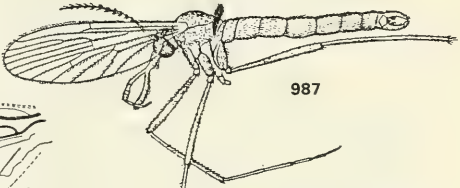

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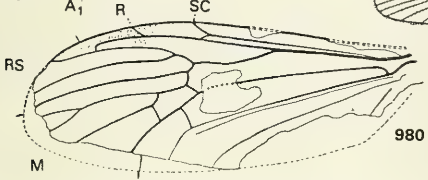

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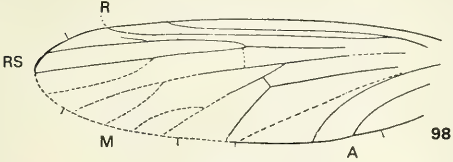

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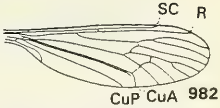

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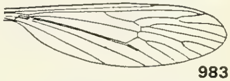

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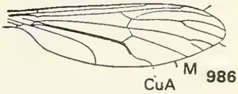

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Figs. 978–988. Superfamilies Tipulidea, Eoptychopteridea.

978. *Dictyotipula densa* Rohdendorf; part of wing, × 30. Upper Triassic, Central Asia (original drawing). 979. *Diplarchitipula multimedialis* Rohdendorf; wing, × 20. Upper Triassic, Central Asia (original drawing). 980. *Architipula radiata* Rohdendorf; wing, × 11. Upper Triassic, Central Asia (original drawing.) 981. *Eolimnobia geinitzi* Handlirsch; wing, × 5.7. Lower Jurassic, Germany (Handlirsch, 1906). 982. *Trichocera* sp.; wing, × 5. Recent, Europe (Curran, 1934). 983. *Tricyphona* sp.; wing, × 3. Recent, Europe (Curran, 1934). 984. *Tipula* sp.; wing, × 1.5. Recent, Europe (Curran, 1934). 985. *Phalacocera* sp.; wing, × 2.4. Recent, Europe (Curran, 1934). 986. *Ptychoptera* sp.; wing, × 4.5. Recent, Europe (Curran, 1934). 987. *Macrochile spectrum* Loew; general view, × 7. Paleogene, Europe (Baltic amber) (Crampton, 1926). 988. *Proptychoptera maculata* Handlirsch; wing, × 12. Lower Jurassic, Germany (Handlirsch, 1939).

and other humid media. Paleogene to Recent. Richly represented in the Recent fauna; about 40 genera known from Tertiary deposits, of which 24 are from the Paleogene of Europe (Baltic amber).

Family TIPULIDAE Leach, 1815

Base of wing narrows sharply; SC terminates on R; bifurcations of M, rm and mcu located far apart, beyond midpoint of wing; A_2 long (Fig. 984). Wings large, rarely of medium size. Larvae live in water or in soil. Paleogene to Recent. Richly represented in the Recent fauna. About 10 genera known, of which two are from the Paleogene of Europe (Baltic amber).

Family CYLINDROTOMIDAE Osten-Sacken, 1809

[nom. transl. Czizek, 1931 (ex Cylindrotomina Osten-Sacken, 1869)]

Base of wing narrow; SC ends freely in costal area; bifurcations of M and crossveins rm and mcu distal to midpoint of wing; R terminates on anterior branch of RS; at end CuA sharply bent backward (Fig. 985). Head capsule of the larvae not distinct; larvae of medium size, live on vegetation in water and moist meadows. Paleogene to Recent. Poorly represented in the Recent fauna; one genus known from the Paleogene and Neogene of North America.

Family LIRIOPEIDAE Hendel, 1936

Base of wing converges sharply; SC terminates on C; bifurcations of M and crossveins rm and mcu located at midpoint of wing; intermedial cell absent (Fig. 986). Head capsule of larva sharply distinct; larvae live in water. Paleogene to Recent. Poor in species, being a relict family; one genus of the Recent fauna known from the Paleogene of Czechoslovakia.

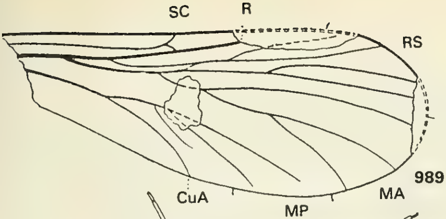
Family TANYDERIDAE Osten-Sacken, 1879

[nom. transl. Alexander, 1920 (ex Tanyderina Osten-Sacken, 1879)]

Base of wing converges somewhat; SC terminates on C, connected with R by a crossvein; RS with four branches, terminates on margin of wing; bifurcations of M and crossveins rm and mcu located at midpoint of wing or more proximally; 314 A_2 indistinct (Fig. 987). Larvae live in moist soil. Paleogene to Recent. Few species, relict among the Recent families; one genus known from the Paleogene of Europe (Baltic amber).

315 Figs. 989–993. Superfamilies Tanyderophryneidea, Dixidea, Culicidea.

989. *Tanyderophryne multinervis* Rohdendorf; wing, × 15. Upper Jurassic, Kazakhstan (original drawing). 990. *Dixamima villosa* Rohdendorf; A—ventral view of fossil, × 7. B—part of wing, × 20. Upper Jurassic, Kazakhstan (Rohdendorf, 1951). 991. *Dixa* sp.; lateral view, × 5.5. Recent, Europe (Curran, 1934). 992. *Mochlonyx* sp.; dorsal view, × 7. Recent, Europe (Curran, 1934). 993. *Culex papiens* Linnaeus; dorsal view, × 7. Recent, Europe (Lindner, 1932).



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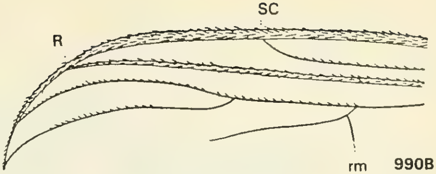

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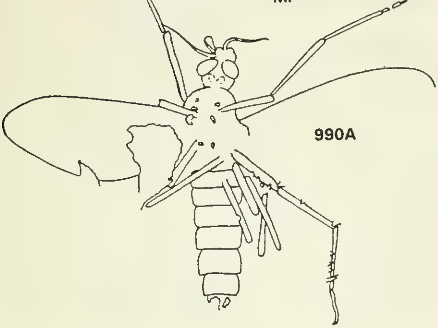

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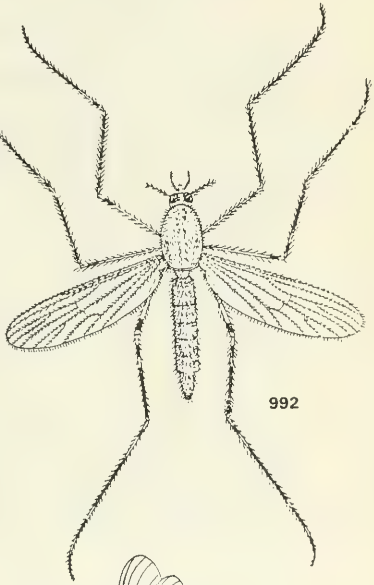

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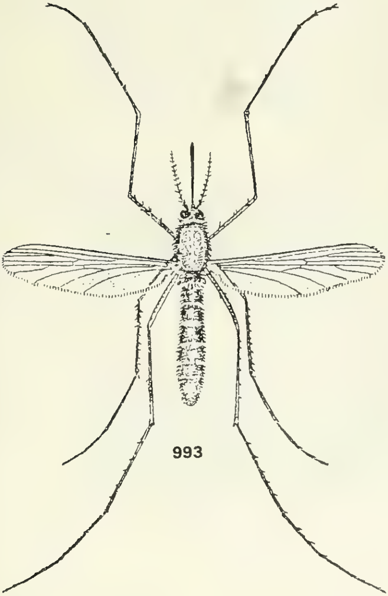

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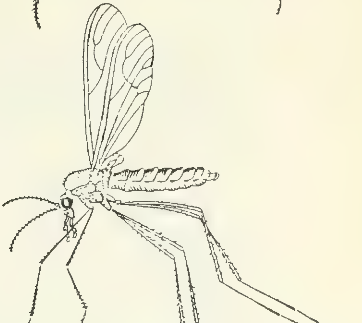

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SUPERFAMILY EOPTYCHOPTERIDEA

Veins of all systems of equal thickness; branches of R not close; intermedial cell very large, almost always distinctly isolated; SC short, one-half of length of wing. One family. Jurassic.

Family EOPTYCHOPTERIDAE Handlirsch, 1906

Broad wing, only 2.5 times as long as it is wide; wing base wide (Fig. 988). Length of wing 4–6 mm. Jurassic. Two genera. Outside the USSR: *Eoptychoptera* Handlirsch, 1906 and *Proptychoptera* Handlirsch, 1939.

SUPERFAMILY TANYDEROPHRYNEIDEA

M, RS and Cu weaker than C, SC and R; branches of R not close; basal stem of M strong, takes off from R; MP isolated from MA; intermedial cells absent; SC is short. Legs of running type. One family. Jurassic.

Family TANYDEROPHRYNEIDAE Rohdendorf, fam. nov.

Wing broad, with length more than 2.75 times of width, and with a narrow base; SC terminates on C, connected with R by a crossvein at end; five branches on RS and not more than four on M; CuA short. Jurassic. One genus.

Tanyderophryne Rohdendorf, gen. nov. Genotype—*T. multinervis* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Posterior branch of RS merged with system of M; four anterior branches of RS form two pairs of parallel veins; MP branches from CuA and forms at least two branches, not united with MA. Length of wing 3.5 mm and of body, about 4.2 mm (Fig. 989). One species. Upper Jurassic of Kazakhstan.

SUPERFAMILY DIXIDEA

Wing three times as long as wide, converges moderately at base; branching of M and crossvein rm close together just behind midpoint of wing; two branches of RS form a pair of parallel veins, uniformly bent backward. Jurassic to Recent. Families: Dixamimidae and Dixidae.

Family DIXAMIMIDAE Rohdendorf, 1957

SC longer than one-half of wing; intermedial cell well isolated; C and R noticeably thicker than other veins. Legs strong, of running type. Jurassic. One genus.

Dixamima Rohdendorf, 1951. Genotype—*D. villosa* Rohdendorf, 1951; Upper Jurassic, Chimkent province (Malm, Karatau). R straight; rm located at extreme base of posterior branch of RS; base of posterior branch of M looks like a crossvein. Length of wing about 5 mm (Fig. 990 a, b). One species. Upper Jurassic of Kazakhstan.

Family DIXIDAE Van der Vulp, 1877

[nom. transl. Brauer, 1880 (ex Dixinae Van der Vulp, 1877)]

SC less than one-half of wing; intermedial crossveins absent; cell not isolated; all veins of roughly equal thickness. Legs of thin type. Larvae live in water (Fig. 991). Paleogene to Recent. Two genera in Recent fauna, of which one also known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CULICIDEA

Narrow wings, at least four times as long as broad, moderately narrow toward base; branching of M and crossvein rm not close; two anterior branches of RS do not form a pair of bent veins running parallel. Larvae live in water. Paleogene to Recent. Families: Chaoboridae and Culicidae.

Family CHAOBORIDAE Hendel, 1936

Proboscis short and soft. Wings without broad scales, with only hair (Fig. 992). Paleogene to Recent. Few genera in the Recent fauna, of which two are also from the Paleogene of Europe (Baltic amber), one (*Chaoborus* Lichtwardt) from the Paleogene of Southern France and one from the Neogene of South Asia (Burmese amber).

Family CULICIDAE Billbergh, 1820

[nom. transl. Stephens, 1829 (ex Culicides Billberg, 1820)]

Proboscis very elongate. Wings covered with broad scales along veins (Fig. 993). Paleogene to Recent. Numerous genera in the Recent fauna, of which three also known from the Paleogene of Western Europe and North America.

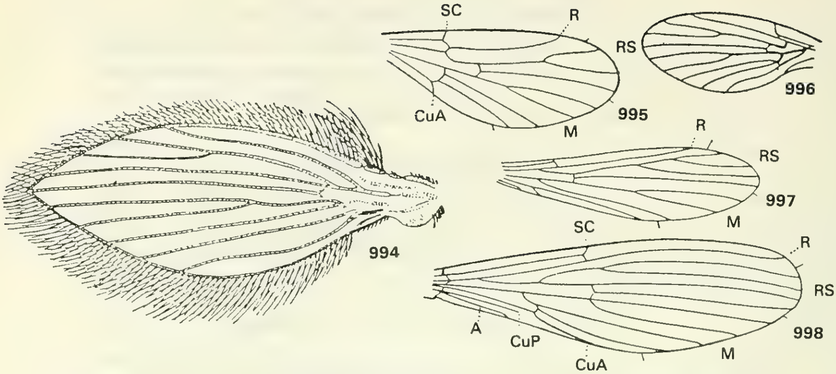
SUPERFAMILY PSYCHODIDEA

Wings with convex anterior margin, narrow at base, covered with dense hair-setae; SC always shorter than one-half of wing; crossvein rm poorly represented; 316 longitudinal veins not displaced, uniformly distributed throughout wing surface. Paleogene to Recent. Families: Psychodidae, Trichomyiidae, Phlebotomidae, Nemopalpidae.

Family PSYCHODIDAE Newman, 1834

[nom. transl. Bigot, 1854 (ex Psychodites Newman, 1834)]

Wings broad, pointed or angular at apex; CuA long, parallel to M; SC almost completely reduced (Fig. 994). Paleogene to Recent. Larvae live in moist places. Two genera from the Recent fauna also known from the Paleogene of Europe (Baltic amber).



Figs. 994–998. Superfamily Psychodidea.

994. *Psychoda* sp.; wing, × 29. Recent, Europe (Hendel, 1928). 995. *Trichomyia* sp.; wing, × 23. Recent, Europe (Curran, 1934). 996. *Sycorax* sp.; wing, × 16. Recent, Europe (Curran, 1934). 997. *Phlebotomus* sp.; wing, × 15. Recent (Brues, Melander and Carpenter, 1954). 998. *Bruchomyia* sp.; wing, × 13. Recent, Australia (Brues, Melander and Carpenter, 1954).

Family TRICHOMYIIDAE Tonnior, 1922

[nom. transl. Rohdendorf, hic (ex Trichomyinae Tonnior, 1922)]

Wings broad, blunt at apex; RS with two or three branches; CuA either very short or elongate; SC very distinct, terminates on C, connected with R by crossvein (Figs. 995, 996). Paleogene to Recent. Two genera from the Paleogene of Europe (Baltic amber).

Family PHLEBOTOMIDAE Rondani, 1840

[nom. transl. Rohdendorf, hic (ex Phlebotominae Rondani, 1840)]

Wings narrow, slightly pointed at apex; RS with four branches; CuA short, terminates on anal margin at basal part of wing; SC prominent, terminates on C, connected with R by a crossvein (Fig. 997). Very small, blood sucking insects. Larvae live in decaying matter and soil. Paleogene to Recent. One genus in the Recent fauna.

Family NEMOPALPIDAE Edwards, 1921

[nom. transl. Rohdendorf, hic (ex Nemopalpinae Edwards, 1921)]

Wings not particularly narrow, with rounded apex; SC long, but somewhat less than one-half of length of wing; A short, descends at right angles and terminates on margin of wing (Fig. 998). Paleogene to Recent. Medium sized, very rare relict insects of the Southern Hemisphere. Development not known. One genus from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CHIRONOMIDEA

Wings with straight anterior margin, sharp costal venation; phragma distinct; anterior veins (C and system R) noticeably stronger than posterior ones (M, Cu and A); vein C does not approach anal margin of wing. Larvae live in water, rarely amidst moist vegetation. Triassic to Recent. Families: Architendipedidae, Protendipedidae, Chironomidae, Ceratopogonidae, Simuliidae.

317 Family ARCHITENDIPEDIDAE Rohdendorf, fam. nov.

Wings elongate with clearly distinguishable venation; crossveins between R and M, M and CuA, in costal area and between branches of RS. Triassic. Two genera.

Architendipes Rohdendorf, gen. nov. Genotype—*A. tshernovskiji* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Costal area with crossveins; basal parts of R and M tough, fused; RS with long anterior branches, comprising two long parallel branches. Length of wing 4.5 mm (Fig. 999). One species. Upper Triassic of Issyk-Kul province.

Paleotendipes Rohdendorf, gen. nov. Genotype—*P. alexii* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Costal area devoid of crossveins; basal parts of R and M very slender and indistinct; anterior branch of RS bent, with small fork at end. Length of wing about 5 mm (Fig. 1000). One species. Upper Triassic of Issyk-Kul province.

Family PROTENDIPEDIDAE Rohdendorf, fam. nov.

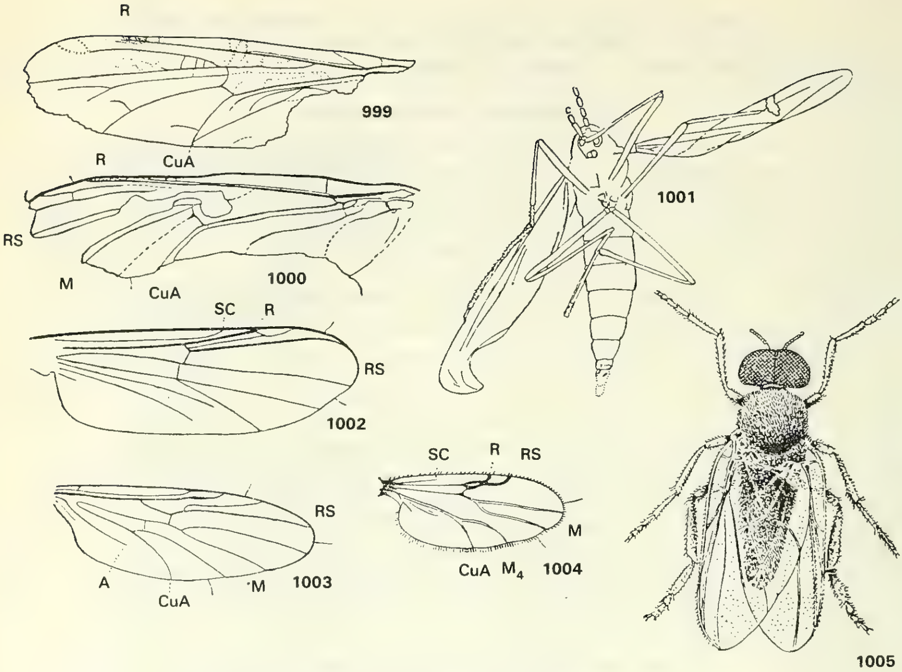
Wings elongate with weak, faint venation, and dense cover of dark hair. Legs thin, very long; anterior metatarsus short. Jurassic. One genus.

Protendipes Rohdendorf, gen. nov. Genotype—*P. dasypterus* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Abdomen elongate and conical; posterior femur slightly longer than posterior tibia. Length of body about 3.25 mm, of wing, 3.5 mm and of posterior femur, 1.35 mm (Fig. 1001). One species. Upper Jurassic of Kazakhstan.

Family CHIRONOMIDAE Macquart, 1838

[nom. transl. Haliday, 1851 (ex Chironomides Macquart, 1838)] (Tendipedidae Grunberg, 1910; Hendel, 1928)

Wings elongate, with weak venation; in neighborhood of anterior margin venation distinct; wings bare or with short, thin hair. Legs, particularly anterior
318 legs, very long and slender. Both branches of M (M_1 and M_4) present, of which, anterior branch simple and isolated from posterior one. Paleogene to Recent.



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Figs. 999–1005. Superfamily Chironomidea.

999. *Architendipes tshermovskiji* Rohdendorf; wing, × 15. Upper Triassic, Central Asia (original drawing). 1000. *Palaeotendipes alexii* Rohdendorf; wing, × 12. Upper Triassic, Central Asia (original drawing). 1001. *Protendipes dasypterus* Rohdendorf; ventral view, × 14. Upper Jurassic, Kazakhstan (original drawing). 1002. *Anatopynia* sp.; wing, × 9.5. Recent, Europe (Brues, Melander and Carpenter, 1954). 1003. *Chironomus* sp.; wing, × 6. Recent, Europe (Brues, Melander and Carpenter, 1954). 1004. *Helea* sp.; wing, × 17. Recent, Europe (Curran, 1934). 1005. *Simulium* sp.; dorsal view, × 14. Recent, Europe (Rubtsov, 1959).

Family rich in species in the Recent fauna and widespread; of seven subfamilies in the Tertiary fauna three well known.

Subfamily Tanypodinae Skuse, 1889
[nom. transl. Enderlein, 1920 (ex Tanypina Skuse, 1889)]
(Pelopiina Hendel, 1928)

Crossvein mcu present; RS well developed and connected with R (Fig. 1002).

Paleogene to Recent. One genus from the Recent fauna also known from the Paleogene of Europe (Baltic amber).

Subfamily Chironominae Macquart, 1838

[nom. transl. Kieffer, 1906 (ex Chironomides Macquart, 1838)]

Crossvein mcu absent; M_4 isolated from M_1 and appears as a branch of CuA; anterior metatarsus longer than tibia. Last segment of genitalia in males directed backward (Fig. 1003). Paleogene to Recent. Many genera in the Recent fauna, of which two also known from the Paleogene of Europe (Baltic amber), Western Europe and North America, and the Neogene of Western Europe.

Subfamily Orthocladiinae Kieffer, 1911

Crossvein mcu absent; anterior metatarsus shorter than tibia; last segment of genitalia in males bent forward. Paleogene to Recent. Three genera of the Recent fauna also known from the Paleogene of Europe (Baltic amber).

Family CERATOPOGONIDAE Skuse, 1889

[nom. transl. Malloch, 1917 (ex Ceratopogonina Skuse, 1889)]
(Heleidae Speiser, 1910)

Wings moderately elongate, rarely long, with very sharp costalized venation; radial veins considerably thicker than others; three branches of M, two anterior ones form a fork. Legs short and of clinging type, with long claws and swollen femora. Larvae live in water and moist soil (Fig. 1004). Paleogene to Recent. Family fairly well distributed in the Recent fauna; one genus known from the Paleogene of Germany.

Family SIMULIIDAE Newman, 1834

[nom. transl. Williston, 1908 (ex Simuliites Newman, 1834)]

Wings large, very broad, fanlike with costalized venation; M with three weak branches; radial veins strong and close. Body short, legs short, of clinging type (Fig. 1005). Larvae live in fast-running streams, winged adults suck blood of vertebrates. Paleogene to Recent. One genus from the Paleogene of Europe (Baltic amber) and the Neogene of Western Europe.

Superfamily RHAETOMYIIDEA

Wings with straight anterior margin, strong veins distributed uniformly over wing surface; phragma well developed, connecting stems of R and CuA; vein C reaches anal margin; crossveins rm and mcu very strong; A weak and reduced. Triassic. Family: Rhaetomyiidae.

Family RHAETOMYIIDAE Rohdendorf, fam. nov.

SC equal to one-half of length of wing, terminates on C; RS divides distal to end

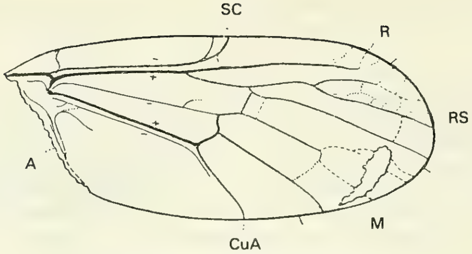


Fig. 1006. Superfamily Rhaetomyiidea.

Rhaetomyia necopinata Rohdendorf; wing, × 17.5. Upper Triassic, Central Asia (original drawing).

of SC into three branches, of which anterior ones have a common stem; M branches into two at level of end of C; CuA strong, with a break. Triassic. One genus.

Rhaetomyia Rohdendorf, gen. nov. Genotype—*R. necopinata* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Main stem of M weaker than R and CuA; anterior branch of M forms a fork and posterior one is simple; CuP slender, runs close to CuA up to middle of its distal segment. Length of wing 3.5 mm, width 1.6 mm (Fig. 1006). One species. Upper Triassic of Issyk-Kul province.

SUPERFAMILY MESOPHANTASMATIDEA

Wings very narrow, with straight anterior margin, converging basal part 319 resembling a stalk; venation strong, not costalized; branches of veins not close; R and CuA thicker than other veins. Jurassic. Family: Mesophantasmatidae.

Family MESOPHANTASMATIDAE Rohdendorf, fam. nov.

Costal vein extends round entire wing; vannus not distinct; anal lobe small; wing apex blunt; A absent. Jurassic. One genus.

Mesophantasma Rohdendorf, gen. nov. Genotype—*M. tipuliforme* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). RS branches halfway along wing, with a double base and three branches; M divided halfway along wing or more distally, has three branches; CuP thin, but quite prominent. Length of wing about 8 mm (Fig. 1007). One species. Upper Jurassic of Kazakhstan.

Infraorder Bibionomorpha

RS with branches, anterior of these branches always terminate on anterior

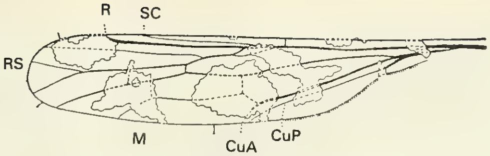


Fig. 1007. Superfamily Mesophantasmatidea.

Mesophantasma tipuliforme Rohdendorf; wing, × 9.2. Upper Jurassic, Kazakhstan (original drawing).

margin of wing or on R. Wing somewhat elongate with large, well-marked apical division. Antennae have uniform segments. Development not associated with water. Triassic to Recent. Nine superfamilies: Pleciodictyidea, Protoligoneuridea, Fungivoridea, Bibionidea, Bolitophilidea, Scatopsidea, Rhyphidea, Phragmoligoneuridea, Cecidomyiidea.

SUPERFAMILY PLECIODICTYIDEA

Regular crossveins between M and CuP; venation weak; only R and CuP sharp and distinct, Triassic. Family: Pleciodictyidae.

Family PLECIODICTYIDAE Rohdendorf, fam. nov.

RS with rows of branches directed to the front resembling irregular crossveins; M system well developed, but weak and difficult to distinguish. Triassic. One genus.

Pleciodictya Rohdendorf, gen. nov. Genotype—*P. modesta* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Not more than three branches of RS terminate on R; crossveins rm take form of three tilted veins; SC weak. Length of wing 2.2 mm (Fig. 1008). One species. Upper Triassic of Issyk-Kul province.

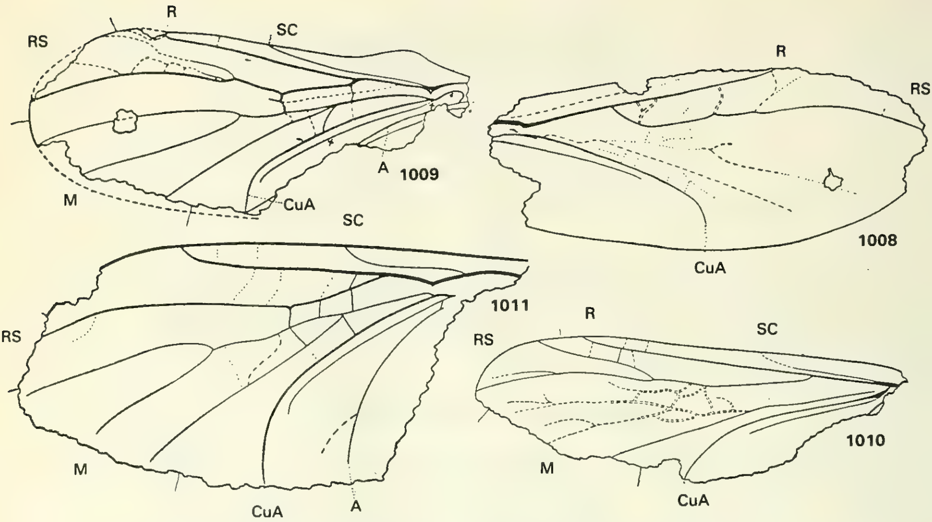
SUPERFAMILY PROTOLIGONEURIDEA

Costal area has sharp projection; rudimentary phragma seen; branches of RS complex, indistinct; with two distinct rm which are far apart. Triassic. Family: Protoligoneuridae.

Family PROTOLIGONEURIDAE Rohdendorf, fam. nov.

M consists of three distinct branches sprouting from a common stem; A has two well developed branches. Triassic. One genus.

Protoligoneura Rohdendorf, fam. nov. Genotype—*P. fusicosta* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC thin, reaches up to middle of wing; common trunk M_{1+2} very short.



320 Figs. 1008–1011. Superfamilies Pleciodictyidea, Protoligoneuridea, Fungivoridea.

1008. *Pleciodictya modesta* Rohdendorf; wing, × 24. Upper Triassic, Central Asia (original drawing). 1009. *Protoligoneura fusicosta* Rohdendorf; wing, × 24. Upper Triassic, Central Asia (original drawing). 1010. *Palaeoplecia rhaetica* Rohdendorf; wing, × 19. Upper Triassic, Central Asia (original drawing). 1011. *Rhaetofungivora reticulata* Rohdendorf; wing, × 35. Upper Triassic, Central Asia (original drawing).

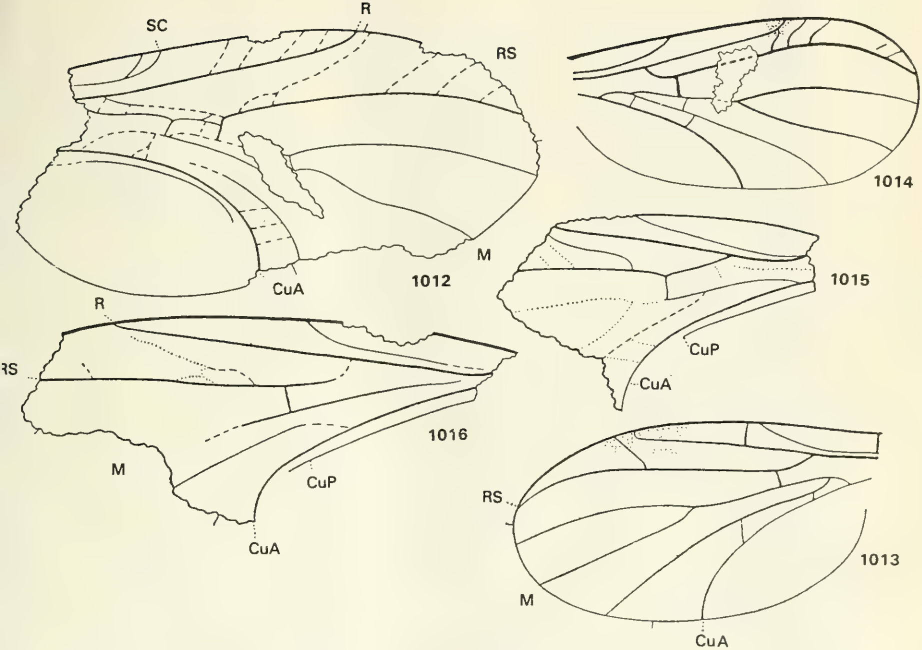
Length of wing 2.5 mm (Fig. 1009). One species. Upper Triassic of Issyk-Kul province.

SUPERFAMILY FUNGIVORIDEA

Costal area without projection; phragma not developed; basal part of CuP not seen. Size small. Legs slender, of running type. Antennae slender, with uniform segments. Intermedial cell not isolated; M with three branches—M_1, M_2 and M_4. Triassic to Recent. 16 families, of which only one is represented in Recent fauna.

Family PALAEOPLECIIDAE Rohdendorf, fam. nov.

R straight at base; RS branches off R at basal one-fourth of wing and has a long anterior branch, parallel to end of R; distinct crossveins between C, R and anterior branches of M; posterior branch of M straight and distinct. Triassic. One genus.



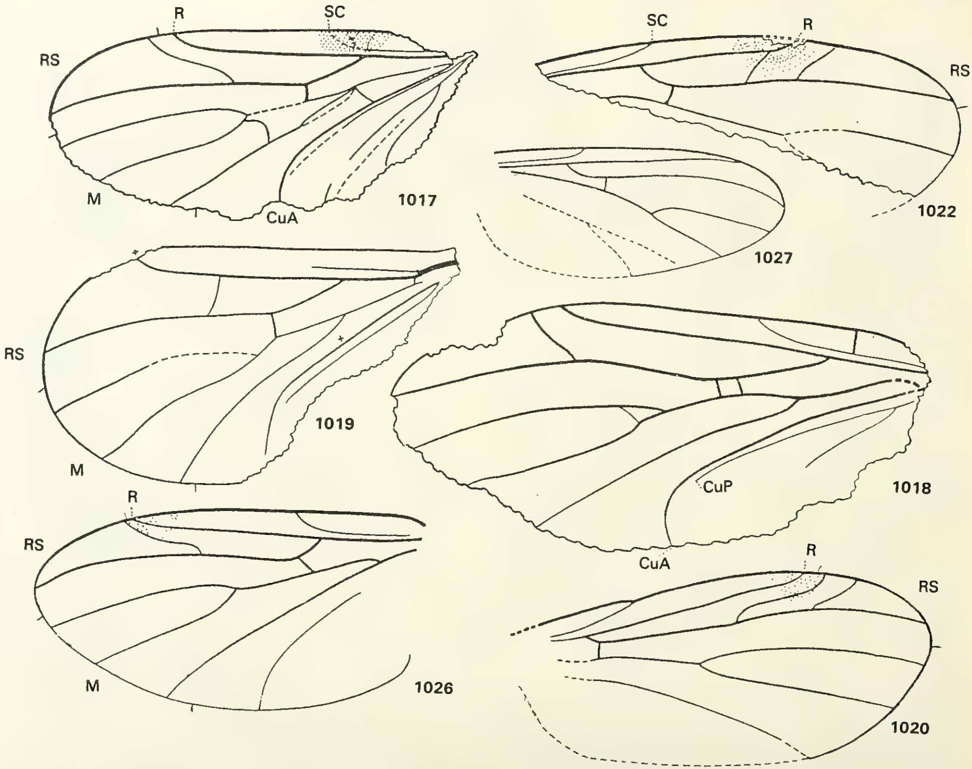
321 Figs. 1012–1016. Superfamily Fungivoridea.

1012. *Rhaetofungivorella analis* Rohdendorf; wing, × 36. Upper Triassic, Central Asia (original drawing). 1013. *Transversiplecia transversinervis* Rohdendorf; wing, × 17.5. Upper Jurassic, Kazakhstan (Rohdendorf, 1946). 1014. *Polyneurisca atavina* Rohdendorf; wing, × 26. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1015. *Rhaetofungivorodes defectivus* Rohdendorf; part of wing, × 17. Upper Triassic, Central Asia (original drawing). 1016. *Protallactoneura turanica* Rohdendorf; part of wing, × 26. Upper Triassic, Central Asia (original drawing).

Palaeoplecia Rohdendorf, gen. nov. Genotype—*P. rhaetica* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC nearly 320 one-third of length of wing, slender; posterior branch of RS has a narrow bifurcation; anterior medial veins irregular and thin. Length of wing about 4 mm (Fig. 1010). One species. Upper Triassic of Issyk-Kul province.

Family PLECIOFUNGIVORIDAL Rohdendorf, 1946

R has a break or a sharp bend at base; RS branches off R at basal one-third of


R
SC
RS
M
CuA
1017
SC
R
RS
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RS
M
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CuP
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R
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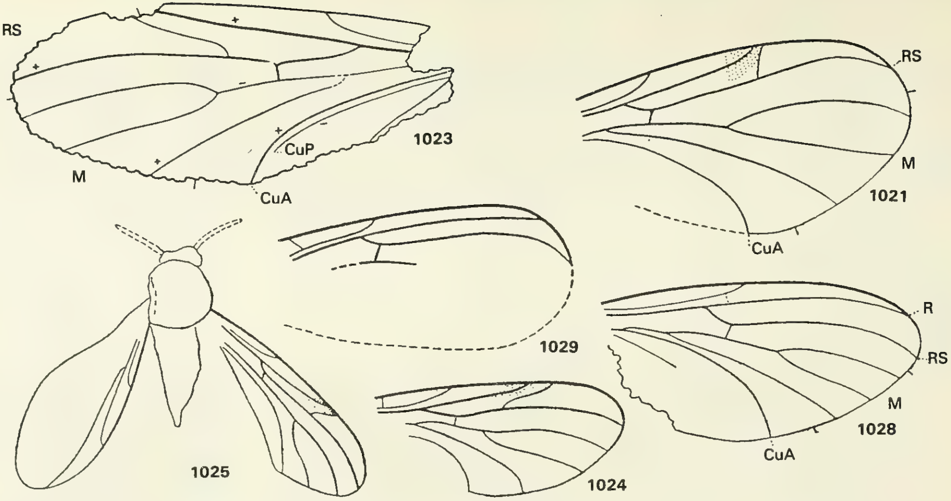

Figs. 1017–1029. Superfamily Fungivoridea.

1017. *Archihesperinus phryneoides* Rohdendorf; wing, × 23. Upper Triassic, Central Asia (original drawing). 1018.*Archipleciofungivora binerva* Rohdendorf; wing, × 20. Upper Triassic, Central Asia (original drawing). 1019. *Archipleciomima obtusipennis* Rohdendorf; wing, × 28. Upper Triassic, Central Asia (original drawing). 1020. *Eopachyneura trisectoralis* Rohdendorf; wing, × 17. Upper Jurassic, Kazakhstan (Rohdendorf, 1946). 1021. *Pleciofungivora major* Rohdendorf; wing, × 16. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1022.*Pleciofungivorella binerva* Rohdendorf; part of wing, × 35. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1023. *Palaeohesperinus longipennis* Rohdendorf; wing, × 17. Upper Triassic, Central Asia (original drawing). 1024. *Prohesperinus abdominalis* Rohdendorf; wing × 13. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1025. *Allactoneurites jurassicus* Rohdendorf; dorsal view, × 11. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1026. *Eohesperinus martynovi* Rohdendorf; wing, × 20. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1027. *Mimalycoria allactoneuroides* Rohdendorf; wing, × 19. Upper Jurassic, Southern Kazakhstan. 1028. *Eoboletina gracilis* Rohdendorf; wing, × 12. Upper Jurassic, Kazakhstan (Rohdendorf, 1946). 1029. *Fungivorites indistinctus* Rohdendorf; part of wing, × 10. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946).

wing and has a varying number of anterior branches; no distinct crossveins between C, end of R and branches of RS; posterior branch of M not thicker than other branches of M. Triassic through Jurassic. Sixteen genera.

Rhaetofungivora Rohdendorf, gen. nov. Genotype—*R. reticulata* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Well-defined vestiges of archedictya seen in form of weak crossveins; rm comprises two or more veins, equal to number of branches of RS; no strong crossveins in subcostal area. Length of wing 1.5–3.25 mm (Fig. 1011). More than 15 species. Upper Triassic of Issyk-Kul province.

Rhaetofungivorella Rohdendorf, gen. nov. Genotype—*R. subcosta* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Numerous weak crossveins between branches of SC, R, RS and branches of M; always with a few rm veins. Length of wing 1.8–2 mm (Fig. 1012). Four species. Upper Triassic of Issyk-Kul province.

Transversiplecia Rohdendorf, 1946. Genotype—*T. transversinervis* Rohdendorf, 1946; Upper Triassic, Chimkent province (Malm, Karatau). Vestiges of archedictyon absent; with a strong crossvein in subcostal area and two crossveins between M and CuA; one inclined branch of RS terminates on C. Length of wing 3.5 mm (Fig. 1013). One species. Upper Jurassic of Kazakhstan.

Polyneurisca Rohdendorf, 1946. Genotype—*P. atavina* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). Anterior branches of RS resembling crossveins terminate on R and C; RS bent sharply backward at base; crossveins between bases of M_{1-2}, M_4 and CuA. Length of wing 1.75 mm (Fig. 1014). One species. Upper Jurassic of Kazakhstan.

Rhaetofungivorodes Rohdendorf, gen. nov. Genotype—*R. defectivus*
321 Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Costal area wide; SC long, reaches to level of base of the slender, inclined anterior branch of RS; with a weak vein between bases of R and M + CuA; M weak. Length of wing about 3 mm (Fig. 1015). One species. Upper Triassic of Issyk-Kul province.

Protallactoneura Rohdendorf, gen. nov. Genotype—*P. turnaica* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC short; branches of RS very delicate and indistinct, seen as vestiges of the system; basal segment of RS three times as long as rm. Length of wing about 2.3 mm (Fig. 1016). One species. Upper Triassic of Issyk-Kul province.

Archihesperinus Rohdendorf, gen. nov. Genotype—*A. phrynecides* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC with branches at end; RS with one slender, bent anterior branch; with crossveins between M_4 and CuA; basal segment of RS more than three times as long as rm. Length of wing 2.6 mm (Fig. 1017). One species. Upper Triassic of Issyk-Kul province.

Archipleciofungivora Rohdendorf, gen. nov. Genotype—*A. binerva* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). Sharp crossvein present in costal area; RS with one strong branch terminating on C; with two rm. Length of wing about 2 mm (Fig. 1018). One species. Upper Triassic of Issyk-Kul province.

Archipleciomima Rohdendorf, gen. nov. Genotype—*A. obtusipennis* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). SC ends freely in wing membrane; RS with one anterior branch resembling a straight crossvein between RS and R; basal segment of RS more than three times as long as rm; anterior margin of wing straight; wing apex blunt. Length of wing 1.9 mm (Fig. 1019). One species. Upper Triassic of Issyk-Kul province.

323 *Eopachyneura* Rohdendorf, 1946. Genotype—*E. trisectoralis* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). Two inclined anterior branches of RS terminate on C; SC terminates on C distal to level of rm; proximal part of C convex up to the point where SC terminates on it; basal segment of RS shorter than rm. Length of wing 3 mm (Fig. 1020). One species. Upper Jurassic of Kazakhstan.

Pleciofungivora Rohdendorf, 1938. Genotype—*P. latipennis* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). One short, weak and slightly inclined anterior branch of RS terminates on C; basal segment of RS 1.5–2 times as long as rm; SC terminates on C at level of rm. Length of wing 2–3 mm (Fig. 1021). Two species. Upper Jurassic of Kazakhstan.

Pleciofungivorella Rohdendorf, 1946. Genotype—*P. binerva* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). Two weak, almost straight, slightly sloping anterior branches of RS terminate on R and C; basal segment of RS 2–2.5 times as long as rm; SC terminates on C at level of or more distal to branching of RS. Length of wing 1.5–1.9 mm (Fig. 1022). Three species. Upper Jurassic of Kazakhstan.

Palaeohesperinus Rohdendorf, gen. nov. Genotype—*P. longipennis* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Issyk-Kul). One long, sloping, slender, cross branch of RS terminates on C; basal segment of RS large, 3.5–5 times as long as the strong rm; SC slender, terminates on C a little distal to base of RS. Length of wing 2–3 mm (Fig. 1023). Two species. Upper Triassic of Issyk-Kul province.

Prohesperinus Rohdendorf, 1946. Genotype—*P. abdominalis* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). One strong inclined cross branch of RS parallel to end segment of R; anterior branch of RS terminates on C; basal segment of RS four times as long as rm; SC strong, terminates on C at level of rm. Length of wing 3.3 mm (Fig. 1024). Two species. Upper Jurassic of Kazakhstan.

Allactoneurites Rohdendorf, 1938. Genotype—*A. jurassicus* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). One strong, inclined anterior branch of RS terminates on C, borders pterostigma, basal segment of RS equal to rm; bifurcation of M strongly separated from rm. Length of wing 3.5 mm (Fig. 1025). One species. Upper Jurassic of Kazakhstan.

Eohesperinus Rohdendorf, 1946. Genotype—*E. martynovi* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). One strong, inclined branch of RS terminates on C, borders pterostigma; basal segment of RS one-and-one-half times as long as rm; bifurcations of M hardly separated from rm. Length of wing 3 mm (Fig. 1026). Two species. Upper Jurassic of Kazakhstan.

Family FUNGIVORITIDAE Rohdendorf, 1957

R always very long, not less than three-fourths of length of wing, straight or bent backward; RS without anterior branches or there may be one branch resembling a crossvein; rm strong, sometimes inclined; all branches of M of equal thickness; no additional crossveins. Jurassic. Five genera.

Mimalycoria Rohdendorf, 1946. Genotype—*M. allactoneuroides* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). rm transverse, isolated from bifurcation of R and RS; SC weak at end, terminates on C at level of basal part of RS; ends of R and RS slightly bent backward. Length of wing 2.75 mm (Fig. 1027). One species. Upper Jurassic of Kazakhstan.

Eoboletina Rohdendorf, 1946. Genotype—*E. gracilis* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). rm has a very slight tilt; basal segment of RS nearly twice as long as rm; R more than 0.9 mm longer than length of wing; C continues a little beyond end of R; SC strong, terminates on C, a little distal to level of rm. Length of wing 4.5 mm (Fig. 1028). One species. Upper Jurassic of Kazakhstan.

Fungivorites Rohdendorf, 1938. Genotype—*F. latimedius* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). rm with very slight
324 slope, equal to or one-half of length of basal segment of RS; R long, almost straight, C runs up to end of RS; SC strong, terminates on C at level of rm. Length of wing 3–5 mm (Fig. 1029). Two species. Upper Jurassic of Kazakhstan.

Mesosciophila Rohdendorf, 1946. Genotype—*M. venosa* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). Crossvein rm

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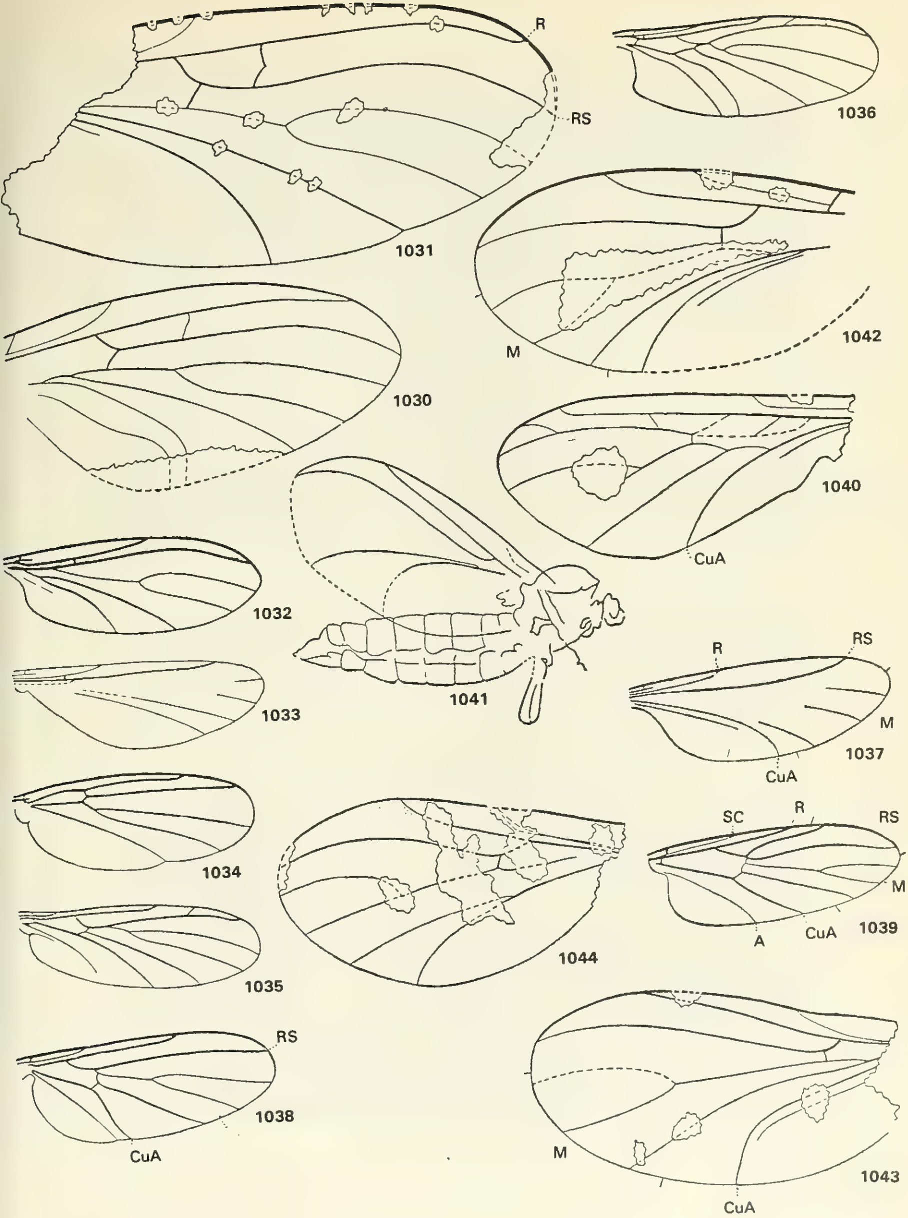
325 Figs. 1030–1044. Superfamily Fungivoridea.

1030. *Mesosciophila venosa* Rohdendorf; wing, × 13. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1031. *Mesosciophilodes similis* Rohdendorf; wing, × 12. Upper Jurassic, Southern Kazakhstan (original drawing). 1032. *Lycoria bicolor* Meigen; wing, × 11. Recent, Europe (Hennig, 1954). 1033. *Manota* sp.; wing, × 11. Recent, Europe (Hendel, 1936). 1034. *Zygomyia notata* Stannius; wing, × 14. Recent, Europe (Hennig, 1954). 1035. *Zelmira fasciata* Meigen, wing, × 9. Recent, Europe (Hennig, 1954). 1036. *Macrocera lutea* Meigen; wing, × 9. Recent, Europe (Hennig, 1954). 1037. *Lygistorrhina* sp.; wing, × 7.6. Recent, Australia (Hendel, 1936). 1038. *Diadocidia ferruginea* Meigen; wing, × 9. Recent, Europe (Hennig, 1954). 1039. *Mycetobia pallipes* Meigen; wing, × 6. Recent, Europe (Hennig, 1954). 1040. *Archizelmira kazakhstanica* Rohdendorf; wing, × 2. Upper Jurassic, Southern Kazakhstan (original drawing). 1041. *Megalyceriomima magnipennis* Rohdendorf; general view, × 18. Upper Jurassic, Southern Kazakhstan (original drawing). 1042. *Lycoriomima ventralis* Rohdendorf; wing, × 32. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1043. *Paralycoriomima sororcula* Rohdendorf; wing, × 30.m Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1044. *Lycorioplecia elongata* Rohdendorf; wing, × 25. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946).



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inclined, equal to basal segment of RS; with an anterior branch of RS resembling an irregular crossvein. Wing broad, only twice as long as it is wide. Length of wing 4.5 mm (Fig. 1030). One species. Upper Jurassic of Kazakhstan.

Mesosciophilodes Rohdendorf, 1946. Genotype—*M. angustipennis* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). Crossvein rm inclined, somewhat longer or shorter than the transversely disposed basal segment of RS; with an anterior branch of RS resembling a strong crossvein. Wing narrow, at least two-and-one-half times longer than it is wide. Length of wing 4–4.5 mm (Fig. 1031). Two species. Upper Jurassic of Kazakhstan.

Family SCIARIDAE Billbergh, 1820

[nom. transl. Bigot, 1852 (ex Sciaraedes Billbergh, 1820)]
(Lycoriidae Hendel, 1928)

R shortened, not more than two-thirds of wing length, usually shorter than one-half of wing; RS without anterior branches, with a sharply isolated basal segment resembling a crossvein; usual crossvein rm resembles base of RS; M and Cu always considerably weaker than radial veins (Fig. 1032). Coxae of all legs moderately enlarged. Compound eyes contiguous behind antennae. Paleogene to Recent. About 40 genera in the Recent fauna, of which 10 also known from the Paleogene of Europe (Baltic amber) and the Neogene of Europe.

Family MANOTIDAE Hendel, 1936

Venation much reduced with rudimentary SC free at its end; basal segment of RS transformed into crossvein; RS in form of simple vein terminating on anterior margin. Antennae planted high on parietal region; proboscis short (Fig. 1033). Paleogene to Recent. One genus in the Recent fauna, also known from the Paleogene of Europe (Baltic amber).

Family FUNGIVORIDAE Latreille, 1809

[nom. transl. Hendel, 1928 (ex Fungivorae Latreille, 1809)]

R of varying length; RS has no anterior branches or has a short branch resembling a crossvein; basal segment of RS sharply isolated transversely disposed; veins of M often weak and closely spaced. Coxae much enlarged. Compound eyes dichoptic (Fig. 1034). Paleogene to Recent. Large family with about 1,500 species and more than 60 genera included in the Recent fauna and grouped under two subfamilies: Sciophilinae and Fungivorinae. In Tertiary faunal complexes representatives of 45 genera (more than 170 species) are found, as yet insufficiently studied.

Family CEROPLATIDAE Rondani, 1856

[nom. transl. Hendel, 1928 (ex Ceroplatina Rondani, 1856)]

R shorter or somewhat longer than one-half of length of wing; rm rarely present, normally absent because basal part of M coalesces with RS at midpoint of wing; M and CuA diverge at base. Antennae distinctly flattened, resembling characteristic multisegmented plates, rarely cylindrical (Fig. 1035). Paleogene to Recent. Seventeen genera found in the Recent fauna. Three genera known from the Paleogene of Europe (Baltic amber).

Family MACROCERATIDAE Rondani, 1856

[nom. transl. Malloch, 1917 (ex Macroceratina Rondani, 1856)]

Venation as observed in preceding family; M_4 parallel to CuA at base. Antennae much enlarged, often longer than body, slender (Fig. 1036). Paleogene. One abundant genus in the Recent fauna also known from the Paleogene of Europe (Baltic amber).

326 Family LYGISTORRHINIDAE Hendel, 1936

Venation reduced; RS completely separated from R; SC very short, free; veins of system M mere terminal divisions. Proboscis sharply elongate (Fig. 1037). Paleogene to Recent. Two genera in the Recent tropical fauna and one from the Paleogene of Europe (Baltic amber).

Family DIADOCIDIIDAE Winnertz, 1863

[nom. transl. Hendel, 1928 (ex Diadocidinae Winnertz, 1863)]

SC strong, terminates on C; RS leaves R at an acute angle, without any branches; basal stem of M reduced; rm and base of M_4 present almost at same level (Fig. 1038). Paleogene to Recent. One genus from the Recent fauna, also known from the Paleogene of Europe (Baltic amber).

Family MYCETOBIIDAE Winnertz, 1863

[nom. transl. Hendel, 1928 (ex Mycetobinae Winnertz, 1863)]

Venation similar to that of preceding family; anterior branch of RS long and strong; veins of CuA and A diverge uniformly (Fig. 1039). Paleogene to Recent. One genus from the Recent fauna, also known from the Paleogene of Europe (Baltic amber).

Family ARCHIZELMIRIDAE Rohdendorf, fam. nov.

R long, more than three-fourths of wing; base of RS weak; two anterior branches of RS, one resembling a crossvein and the other terminating on C; M_{1+2} weak; with short rm. Jurassic. One genus.

Archizelmira Rohdendorf, gen. nov. Genotype—*A. kazakhstantica* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). SC slender, terminates on C at level of base of M; radial area narrow. Length of wing 3 mm (Fig. 1040). One species. Upper Jurassic of Kazakhstan.

Family PLECIOMIMIDAE Rohdendorf, 1946

R short, not more than three-fourths of length of wing and usually shorter; base of RS always strong; RS always without branches; no crossveins between M_4 and CuA. Wings broad, usually rounded at apex. Jurassic. Thirteen genera.

Megalycoriomima Rohdendorf, gen. nov. Genotype—*M. magnipennis* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). R long, straight, about three-fourths length of wing; rm indistinct; upper one-third of RS strongly bent backward; M_{1+2} very weak, indistinct. Length of wing 1.6 mm (Fig. 1041). One species. Upper Jurassic of Kazakhstan.

Mycoriomima Rohdendorf, 1946. Genotype—*L. ventralis* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R weakly bent forward at apex, not more than two-thirds length of wing; rm one-half length of basal segment of RS, which gradually bends backward; M and SC weak; CuP prominent. Length of wing 1.75 mm (Fig. 1042). One species. Upper Jurassic of Kazakhstan.

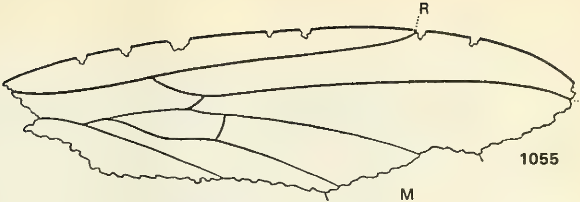
Paralycoriomima Rohdendorf, 1946. Genotype—*P. sorocula* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R almost perfectly straight, almost two-thirds length of wing; rm two-thirds of basal segment of RS, which gradually bends backward; M and SC not particularly weak; CuP well developed. Length of wing 1.75 mm (Fig. 1043). One species. Upper Jurassic of Kazakhstan.

Lycorioplecia Rohdendorf, 1946. Genotype—*L. elongata* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R bent forward at its apex, about two-thirds length of wing; rm located close to fork of RS, which is strongly and uniformly bent back. M and SC not particularly weak; CuP indistinct; with a weak pterostigma. Length of wing 2.5 mm (Fig. 1044). One species. Upper Jurassic of Kazakhstan.

Lycoriomimodes Rohdendorf, 1946. Genotype—*L. deformatus* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R

Figs. 1045–1055. Superfamily Fungivoridea.

1045. *Lycoriomimodes deformatus* Rohdendorf; wing, × 30. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1046. *Lycoriomimella minor* Rohdendorf; wing, × 48. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1047. *Pleciomima secunda* Rohdendorf; wing, × 25. Upper Jurassic, Kazakhstan (Rohdendorf, 1946). 1048. *Pleciomimella karatavica* Rohdendorf, general view, × 14. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1049. *Mimallactoneura vetusta* Rohdendorf; wing, 18. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1050. *Antefungivora prima* Rohdendorf; wing, × 32. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1051. *Antiquamedia tenuipes* Rohdendorf; dorsal view, × 15. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1052. *Archilycoria magna* Rohdendorf; wing, × 15. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1053. *Paritonida brachyptera* Rohdendorf; general view, × 16. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1054. *Tipuloplecia breviventris* Rohdendorf; parts of wings, × 15. A—left wing, B—right wing. Upper Jurassic, Southern Kazakhstan (original drawing). 1055. *Sinemedia angustipennis* Rohdendorf; part of wing, × 24. Upper Jurassic, Southern Kazakhstan (original drawing).



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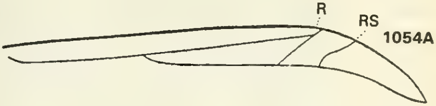

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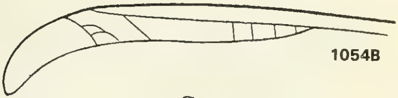

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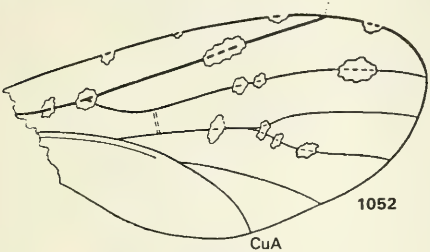

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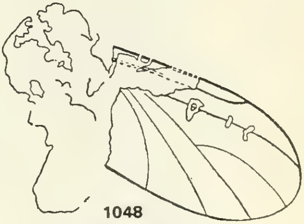

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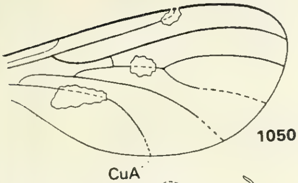

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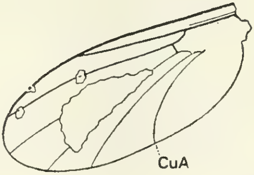

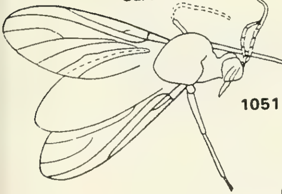

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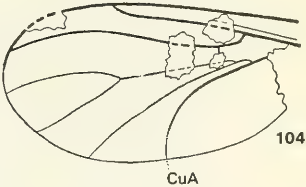

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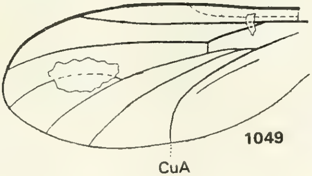

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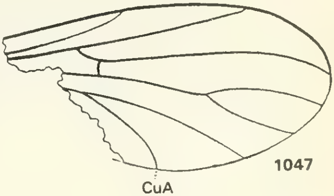


1047

only slightly bent forward in the very end, equals 2/3 of wing, rm only slightly shorter than basal segment of RS, which is strongly bent backward; M and SC not particularly weak; pterostigma absent; CuP indistinct. Length of wing 1.6 mm (Fig. 1045). Two species. Upper Jurassic of Kazakhstan.

Lycoriomimella Rohdendorf, 1946. Genotype—*L. minor* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R irregularly wavy, about two-thirds of length of wing; rm two-thirds length of RS, distal part of latter almost straight; SC strong, bent at end. Length of wing is 1.25 mm (Fig. 1046). One species. Upper Jurassic of Kazakhstan.

Pleciomima Rohdendorf, 1938. Genotype—*P. secunda* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). R almost straight, two-thirds of length of the wing; rm one-half of length of basal segment of RS, which is strongly bent back, particularly the terminal half; M and SC strong. Length of wing 2.25–2.5 mm (Fig. 1047). Two species. Upper Jurassic of Kazakhstan.

Pleciomimella Rohdendorf, 1946. Genotype—*P. karatavica* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R straight almost throughout, scarcely bending at apex; rm only seven-eights of length of basal segment of RS, which is weakly bent at terminal half; SC weak at top; M not particularly slender. Length of wing 2.1 mm (Fig. 1048). One species. Upper Jurassic of Kazakhstan.

Mimallactoneura Rohdendorf, 1946. Genotype—*M. vetusta* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R straight almost throughout; basal segment of RS five times as long as rm; distal segment of RS very slightly bent back; SC very weak, indistinct; M and CuP prominent. Length of wing 3 mm (Fig. 1049). One species. Upper Jurassic of Kazakhstan.

Antefungivora Rohdendorf, 1938. Genotype—*A. prima* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). R straight; rm less than one-sixth of basal segment of RS, its distal segment very strongly bent backward in terminal half; SC weak, short, terminates on C; M_4 long, connected with M_{1+2}. Length of wing 1.5 mm (Fig. 1050). One species. Upper Jurassic of Kazakhstan.

Antiquamedia Rohdendorf, 1938. Genotype—*A. tenuipes* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). R weakly bent forward; rm indistinct, RS gradually bends back at distal half; SC short, bent backward terminates on R; M_4 long, connected with M. Length of wing 2 mm (Fig. 1051). One species. Upper Jurassic of Kazakhstan.

Archilycoria Rohdendorf, 1946. Genotype—*A. magna*Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R straight and long; rm one-third of basal segment of RS; Rs uniformly and gently bent backward; SC ends freely; M_4 in form of long branch of CuA. Length of wing 3.6 mm (Fig. 1052). One species. Upper Jurassic of Kazakhstan.

Paritonida Rohdendorf, 1946. Genotype—*P. brachyptera* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R slightly bent at apex; rm less than one-sixth of basal segment of RS; distal segment of RS uniformly bent backward; SC ends freely; M_4 in the form of a long branch of CuA, separated from M_{1+2}. Length of wing 1.75 mm (Fig. 1053). One species. Upper Jurassic of Kazakhstan.

Family TIPULOPLECIIDAE Rohdendorf, fam. nov.

Legs thin; wings considerably longer than abdomen, broad; few anterior branches of RS present; venation delicate except for the strong C. Jurassic. One genus.

Tipuloplecia Rohdendorf, 1946. Genotype—*T. breviventris* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). R slender, straight; up to six anterior branches of RS, of which many look like crossveins between RS and R, only a few terminate on C; RS strongly bent. Length of wing 3.25 mm (Fig. 1054). One species. Upper Jurassic of Kazakhstan.

Family SINEMEDIIDAE Rohdendorf, fam. nov.

Legs strong, of running type. Wings narrow, not particularly long; anterior branches of RS absent. Venation strong; weak intermedial crossvein present between anterior branches of M. Jurassic. One genus.

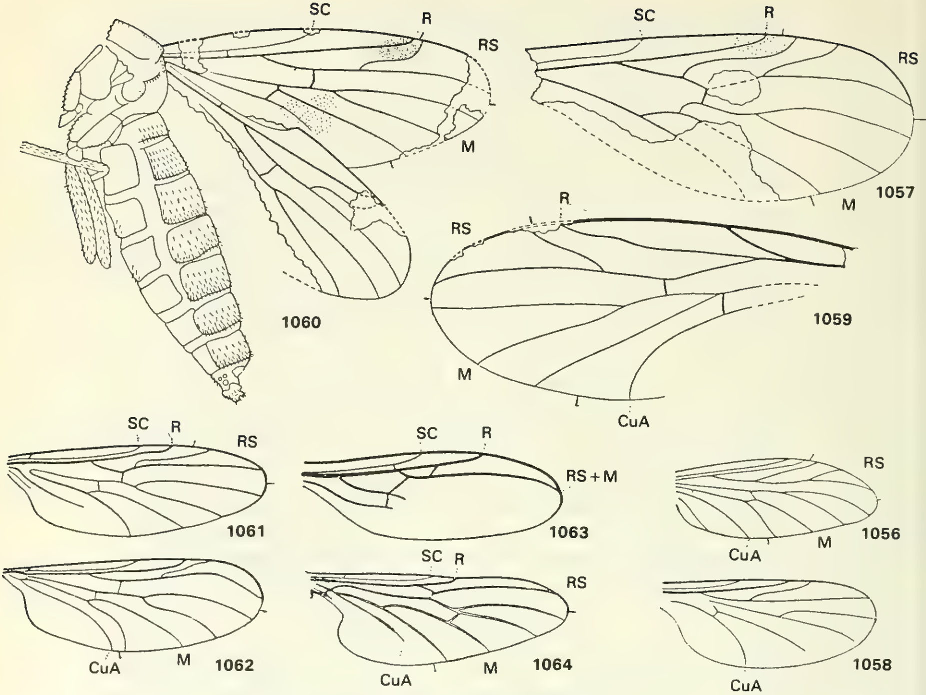
Sinemedia Rohdendorf, gen. nov. Genotype—*S. angustipennis* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). R strong, slightly bent forward; rm slanting, one-third of length of basal segment of RS; distal segment of RS slightly bent back; veins of M not particularly weak. Length of wing 2.25 mm (Fig. 1055). One species. Upper Jurassic of Kazakhstan.

SUPERFAMILY BIBIONIDEA

Costal area without projection; phragma not developed. Legs clinging, rarely of running type. Antennae thin or shortened. Intermedial cell not isolated; RS 329 almost always has anterior branches, if anterior branches of RS not present, then M and CuA considerably weaker and lighter than R, but they are long; SC always long, usually more than one-half of wing length. Wing size usually medium to large, rarely small. Jurassic to Recent, Families: Eopleciidae, Paraxymyiidae, Protopleciidae, Penthetriidae, Hesperinidae, Bibionidae, Axymyiidae; last family not known in fossil form.

Family EOPLECIIDAE Rohdendorf, 1946

Two strong, long branches of RS located on either side of rm; mcu placed between CuA and M_4; A has two branches. Length of wing 3.5 mm (Fig. 1056). Lower Jurassic of Germany. One genus.



Figs. 1056–1064. Superfamily Bibionidea.

1056. *Eoplecia primitiva* Handlirsch; wing, × 12. Lower Jurassic, Germany (Handlirsch, 1939). 1057. *Paraxymyia quadriradialis* Rohdendorf; wing, × 27. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1058. *Protoplecia liasina* Geinitz; wing, × 10. Lower Jurassic, Germany (Handlirsch, 1906). 1059. *Mesopleciella minor* Rohdendorf; wing, × 16. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1060. *Mesoplecia stigma* Rohdendorf; general view, × 9. Upper Jurassic, Southern Kazakhstan (original drawing). 1061. *Penthetria funebris* Melgen; wing, × 3.7. Recent, Europe (Hennig, 1954). 1062. *Hesperinus imbecillus* Loew; wing, × 5.7. Recent, Europe (Hennig, 1954). 1063. *Protobibio jurassicus* Rohdendorf; wing, × 30. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1064. *Bibio mare* Linnaeus; wing, × 32. Recent, Europe (Hennig, 1954).

Family PARAXYMYIIDAE Rohdendorf, 1946

Two strong, long branches of RS located on either side of rm; basal segment of M reduced; SC less than one-half of wing length. Jurassic. One genus.

Paraxymyia Rohdendorf, 1946. Genotype—*P. quadriradialis* Rohdendorf, 1946. Upper Jurassic, Chimkent province (Malm, Karatau). Pterostigma present; SC slender; anterior branch of RS runs parallel to R. Length of wing 2.25 mm (Fig. 1057). One species. Upper Jurassic of Kazakhstan.

Family PROTOPLECIIDAE Rohdendorf, 1946

One branch of RS located distal to rm; mcu resembles a crossvein between CuA and M; SC occupies different positions. Jurassic. Three genera.

130 *Protoplecia* Handlirsch, 1906. Genotype—*P. liasina* Geimitz, 1884; Lower Jurassic, Germany. SC somewhat shorter than one-half of wing; bifurcation of M_{1+2} more distal than level where RS branches. Length of wing 3.5 mm (Fig. 1058). One species. Lower Jurassic of Germany.

*Mesopleciella*Rohdendorf, 1946. Genotype—*M. minor* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). SC appreciably shorter than one-half of wing; bifurcations of M_{1+2} slightly more proximal than level of forking of RS; mcu connects CuA and common stem of M. Length of wing 3.75 mm (Fig. 1059). One species. Upper Jurassic of Kazakhstan.

Mesoplecia Rohdendorf, 1938. Genotype—*M. jarassicua* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). SC about one-half of length of wing; bifurcations of M_{1+2} located markedly proximal to bifurcations of RS; mcu connects CuA and M_4; wings large. Length of wings 7–8.2 mm (Fig. 1060). Two species. Upper Jurassic of Kazakhstan.

Family PENTHETRIIDAE Rohdendorf, 1946

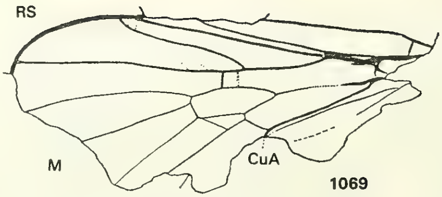
RS with one branch. Wings of medium or large size; veins of all systems of roughly same thickness; SC always long; mcu slanting, resembles basal segment of M_4 and actual base of M_4 resembles a crossvein. Legs without spines. Antennae short, less than length of thorax (Fig. 1061). Paleogene to Recent. Two genera in the Recent fauna, also found in the Paleogene of Europe (Baltic amber).

Family HESPERINIDAE Hendel, 1928

RS with one branch; veins nearly of same thickness; SC very long, more than one-half of wing; basal segment of M_4 resembles a crossvein. Antennae slender and as long as thorax. Legs slender. Length of wing 5–7 mm (Fig. 1062). Neogene to Recent. One genus in Recent fauna and one from the Neogene of America.

Family PROTOBIBIONIDAE Rohdendorf, 1946

RS with one branch resembling a crossvein; venation strongly costalized with strong radial veins and weak, indistinct M and CuA. Wings very small. Length of wing 1.5 mm. Jurassic. One genus.



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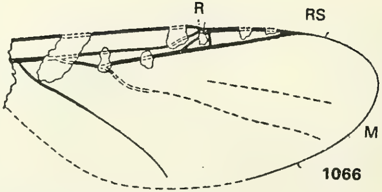

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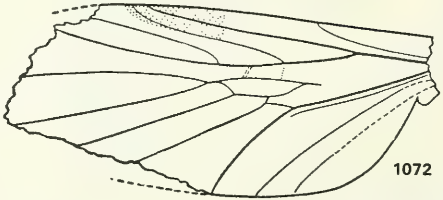

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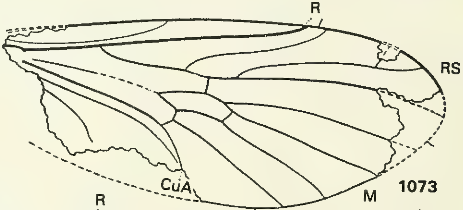

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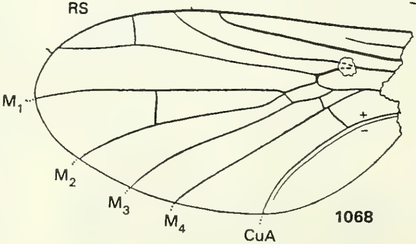

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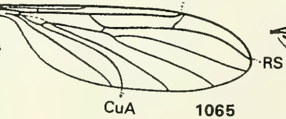

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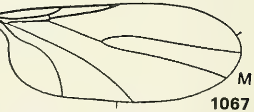

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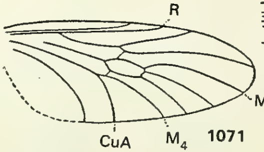

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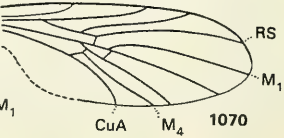

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Protobibio Rohdendorf, 1946. Genotype—*P. jurassicus* Rohdendorf, 1946; Upper Jurassic, Chimkent province (Malm, Karatau). SC shorter than one-half of wing; rm long and slanting; wing narrow (Fig. 1063). One species. Upper Jurassic of Kazakhstan.

Family BIBIONIDAE Newman, 1834

[nom. transl. Kirby, 1837 (ex Bibionides Newman, 1834)]

RS simple, without branches. Venation strongly costalized; radial veins, base of M and rm strong and dark and differ sharply from pale posterior veins M and CuA; rm looks like basal segment of RS, sometimes it is absent because of strong fusion of M with RS; M_4 sharply isolated from M_{1+2}, forms a branch of CuA, its free base resembles a crossvein strongly displaced distally (Fig. 1064). Paleogene to Recent. Three genera in the Recent fauna, of which two genera also known in Tertiary faunal complexes.

SUPERFAMILY BOLITOPHILIDEA

Costal area without projection; phragma absent and in its place base of wing has highly thickened basal part of CuA. Wings reduced. Antennae slender and long. Intermedial cell not isolated; M with three branches. Paleogene to Recent. Families: Bolitophilidae and Arachnocampidae; latter known only in Recent fauna.

Family BOLITHOPHILIDAE Winnertz, 1863

[nom. transl. Malloch, 1917 (ex Bolithophilinae Winnertz, 1863)]

RS with anterior branch; mcu located proximal to branching of RS; basal stem of M reduced; SC a little shorter than one-half of length of wing (Fig. 1065). Paleogene. One genus from the Paleogene of Europe (Baltic amber).

SUPERFAMILY SCATOPSIDEA

Costal area broad, with reduced SC, free at end; phragma may or may not be present. Body short and strong. Legs short and of clinging type. Antennae slender, often short. Intermedial cell not isolated. M with three branches.

331 Figs. 1065–1073. Superfamilies Bolitophilidea, Scatopsidea, Rhyphidea.

1065. *Boiitophila hybrida* Meigen; wing, × 6.4. Recent, Europe (Hennig, 1954). 1066. *Protoscatopse jurassica* Rohdendorf; wing, × 28. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1946). 1067. *Scatopse fuscipes* Meigen; wing, × 9. Recent, Europe (Hennig, 1954). 1068. *Oligophryne fungivoroides* Rohdendorf; wing, × 26. Upper Triassic, Central Asia (original drawing). 1069. *Protolbiogaster rhaetica* Rohdendorf; wing, × 13. Upper Triassic, Central Asia (original drawing). 1070. *Mesorrhyphoides anomalis* Handlirsch; wing, × 13. Lower Jurassic, Germany (Hennig, 1954). 1071. *Mesoryphus nanus* Handlirsch; wing, × 10. Lower Jurassic, Germany (Hennig, 1954). 1072. *Archirhyphus asiaticus* Rohdendorf, wing, × 20. Upper Jurassic, Southern Kazakhstan (original drawing). 1073. *Protorhyphus turanicus* Rohdendorf; wing, × 22. Upper Triassic, Central Asia (original drawing).

Jurassic to Recent. Families: Protoscatopsidae, Scatopsidae, Canthyloscelididae, Synneuridae; last two known only in Recent fauna.

Family PROTOSCATOPSIDAE Rohdendorf, 1946

Antennae short, slightly longer than head; venation sharply costalized; much of
331 wing surface devoid of veins; SC absent; RS has two short anterior branches terminating on C just behind end of SC; all radial veins short and close. Jurassic. One genus.

Protoscatopse Rohdendorf, 1946. Genotype—*P. jurassica* Rohdendorf, 1936; Upper Jurassic, Chimkent province (Malm, Karatau). M_{1+2} considerably more slender than RS, difficult to distinguish; CuA almost straight, strong at base, gradually tapering toward end. Length of wing 2 mm (Fig. 1066). One species. Upper Jurassic of Kazakhstan.

Family SCATOPSIDAE Newman, 1834

[nom. transl. Williston, 1917 (ex Scatopsites Newman, 1834)]

Antennae shorter than head. Venation sharply costalized; SC in form of a small rudiment; RS without anterior branches. Size of body varies from 1 to 4 mm (Fig. 1067). Paleogene to Recent. 10 genera in the Recent fauna, of which one also known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY RHYPHIDEA

Costal area broad; phragma usually well-developed. Size small or medium. Legs of running type or slender. Antennae long and slender. Intermedial cell sharply isolated; M always has four branches. Mesozoic to Recent. Families: Oligophryneidae, Protolbiogastridae, Olbiogastridae, Rhyphidae, Protorhyphidae, Cramptonomyiidae; last one occurs only in the Recent fauna.

332 Family OLIGOPHRYNEIDAE Rohdendorf, fam. nov.

RS has two anterior branches: a long proximal one and a very short distal one, which resemble crossveins; SC short, three additional crossveins; intermedial cell very small. Triassic. One genus.

Oligophryne Rohdendorf, gen. nov. Genotype—*O. fungivoroides* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Sogyuty). SC free at apex; R strong. Length of wing 2 mm (Fig. 1068). One species. Upper Triassic of Issyk-Kul province.

Family PROTOLBIOGASTRIDAE Rohdendorf, fam. nov.

One long bent anterior branch of RS terminates on C; costal area broad and convex; phragma strong and complex; basal stem of M much weakened; with additional crossveins between RS and M and between M_3 and M_4; SC long, extending to level of apex of intermedial cell. Triassic. One genus.

Protolbiogaster Rohdendorf, gen. nov. Genotype—*P. rhaetica* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Sogyuty). More distal anterior branches of RS present with traces of other branches; veins of system M evidently weaker than R and CuA. Length of wing 4.7 mm (Fig. 1069). One species. Upper Triassic of Issyk-Kul province.

Family OLBIOGASTRIDAE Hennig, 1948

RS has one branch terminating on C or R; SC short, reaching up to level of first bifurcation of M; basal stem of M not weakened; additional crossveins absent (Fig. 1070). Jurassic to Recent. Two genera in Recent fauna and two genera from the Jurassic of Western Europe.

Family RHYPHIDAE Newman, 1834

[nom. transl. Macquart, 1838 (ex Rhyphites Newman, 1834)]
(Phryneidae Hendel, 1928)

One branch of RS terminates on C; SC long, with its apex extending up to level of rm; basal stem strong (Fig. 1071). Jurassic to Recent. Two genera.

Family PROTORHYPHIDAE Handlirsch, 1906

Two branches of RS, arise on either side of rm and terminate on C; SC short, barely extending to level of basal end of intermedial cell; basal stem of M often weakened. Triassic to Jurassic. Two genera.

Archirhyphus Handlirsch, 1939. Genotype—*A. geinitzi* Handlirsch, 1939; Lower Jurassic, Germany. M_1 and M_2 with a common stalk emerging from cell. Length of wing 3 mm (Fig. 1072). Two species. Lower Jurassic of Germany and Jurassic of Kazakhstan.

Protorhyphus Handlirsch, 1906. Genotype—*Phryganidium simplex* Geinitz, 1887; Lower Jurassic, Germany. M_1 and M_2 leave intermedial cell independently, not forming a common stalk. Length of wing 2.5–3 mm (Fig. 1073). Two species. Upper Triassic, Issyk-Kul province and Lower Jurassic of Germany.

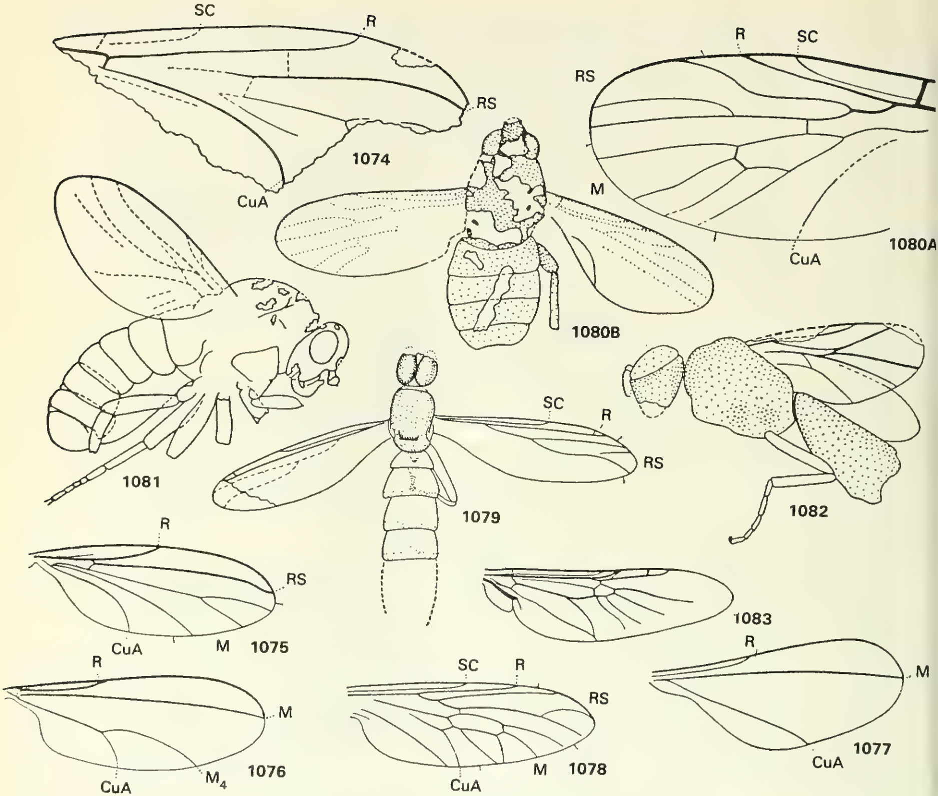
SUPERFAMILY PHRAGMOLIGONEURIDEA

Costal area without projection; phragma prominent; intermedial cell not isolated; M consists of three branches. Triassic. Family: Phragmoligoneuridae.

Family PHRAGMOLIGONEURIDAE Rohdendorf, fam. nov.

Basal segments of RS and M reduced; RS with one anterior branch resembling a crossvein. Triassic. One genus.

Phragmoligoneura Rohdendorf, gen. nov. Genotype—*P. incerta* Rohdendorf, sp. nov.; Upper Triassic, Issyk-Kul province (Rhaetian, Sogyuty).



333 Figs. 1074–1083. Superfamilies Phragmoligoneuridea, Cecidomyiidea, Stratiomyiidea.

1074. *Phragmoligoneura incerta* Rohdendorf; wing, × 22. Upper Triassic, Central Asia (original drawing). 1075. *Catocha* sp.; wing, × 10. Recent, North America (Hennig, 1954). 1076. *Asphondylia sarothamni* Loew; wing, × 15. Recent, Europe (Hennig, 1954). 1077. *Miastor hastatus* Kieffer; wing, × 14. Recent, Europe (Hennig, 1954). 1078. *Protobrachyceron liasinum* Handlirsch; wing, × 9.5. Lower Jurassic, Germany (Hennig, 1954). 1079. *Archisargus pulcher* Rohdendorf; dorsal view, × 2.3. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1080. *Palaeostratiomyia* pygmaea Rohdendorf; A—wing, × 24. B—dorsal view, × 11. Upper Jurassic, Southern Kazakhstan (Rohdendorf; 1938). 1081. *Eomyia veterrima* Rohdendorf; lateral view, × 27. Upper Jurassic, Southern Kazakhstan (original drawing). 1082. *Protocyrtus jurapsicus* Rohdendorf; lateral view, × 7.5. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1083. *Hermione locuples* Loew; × 6.5. Recent, Europe (Hennig, 1954).

SC weak, terminates on C. M_{1+2} not far from rm. Length of wing 2.4 mm (Fig. 1074). One species. Upper Triassic of Issyk-Kul province.

SUPERFAMILY CECIDOMYIIDEA
(Itonidoidea)

Size small. Legs slender, not of running type. Phragma not developed. Antennae very slender, often with well demarcated segments or peculiar outgrowths. Venation usually sharply reduced. Wings weak and without trace of costalization. Paleogene to Recent. Families: Lestremiidae, Cecidomyiidae, Heteropezidae.

Family LESTREMIIDAE Rondani, 1841
[nom. transl. Rohdendorf, hic. (ex Lestriminae Rondani, 1841)]

M_{1+2} always developed, usually in the form of a fork; A visible. First segment of tarsus always longer than second. Ocelli present (Fig. 1075). Paleogene to 333 Recent. About 15 genera known in the Recent fauna, of which one also known from the Paleogene of Europe (Baltic amber).

Family CECIDOMYIIDAE Newman, 1834
[nom. transl. Macquart, 1938 (ex Cecidomiites Newman, 1834)]
(Itonididae Grunberg, 1910)

M_{1+2} absent or present as a simple vein; SC rudimentary or absent on wing surface. First segment of tarsus rarely present (Fig. 1076). Paleogene to Recent. Large family: over 3,000 species, and more than 100 genera in the Recent fauna; eleven genera from the Paleogene of Europe (Baltic amber).

Family HETEROPEZIDAE Kertesz, 1902
[nom. transl. Hendel, 1928 (ex Heteropezinae Kertesz, 1902)]

Ocelli absent. First segment of tarsus longer than second or tarsi two to four 334 segmented. M absent or resembles a simple fold (Fig. 1077). Paleogene to Recent. About 10 genera in the Recent fauna, of which three, *Miastor* Meinert, *Heteropeza* Winnertz and *Frirenia* Kieffer, also known from the Paleogene of Europe (Baltic amber).

Infraorder Asilomorpha

Always at least one long branch of RS terminates on C, arising proximal to rm. Apical division of wing prominent. Antennae almost always with a complex upper division, termed "third" segment. Jurassic to Recent. Superfamilies: Stratiomyiidea, Tabanidea, Asilidea, Bombilidea, Empididea.

SUPERFAMILY STRATIOMYIIDEA

Propleurae fused with prosternite, encircling socket of anterior coxae in front.

C does not extend around entire margin of wing; intermedial cell as usual shortened. Empodium broad, resembles pulvilli. Jurassic to Recent. Families: Protobrachyceridae, Archisargidae, Palaeostratiomyiidae, Eomyiidae, Protocyrtidae, Stratiiomyiidae, Xylophagidae, Rachiceridae, Acroceridae, Solvidae, Chiromyzidae; last two known only in the Recent fauna.

Family PROTOBRACHYCERIDAE Rohdendorf, fam. nov.

Venation not costalized; all veins strong; M_4 and M_3 leave intermedial cell, terminate on margin of wing, converging noticeably; intermedial cell elongated. Length of wing 4.5 mm (Fig. 1078). Jurassic. One genus from the Lower Jurassic of Germany. Family immediate ancestor of the Recent Solvidae.

Family ARCHISARGIDAE Rohdendorf, fam. nov.

Wing long, narrow, converges toward base; SC and R stronger than other veins; R has a short branch at end; RS which is weak and hard to distinguish has three branches. Body elongate. Size large. Jurassic. One genus.

Archisargus Rohdendorf, 1938. Genotype—*A. pulcher* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). SC extends more than one-half of wing; R almost perfectly straight. Head as broad as thorax; eyes very large. Thorax longitudinal, with blunt angular scutellum. Abdominal segments with dark markings. Legs slender. Length of body about 20 mm and of wing, 16 mm (Fig. 1079). One species. Upper Jurassic of Kazakhstan.

Family PALAEOSTRATIOMYIIDAE Rohdendorf, 1951

Wing blunt, broad and somewhat narrow at base; all veins of roughly equal thickness; only SC and, to some extent, M weaker than others; all branches of M emerge from intermedial cell. Body short. Abdomen blunt and egg-shaped. Size small. Jurassic. One genus.

Palaeostratiomyia Rohdendorf, 1938. Genotype—*P. pygmaea* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). SC shorter than one-half length of wing; R slightly bent forward; proximal branch of RS sharply bent, its distal branch almost straight and parallel to basal stem of RS; rm at level of end of SC. Head slightly narrower than thorax; eyes of medium size. Legs strong. Abdomen consists of four distinct segments and lighter than thorax. Length of body 2.75 and of wing 2.5 mm (Fig. 1080 A, B). One species. Upper Jurassic of Kazakhstan.

Family EOMYIIDAE Rohdendorf, fam. nov.

Wing short, slightly pointed at end; venation delicate and hard to distinguish; only C clearly visible along anterior margin. Body with a convex back and a small head with short antennae and small compound eyes. Abdomen seven-segmented. Legs strong and of clinging type. Size small. Jurassic. One genus.

Eomyia Rohdendorf, gen. nov. Genotype—*E. veterrima* Rohdendorf, sp. nov.; Upper Jurassic, Chimkent province (Malm, Karatau). Cheeks slightly narrower than length of eyes. Antennae have a rounded third segment and terminal arista. Apex of abdomen rounded. Length of body 2.25 mm and of wing, 1.5 mm (Fig. 1081). One species. Upper Jurassic of Kazakhstan.

Family PROTOCYRTIDAE Rohdendorf, 1958

Body and wings short. Venation strong and prominent; R straight. RS without branches and curved; M two-branched. Head large. Thorax convex. Abdomen short. Legs strong, of clinging type. Size small. Jurassic. One genus.

Protocyrtus Rohdendorf, 1938. Genotype—*P. jurassicus* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Crossvein inclined. Cheek very broad and swollen posteriorly. Segments of abdomen indistinct. Length of body 5 mm and of wing, 3.5 mm (Fig. 1082). One species. Upper Jurassic of Kazakhstan.

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Family STRATIOMYIIDAE Newman, 1834

[nom. transl. Rohdendorf, hic (ex Stratiomites Newman, 1834)]

C does not approach anal margin; venation always costalized; anterior veins stronger than posterior ones and shifted toward anterior margin; intermedial cell short. Body flat. Head large; proboscis short. Medium or large sized, rarely small (Fig. 1083). Paleogene to Recent. Richly represented in the Recent fauna with over 1,600 species; six genera discovered in Tertiary faunal complexes.

Family XYLOPHAGIDAE Fallen, 1810

[nom. transl. Stephens, 1829 (ex Xylophagei Fallen, 1810)]
(Erinnidae Kertesz, 1908)

C does not approach anal margin; venation not costalized, not shifted toward anterior margin; intermedial cell large; M_4 branches from mcu, terminates on margin of wing. Anterior tibia with terminal spur. Body elongate. Medium to large sized (Fig. 1084). Paleogene to Recent. One genus of the Recent fauna also known from the Paleogene of Europe (Baltic amber).

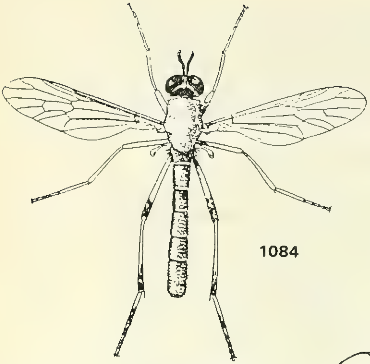
Family RACHICERIDAE Handlirsch, 1907

C does not approach anal margin; venation not costalized; intermedial cell large; M_4 branches from mcu terminates on M_3. Anterior tibiae without spurs. Antennae 20 to 36 segmented (Fig. 1085). Paleogene to Recent. One genus of the Recent fauna known from the Paleogene of Europe (Baltic amber).

Family ACROCERIDAE Leach, 1815

[nom. transl. Leach, 1819 (ex Acrocerides Leach, 1815)]
(Cyrtidae Hendel, 1928)

C extends completely around wing or terminates at wing apex; venation variable,



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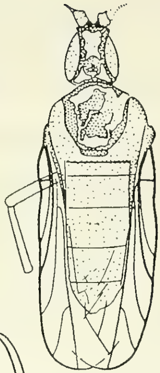

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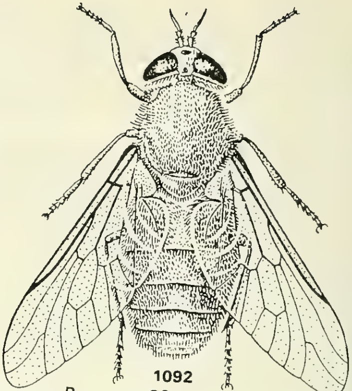

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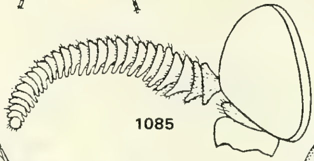

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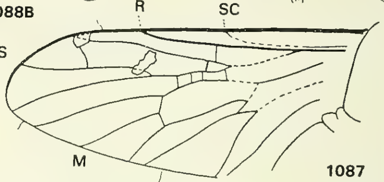

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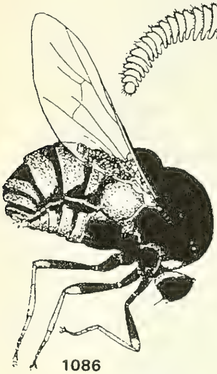

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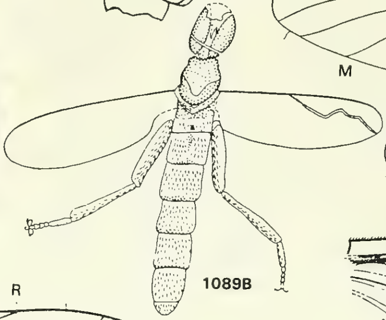

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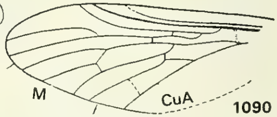

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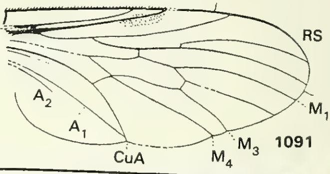

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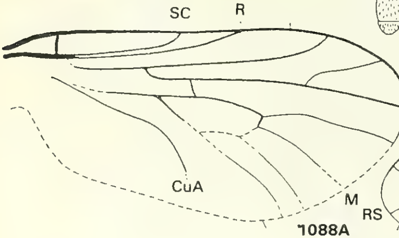

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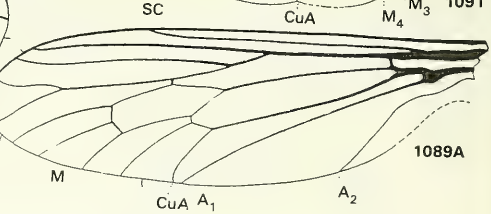

1089A

costalized or uniformly distributed on wing surface. Head very small. Abdomen greatly enlarged. Antennae greatly shortened, three-segmented. Thoracic scales very large (Fig. 1086). Paleogene to Recent. Few genera in Recent fauna, of which one is also known from the Paleogene of America.

SUPERFAMILY TABANIDEA

Propleurites separate from prosternite, do not encircle anterior coxal socket. Venation complete, not costalized; C almost always runs right around wing margin; intermedial cell large. Empodium resembles pulvilli and is broad. Jurassic to Recent. Families: Eostratiomyiidae, Rhagionempididae, Rhagionidae, Coenomyiidae, Tabanidae, Nemestrinidae, Acanthomeridae; last one represented only in the Recent fauna.

Family EOSTRATIOMYIIDAE Rohdendorf, 1951

SC shorter than one-half of wing length, and weak; crossveins present between R, RS_{1+2} and RS_{3+4}; a few rm crossveins. Wing with straight anterior margin and sharply demarcated apex; M_4 branches off mcu; bifurcation of RS_{3+4} long and narrow. Size large. Jurassic. One genus.

Eostratiomyia Rohdendorf, 1951. Genotype—*E. avia* Rohdendorf, 1951; Upper Jurassic, Chimkent province (Malm, Karatau). Four rm crossveins; crossveins between R and RS_{1+2} and between RS_{1+2} and RS_{3+4} located at level between crossveins rm_1 and rm_2, immediately distal to termination of SC; fork of RS_{3+4} widens sharply at its apex; all cells of M open, as also those of C. Length of wing 7 mm and of body, about 10 mm (Fig. 1087). One species. Upper Jurassic of Kazakhstan.

Family RHAGIONEMPIDIDAE Rohdendorf, fam. nov.

SC strong, shorter than one-half of wing length; additional crossveins absent; anterior margin of wing convex, apex not very distinct; M_4 branches from cell; fork of R_{3+4} short and broad. Head long, with a broad forehead and short

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335 Figs. 1084–1092. Infraorder Asilsomorpha.

1084. *Erinna atra* Fabricius; dorsal view, × 4.2. Recent, Europe (Verrall, 1909). 1085. *Rachicerus* sp.; head in profile, × 18. Recent. North America (Curran, 1934). 1086. *Acrocera snaguinea* Meigen; lateral view, × 6. Recent Europe (Sack, 1936). 1087. *Eostratiomyia avia* Rohdendorf; wing, × 7.6. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1951). 1088. *Rhagionempis tabanicornis* Rohdendorf; A—wing, × 15. B—ventral view, × 14. Upper Jurassic, Kazakhstan (Rohdendorf, 1938). 1089. *Archirhagio obscurus* Rohdendorf; A—wing, × 4.B—ventral view, × 2.4. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1090. *Protorhagio capitatus* Rohdendorf; wing, × 9.3. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1091. *Rhagiophryne bianalis* Rohdendorf; wing, × 12. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1951). 1092. *Silvius vituli* Fabricius; dorsal view, × 5. Recent, Europe (Olsufev, 1937).

antennae; antennae have a broad third segment and apical arista. Size small. Jurassic. One genus.

Rhagionempis Rohdendorf, 1938. Genotype—*R. tabanicornis* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Apex of SC reaches level of rm. All cells of M open. Length of wing 3.5 mm and of body, 3.75 mm (Fig. 1088A, B). One species. Upper Jurassic of Kazakhstan.

Family RHAGIONIDAE Latreille, 1802

[nom. transl. Bezzi, 1913 (ex Rhagionides Latreille, 1802)]

SC strong, always shorter than one-half of wing; apex of wing indistinctly delimited; fork of R_{3+4} long and uniform. Third segment of antennae swollen, short, not annulated. Head short. In males forehead always narrow. Medium or rarely small sized. Jurassic to Recent. Three Jurassic genera, and about 12 genera in the Recent fauna, of which five also known from the Paleogene of Europe (Baltic amber).

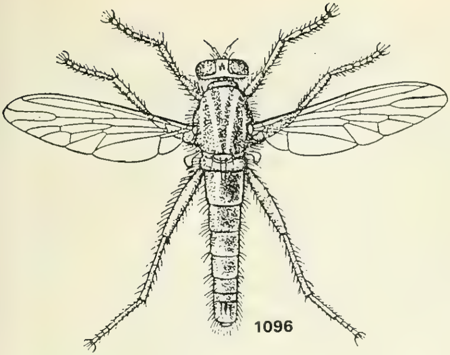
Archirhagio Rohdendorf, 1938. Genotype—*A. obscurus* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Wing narrow, long, without halteres; fork of R_{3+4} relatively short and wide; basal divisions of R, M and CuA long; bifurcation of M distal to midpoint of wing. Length of body 21.5 mm and of wing, 13 mm (Fig. 1089A). One species. Upper Jurassic of Kazakhstan.

Protorhagio Rohdendorf, 1938. Genotype—*P. capitatus* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Wing broad; basal divisions of R, RS and M short; M placed at basal half of wing; R and R_1 bent, parallel and very close together. rm proximal to apex of SC; A_1 and CuA not connected. Length of wing 5 mm (Fig. 1090). One species. Upper Jurassic of Kazakhstan.

Rhagiophryne Rohdendorf, 1951. Genotype—*R. bianalis* Rohdendorf, 1951; Upper Jurassic, Chimkent province (Malm, Karatau). Wing broad; basal divisions of R, RS and M short; bifurcation of M located at basal half of wing; R_1 and R gradually diverge, so that their apices are far apart; rm somewhat distal to end of SC; A_1 and CuA connected in front of margin of wing. Length of wing 4.5 mm (Fig. 1091). One species. Upper Jurassic of Kazakhstan.

Figs. 1093–1101. Infraorder Asilomorpha.

1093. *Nemestrinus fasciatus* (Olivier); dorsal view, × 2.7. Recent, Europe (Sack, 1933). 1094. *Protomphrale martynovi* Rohdendorf; lateral view, × 15. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1095. *Thereva nobilitata* Fabricius; dorsal view, × 5. Recent, Europe (Verrall, 1909). 1096. *Philonicus albiceps* Meigen; dorsal view, × 3. Recent, Europe (Verrall, 1909). 1097. *Brachystoma* sp.; wing, × 5.5. Recent, North America (Curran, 1934). 1098. *Empis* sp.; wing, × 3. Recent. Europe. 1099. *Tachypeza* sp.; wing, × 14. Recent, Europe (Curran, 1934). 1100. *Hilarimorpha* sp.; wing, × 7. Recent, Europe (Curran, 1934). 1101. *Dolichopus popularis* Wiedemann; dorsal view, × 8. Recent, Europe (Hendel, 1936).



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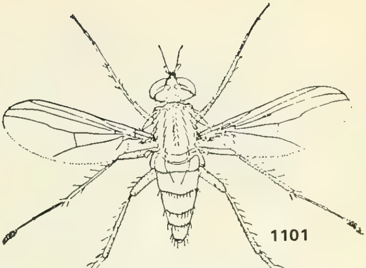

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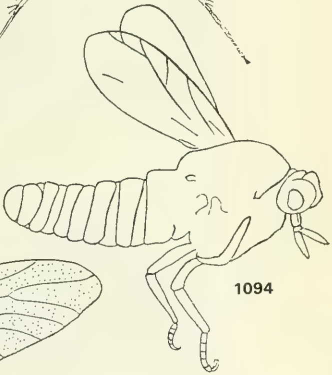

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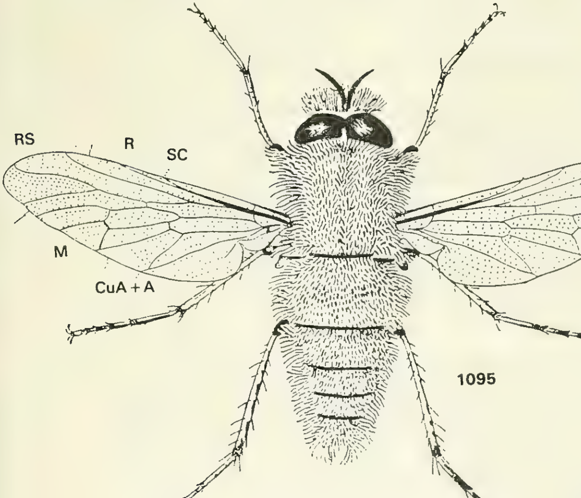

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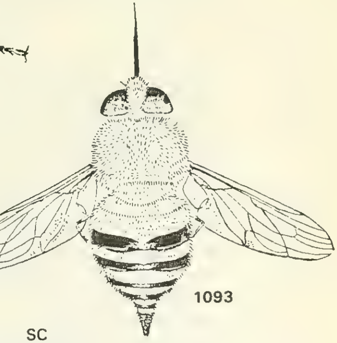

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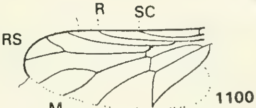

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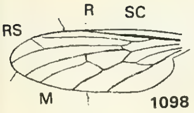

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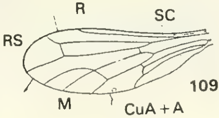

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Family COENOMYIIDAE Westwood, 1840

Fork of R_{3+4} diverges markedly and covers apex of wing. Middle tarsus with a spur. Thoracic scales small. All cells of M visible. Antennae with fine, multiannulated third segments. Size large. Paleogene to Recent. Several genera found in the Recent fauna, of which one also occurs in the Paleogene of Europe (Baltic amber).

Family TABANIDAE Leach, 1819. Horse-flies

Fork of R_{3+4} rather short, sharply divergent, encloses apex of wing. Head short, with piercing proboscis in females; antennae with broad third segment provided with an outgrowth. Thoracic scales well developed. Size large, rarely medium (Fig. 1092). Paleogene to Recent. Most genera from the Recent fauna, of which three also known from the Paleogene of Europe (Baltic amber) and the Neogene of Western Europe.

Family NEMESTRINIDAE Macquart, 1834

Fork of R_{3+4} very narrow, with parallel branches running toward anterior margin, both anterior branches of M also do so; with a special 'diagonal vein' consists of segments of RS and M; only CuA and "diagonal vein" run toward anal margin of wing and sometimes 'diagonal vein' does not extend to wing margin. Size large (Fig. 1093). Jurassic to Recent. More than 200 Recent species from 15 genera known, of which three genera represented by a few species occur in the Paleogene of Europe and the Neogene of North America; one genus described from the Upper Jurassic of Germany.

SUPERFAMILY ASILIDEA

Propleurae usually fused with prosternum. Empodium slender, setiferous. Venation complete, not reduced; intermedial cell large. Jurassic to Recent. Families: Protomphralidae, Therevidae, Mydaidae, Asilidae, Omphralidae, Apioceridae; last two found only in the Recent fauna.

Family PROTOMPHRALIDAE Rohdendorf, 1938

Veins of RS shifted toward middle of wing, with four branches running toward anterior margin. Antennae three-segment, last segment large, without arista. M and Cu weaker than anterior veins. Jurassic. One genus.

Protomphrale Rohdendorf, 1938. Genotype—*P. martynovi* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Abdomen seven-segmented, tapers at end. Wing narrow with a convex anterior margin. Legs of clinging type (Fig. 1094). One genus. Upper Jurassic of Kazakhstan.

Family THEREVIDAE Newman, 1834

[nom. transl. Westwood, 1840 (ex Therevites Newman, 1834)]

Veins distributed uniformly over wing surface, not displaced; M with four branches running toward anal margin. Parietal region convex; head with a short proboscis; antennae with terminal arista. Body without bristles, but sometimes with fine hair. Legs slender, of running type. Size medium (Fig. 1095). Paleogene to Recent. About 25 genera in the Recent fauna, of which one also known from the Paleogene (Baltic amber) and Neogene of Europe.

Family MYDAIDAE Latreille, 1806

[nom. transl. Coquillet, 1901 (ex Mydasii Latreille, 1806)]

Usually one, rarely two veins run into anal margin of wing; all branches of radial system and almost all of M bent forward and extend to anterior margin. 339 Antennae long, swollen at tip; head large, broader than thorax. Body without setae. Legs of clinging type. Size large (15–50 mm). About 250 species from 30 genera in the Recent fauna and the Miocene of North America which have not been studied so far.

Family ASILIDAE Latreille, 1802

[nom. transl. Leach, 1819 (ex Asilici Latreille, 1802)]

Veins uniformly disposed over the wing, not displaced; rarely, ends of M weakened. Parietal region concave, lies below projecting borders of eyes. Body always with numerous setae. Legs strong, with large clinging claws. Antennae with terminal arista. Medium or large sized (Fig. 1096). Paleogene to Recent. More than 4,500 species under numerous genera in the Recent fauna; fifteen genera from the Paleogene of Europe (Baltic amber) and the Neogene of Europe and North America.

SUPERFAMILY BOMBYLIIDEA

Propleurae reduced, not fused with sternum. Empodium in form of slender seta. Venation often reduced; M has only three or even two veins; intermedial cell large but sometimes absent because of reduction of branches of M. Legs weak and slender. Paleogene to Recent. Family: Bombyliidae.

Family BOMBYLIIDAE Latreille, 1802

[nom. transl. van der Wulp, 1877 (ex Bombylarii Latreille, 1802)]

Antennae with elongate or thickened third segment provided with terminal arista or tuft of setae. Wings have well-developed base and almost always a phragma. Often there is an elongated proboscis. Head globular, almost always swollen posteriorly; eyes often notched at back and with dividing line. Paleogene to Recent. More than 3,000 species, under numerous and varied genera, found in the Recent fauna; in Tertiary fauna a few species belonging to five genera which have been studied very little.

SUPERFAMILY EMPIDIDEA

Propleurae fused with sternum, rarely reduced. Empodium setiform. Posterior branch of RS simple or has a very short bifurcation; cubital cell usually short, rarely long; M has two or three branches; intermedial cell large, rarely absent. Paleogene to Recent. Families: Empididae, Hilarimorphidae, Dolichopodidae.

Family EMPIDIDAE Latreille, 1804

[nom. transl. Leach, 1819 (ex Empides Latreille, 1804)]

Proboscis often elongate. Cubital cell short, rarely elongate, M sometimes has three branches, in which case cubital cell shorter than posterior basal. Thorax often inflated on dorsal side (Figs. 1097–1099). Paleogene to Recent. More than 3,000 species belonging to numerous genera in the Recent fauna, of which about 20 representatives also found in Tertiary fauna, mainly in the Paleogene of Europe (Baltic amber).

Family HILARIMORPHIDAE Hendel, 1936

Propleurae reduced. No intermedial cell; cubital cell long, reaching margin of wing (Fig. 1100). Paleogene to Recent. A few species of genus *Hilarimorpha* Krober from the Recent fauna. One genus found in the Paleogene of Europe (Baltic amber).

Family DOLICHOPODIDAE Latreille, 1809

[nom. transl. Geistacker, 1863 (ex Dolichopodes Latreille, 1809)]

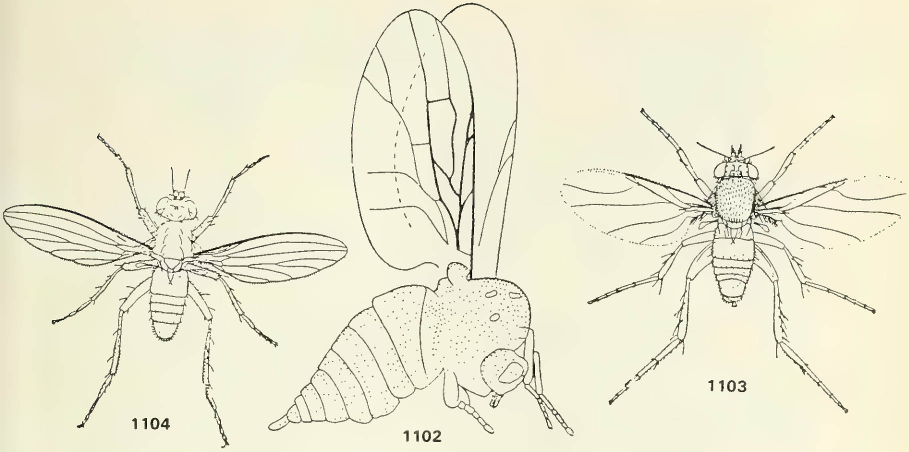
Propleurae reduced. Intermedial cell large, fused with basal cell; cubital cell very short, almost absent; always there are two or three branches of RS, and usually two of M. Thorax very large, inflated; legs of running type. Color usually metallic green. Body with strong setae (Fig. 1101). Paleogene to Recent. More than 3,600 species of numerous genera found in the Recent fauna. About 20 genera known from the Paleogene of Europe (Baltic amber).

Infraorder Phoromorpha

Venation always sharply costalized; all veins of RS extend toward anterior margin. Antennae three-segmented, located close to oral margin; frons always broad, uniformly sclerotized, with strong setae. Jurassic to Recent. Superfamily: Phoridea.

SUPERFAMILY PHORIDEA

Venation sharply costalized, displaced to anterior margin; cubital cell absent;



340 Figs. 1102–1104. Infraorders Phoromorpha, Musidoromorpha.

1102. *Palaeophora ancestris* Rohdendorf; lateral view, × 25. Upper Jurassic, Southern Kazakhstan (Rohdendorf, 1938). 1103. *Chaetoneurophora caliginosa* Meigen; dorsal view, × 14. Recent, Europe (Verrall), 1909. 1104. *Musidora lutea* Panzer; dorsal view, × 7.5. Recent, Europe (Verrall, 1909).

anterior veins of R and RS much thicker than others. Paleogene to Recent. Families: Phoridae, Aenigmatiidae, Thaumatoxeniidae; last two not known in fossil form.

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Family PHORIDAE Newman, 1834

[nom. transl. Haliday, 1851 (ex Phorites Newman, 1834)]

Intermedial cell and bifurcation on M absent; crossvein rm indistinct, being much shortened and displaced toward base of wing. Thorax does not overhang head; legs strong (Fig. 1103). Paleogene to Recent. About 1,500 species belonging to many genera found in Recent fauna; few species known from the Paleogene of Europe (Baltic amber).

Phoromorpha Incertae sedis

Family PALAEOPHORIDAE Rohdendorf, 1954

Intermedial cell, bifurcations on M_3 and RS_{1+2}, and two crossveins rm present. Head small. Thorax strongly inflated, overhangs head; legs weak. Abdomen many-segmented, conical. Jurassic. One genus.

Palaeophora Rohdendorf, 1951 (*Archiphora* Rohdendorf, 1938, nec Schmitz, 1929). Genotype—*Archiphora ancestrix* Rohdendorf, 1938; Upper Jurassic, Chimkent province (Malm, Karatau). Fork of M_3 distal to level of crossvein between RS and M_{1+2}; CuA curved, does not reach wing margin. Length of body 2 mm and of wing, 1.9 mm (Fig. 1102). One species. Upper Jurassic of Kazakhstan.

Infraorder Musidoromorpha

Veins uniformly distributed on wing surface; devoid of traces of costalization; C runs right round wing margin. Face flat, frons broad; antennae three-segmented, with slender arista. Paleogene to Recent. Family: Lonchopteridae.

Family LONCHOPTERIDAE Macquarts, 1835

[nom. transl. Walker, 1851 (ex Lonchopterinae Macquart, 1835)]
(Musidoridae Kertesz, 1909)

Wings distinctly pointed at apex. Body has strong setae. Legs of running type and strong (Fig. 1104). Paleogene to Recent. A few species of genus *Musidora* Meigen found in the Recent fauna and Baltic amber.

Infraorder Myiomorpha

All three veins of system R reach anterior margin; sometimes C does not continue beyond apex of M_1, i.e. it does not reach posterior to apex of wing. Antennae always separated from margin of mouth by large frons, three-
341 segmented with three-segmented arista. Larvae without head, meta- and amphipneustic. Tertiary to Recent. Abundant and varied group of Dipterans that first appeared in the Paleogene and Recent times, including more than 30,000 species under six superfamilies and numerous families. Superfamilies: Platypezidea, Syrphidea, Conopidea, Muscidea, Hippoboscidea, Gastrophilidea.

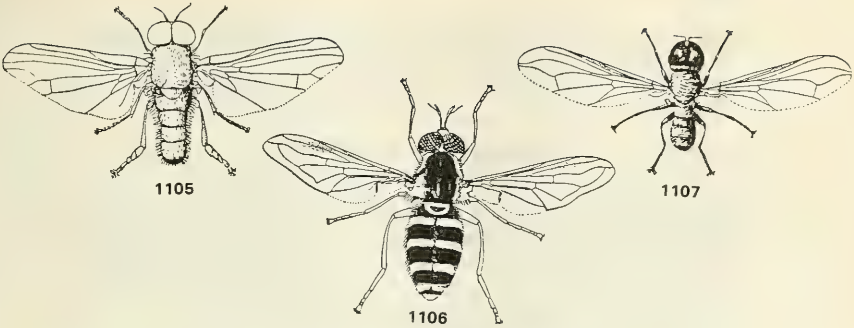
SUPERFAMILY PLATYPEZIDEA

Antennae with terminal arista. Posterior tibiae and bases of posterior tarsi somewhat broad. Crossvein rm always displaced toward base of wing. Paleogene to Recent. Families: Platypezidae and Sciadoceridae; latter known only in the Recent fauna.

Family PLATYPERZIDAE Fallen, 1817

[nom. transl. Walker, 1851 (ex Platypezinae Fallen, 1817)]
(Clythiidae Kertesz, 1910)

Cubital cell always prominent, sometimes quite large; SC long, always terminates on C; intermedial crossvein invariably present (Fig. 1105). Paleogene to Recent. More than 120 species under nearly 10 genera found in the Recent



Figs. 1105–1107. Superfamilies Platypezidea, Syrphidea.

1105. *Clythia picta* Meigen; dorsal view, × 8. Recent, Europe (Verrall, 1909). 1106. *Chrysotoxym festivum* Linnaeus; dorsal view, × 2.5. Recent, Europe (Verrall, 1909). 1107. *Dorylas campestris* Latreille; dorsal view, × 7. Recent, Europe (Verrall, 1909).

fauna, of which three also known from the Paleogene and Neogene of Europe and North America, including the Paleogene of Europe (Baltic amber).

SUPERFAMILY SYRPHIDEA

Antennae normally with a dorsal arista. Posterior tibiae and tarsi not broad. Crossvein rm located in middle of wing. Setae on body few or absent. Head without lunule at base of antennae. Cubital cell always large, almost reaches wing margin. Microtomentum weakly developed. Paleogene to Recent. Families: Syrphidae and Pipunculidae.

Family SYRPHIDAE Latreille, 1802

[nom. transl. Leach, 1819 (ex Syrphine Latreille, 1802)]

Anterior branch of M terminates on RS_{3+4}, forming a closed cell; a peculiar fold—"vena spuria" extends between RS and M and intersecting crossvein rm. Head of moderate size, with broad face; eyes distinctly projecting forward in profile. Size variable, often large (Fig. 1106). Paleogene to Recent. More than 400 species belonging to numerous genera found in the Recent fauna; twenty-two genera known from the Paleogene of Europe (Baltic amber) and the Neogene of Europe.

Family PIPUNCULIDAE Zetterstedt, 1844

[nom. transl. Curtis and Walker, 1854 (ex Pipunculini Zetterstedt, 1844)]

(Dorylaidae Kertesz, 1910)

Anterior branch of M terminates on C or completely absent, so there is no closed cell; additional longitudinal fold, "vena spuria", absent. Head relatively very large; vertex and face very narrow, not prominent in profile. Size small (Fig. 1107). Paleogene to Recent. About 350 species belonging to a few genera found in the Recent fauna, of which two also known from the Paleogene of Europe (Baltic amber).

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SUPERFAMILY CONOPIDEA

(Acalypterata; Holometopa)

Antennae almost always with dorsal arista, rarely located at tip of third segment or completely absent; head with transverse slit or lunule above base of antennae. Thoracic and wing scales absent or weakly developed. M_1 usually terminates on margin of wing, always without an angular bend; cubital cell short, rarely long. Primarily shining without microtomentum. Paleogene to Recent. A very varied group comprising not fewer than 13 families: Conopidae, Ortalididae, Neriidae, Sepseidae, Sciomyzidae, Lauxaniidae, Drosophilidae, Chloropidae; families Pyrgotidae, Tachiniscidae, Agromyzidae, Celyphidae and Milichiidae not known in fossil record so far. Taxonomy of this superfamily has not been studied much to date.

Family CONOPIDAE Latreille, 1802

[nom. transl. Stephens, 1829 (ex Conoparise Latreille, 1802)]

M_1 usually connected with RS_{3+4} or very close to it; cubital cell usually long. Parafrontalia and cheeks broad, proboscis almost always long; arista often terminal. Paleogene to Recent. More than 600 species belonging to nearly 25 genera found in Recent fauna; one genus from the Paleogene of Europe (Baltic amber).

Family ORTALIDIDAE Fallen, 1810

[nom. transl. Macquart, 1835 (ex Ortalides Fallen, 1810)]
(Trypetidae Schiner, 1863; Trypaneidae Bezzi, 1911; Otitidae Hennig, 1950)

Base of ovipositor in the form of a more or less elongated segment of abdomen. Cubital and posterior basal cells isolated. Legs not slender, of clinging or running type, with numerous setae. Paleogene to Recent. More than 4,200 species distributed in the Recent fauna, represented by many subfamilies, tribes and about 100 genera; five genera from the Tertiary faunas of Europe and North America.

Family NERIIDAE Haliday, 1839

[nom. transl. Hendel, 1922 (ex Neriides Haliday, 1839)]
(Tylidae Hendel, 1928)

Ovipositor soft, retracted into abdomen, without large basal segment. Venation not reduced. Legs elongated, slitlike. C without breaks. Paleogene to Recent. More than 550 species found in the Recent fauna, mainly in tropics;

representatives of tribe Trepidariini from the Paleogene of Europe (Baltic amber) have not yet been studied.

Family SEPSIDAE Macquart, 1835

Ovipositor without enlarged basal segment. C with breaks or complete. Venation complete. Mainly small flies with black lustrous coloration resembling ants. Paleogene to Recent. More than 500 species of the Recent fauna under six subfamilies, whose interrelationships have not yet been sufficiently studied; four genera have been reported from the Paleogene of Europe (Baltic amber) and the Neogene of Europe.

Family SCIOMYZIDAE Fallen, 1820

[nom. transl. Macquart, 1835 (ex Sciomyzides Fallen, 1820)]

Ovipositor retracted. C usually without breaks. Venation complete without reduction. Occipital setae diverge. Medium, sometimes large sized flies, as a rule light-colored and usually with a more or less dull microtomentum on body. Legs strong. Abdomen short. Paleogene to Recent. About 40 genera in the Recent fauna; three little-studied genera from the Paleogene of Western Europe and North America.

Family LAUXANIIDAE Macquart, 1835

Ovipositor retracted. C complete or with breaks. Venation complete. Occipital setae converge and intersect. Small flies of varied colors, with weak legs and short body. Paleogene to Recent. About 1,900 species under six subfamilies; most genera, which need further detailed study, from Tertiary fauna.

Family DROSOPHILIDAE Rondani, 1856

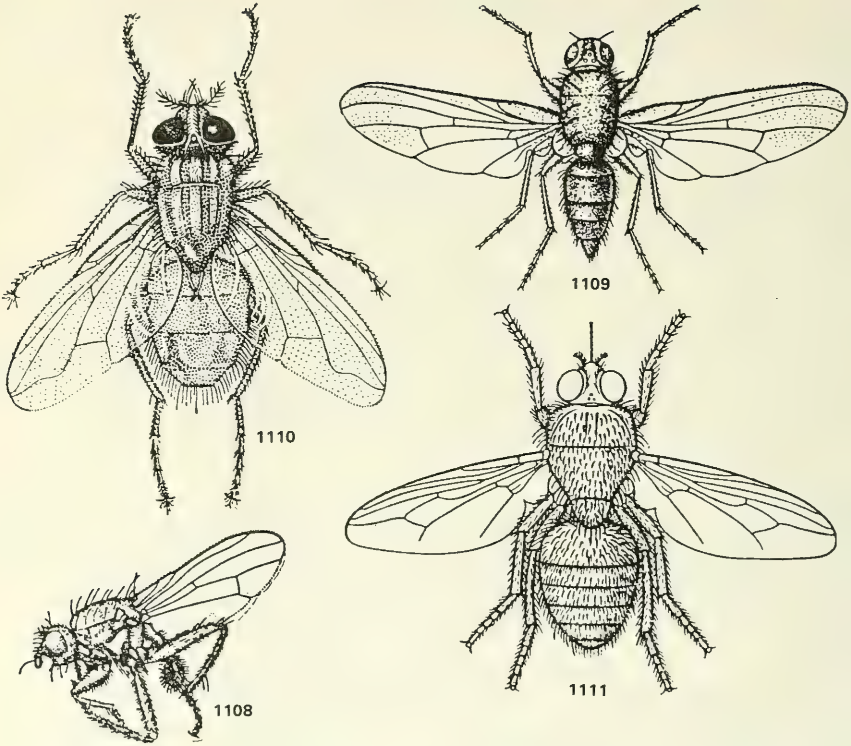
[nom. transl. Osten-Sacken, 1878 (ex Drosophilina Rondani, 1856)]

Ovipositor retracted. C always has one or two breaks; SC in form of weak fold; posterior basal and cubital cells often fused with adjacent cells or reduced. Occipital setae converge or diverge. Small, rarely medium sized flies of different colors with strong legs and short body. Setae on body well developed. Paleogene to Recent. About 3,000 species belonging to numerous genera under four
43 subfamilies found in the Recent fauna; four genera in the Paleogene and Neogene of Western Europe and the Paleogene of Europe (Baltic amber).

Family CHLOROPIDAE Schiner, 1864

[nom. transl. Verall, 1901 (ex Chloropinae Schiner, 1864)]

Ovipositor retracted. C always with break, reduced; cubital cell absent and posterior basal cell fused with intermedial. Occipital setae converge. Small, rarely medium sized flies with miscellaneous colors, almost devoid of setae on



Figs. 1108–1111. Superfamilies Muscidea, Hippoboscidea.

1108. *Scopeuma* sp.; lateral view, × 3.7. Recent, Europe (Curran, 1934). 1109. *Phorbia antiqua* (Meigen); × 6.5. Recent, Europe (Shtakelberg, 1933). 1110. *Musca domestica* Linnaeus; dorsal view, × 7. Recent, Europe (Zimin, 1951). 1111. *Glossina oligocoena* (Scudder); dorsal view (reconstruction), × 5.2. Miocene, North America (Piveteau, 1954).

body. Paleogene to Recent. In the Recent fauna about 1,200 species belonging to numerous genera, of which two also known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY MUSCIDEA

Antennae always with dorsal arista; head with prominent transverse slit or lunule over base of antennae. Thoracic and wing scales almost always well developed and large. M_1 often sharply bent forward, terminating at margin of wing near apex of RS_{3+4}, sometimes fused with it forming a closed cell; cubital cell always short. Body usually with a dull microtomentum and covered with numerous setae, rarely lustrous or bare. Paleogene to Recent. Abundant group includes not fewer than 6,000 species. Of 16 families, following six known from Tertiary fauna: Cordyluridae, Anthomyiidae, Muscidae, Hypodermatidae, Sarcophagidae, Tachinidae.

344 Family CORDYLURIDAE Macquart, 1835

Thoracic and wing scales very small. Body elongate. Hypopleural setae absent. M_1 straight, not close to RS_{3+4}. Abdomen cylindrical. Body and legs with innumerable, upright setae. Size medium (Fig. 1108). Paleogene to Recent. About 50 genera found in the Recent fauna, of which three also known from the Paleogene of Europe (Baltic amber), the Oligocene and Miocene of Western Europe.

Family ANTHOMYIIDAE Rondani, 1856

[nom. transl. Low, 1862 (ex Anthomyna Rondani, 1856)]

Scales well developed. Body with inflated thorax. M_1 straight, without bend. Hypopleural setae absent. Size medium (Fig. 1109). Paleogene to Recent. About 1,500 species found in the Recent fauna; a few sufficiently studied remains known from Tertiary deposits.

Family MUSCIDAE Fallen, 1849

[nom. transl. Robineau Desvoidy, 1830 (ex Muscides Fallen, 1810)]

Scales well developed. Body short, with large head and short abdomen. M_1 bent forward in form of arc or angle. Hypopleural setae absent. Size variable (Fig. 1110). Paleogene to Recent. More than 400 species belonging to nearly 20 genera in the Recent fauna. Indications of the occurrence of the ''genus'' *Musca* in Tertiary deposits have not been substantiated so far.

Family HYPODERMATIDAE Rondani, 1856

[nom. transl. Townsend, 1916 (ex Hypodermina Rondani, 1856)]

Scales moderately developed. Body large, elongate, covered with dense hair, rarely bare. M_1 bent forward. Hypopleural setae hair-like. Puparia very large. Paleogene to Recent. About 30 species found in the Recent fauna; remains of puparia from Tertiary fauna of North America have been little studied.

Family SARCOPHAGIDAE Macquart, 1835

[nom. transl. Brauer and Bergenstamm, 1889 (ex Sarcophagii Macquart, 1835)]

Scales large. Body setaceous. Head often with hairy arista. M_1 always bent at an angle in front. Hypopleural setae strong. Puparia usually with deep posterior slit. Neogene to Recent. About 3,000 species found in the Recent fauna; remains of puparia have been discovered in the Neogene and Quaternary deposits, but have been little studied so far.

Family TACHINIDAE Robineau and Desvoidy, 1830

[nom. transl. Loew, 1862 (ex Tachinariae Robineau and Desvoidy, 1830)]

Scales very large. Body with long, strong setae. Head with bare arista. M_1 usually sharply bent at an angle or curved in front. Hypopleural setae always present. Puparia without posterior slits. Paleogene to Recent. More than 5,000 species found in the Recent fauna. Indications of occurrence of representatives of this family in Tertiary faunas have not been verified.

SUPERFAMILY HIPPOBOSCIDEA

Arista covered with branching hairs. Pronotum highly reduced. All sterna of abdomen (except first) highly reduced. Membrane of abdomen well developed and hairy. Venation strongly costalized, displaced toward anterior margin. Sometimes wings reduced. Viviparous (pupiparous). Normally bloodsuckers of mammals and birds. Paleogene to Recent. Family: Glossinidae and Hippoboscidae.

Family GLOSSINIDAE Townsend, 1935

Wings large, moderately costalized. Apical part of vein M_{1+2} prominent, separating cell R_5. Body not dorso-ventrally flattened, with protruding antennae and thin legs. Size large (Fig. 1111). Paleogene to Recent. In the recent fauna about 30 species of genus *Glossina* Wiedemann in Tropical Africa. One species of this genus found in the Miocene of North America.

Family HIPPOBOSCIDAE Leach, 1815

Wings exhibit very strong costalization, venation sometimes reduced or even absent; apical part of M_{1+2} not isolated and not bent toward front. Body flat, with strong, short clinging legs. Size medium. Paleogene to Recent. In the Recent fauna more than 100 species belonging to 20 genera; one from the Paleogene of Germany.

345 Order APHANIPTERA. Fleas

(A.G. Sharov)

Small, secondarily wingless insects, with parasitic adaptations to live on warm-blooded vertebrates. Body laterally flattened, covered with backwardly directed setae, hairs or combs of spines. Antennae short, mouth parts in form of piercing

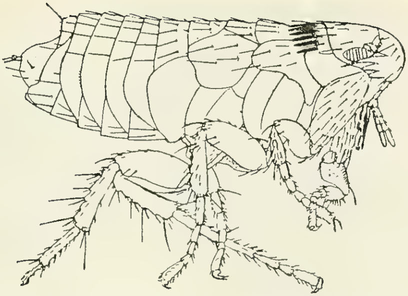


Fig. 1112. Aphaniptera.

Palaeopsylla debsiana Dampf; lateral view, × 20. Paleogene, Europe (Baltic amber) (Handlirsch, 1925).

stylets. Legs of jumping type: coxae large, tarsi long. Paleogene to Recent. Six families in the Recent fauna; one in fossil form.

Family HYSTRICHOPSYLLIDAE Tiraboschi, 1904

Head with combs of spines on cheek. Terga of abdomen with single row of setae. Eyes usually present (Fig. 1112). Paleogene to Recent. Of the many genera in Recent fauna, two genera also known in fossil form from the Paleogene of Western Europe and Europe (Baltic amber).

SUPERORDER HYMENOPTEROIDEA. Hymenopteroid insects

(B.B. Rohdendorf)

Wings membranous, sharply dissimilar, forewings longer than hindwings, often strongly costalized. Shape of two wings sharply different; forewing always with sharply demarcated apical part and well-defined apical margin. Venation reduced, with few strong veins forming large cells, a broad area without veins usually present at apical margin. Mouth parts of biting type, adapted for intake of liquid food. Larvae eruciform or vermiform with short legs or legless. Live in tissues or on surface of plants; many parasitic on other insects. Great variation in development of progeny. Closest to certain neuropteroids. Triassic to Recent. Phylogenetic relationship with other groups of Neoptera not clear. Suggested links with mecopteroids not feasible. Evolution of this group undoubtedly involves perfection of breeding and, above all, care of progeny. There is every reason to believe that this group of winged insects is the most advanced.

Order HYMENOPTERA. Membranous winged insects

(O.M. Martynova)

Two pairs of membranous, sharply costalized wings; wingless forms: ants, velvet ants etc.—rare; hindwings always shorter than forewings, during flight linked with latter. Venation greatly reduced, usually shifted toward anterior margin; only in suborder Symphyta SC preserved in one form or another; in parasitic and stinging Hymenoptera SC fused with radius; RS divided into two branches, of which anterior one sometimes branches, and posterior one fuses with anterior branch of medial vein for a considerable distance; M divides in distal half of wing into two simple branches, an anterior MA fused with posterior branch of RS; free base of MA very short; crossveins r-rs and rs-m 346 (basal vein) always present; basal crossvein in parasitic hymenopterans long, because base of RS usually reduced, connects M and R; R and M fused at base; CuA free and simple; CuP occasionally preserved in form of indistinct fold in Symphyta; one or two anal veins; between bases of radius and M radial cell rc located; distal part cell rc borders stem of RS and basal crossvein; between radius and RS lie radial cells r_1, r_2 and r_3; cell bordering basal crossvein and parts of RS and MA—subordial cell (sr).

Head usually hypognathous and mobile; mouth parts of biting-lapping type. Large compound eyes of oval shape, rarely round; three ocelli usually seen on parietal region; antennae of varied shape with three or more segments, first two segments distinctly different from others (flagellum) in shape and size.

Thoracic segments closely fused together; mesothorax most well developed. Anterior segment of abdomen fused with metathorax, in Apocrita it is in the form of an auxillary thoracic segment; second abdominal segment forms pedicel of varying length; usually tarsi five-, rarely three- or four-segmented; last segment with two claws with a pulvillus between them.

In most forms, larvae worm-like, without eyes or legs; in primitive Symphyta larvae with three pairs of thoracic legs. Pupa of exarate type. Except pupa, all other stages can hibernate. Adults feed on nectar, sugary excretions of aphids, coccids etc., rarely on animal food. Larvae feed on plant or animal food. Triassic to Recent. Suborders: Symphyta, Apocrita.

Suborder SYMPHYTA. Sawflies

Wings usually well developed, particularly forewings; venation most complete; often SC present or its vestiges seen as crossveins; subradial and discoidal cells always in contact; one or two anal veins; a small anal area present in hindwings. Trochanter always two-segmented; tarsi five-segmented. Abdomen sessile; ovipositors of varying shape; usually ovipositor consists of two comparatively short serrate plates. Larvae herbivorous, with thoracic and often abdominal legs. Triassic to Recent. Superfamilies: Megalodontidea, Siricidea, Orussidea, Cephidea, Tenthredinidea.

SUPERFAMILY MEGALODONTIDEA

In forewings SC often free; three almost equal radial cells between R and RS; straight crossveins of almost equal length divide them; anal vein present. Triassic to Recent. Families: Anaxyelidae, Xyelidae, Pamphiliidae, Megalodontidea; last family not known in fossil form.

Family ANAXYELIDAE Martynov, 1925

Free SC absent in forewings; RS_1 has no bifurcation; cell r_3 long, equal in length to combined lengths of first two cells. Larvae not known. Upper Jurassic. One genus.

Anaxyela Martynov, 1925. Genotype—*A. gracilis* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Four crossveins in costal area of forewing; pterostigma weak; crossveins r-rs run parallel; free base of posterior branch of RS short. Length of forewing 7 mm. Ovipositor 4.6 mm (Fig. 1113). Two species. Upper Jurassic of Kazakhstan.

Family XYELIDAE Haliday, 1840

SC free in forewings; anterior branch of RS with fork; cells r and r_3 almost of same length, longer than r_2; discoidal cell and second cell between branches of RS equal and elongated. Antennae with 9–12 segments, differ from other families in having a strongly elongate, thick third segment. Ovipositor moderately or very long. Larvae have legs on every abdominal segment; live on leaves and in flowers. Triassic to Recent. Five genera in the Recent fauna of Holarctic region; five genera in fossil record.

Liadoxyela Martynov, 1937. Genotype—*L. praecox* Martynov, 1937; Lower Jurassic, Central Asia (Lower Liassic, Kizil-Kiya). In forewings RS arise at same level as apex of SC; branches of anterior branch of RS not bent forward; basal crossvein (rs-m) short; cell dc and last cell between branches of RS elongate. Length of forewing 12 mm (Fig. 1114). One species. Lower Jurassic of Asia.

Outside the USSR: *Archexyela* Riek, 1955 from the Triassic of Australia; two genera from the Oligocene of Western Europe and one genus from the Miocene of North America.

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Family PAMPHILIIDAE Dalla-Torre, 1894. Leaf-Rollers

[nom. transl. Viereck, 1916 (ex Pamphiliinae Dalla-Torre, 1894)]

SC free in forewings. Anterior branch of RS without fork, bent forward; cell r_3 a little longer than following cell rs_2. Larvae with well-developed thoracic legs; abdominal legs absent; live gregariously on coniferous and broad leaved trees, in webs or rolled-up leaves (Fig. 1115). Paleogene to Recent. Eight genera found in the Recent fauna of the Holarctic; two genera in fossil form from the Paleogene of Europe (Baltic amber) and the Miocene of North America.

SUPERFAMILY SIRICIDEA

Three radial cells of varying size; r_1 smaller than r_2; cross veins r-rs slanting, not 348 parallel, proximal one shorter than distal; one anal vein. Ovipositor needle- or horn-shaped. Jurassic to Recent. Families: Syntexidae, Xiphydriidae, Siricidae, Pseudosiricidae; first two not known as fossils; last one from the Jurassic of Western Europe.

Family SIRICIDAE Kirby, 1937. Horntails

Traces of SC seen in forewings; base of RS and basal crossvein in one straight line; end of anterior branch of RS bent forward; free base of posterior branch of RS long; cell dc almost twice as long as cell rs_2. Body black with yellow markings. Larvae live in wood, without eyes. Thoracic legs highly reduced; abdominal legs absent. Few genera in the Recent fauna, of forest zone (Fig. 1116); two genera in fossil record from the Paleogene of Europe (Baltic amber) and the Miocene of Southern Europe.

SUPERFAMILY ORUSSIDEA

Free SC absent in forewings; two radial cells; base of anterior branches of RS reduced; crossvein r-rs slanting, joins anterior branch of RS to form a single vein convex from behind; RS_2+M_1 also convex from behind; Cu and A fused at base. Larvae highly specialized parasites of beetles of families Buprestidae and Cerambycidae, living in wood. Widely distributed, relict group in the Recent fauna. Jurassic to Recent. Families: Paroryssidae and Orussidae.

Family PARORYSSIDAE Martynov, 1925

Two close crossveins in forewing between branches of RS; only bases of branches of M preserved, arranged at right angles to stem of M. Upper Jurassic. One genus.

Paroryssus Martynov, 1925. Genotype—*P. extensus* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Costal margin of forewing much strengthened; fused SC and R form a thick vein; pterostigma oval. Length of body with ovipositor 11 mm; length of forewing 3.4 mm (Fig. 1117). One species. Upper Jurassic of Kazakhstan.

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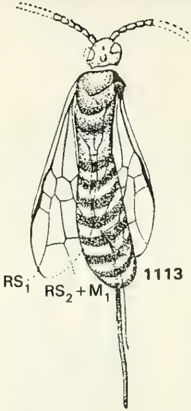
347 Figs. 1113–1119. Suborder Symphyta.

1113. *Anaxyela gracilis* Martynov; ventral view, × 5. Upper Jurassic, Kazakhstan (Martynov, 1925). 1114. *Liadoxyella praecox* Martynov; forewing, × 5. Lower Jurassic, Central Asia (Martynov, 1937). 1115. *Lyda nemoralis* Thomson; dorsal view, × 3.5. Recent (Gussakovsky, 1935). 1116. *Sirex gigas* Linnaeus; dorsal view, × 1. Recent (Gussakovsky, 1935). 1117. *Paroryssus extensus* Martynov; ventral view, × 4. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 1118. *Cephus pygmaeus* Linnaeus; lateral view, × 5.5. Recent (Gussakovsky, 1935). 1119. *Pteronidea ribesii* Scopoli; dorsal view, × 5.5. Recent (Gussakovsky, Guide to Insects, 1948).



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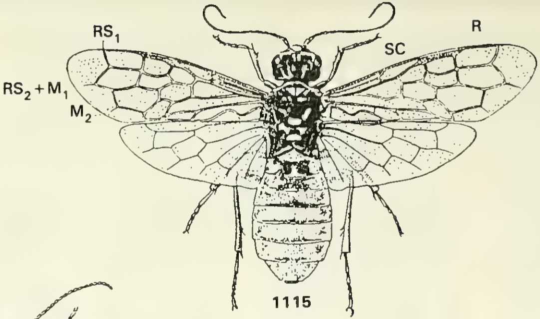

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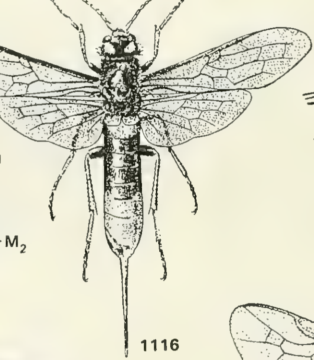

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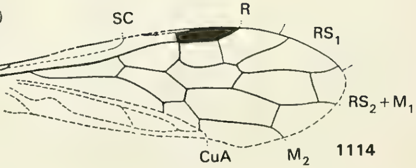

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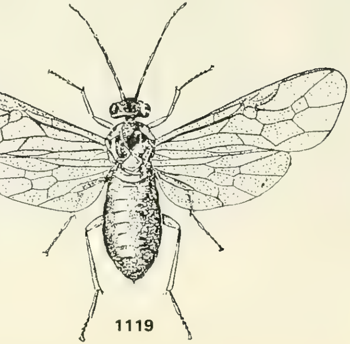

1119

SUPERFAMILY CEPHIDEA

Free SC absent in forewings; three radial cells (r_{1-3}), of which middle one shorter than other two; crossveins r-rs slanting, run closely parallel, of equal length; one anal vein present. Fairly large forms with antennae often thickened at apex. Paleogene to Recent. Family: Cephidae.

Family CEPHIDAE Haliday, 1840. European wheat stem sawflies

Base of RS considerably shorter than crossvein rs-m in forewings; anterior branch of RS simple, not bent forward; cell r_1 shorter than r_3; discoidal cell (dc) elongate, longer than cell rs_2. Larvae with three pairs of reduced thoracic legs; abdominal legs absent; antennae four or five segmented; ocelli present; live in stems of plants (Fig. 1118). Paleogene to Recent. A few genera of Recent fauna from the Holarctic; one from Madagascar; four genera in fossil record found in the Paleogene of Europe (Baltic amber) and the Miocene of Western Europe and North America.

SUPERFAMILY TENTHREDINIDEA

SC resembles a crossvein in forewing; two or three radial cells; cell r_1 not very big; crossvein r-rs very short; RS leaves R distal to crossvein, i.e. basal crossvein r-m, not rs-m; Cu forms a loop in both pairs of wings. Paleogene to Recent. Families: Tenthredinidae, Cimbicidae, Diprionidae, which occur as fossils in areas outside the USSR.

Family TENTHREDINIDAE Leach, 1817. True sawflies

[nom. transl. Leach, 1819 (ex Tenthredinidea Leach, 1817)]

Costal margin of forewings thickened; pterostigma large; basal crossvein twice as long as base of RS; anterior branch of RS convex from behind; cell r_1 considerably smaller than r_2. Larvae strongly resemble caterpillars, with three pairs of thoracic legs and abdominal legs on segments 2 to 8 and segment 10 of abdomen; feed on leaves, fruit and galls; few are miners (Fig. 1119). Paleogene to Recent. About 4,000 species under seven subfamilies in the Recent fauna. A few genera known from the Paleogene of Europe (Baltic amber) and the Miocene of Western Europe and North America.

Family CIMBICIDAE Leach, 1817

[nom. transl. Kirby, 1837 (ex Cimbicinae Leach, 1817)]

Differs from other families of superfamily by reduced base of RS_1. Paleogene to Recent. A few genera in the Paleogene of Europe (Baltic amber) and the Miocene of Western Europe and North America.

Family DIPRIONIDAE Rohwer, 1911

Differs from other families of superfamily by presence of teeth or plumose-structures on more than nine segments of antennae. Larvae live on conifers. Paleogene to Recent. A few genera in the Paleogene of Europe (Baltic amber) and the Miocene of Western Europe and North America.

Suborder Apocrita

Wings well developed or rudimentary; venation often reduced; free SC never present; radial cells not more than two; if subradial and discoidal cells present in forewing, then they never touch (Parasitica) or are in contact for a short distance (few Aculeata); anal veins absent; hindwings without a separate anal area. Abdomen not sessile; second abdominal segment narrower than others and occasionally elongate; typically abdomen petiolate or pendulous; if in certain forms abdomen happens to be sessile, then venation of wings highly reduced; ovipositor acicular, often retracted into abdomen and transformed into a sting. Larvae legless, eyeless, wormiform and barely mobile. Upper Jurassic to Recent. Superfamilies: Ichneumonidea, Cynipidea, Chalcididea, Proctotrupidea, Bethylidea, Cretavidea, Scoliidea, Formicidea, Pompilidea, Apidea, Vespidea; last found as fossils in areas outside the USSR.

SUPERFAMILY ICHNEUMONIDEA

Venation of forewings fairly complete; RS branches distal to branching of M; often base of RS reduced and fused into one line with basal crossvein; pterostigma always present; branching of M and its two branches clearly visible; CuA present. Antennae geniculate with 10 or more segments. Trochanter with two segments. Larvae usually parasites, mainly on insects. One of the most widespread families, with about 16,000 species. Upper Jurassic to Recent. Nine families in the Recent fauna; families with fossil forms: Pelecinopteridae, Ephialtitidae, Braconidae, Megalyridae, Evaniidae, Adulacidae, Stephanidae, Trigonalidea, Ichneumonidae; only first two extinct.

Family PELECINOPTERIDAE Brues, 1933

Length of forewing about 14 mm, half of very long abdomen; pterostigma indistinct in forewings, looks like a thick vein; stem of RS reduced; RS branches distal to pterostigma, with end of anterior branch bent backward; cell dc open; basal crossvein not visible; medial cell open. Head large, with large eyes and three ocelli. Antennae 13 segmented. Thorax long. Abdomen in females consists of six segments of almost equal length; ovipositor not retracted (Fig. 1120). Paleogene. One genus from the Paleogene of Europe (Baltic amber).


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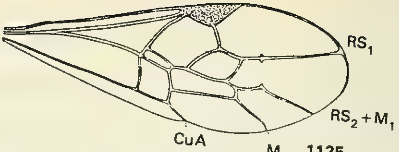

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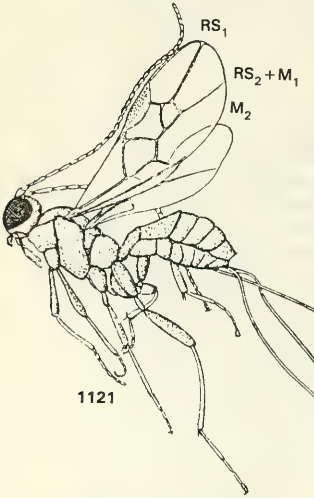

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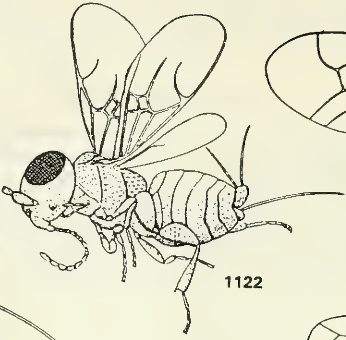
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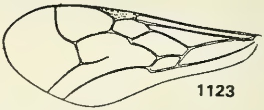
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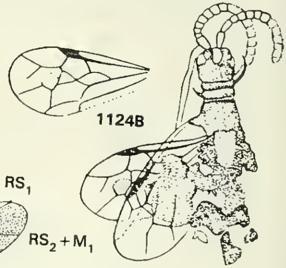
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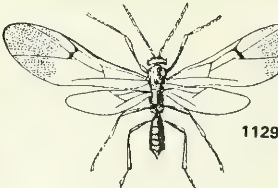

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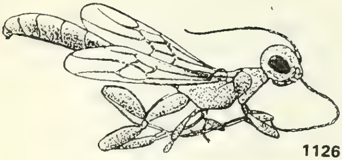
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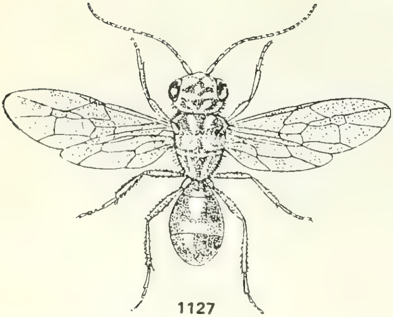
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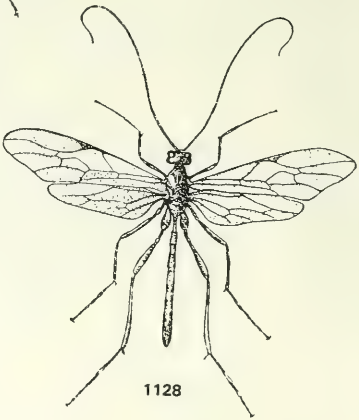
1128

Family BRACONIDAE Burmeister, 1829. Ichneumon wasps—Braconids

[nom. transl. Kirby, 1837 (ex Braconoides Burmeister, 1829)]

Length of wing exceeds slightly length of abdomen; pterostigma distinct, rounded on forewings; stem of RS usually not reduced, branches at level of pterostigma; free base of posterior branch of RS absent; end of anterior branch of RS slightly bent toward front or straight; cell dc closed, smaller than sr, r_1 and r_2; no cell m_1. Head transverse or cuboidol, bears three ocelli and long filiform antennae. Abdomen joined with lower part of propodeum; articulation between second and third segments immobile (Fig. 1121). Larvae parasitic on insects, often on beetles. Paleogene to Recent. 16 subfamilies in the Recent fauna, of which following 13 have fossil representatives: Braconinae, Spathiinae, Doryctinae, Rhogadinae, Cheloninae, Triaspinae, Neoneurinae, Microgasterinae, Blacinae, Euphorinae, Meteorinae, Aphidinae, Alysiinae from the Paleogene of Europe (Baltic amber), Western Europe and North America.

Family MEGALYRIDAE Schletterer, 1889

Forewings somewhat longer than abdomen; costal area narrow; pterostigma narrow and indistinct; basal crossvein short, borders a small and almost quadrate subradial cell (sr), slightly smaller than posteriorly located second cubital cell; base of anterior branch of RS reduced, resembles a curved, long r-rs; posterior branch of RS short, does not reach wing margin; dc and m_1 absent. Abdomen stalklike; ovipositor often longer than body (Fig. 1122). Paleogene to Recent. Two genera in the Recent fauna with 19 species in Australia and one species in South America; one extinct genus known from the Paleogene of Europe (Baltic amber).

350

Family EVANIIDAE Leach, 1812

[nom. transl. Westwood, 1840 (ex Evaniades Leach, 1812)]

Pterostigma of forewings distinct, longitudinal; stem of RS fully preserved, branches at level of origin of pterostigma; anterior branch of RS forms an arcuate bend in front, ends at anterior margin of wing; cell dc closed, large, of same length as sr, but wider; basal crossvein long; cell m_1 absent. Antennae 13

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351 Figs. 1120–1129. Suborder Apocrita; Superfamilies Ichneumonoidea, Cynipoidea.
1120. *Pelecinopteron tubuliforme* Brues; lateral view, × 4.5. Paleogene, Europe (Baltic amber) (Brues, 1933). 1121. *Microtypus longicornis* Brues; lateral view, × 18. Paleogene, Europe (Baltic amber) (Brues, 1933). 1122. *Prodinapsis minor* Brues; lateral view, × 20. Paleogene, Europe (Baltic amber) (Brues, 1933). 1123. *Evania brevis* Brues; forewing, × 13.6. Paleogene, Europe (Baltic amber) (Brues, 1933). 1124. *Mesaulacinus oviformis* Martynov; A—general view, B—forewing, × 12. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 1125. *Micraulacinus prisculus* Brues; forewing, × 10. Paleogene, Europe (Baltic amber) (Brues, 1933). 1126. *Electrostephanus petiolatus* Brues; lateral view, × 6. Paleogene, Europe (Baltic amber) (Brues, 1933). 1127. *Poecilogonalis thwatesti* Linnaeus; dorsal view, × 8.5. Recent (Clausen, 1940). 1128. *Ophion luteus* Linnaeus; dorsal view, × 3.5. Recent (Meier, 1935). 1129. *Neuroterus lenticularis*; dorsal view, × 7.7. Recent (Sharp, 1905).

or 14 segmented. Abdomen short, stalklike, connected to upper region of propodeum, much higher than base of posterior legs; ovipositor short, does not extend beyond tip of abdomen (Fig. 1123). Paleogene to Recent. A few hundred species occur in the Recent fauna at various latitudes. Parasites of eggs of cockroaches. Two genera from the Paleogene of Europe (Baltic amber).

Family AULACIDAE Schuckard, 1841

Pterostigma clearly visible, longitudinal; stem of RS long, branches at level of origin of pterostigma; free base of posterior branch of RS absent; end of stem of RS fused with anterior branch of M; anterior branch of RS straight or with end gently bent in front; basal crossvein short, forms long, narrow cell sr; discoidal (dc) and medial cells closed. Antennae 13 or 14 segmented. Abdomen joined to upper part of propodeum, much higher than base of hindlegs, longer than thorax; ovipositor clearly projects beyond tip of abdomen, usually longer than whole body. Parasites of beetle larvae living in wood; often parasitic on larvae of Xiphydriidae. Upper Jurassic to Recent. About 100 widely distributed species in the Recent fauna; nine genera found in fossil record.

Mesaulacinus Martynov, 1925. Genotype— *M. oviformis* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Forewings wide, rounded; subradial cell rhomboidal, larger than triangular discoidal cell (dc); vestiges of second crossvein preserved between branches of RS. Length of forewing 2.1 mm (Fig. 1124). One species. Upper Jurassic of Kazakhstan.

Paraulacus Ping, 1928 from the Cretaceous of China; seven genera in Tertiary deposits of Europe (Fig. 1125), Asia and America.

Family STEPHANIDAE Leach, 1815

[nom. transl. Haliday, 1840 (ex Stephanidia Leach, 1815)]

Size varied, length ranges from 4 to 36 mm. Wings shorter than body; pterostigma prominent, longitudinal; costal area narrow, of uniform width; RS branches on meeting anterior branch of M at a level halfway along pterostigma, branches not bent; crossvein r-rs short, diverges from distal end of pterostigma; discoidal cell open; basal crossvein borders rhomboidal subradial cell; medial cell open. Antennae long, 30-segmented. Ovipositor longer than body. Parasitic on wood-boring insects (Fig. 1126). More than 100 species of 10 genera found in the Recent fauna, primarily in hot climates; two extinct genera from the Paleogene of Europe (Baltic amber) and the Miocene of North America.

Family TRIGONALIDAE Cresson, 1867

Insects of medium size. Wings longer than abdomen; pterostigma narrow, not wider than costal area; stem of RS bent at right angles; basal crossvein short; RS branches at level of midpoint of pterostigma, branches not bent; crossvein r-rs long, borders large radial cell (r_1); two crossveins between branches of RS;

discoidal cell long and narrow; basal crossvein borders trapezoidal subradial cell (sr); medial cell closed. Abdomen joined to lower part of propodeum above base of hind legs. Eggs laid on leaves. Larvae devour pseudo-caterpillars of sawflies or caterpillars of Lepidoptera (Fig. 1127). Neogene to Recent. About six genera in the Recent fauna, of which one also known from Neogene of South Asia (Burmese amber) and Germany.

352 Family ICHNEUMONIDAE Latreille, 1802. True ichenumons

[nom. transl. Leach, 1817 (ex Ichneumonides Latreille, 1802)]

Pterostigma of forewings distinct, triangular; costal area absent; base of stem of RS inclined backward, fused with basal crossvein, reduced farther; subradial cell fused with first radial, closed by a short crossvein; crossvein r-rs long, tilted passes into anterior branch of RS; medial cell closed, large. Parasitic on all insects, primarily on insect larvae which live in wood (Fig. 1128). Paleogene to Recent. Subfamilies: Ichneumoninae, Cryptinae, Pimplinae, Ophioninae, Tryphoninae, known from the Paleogene of Western Europe and North America.

SUPERFAMILY CYNIPIDEA

Small insects: length varies from 1 to 4 mm. Costal area present; pterostigma absent. Differs from Ichneumonidea in absence of distal part of medial vein with branches and complete reduction of Cu. Parasitic on hymenopterans, dipterans and aphids; some of them form galls (Fig. 1129). Paleogene to Recent. Families: Ibaliidae, Figitidae, Eucoilidae, Charipidae, Cynipidae;last one found as fossil.

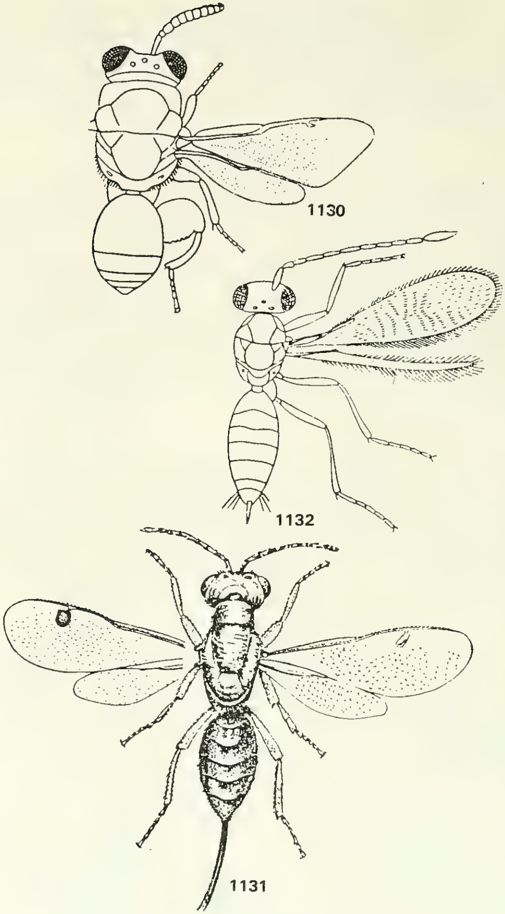
Family CYNIPIDAE Linnaeus, 1758. Gall wasps

[nom. transl. Haliday, 1840 (ex Cynipes Linnaeus, 1758)]

First radial cell (r_1) closed, four times as long as it is wide. Antennae simple, not more than 16 segmented. Early stages live in plant tissues and form galls. Paleogene to Recent. 10 subfamilies, of which one known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CHALCIDIDEA. Chalcids

Insects measuring from less than 1 mm to 20 mm; normal size 2–3 mm, occasionally with more or less shortened wings. Venation reduced to one vein: SC + R. Antennae geniculate, usually with annulated segments between second segment and flagellum. Tarsi three- to five-segmented. Parasitic on insects, sometimes on other arthropods (spiders, ticks and mites). Few families and some genera phytophages. Paleogene to Recent. In the Recent fauna about 27 families: families found as fossils Chalcididae, Torymidae, Mymaridae, Eurytomidae, Agaonidae, Perilampidae, Pteromalidae, Eulophidae, Encyrtidae; last six occur outside the USSR.



Figs. 1130–1132. Superfamily Chalcidoidea.

1130. *Brachymeria intermedia* Nees; dorsal view, × 12. Recent (Nikolskaya, 1952). 1131. *Megastigmus juniperi* Nikolskaya; dorsal view, × 20. Recent (Nikolskaya, 1952). 1132. *Gonatocerus cicadellae* Nikolskaya; dorsal view, × 20. Recent (Nikolskaya, 1957).

353 Family CHALCIDIDAE Walker, 1835

Fairly large forms, rarely less than 5 mm in length. Posterior coxae long and cylindrical; posterior femurs thickened with teeth along outer margin; posterior tibiae curved. Ovipositor, if present attached to last, elongated tergum (Fig. 1130). Neogene to Recent. Six subfamilies and more than 100 genera in the Recent fauna; four genera from these known from the Miocene of Western Europe and Quaternary deposits of East Africa.

Family TORYMIDAE Walker, 1833

(Callimomidae Viereck, 1916)

Body measurements range from 1.5 to 7 mm. Differs from preceding family in its smaller size. Posterior coxae trihedral; usually posterior femurs not thickened. Ovipositor more or less long (Fig. 1131). Paleogene to Recent. About 60 genera and more than 500 species in the Recent fauna; three genera from the Paleogene of Europe (Baltic amber) and the Neogene of North America.

Family MYMARIDAE Haliday, 1833

[nom. transl. Haliday, 1840 (ex Mymares Haliday, 1833)]

Small forms, usually less than 1 mm long. Most of them egg parasites. Wings narrow, with long fringe along margin. Venation highly reduced; only base of R preserved; hindwings sometimes setiform. Antennae 8–13 segmented, in females often with a club. Tarsi four- or five-segmented (Fig. 1132). Paleogene to Recent. In the Recent fauna about 40 genera and more than 200 species; nine genera found in fossil form (two of these extinct), known from the Paleogene of Europe (Baltic amber), North America and East Africa (Copal).

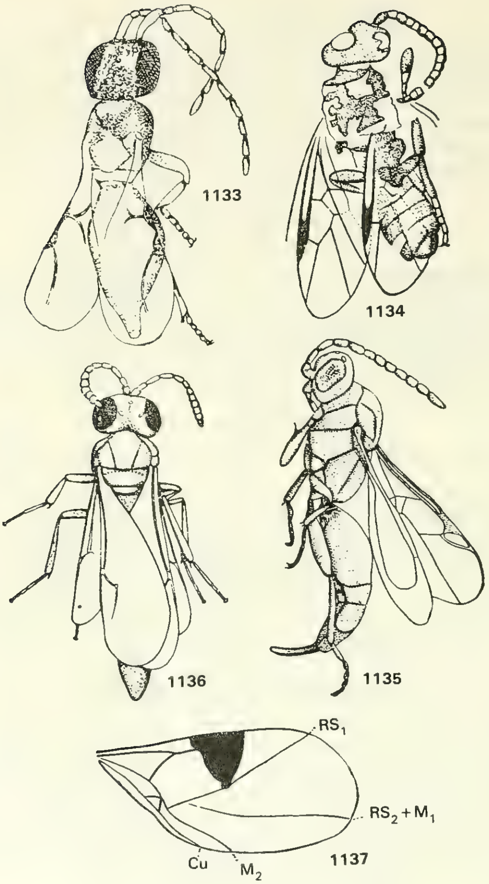
SUPERFAMILY PROCTOTRUPIDEA

Small insects, usually wingless. Venation sometimes reduced to one vein, when SC + R short and unconnected with C; if veins large then discoidal cell (dc) always open, subradial cell (sr) always small, usually triangular; cells do not touch; pterostigma sometimes very large. Antennae simple, if geniculate, then without annulated segments. Ovipositor projects from extreme tip of abdomen. Parasitic on arthropods and their eggs. Upper Jurassic to Recent. In the Recent fauna 12 families; following families known to have fossil representatives: Megaspilidae, Heloridae, Proctotrupidae, Scelionidae, Serphitidae.

Family MEGASPILIDAE Ashmead, 1893

[nom. transl. Ashmead, 1903 (ex Megaspilini Ashmead, 1893)]

Small forms, length varying from 0.6 to 3.3 mm, often wingless. In forewing C, SC and R fused into one vein, remaining veins vestigial; basal crossvein from the



Figs. 1133–1137. Superfamily Proctotrupoidea.

1133. *Conostigmus succinalis* Brues; dorsal view, × 24. Paleogene, Europe (Baltic amber) (Brues, 1946). 1134. *Mesohelorus muchini* Martynov; dorsal view, × 9. Upper Jurassic, Southern Kazakhstan (Martynov, 1925). 1135. *Cryptoserphus pinorus* Brues; lateral view, × 22. Paleogene, Europe (Baltic amber) (Brues, 1940). 1136. *Ceratoteleia proleptica* Brues; dorsal view, × 15. Paleogene, Europe (Baltic amber) (Brues, 1940). 1137. *Serphites paradoxus* Brues; forewing, × 39. Upper Cretaceous, North America (Canadian amber) (Brues, 1937).

small curved base of RS, crosses entire wing up to its anal margin; crossvein r-rs 354 continues as anterior branch of RS, forming one curved vein; pterostigma present. Parasitic on aphids, scale insects and dipterans (Fig. 1133). Paleogene to Recent. Many widely distributed genera in the Recent fauna; three genera in the Paleogene of Europe and North America (Baltic and Canadian amber).

Family HELORIDAE Forster, 1856

Small insects, length varying from 3 to 6.5 mm. Forewings with relatively rich venation; base of RS between R and basal crossvein often absent; subradial cell triangular; first radial cell broad; pterostigma present. Parasitic on neuropterans. Upper Jurassic to Recent. Only one genus known in the Recent fauna of Northern Hemisphere, one genus extinct.

Mesohelorus Martynov, 1925. Genotype—*M. muchini* Martynov, 1925; Upper Jurassic, Chimkent province (Malm, Karatau). Forewings with elongate pterostigma and narrow costal area; stem of RS completely preserved; branches of RS straight, not curved; rudiments of crossvein close discoidal cell. Length of forewing 5 mm (Fig. 1134). One species. Upper Jurassic of Kazakhstan.

Family PROTOTRUPIDAE Cresson, 1887
(Serphidae Kieffer, 1909)

Length of insects varies from 2 to 7 mm. Forewings with highly reduced venation; with fully preserved SC + R and large pterostigma; RS usually reduced; if stem of RS preserved (in Tertiary forms), then anterior branch of RS deviates to front; RS close to distal part of pterostigma; crossvein r-rs very short; only base of M retained up to point of branching; subradial cell small. Parasitic on dipterans and beetles (Fig. 1135). Paleogene to Recent. Few widespread genera in Recent fauna; three genera known from the Paleogene of Europe (Baltic amber) and the Neogene of North America; few genera of the Recent fauna encountered in the Quaternary deposits of East Africa.

Family SCELIONIDAE Haliday, 1840

Small insects, from 0.45 to 5 mm long. Often wingless. Pterostigma absent from forewings; SC + R terminates on anterior margin of wing, whence the slanting crossvein r-rs takes off a little more distally; sometimes this crossvein is only a rudiment not reaching margin of forewing or anterior branch of RS; other veins vestigial. Parasitic, mainly on eggs of Lepidoptera, Hymenoptera and Orthoptera (Fig. 1136). Paleogene to Recent. A large number of widespread genera in the Recent fauna; twenty-six genera from the Paleogene of Europe (Baltic amber), the Neogene of Western Europe and North America and from West Africa (Copal).

Family SERPHITIDAE Brues, 1937

Differs from Proctotrupidae in unusually large pterostigma located halfway along forewing, occupying almost one-half of its width; basal crossvein fused with base of RS, rest of RS reduced. Length of forewing 1.2 mm (Fig. 1137). Paleogene. One genus, *Serphites* Brues, 1937, from the Upper Cretaceous of North America (Canadian amber).

SUPERFAMILY BETHYLIDEA

In forewings basal crossvein usually connects medial vein with radius, not with stem of RS; stem of RS long, if branching retained then it takes place distal to branching of M; more often base of RS_1 lost and anterior branch of RS emerges as an extension of crossvein r-rs, curved forward; pterostigma narrow, resembles thick vein; medial cell open; Cu present. Antennae with 10 to 28 segments, with the same number in both sexes. Paleogene to Recent. Six families in Recent fauna, of which following also found as fossils: Embolemidae, Bethylidae, Chrysididae, Dryinidae.

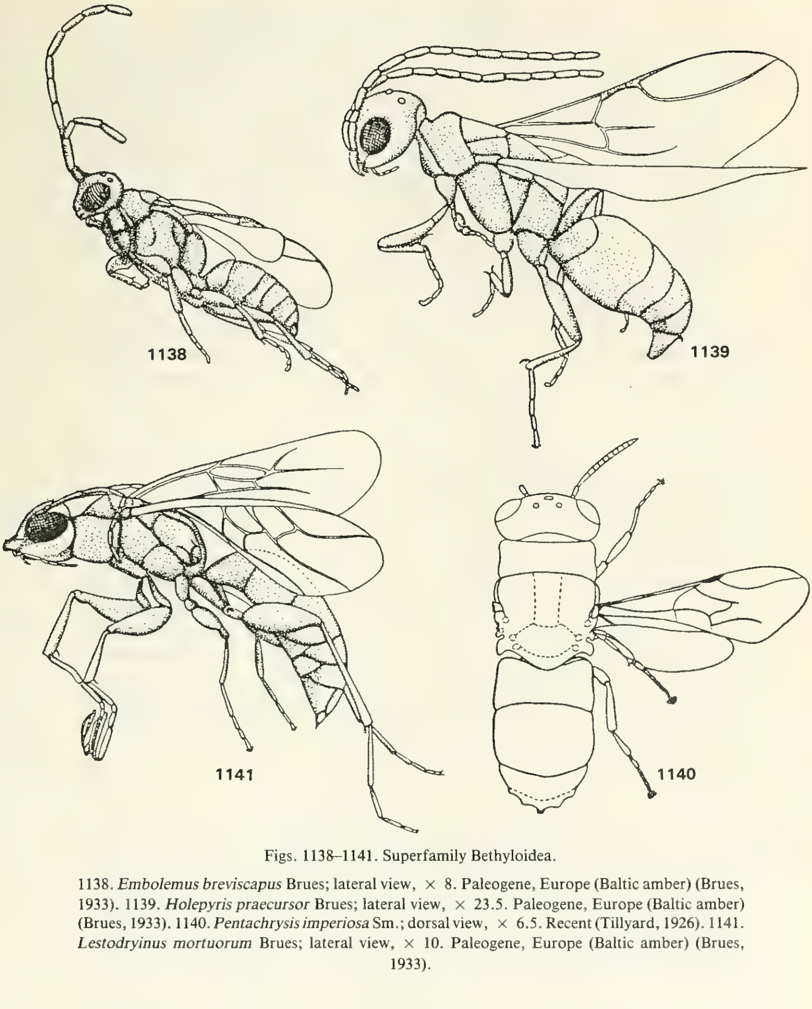
Family EMBOLEMIDAE Forster, 1856

[nom. transl. Handlirsch, 1925 (ex Embolemoidae Forster, 1856)].

Small insects. Females wingless. Pterostigma very small in forewings; crossveins absent; subradial cell closed; base of anterior branches of RS reduced; radial cell fused with discoidal. Head rounded, hypognathous, narrows at base, with a metallic luster. Antennae with ten segments, thin, attached above clypeus. Anterior tarsi simple, without pincerlike claws. Abdomen of hanging type, with first segment not separated from second segment by furrow or constriction. Length 3–5 mm (Fig. 1138). Paleogene to Recent. Three genera in the Recent fauna of the Holarctic (eight species), of which two also known from the Paleogene of Europe (Baltic amber).

355 Family BETHYLIDAE Haliday, 1840

Small or medium sized forms. Females wingless. In forewings of males costal area very narrow, hardly distinguishable. Pterostigma resembles a thickened vein; crossvein r-rs extends from apex of pterostigma up to middle of wing and continues further as anterior branch of RS, which occurs as a semicircle with convexity toward posterior side; stem of RS and its posterior branches absent; basal crossvein (r-m) straight; M branches proximal to middle of wing; both branches of M do not reach up to wing margin; Cu continues as posterior branch of M. Head prognathous; antennae, attached low, with 12 or 13 segments. Parasitic on larvae of beetles and Lepidoptera (Fig. 1139). Paleogene to Recent. About 100 genera found in Recent fauna (700 species); twenty-three genera from the Paleogene of Europe (Baltic amber), the Paleogene of Western Europe and the Neogene of South Asia (Burmese amber); two Recent genera also known from the Quaternary deposits of East Africa.



Figs. 1138–1141. Superfamily Bethyloidea.

1138. *Embolemus breviscapus* Brues; lateral view, × 8. Paleogene, Europe (Baltic amber) (Brues, 1933). 1139. *Holepyris praecursor* Brues; lateral view, × 23.5. Paleogene, Europe (Baltic amber) (Brues, 1933). 1140. *Pentachrysis imperiosa* Sm.; dorsal view, × 6.5. Recent (Tillyard, 1926). 1141. *Lestodryinus mortuorum* Brues; lateral view, × 10. Paleogene, Europe (Baltic amber) (Brues, 1933).

Family CHRYSIDIDAE Latreille, 1802. Cuckoo wasps

[nom. transl. Bomer, 1919 (ex Chrysidides Latreille, 1802)]

Small or medium sized insects. Length 2–18 mm. Body colored, with a metallic luster. Costal area narrow, but clearly distinguishable; pterostigma distinct; basal crossvein (r-m) curved as a semicircle, terminates on radius at place of origin of stem of RS; RS long, smoothly curved, with convexity toward posterior side, connected with anterior branch of M; anterior branch of RS with a reduced
356 base, directly leaving crossvein r-rs somewhat distal to middle of wing, with straight tip; M branches at middle of wing; Cu ends at anal margin of wing, at level of branching of M. Head as broad as thorax; antennae attached low, with 13 segments. Abdomen of females with three, rarely four segments (in males with three to five), remaining segments transformed into tubelike ovipositor, retracted into abdomen. Parasitic in nests of Vespidae and Sphecidae (Fig. 1140). Paleogene to Recent. In the Recent fauna about 40 genera and 1,500 species distributed mainly in tropics and subtropics; three genera from the Paleogene of Europe (Baltic amber) and the Miocene of North America.

Family DRYINIDAE Haliday, 1833

Small insects, resemble ants. Size ranges from 2.4 to 7 mm. Females often wingless. In forewings costal area narrow, but distinct; pterostigma oval; basal crossvein short and slanting; RS leaves R proximal to middle of wing; stem of RS slanting, branches at level of origin of crossvein r-rs; crossvein inclined, appears to continue as curved anterior branch of RS; free base of anterior branch of RS resembles a crossvein; subradial and first radial cells elongate, inclined; M branches a little distal to origin of RS, both its branches reach wing margin; Cu continues as posterior branch of M. Head large, transverse, hypognathous; antennae attached on dorsal part of clypeus, with 10 segments. Prothorax often elongated; femora inflated at base; anterior tarsi with pincer-like segment and claw. Abdomen pendulous. Parasitic on nymphs and adults of Fulgoridae and Cicadellidae (Fig. 1141). Paleogene to Recent. About 16 widely distributed genera in the Recent fauna, of which three also known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CRETAVIDEA

Differ from all known hymenopterans in the well-preserved branching of branches of RS and M, which make them resemble primitive Mecopterans; first radial cell located over subradial, placed slightly one above the other; discoidal cell closed, in close contact with the subradial cell for a long distance. Cretaceous. Family: Cretavidae.

Family CRETAVIDAE Sharov, 1957

Costal area clearly visible, wider than usual; pterostigma not large; inclined basal crossvein directly passes over to base of RS; two crossveins between branches of RS, proximal one continues as crossvein r-rs; M branches almost at middle of wing; two crossveins between M and Cu; Cu ends at anal margin of wing at level of branching of RS. Cretaceous. One genus.

Cretavus Sharov, 1957. Genotype—*C. sibiricus* Sharov, 1957; Lower Cretaceous, Krasnoyarski district (Senonian, B. Kas). RS branches slightly proximal to point of fusion of its posterior branch with anterior branch of M; two cells between branches of RS; discoidal cell triangular, narrow, smaller than adjacent cell; subradial cell larger than discoidal cell, and somewhat smaller than first radial cell; crossvein r-rs and vein closing discoidal cell in a single line. Length of forewing 10 mm (Fig. 1142). Lower Cretaceous of East Siberia.

SUPERFAMILY SCOLIIDEA

Usually large insects. Females wingless. Costal area absent; pterostigma small; two crossveins lie between branches of RS, but base of anterior branch of RS reduced; subradial and discoidal cells do not touch; medial cell closed, broad, stretched along its width. Paleogene to Recent. Families: Scoliidae (outside the USSR) and Mutillidae represented in fossil form.

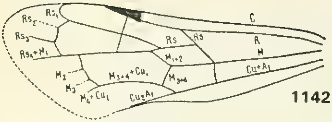
Family MUTILLIDAE Latreille, 1802. Velvet-ants

[nom. transl. Stephens, 1829 (ex Mutillariae Latreille, 1802)]

Varied size; length ranges from 5 to 30 mm. Females wingless. Head hypognathous; antennae simple with 12 or 13 segments, attached low. Pronotum with a grooved posterior margin; middle coxae in close contact; fore femora not thickened; first segment of hind tarsi cylindrical. Abdomen, pendulous, with six or seven segments; first segment separated from the second by a deep furrow or constriction. Parasites of larvae and pupae of bees and wasps, as an exception, of beetles (Fig. 1143). Paleogene to Recent. In the Recent fauna 11 genera and several thousand species, mainly in tropics and subtropics; one extinct genus known from Baltic amber.

357 SUPERFAMILY FORMICIDEA. Ants

Forms of varying size; from 2 to 25 mm in length. Divided into winged males and females and infertile, wingless female workers. Wings with few veins; costal area present; pterostigma well developed; basal vein terminates on RS, forming a nearly quadrate subradial cell, as if "suspended" in the corner, without touching discoidal cell; one crossvein, between branches of RS or it may be absent; medial cell open; Cu ends at anal margin of wings; abdomen short, with pedicel; pedicel made up of first two segments; if only one segment in pedicel then with an outgrowth projecting upward seen on it. Paleogene to Recent. One family, Formicidae, with more than 5000 species in Recent fauna, particularly in the tropics; a few subfamilies, the following of which are known in fossil form: Ponerinae, Dolichoderinae, Myrmicinae, Formicinae; Pseudomyrmicinae; last one found outside the USSR.



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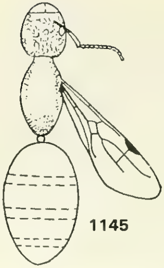

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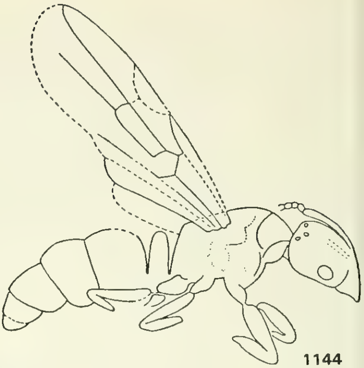

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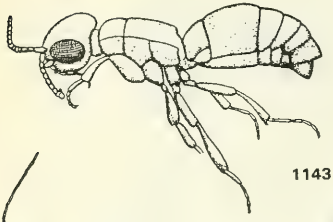

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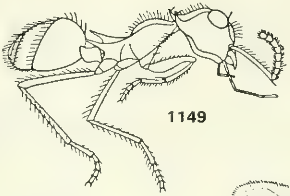

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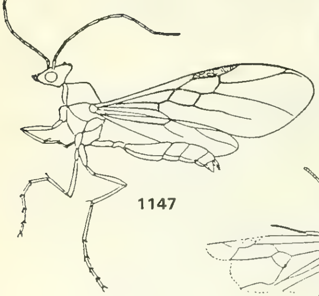

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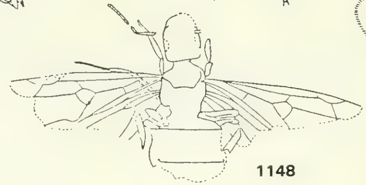

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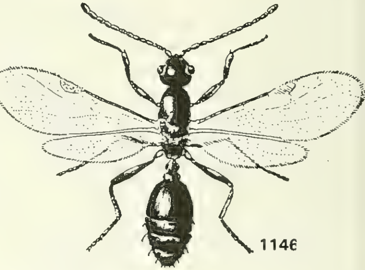

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Figs. 1142–1149. Superfamilies Cretavoidea, Formicoidea, Scolioidea.

1142. *Cretavus sibiricus* Sharov; forewing, × 4.7. Upper Cretaceous, Krasnoyarski region (Sharov, 1956). 1143. *Promutilla megalophthalma* Brues; lateral view, × 10. Paleogene, Europe (Baltic amber) (Brues, 1933). 1144. *Ponera umbrata* Popov; lateral view, × 10. Miocene, Caucasus (Popov, 1932). 1145. *Dolichoderus antiquus* Carpenter; dorsal view, × 6. Miocene, North America (Carpenter, 1930). 1146. *Monomorium minimum* Buckley; dorsal view. Recent (Essig, 1942). 1147. *Aeromyrma sophiae* Emery; lateral view, × 12. Mid Miocene, Amber of Sicily (Emery, 1890). 1148. *Lasius martynovi* Popov; dorsal view, × 3.7. Paleogene, Caucasus (Popov, 1932). 1149. *Gaesomyrmex corniger* Emery; lateral view, × 7.5. Mid Miocene, Amber of Sicily (Emery, 1890).

Subfamily Ponerinae Smith, 1851

[nom. transl. Dalla-Torre, 1893 (ex Poneridae Smith, 1851)]

Pedicel of abdomen made up of one segment, with a large, upright scale; postpedicel very large, as also third segment of abdomen, separated from fourth

358 by constriction. Forewing with large pterostigma; RS and M straight, almost parallel; discoidal cell closed, long (Fig. 1144). Paleogene to Recent. A few genera known from the Northern Hemisphere in the Recent fauna, mainly from the tropics; thirteen genera known from the Paleogene of Europe (including Baltic amber), the Caucasus, North and Southern America.

Subfamily Dolichoderinae Forel, 1878

[nom. transl. Dalla-Torre, 1893 (ex Dolichoderidae Forel, 1878)]

Small ants. Abdominal pedicel consists of one segment, sting rudimentary. In forewing small pterostigma present; RS coalesces with M up to its branching and hence closed discoidal cell appears to be sitting on the stalk; RS and M curved, do not reach wing margin (Fig. 1145). Paleogene to Recent. In the Recent fauna, primarily in the tropics; in fossil form 17 genera known from the Paleogene of Europe (Baltic amber), Western Europe and North America.

Subfamily Myrmicinae Smith, 1851

[nom. transl. Dalla-Torre, 1893 (ex Myrmicidae Smith, 1851)]

Largest and most widely distributed subfamily of ants. Pedicel consists of two segments, sting strongly developed. Forewings with fairly large pterostigma; RS coalesces with M up to its branching, but discoidal cell open; basal crossvein terminates on extreme base of RS; both branches of RS reach wing margin (Figs. 1146, 1147). Paleogene to Recent. 36 genera in fossil form from the Paleogene of Europe (Baltic amber), Western Europe and North America and the Quaternary deposits of East Africa.

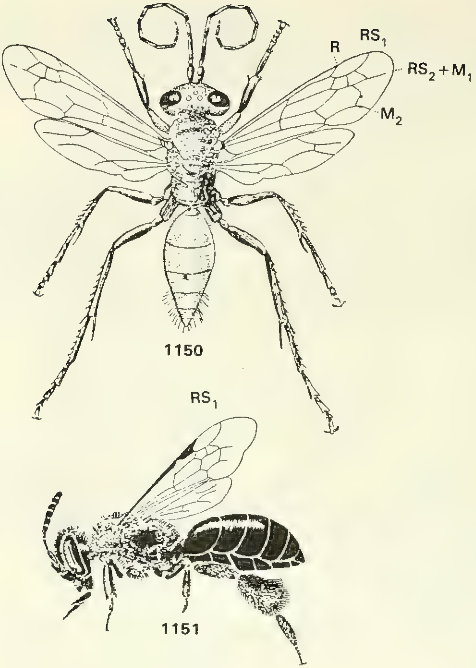
Subfamily Formicinae Mayr, 1855

[nom. transl. Ashmead, 1901 (ex Formicidae Mayr, 1855)]

Length of ants ranges from 2 to 20 mm. Pedicel consists of one segment. Cloacal opening produced into a tube, surrounded by a ring of hairs; sting absent. Venation usually highly reduced; either anterior branch of RS (*Lasius*) or posterior branch of M (*Camponotus*) may be absent; in the first case, closed subradial cell retained (Figs. 1148, 1149). Paleogene to Recent. In Recent fauna many widely distributed species (predominantly, warmth-loving); fifteen genera in fossil form known from the Paleogene of Europe (Baltic amber), Caucasus, Western Europe, Japan and North America.

SUPERFAMILY POMPILIDEA. Spider-wasps

Medium and large sized insects, length ranging from 5 to 27 mm. Variously colored, with metallic luster. In forewing costal area, pterostigma and basal crossvein rs-m clearly seen; RS branches up to its coalescence with M, hence subradial and discoidal cells in close contact; subradial cell long, longer than cells dc and rs_2 put together and longer than first radial cell; dominant radial



Figs. 1150–1151. Superfamilies Pompiloidea, Apoidea.

1150. *Calicurgus hyalinatus* Fabricius; dorsal view, × 4. Recent (Sharp, 1910). 1151. *Andrena* sp.; lateral view, × 5. Recent (Essig, 1942).

cell between R and M shorter than one-half of length of wing; medial cell closed; Cu ends distal to middle of wing on anal margin. Head as broad as or wider than pronotum; antennae long; eyes without distinct notch along inner margin. Legs long; posterior tibiae extend beyond tip of abdomen (Fig. 1150). Paleogene to Recent. Families: Pompilidae and Rhopalosomatidae; latter not known in fossil form.

359 Family POMPILIDAE Leach, 1815

[nom. transl. Leach, 1819 (ex Pompilidae Leach, 1815)]

Abdomen on a thin pedicel. Parasitic on spiders and a few hymenopterans. Paleogene to Recent. About 50 genera (3,000 species) in the Recent fauna, most widespread in the hot belt; seven genera known in fossil form from the Paleogene of Europe (Baltic amber), Western Europe and North America.

SUPERFAMILY APIDEA. Bees

Medium or large sized insects. Usually body hairy, rarely bare. Venation of wings very similar to that of Pompilidae, but differs in less obvious costal area and longer basal radial cell (r), which is one-half of wing length or more. Antennae geniculate, usually short. Pronotum with distinct protuberances in antero-lateral region; first segment of posterior tarsi usually broad, densely covered on inner side with hair, like a brush (Fig. 1151). Paleogene to Recent. Six families in the Recent fauna; only Apidae has fossil representatives.

Family APIDAE Latreille, 1802

[nom. transl. Leach, 1817 (ex Apiariae Latreille, 1802)]

Antennal socket connected with suture of fronto-clypeus by a simple suture; labial palps with two elongate segments; width of labrum greater than its length. Parasitic and social insects. Paleogene to Recent. Four subfamilies: many genera known in fossil form from the Paleogene of Europe (Baltic amber), East Siberia, South Asia (Burmese amber) and North America.

REFERENCES

360-374 Alexander, C.P. 1931. Crane-flies of the Baltic Amber (Diptera). Bernst-Forsch., No. 2. pp. 1–135.

Ander, K. 1939. Systematische Eintenung und Phylogenie der Ensileren (Saltatoria) aui Grund vergleichend-anatomischer Untersuchungen. Verh. VII. Intern. Kongr. f. Entomol. pp. 621–627.

Ander, K. 1942. Die Insekteniauna des Baltischen Bernstein nebst damit verknupft zoogeographischen Probleme. *Klng. Fyziograf.*, Sallsk. Handl., n.f., vol. 53, pp. 1–82.

André, E. 1895. Notice sur les fourmis fossiles de l'ambre de la Baltique et description de deux especes nouvelles. *Bull. Sec. Zool.* France, vol. 20, pp. 80–84.

Andrée, K. 1929. Bernsteinforschung einst und jetzt. *Bernst. Forsch.*, No. I, pp. 1–32.

Andrée, K. 1936. Die wissenschaftliche Bedeutung des Bernsteins und neuere Bernsteinforschungen. *Forsch. u. Fortschr.*, vol. 12, pp. 357–359.

Andrusov, N. 1916. Trubki chervei iz semeistva Amphictenidae v russkom miotsene. (Worm tubes of the family Amphictenidae from the Russian Miocene). *Izv. imp. Acad. Nauk.* SPb., pp. 227–232.

Assmann, A. 1870. Beitrage zur Insektenfauna die Vorwelt. Ztschr. f. Entomolgie Herausgeg. vom. Verein fur Schles. Insektenkunde zu Breslau (N.F.), I Heft. Breslau.

Assmann, A. 1877. Uber die von Germar beschriebenen und im palaeontologischen Museum zu Munchen befindlichen Insecten aus dem litographischen Schiefer in Bayern. Amtl. Bericht. der 50 Versamml. deufsch. Naturf und Arzte I. Munchen, pp. 191–192.

Backer, A.L. 1920. The generic classification of the Hemipterous family Aphididae. U.S. Dept. Agric. Bull. No. 826, p. 89.

Backer, A.L. 1922. Two new aphids from Baltic Amber. *J. Wash. Acad. Sci.*, vol. 12, pp. 353–358.

Backer, A.L. 1930. Beitrage zu einem System Blattlause. *Arch. f. klassifikatorische u. phylogenetische Entomol*; vol. 1, No. 2, pp. 115–194.

Bagnal, R.S. 1912. Some considerations in regard to the classification of the order Thysanoptera. *Ann. Mag. Nat. Hist.*, vol. 10, No. 8, pp. 220–222.

Bagnal, R.S. 1914. On *Stenurothrips succineus* gen. et. sp. nov., an interesting tertiary Thysanopteron. *Geol. Mag.*, vol. I, pp. 483–485.

Bagnal, R.S. 1923. Fossil Thysanoptera. I. Terebrantia, Pt. I. *Entomol. Monthly Mag. London*, vol. 59, pp. 35–38.

Bagnal, R.S. 1924. Von Schlechtendal's work on fossil Thysanoptera in the light of recent knowledge. *Ann. Mag. Nat. Hist. London*, ser. 9, vol. 14, pp. 156–161.

Bagnal, R.S. 1924. Fossil Thysanoptera II–III. *Entomol. Monthly Mag. London*, vol. 60, pp. 130–132, 251–252.

Bagnal, R.S. 1926. Fossil Thysanoptera. IV. *Entomol. Monthly Mag.*, vol. 62, pp. 16–17.

Bagnal, R.S. 1920. On the Australian Thysanoptera allied to the genus *Odontothrips. Entomol. Monthly Mag.*, vol. 65, pp. 47–49.

Bakkendorf, O. 1948. A comparison of a Mymarid from Baltic famber with a recent species, *Petiolaria anòmala* (Microhymen). *Entomol. Medd., Compenhagen*, vol. 25, pp. 213–218.

Barbu, J.Z. 1942. *Pentatoma* sp. dans la sarmatien de Mehn (dep. de Silin). *Bull. Sect. Sci. Acad.* Roumaine Bukarest., vol. 24, pp. 562–564.

Bei-Bienko, G.Ya. 1936. Nasekomye Kozhistokrylye. *Fauna SSSR* (Insects: Earwigs. Fauna USSR). *Izd. Zool. in-ta AN SSSR*, Nov. Ser., No. 5, pp. 1–239.

Bei-Bienko, G.Ya. 1950. Nasekomye tarakanobye. *Fauna SSSR* (Insects: Cockroaches. Fauna USSR). *Izd. Zool. in-ta AN SSSR*. Nov. Ser., No. 40.

Bekker, E.G. 1952–1954. K. Voprosu o proickhozhlenii kryla Nasekomykh (On origin of wings of insects). Pt. 1. *Vestn. Mosk. Un-ta*, 1952, No. 9, pp. 59–68; Pt. 2, 1954, No. 5, pp. 119–130.

Bekker-Migdisova, E.E. 1940. Iskopaemye permckie tsikadi semeistva Prosbolidae s.r. Soyany (Permian fossil cicadas of family Prosbolidae from Soyan). *Tr. Paleontol. in-ta. AN* SSSR, vol. 9, No. 2, pp. 5–79.

Bekker-Migdisova, E.E. 1946, 1948. Ocherki po sravnitelnoi morphologii sovremenykh i permskikh Homoptera (Essays on the comparative morphology of Recent and Permian Homoptera). Pt. 1, *Iz. AN SSSR, Ser. biol.* No. 6 (1946), pp. 741–766; Pt. 2, *Ser. biol.*, No. 1 (1948), pp. 123–142.

Bekker-Migdisova, E.E. 1947. *Cicadoprosbole* gen. et. sp. nov.—perekhodnaya forma Mezhdy permskimi Prosbolidae i sovremennymi Cicadidae (*Cicadoprosbole* gen. et. sp. nov.—transitional form between Permian Prosbolidae and Recent Cicadidae). *Dokl. AN SSSR*, No. 5, pp. 445–448.

Bekker-Migdisova, E.E. 1948. Tipy izmenchivosti zhilkobaniya Krylev Homoptera (Types of variability in wing venation of Homoptera). *Izv. AN SSSR*. Ser. biol., No. 2, pp. 87–92.

Bekker-Migdisova, E.E. 1948. Permskie tsikady semsistva Scytinopteridae s.r. Soyany. (Permian Cicadadas of family Scytinopteridae from Soyan). *Tr. Paleontol. in-ta AN SSSR*, vol. 15, No. 2, pp. 1–42.

Bekker-Migdisova, E.E. 1949a. Mezozoiskie Homoptera Srednei Azii (Mesozoic Homoptera of Central Asia). *Tr. Paleontol. in-ta AN SSSR*, vol. 22, pp. 1–68.

Bekker-Migdisova, E.E. 1949b. Novoe permskoe semeistvo Boreoscytidae i voproc o fylogenii predkov Homoptera (New Permian family Boreoscytidae and problem of phylogeny of ancestors of Homoptera). *Tr. Paleontol. in-ta AN SSSR*, vol. 20, pp. 171–182.

Bekker-Migdisova, E.E. 1950. Yuriskie Paleontinidae novogo mestonakhozhdeniya na r. Ii (Jurassic Paleontinidae from a new locality on r. Ii). *Dokl. AN SSSR*, vol. 71, No. 6, pp. 1105–1108.

Bekker-Migdisova, E.E. 1951. Svoeobrasnye novye iskopaemye nasekomye iz gruppy paraneopter (Peculiar new fossil insects from paraneopterous groups). *Dokl. AN SSSR*, vol. 78, No. 6, pp. 1207–1210.

Bekker-Migdisova, E.E. 1952. Novye ravnokrylye is permi Kuzbassa i nekototye zamechaniya ob ipsvichiidakh (New Homoptera from Permian Kuznetsk basin and some observations on ipsviichids). *Tr. Paleontol. in-ta AN SSSR*, vol. 40, pp. 177–186.

Bekker-Migdisova, E.E. 1953a. Obzor fauny ravnokrylykh i senoedov erunakovskoiu kuznetskoi svit Kuzbassa (A survey of homopteran and book lice fauna from the Erunakovian and Kuznetski series of Kuznetsk Basin). *Dokl. AN SSSR*, vol. 90, No. 1, pp. 97–100.

Bekker-Migdisova, E.E. 1953b. Pervaya naxodka senoeda (Psocoptera) iz Kuznetskogo basseina (First discovery of book lice (Psocoptera) from the Kuznetsk Basin). *Dokl. AN SSSR*, vol. 90, No. 2, pp. 279–282.

Bekker-Migdisova, E.E. 1953c. Dva predstavitelya poluzhestkokrylykh Nasekomykh iz urochisha Madygen (Two representatives of heteropterous insects from Madgeny area). *Dokl. AN SSSR*, vol. 90, No. 3, pp. 461–464.

Bekker-Migdisova, E.E. 1954. Nakhodka yuzhnoi tsikady v Miiotsene zapadnoi Sibiri. Voprosy geologic Asii (Discovery of a southern cicada from the

Miocene of Western Siberia. Problems on geology of Asia). vol. 1, *Izd. AN SSSR*, pp. 799–805.

Bekker-Migdisova, E.E. 1955. Iskonaemye Nasekomye iz Triasa Sibiri (Fossil Insects from the Triassic of Siberia). *Dokl. AN SSSR*, vol. 105, No. 5, pp. 1100–1103.

Bekker-Migdisova, E.E. 1957. K voprosy ob evolyutsii ravnokrylykh (Homoptera) (On the evolution of the Homoptera) Tezisy. dokladov III soveshch, Vses. *Entomol. Ob-va.*

Bekker-Migdisova, E.E. 1958. Novye iskopaemye ravnokrylye (New fossils of Homoptera). Pt. 1. 1—Novye drevnee kamennougalnoe ravnokrylye iz Kuznetskogo basseina. (New early Carboniferous Homoptera from the Kuznetsk basin). 2—Novoe semeistvo Cicadocaridae i drevnie Coleorrhyncha. (New family Cicadocaridae and ancient Coleorrhyncha). 3—Predstaviteli cemeistva Membracidae iz verkhnego triasa Srednei Azii. (Representatives of the family Membracidae from the Upper Triassic of Central Asia). Materialy K "*Osnovam paleontologii*", vol. 2, pp. 57–67.

Bekker-Migdisova, E.E. 1959. Novye rod Borisrohdendorfia (Homoptera) iz Kuznetskogo basseina (New genus Borisrohdendorfia (Homoptera) from the Kuznetsk Basin). *Paleontol. Zhurn.*, No. 3, pp. 138–140.

Bekker-Migdisova, E.E. 1960a. Novye permskie ravnokrylye Evropeiskoi chasti SSSR (New Permian Homoptera from the European part of USSR). *Tr. Paleontol. In-ta AN SSSR*, vol. 76, pp. 1–112.

Bekker-Migdisova, E.E. 1960b. Nekotorye novye predstaviteli gruppy sternorinkh iz permi i mezozoya SSSR (Some new representatives of Sternorhyncha from the Permian and Mesozoic of USSR). Materialy K '*Osnovam Paleontologii*', vol. 3, pp. 109–116.

Bekker-Migdisova, E.E. 1960c. Paleozoiskie ravnokrylye SSSR i voprosy filogenii otryada (Paleozoic Homoptera of the USSR and problems of phylogeny of the order). *Paleontol. Zhurn.*, No. 3, pp. 28–42.

Bekker-Migdisova, E.E. 1960. Die Archescytinidae als vermutliche Vorfahren der Blattlause. *XI Intern. Kongress f. Entomol. Verhandlungen.* vol. 1, pp. 298–301.

Bekker-Migdisova, E.E. 1962. Nekotorye Novye poluzhestkokrylye u senoedy (Some new Heteroptera and book lice). *Paleontol. Zhurn.*, No. 1, pp. 89–104.

Bekker-Migdisova, E.E. and O.M. Martynova. 1951. Mestonokhozhgenie miotsenovykh Nasekomykh v Terskom Alatay i tsikada iz nego (Occurrence of Miocene insects in Tersk Altai and cicadas therefrom). *Dokl. AN SSSR*, vol. 78, No. 4, pp. 761–763.

Bequaert, J.C. 1947. Catalogue of recent and fossil Nemestrinidae of North America. *Psyche*, vol. 54, pp. 194–207.

Berendt, G.C. 1830. Die Insekten im Bernstein, ein Beitrag zur Tiergeschichte der Vorwelt. Danzig, 4°, No. 1. pp. 1–38.

Berendt, G.C. 1856. Die in Bernstein befindlichen organischen Reste der

Vorwelt, vol. II. I. Abt. Die im Bernstein befindlichen Hemipteren und Orthopteren der Vorwelt.

Bischoff, H. 1916. Bernsteinhymenopteren. *Schr. phys.-okon. Ges. Konigsberg*, vol. 56, pp. 139–144.

Bode, A. 1953. Die Insekteniauna des Ostnicdersachsischen oberen Lias. *Palaeontographica*, vol. 103. Abt. A. Lief. 1–4, pp. 1–375.

Bogachev, A.E. 1948. Fauna binagadinskikh kirovykh plastov. Zhyki: Coleoptera (Fauna of the Binagadinian and Kirovian beds. Beetles: Coleoptera). *Tr. Est. istor. myzeya* AN Azerb SSR, byp. I and II, pp. 137–160.

Bolivar, C. 1926. Sobre une nuova familia de Coleopteros. *Eos*, vol. 2, pp. 202–204.

Bolton, H. 1910. On a new species of fossil Cockroach from the South Wales Coalfield. *Geol. Mag.*, vol. 7, pp. 147–151.

Bolton, H. 1912. Insect remains from the Midland and South-Eastern Coal Measures. *Quart. Journ. Geol. Soc. London*, vol. 68, pp. 310–323.

Bolton, H. 1916. The Mark Stirrup Collection of Fossil Insects. *Mem. Proc. Machester Soc.*, vol. 61, No. 2, pp. 1–24.

Bolton, H. 1917. On Blattoid and other insect remains from the South Staffordshire Coalfield. *Mem. and Proc., Birmingham Nat. Hist. and Phil. Soc.*, vol. 14, pp. 100–106.

Bolton, H. 1919. A monograph of the fossil insects of the British Coal Measures. Pt. I. *Paleontographical Soc.*, vol. 73.

Bolton, H. 1920. *Paleontographical Soc.*, pt. II, pp. 81–159.

Bolton, H. 1921. A new species of Blattoid (*Archimylacris*) from the Keele Group (Radstockian) of Shrophshire. *Quart. Journ. Geol. Soc. London*, vol. 77, pp. 23–29.

Bolton, H. 1921. A monograph of the fossil insects of the British Coal Measures. *Palaeontographical Soc.*, pts. I, II; pp. 1–80, 81–105.

Bolton, H. 1923. On a New Blattoid wing from the Harrow Hill Mine, Drybrook (Forest of Dean). *Abst. Proc. Geol. Soc. London*, vol. 23, p. 93.

Bolton, H. 1924. On a new form of Blattoid from the Coal Measures of the Forest of Dean. *Quart. Journ. Geol. Soc. London*, vol. 80, pp. 17–21.

Bolton, H. 1925. Insects from the Coal Measures of Commentry. *Brit. Mus., fossil insects*, No. 2, pp. 1–56.

Bolton, H. 1930. Fossil insects of the South Wales Coalfield, pt. I. *Quart. Journ. Geol. Soc. London*, vol. 86, pp. 9–19.

Bolton, H. 1932. On the occurrence of a Blattoid hindwing in the Bristol Coal Measures. *Rep. Bristol Nat. Soc.* (1931), vol. 7(4), pp. 259–260.

Bolton, H. 1934. New forms from the insect fauna of British Coal Measures. *Quart. Journ. Geol. Soc. London*, vol. 20, pt. 3, pp. 277–301.

Borkhsenius, N.S. 1950. Chervetsy i schitovki SSSR (Scales and armored scales of the USSR). *Izd. AN SSSR*, pp. 1–250.

Brauer, F., J. Redtenbacher and L. Ganglbauer. 1889. Fossile Insekten aus der

Juraformation Ost-Sibiriens. *Zap. imp. akad. nauk. SPb.*, Ser. t, vol. 36, No. 15, pp. 1–22.

Brauer, F. 1851. Verwandlungsgeschichte des Osmylus maculatus. *Arch. Natürg.*, Jahrg. 17. vol. 1, p. 255.

Brauer, F. 1886. Ansichten uber die palaeozoischen Insekten und deren Deutung. *Ann. kk. Naturh. Holmus.*, Wien, vol. 1, pp. 87–125.

Brauer, F., J. Redtenbacher and L. Ganglbauer. 1889. Fossile Insekten aus der Juraformation Ost-Sibiriens. *Mem. Acad. Imp. Sic. St. P.* ser. 7, t. 36, No. 15, pp. 1–22.

Brischke, D. 1886. Die Hymenopterenddes Bernsteins. *Schr. Naturf. Ges. Danzig*, n. f., vol. 6, No. 3, pp. 278–279.

Britten, H. 1936. Insects Remains from Peat Beds of Rhyl. and Prestatyn. *Proc. Liverpool Geol. Soc.*, vol. 17, pp. 61–63.

Brodie, P.B. 1845. A history of the fossil insects in the secondary Rocks of England. London, pp. 1–130.

Brodie, P.B. 1854. On the Insect Beds of the Purbeck Formation in Wiltshire and Dorsetshire. *Quart. Journ. Geol. Soc. London*, vol. 10, pp. 475–482.

Brodie, P.B. 1873. The distribution and correlation of fossil insects, and the supposed occurrence of Lepidoptera and Arachnidae in British and Foreign Strata, chiefly in the Secondary rocks. *Ann. Rep. Warwickshire Nat. Hist. Soc.*, vol. 37, pp. 12–18.

Brongniart, C. 1885. Les Insectes fossiles des terrains primaires. *Bull. Soc. Amis Sci. Nat. Rouen*, vol. 21, No. 3, pp. 50–68.

Brongniart, C. 1893. Recherches pour servir a l'histoire des insectes fossiles de temps primaires. Etudes sur le terrain houiller de Commentry. III. Faune entomologique. Saint-Etienne.

Brues, C.T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bull. Mus. Comp. Zool.*, vol. 54, pp. 1–125.

Brues, C.T. 1910. Some notes on the geological history of the parasitic Hymenoptera. *N.Y. Journ. Ent. Soc.*, vol. 18, pp. 1–22.

Brues, C.T. 1923. Some new fossil parasitic Hymenoptera from Baltic amber. *Proc. Amer. Acad. Arts and Sci. Boston*, vol. 53, pp. 327–346.

Brues, C.T. 1923. A fossil genus of Dinapsidae from Baltic amber. *Psyche. Boston. Mass.*, vol. 30, pp. 31–35.

Brues, C.T. 1923. Ancient insects; fossils in amber and other deposits. *Sci. Monthly*, vol. 17, No. 19, pp. 280–304.

Brues, C.T. 1926. A species of *Urocerus* from Baltic amber. *Psyche. Boston. Mass.*, vol. 33, pp. 168–169.

Brues, C.T. 1933. Progressive change in the insect population of forests since the early Tertiary. *Amer. Nat.*, vol. 67, pp. 385–406.

Brues, C.T. 1933. The Parasitic Hymenoptera of the Baltic amber. *Bernst. Forsch.*, No. 3, pp. 4–178.

Brues, C.T. 1937. Insects and Arachnids from Canadian amber. *Univ. Toronto Stud., geol. ser.*, No. 40, pp. 7–55.

Brues, C.T. 1939. Fossil Phoridae in Baltic amber. *Bull. Mus. Comp. Zool. Harvard*, vol. 85, No. 6, pp. 1–26.

Brues, C.T. 1939. New Oligocene Braconidae and Bethylidae from Baltic amber. *Ann. ent. Soc. Amer. Columbus*, vol. 32, pp. 251–263.

Brues, C.T. 1940. Serphidae in Baltic amber, with the description of a new living genus. *Proc. Amer. Acad. Arts and Sci.*, vol. 73, No. 9, pp. 259–269.

Brues, C.T. 1940. Fossil parasitic Hymenoptera of the family Scelionidae from Baltic amber. *Proc. Amer. Acad. Arts and Sci.*, vol. 74, pp. 69–90.

Brues, C.T. and A.L. Melander. 1932. Classification of insects. *Bull. Mus. Compar. Zool. at Harward College*, vol. 73, pp. 61–65.

Burchardt, 1929. List of genera of insects found in Upper Triassic. *Abh. Schweiz. Paleontol. Ges.*, vol. 49, No. 4, p. 123.

Burr, M. 1899. Essai sur les Eumastacides. *Ann. Soc. Esp. Hist. Nat.*, vol. 28, pp. 1–94.

Burr, M. 1903. Eumastacidae. Genera Insectorum, fasc. 15.

Burr, M. 1909. Notes on the classification of the Dermaptera. *Dtsch. Entomol. Zfschr.*, p. 320.

Burr, M. 1911. Dermaptera preserved in amber from Prussia. *Trans. Linn. Soc. London*, 2, ser., vol. 2, pt. 8, pp. 145–150.

Cabrera, A. 1928. Un segundo ortoptero del Triasico Argentino, *Eos*, vol. 4, pp. 371–373.

Carpenter, F.M. 1926. Fossil insect from the Lower Permian of Kansas. *Bull. Mus. Comp. Zool. Harward Coll.*, vol. 67, No. 13, pp. 437–444.

Carpenter, F.M. 1929. A Jurassic Neuropteron from the lithographic limestone of Bavaria. *Psyche*, vol. 36, No. 3, pp. 190–194.

Carpenter, F.M. 1930a. The fossil ants of North America. *Bull. Mus. Comp. Zool. Harvard Coll.*, vol. 70, No. 1, pp. 1–66.

Carpenter, F.M. 1930b. Um Blattide Permiano do Brasil. *Boletin Servico Geologico E. Mineralogico do Brasil*, vol. 50, pp. 5–10.

Carpenter, F.M. 1930c. The Lower Permian insects of Kansas, pt. I. Introduction and the order Mecoptera. *Bull. Mus. Comp. Zool. Harvard Coll.*, vol. 70, No. 2, pp. 69–101.

Carpenter, F.M. 1931. The Affinities of *Holcorpa maculosa* Scudder, and other Tertiary Mecoptera. *Journ. N.Y. Entomol. Soc.*, vol. 39, pp. 405–414.

Carpenter, F.M. 1931a. Revision of the Nearctic Mecoptera. *Bull. Mus. Comp. Zool. Harvard Coll.*, vol. 72, pp. 205–277.

Carpenter, F.M. 1931b. Insects from the Miocene (Latah) of Washington. 6. Tricoptera. *Ann. Entomol. Soc. Amer.*, vol. 24, No. 2, pp. 319–322.

Carpenter, F.M. 1931c. The Lower Permian insects of Kansas, pt. 2. The orders Palaeodictyoptera, Protodonata, and Odonata. *Amer. Journ. Sci.*, vol. 21, pp. 97–139.

Carpenter, F.M. 1931d. The Lower Permian insects of Kansas, pt. 3. The Protohymenoptera. *Psyche*, vol. 37, No. 4, pp. 343–374.

Carpenter, F.M. 1931e. The Lower Permian insects of Kansas, pt. 4. The order

Hemiptera, and additions to the Paleodictyoptera and Protohymenoptera. *Amer. Journ. Sci.*, vol. 22, pp. 113–130.

Carpenter, F.M. 1932a. Critical Notes on Jurassic insects from Solenhofen, Bavaria. *Ann. Carnegie Mus.*, vol. 21, No. 3, pp. 97–129.

Carpenter, F.M. 1932b. The Lower Permian insects of Kansas, pt. 5. Psocoptera and addition to the Homoptera. *Amer. Journ. Sci. New Haven*, vol. 24(5), pp. 1–22.

Carpenter, F.M. 1933a. A new Megasecopteron from the Carboniferous of Kansas. *Bull. Univ. Kansas*, vol. 21, No. 10, pp. 365–367.

Carpenter, F.M. 1933b. The Lower Permian insects of Kansas, pt. 6. Delopteridae. Protelytroptera, Plectoptera and a New Collection of Protodonata, Odonata, Megasecoptera, Homoptera, and Psocoptera. *Proc. Amer. Acad. Arts and Sci.*, vol. 68, No. 2, pp. 411–503.

Carpenter, F.M. 1934. Carboniferous insects from Pennsylvania in the Carnegie Museum and the Museum of Comparative Zoology. *Ann. Carnegie. Mus. Pittsburg*, vol. 22, pp. 323–342.

Carpenter, F.M. 1935a. Tertiary insects of the family Chrysopidae. *Journ. Paleontol.*, vol. 9, No. 3, pp. 259–271.

Carpenter, F.M. 1936a. Lower Permian insects of Kansas, pt. 7. The order Protoperlaria. *Proc. Amer. Acad. Arts and Sci.*, vol. 70, No. 4, pp. 101–146.

Carpenter, F.M. 1936b. Revision of the nearctic Raphidiodea (recent and fossil). *Proc. Amer. Acad. Arts and Sci.*, vol. 71, No. 2, pp. 89–157.

Carpenter, F.M. 1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Amer. Journ. Sci.*, vol. 36, No. 216, pp. 445–452.

Carpenter, F.M. 1939. The Lower Permian Insects of Kansas, pt. 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plecoptera and Protoperlaria. *Proc. Amer. Acad. Arts and Sci.*, vol. 73, No. 3, pp. 29–70.

Carpenter, F.M. 1940. Carboniferous insects from the Stanton Formation, Kansas. *Amer. Journ. Sci.*, vol. 38, pp. 636–642.

Carpenter, F.M. 1943a. Osmvlidae of the Florissant shales, Colorado. *Amer. Journ. Sci.*, vol. 241, pp. 753–760.

Carpenter, F.M. 1943b. Studies on carboniferous insects from Commentry, France, pt. I. Introduction and families Protogriidae, Meganeuridae and Campylopteridae. *Bull. Geol. Soc. Amer.*, vol. 54, pp. 527–554.

Carpenter, F.M. 1943c. The Lower Permian insects of Kansas, pt. 9. The orders Neuroptera, Raphidiodea, Caloneurodea and Protorthoptera (Probnisidae), with additional Protodonata and Magasecoptera. *Proc. Amer. Acad. Arts and Sci.*, vol. 75, No. 2, pp. 55–84.

Carpenter, F.M. 1943d. Carboniferous insects from the vicinity of Mazon Greak, Illinois, State of Illinois. *Scientif. Papers*, vol. 3, pt. I, pp. 9–20.

Carpenter, F.M. 1947. Lower Permian insects from Oklahoma, pt. I. Introduction and the orders Megasecoptera, Protodonata and Odonata.

Proc. Amer. Acad. Arts and Sci., vol. 76, No. 2, pp. 25–54.

Carpenter, F.M. 1956. The Lower Permian insects of Kansas, pt. 10. The order Protorthoptera, the family Liomopteridae and its relatives. *Proc. Amer. Acad. Arts and Sci.*, vol. 78, No. 4, pp. 185–218.

Carpenter, F.M. 1951. Studies on Carboniferous insects from Commentry, France, pt. II. The Megasecoptera. *Journ. Paleontol.*, vol. 25, No. 3, pp. 336–355.

Carpenter, F.M. 1954. The Baltic amber Mecoptera. *Psyche*, vol. 61, No. 1, pp. 31–40.

Carpenter, F.M. and F.M. Hull. 1939. The fossil Pipunculidae. *Berast.-Forsch.* No. 4, pp. 8–17.

Carpenter, F.M. and A.K. Miller. 1937. A Permian insect from Coahuila, Mexico. *Journ. Paleontol.*, vol. 10, No. 5, pp. 395–409.

Carpenter, F.M., T.E. Snyder, C.P. Alexander, M.T. James and F.M. Hull. 1938. Fossil insects from the Creide Formation, Colorado, pt. I. Introduction, Neuroptera, Isoptera and Diptera. *Psyche*, vol. 45, No. 23, pp. 105–118.

Candell, A.N. 1911. Orthoptera fam. Locustidae. Subfam. Prophalangopsidae. *Genera Insectorum*, fasc. 120. 7 pp, Brussels.

Chernova, O.A. 1961. O sistematicheskom polozhenii i geologicheskom vozraste podenok roda Ephemeropsis Eichwald (Ephemeroptera, Hexagenitidae) [On the systematic position and geological age of the mayflies of the genus *Ephemeropsis* Eichwald (Ephemeroptera, Hexagenitidae)]. *Entomol. Obozren.*, vol. 40, No. 4, pp. 858–869.

Chernova, O.A. 1962. Lichinki podenki iz Neogena zapadnoi Sibiri (Ephemeroptera, Heptagenitidae) [Larvae of Ephemeroptera from the Neogene of Western Siberia (Ephemeroptera, Heptagenitidae)]. *Zoolog. zhurn.*, vol. 41, No. 6, pp. 943–945.

Chopard, L. 1936. Un remarquable genre d'Orthopteres de l'ambre de la Baltique. Livre Jubilaire E.L. Bouvier, Paris, pp. 163–168.

Chopard, L. 1936. Orthopteres fossiles et sub-fossiles de l'ambre et du Copal. *Ann. Soc. Ent. France*, vol. 105, pp. 375–386.

Cockerell, T.D.A. 1906a. A fossil Cicada from Florissant, Colorado. *Bull. Amer. Mus. Nat. Hist.*, vol. 22, pp. 457–458.

Cockerell, T.D.A. 1906b. Fossil Hymenoptera from Florissant, Colorado. *Bull. Mas. Compar. Zool. Harward Coll.*, vol. 50, No. 2, pp. 33–57.

Cockerell, T.D.A. 1908a. Description of tertiary insects. *Amer. Journ. Sci.*, vol. 25, pp. 51–52.

Cockerell, T.D.A. 1908b. Descriptions of tertiary insects, pt. IV. Dragonflies from Florissant, Colorado. *Amer. Journ. Sci.*, vol. 26, pp. 69–75.

Cockerell, T.D.A. 1908c. Fossil insects from Florissant. *Bull. Amer. Mus. Nat. Hist.*, vol. 24, pp. 59–69.

Cockerell, T.D.A. 1909a. A catalogue of the generic names based on American insects and Arachnids from the Sartiary Rocks with indications of the type species. *Bull. Amer. Mus. Nat. Hist.*, vol. 26, p. 78.

Cockerell, T.D.A. 1909b. Descriptions of Hymenoptera from Baltic amber. Schr. phys. okon. Ges. Konigsberg, vol. 50, No. 1, pp. 1–20.

Cockerell, T.D.A. 1909c. Some additional bees from Prussian amber. *Schr. phys. okon. Ges.* Konigsberg, pp. 21–25.

Cockerell, T.D.A. 1911. Fossil insects from Florissant, Colorado. *Bull. Amer. Mus. Nat. Hist.*, vol. 30, pp. 71–82.

Cockerell, T.D.A. 1912. The oldest American Homopterous insect. *Canad. Entomol.*, vol. 44, pp. 93–95.

Cockerell, T.D.A. 1912. *Entomol. News*, vol. 23, p. 228.

Cockerell, T.D.A. 1913. Bees of the genus *Megachile* from Australia. *Entomologist*, London, vol. 46, pp. 165–168.

Cockerell, T.D.A. 1914. New and little known insects from the Miocene of Florissant, Colorado. *Journ. Geol. Chicago*, vol. 22, pp. 714–724.

Cockerell, T.D.A. 1915. British fossil insects. *Proc. U.S. Nat. Mus.*, vol. 49, No. 2119, pp. 469–499.

Cockerell, T.D.A. 1916. Insects in Burmese amber. *Amer. Journ. Sci.*, vol. 42, pp. 135–138.

Cockerell, T.D.A. 1917. Arthropods in Burmese Amber. *Amer. Journ. Sci.*, vol. 44, 4 seri., pp. 360–368.

Cockerell, T.D.A. 1917. Some fossil insects from Florissant, Colorado. *Proc. U.S. Nat. Mus.*, vol. 53, No. 2210, pp. 389–392.

Cockerell, T.D.A. 1919 (1918). New species of North American Fossil Beetles, Cockroaches and Tsetse Flies. *Proc. U.S. Nat. Mus.*, vol. 54, No. 2237, pp. 301–311.

Cockerell, T.D.A. 1920. Fossil Arthropods in the British Museum. *Ann. Mus. Nat. Hist. London*, vol. 5, pp. 273–279.

Cockerell, T.D.A. 1921a. Eocene insects from the Rocky Mountains. *Proc. U.S. Nat. Mus.*, vol. 57, pp. 233–260.

Cockerell, T.D.A. 1921b. Fossil Arthropoda in the British Museum. V. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 7, pp. 1–25.

Cockerell, T.D.A. 1921c. Fossil Arthropoda in the British Mus. VII. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 8, pp. 541–545.

Cockerell, T.D.A. 1922a. Some Eocene insects from Colorado and Wyoming. *Proc. U.S. Nat. Mus.*, vol. 59(1921), pp. 29–59.

Cockerell, T.D.A. 1922b. Fossil Arthropods in the British Museum, pt. VIII. Homoptera from Gurnet Bay, Isle of Wight. *Ann. Mag. Nat. Hist. London*, vol. 10, ser. 9, No. 55, pp. 157–161.

Cockerell, T.D.A. 1924. Fossil insects in the United States National Museum. *Proc. U.S. Nat. Mus.*, vol. 64, pp. 1–15.

Cockerell, T.D.A. 1925a. Plant and insect fossils from the Green River, Eocene of Colorado. *Proc. U.S. Nat. Mus.*, Washington D.C., vol. 66, No. 2586, p. 13.

Cockerell, T.D.A. 1925b. Tertiary insects from Kudia River, Maritime province, Siberia. *Proc. U.S. Nat. Mus.*, vol. 68, pp. 1–16.

Cockerell, T.D.A. 1926a. Tertiary fossil insects from Argentina. *Amer. Journ. Sci. New Haven Conn.*, vol. 2(5), pp. 501–504.

Cockerell, T.D.A. 1926b. Some tertiary fossil insects. *Ann. Mag. Nat. Hist. London*, vol. 18, pp. 313–324.

Cockerell, T.D.A. 1927a. Fossil insects in the British Museum. *Ann. Mag. Nat. Hist.*, vol. 20, ser. 9, pp. 585–594.

Cockerell, T.D.A. 1927b. The Carboniferous Insects of Maryland. *Ann. Mag. Nat. Hist. London*, ser. 9, vol. 19, pp. 385–416.

Cockerell, T.D.A. 1928. The Jurassic insects of Turkestan. *Psyche.*, vol. 35, No. 2, pp. 126–130.

Cockerell, T.D.A. and Sandhouse. 1922. Some Eocene insects of the family Fulgoridae. *Proc. U.S. Nat. Mus. Washington*, vol. 59, pp. 455–457.

Comstock, J.H. 1918. The Wings of Insects. New York, pp. 1–430.

Cooper, K.W. 1941. *Davispia bearcreekensis* Cooper, a new Cicada from the Paleocene, with a brief review of the fossil Cicadidae. *Amer. Journ. Sci. New Haven*, No. 239, pp. 286–304.

Cosmovici, N. and M. Pauca. 1955. Odonat fossil din Oligocenul de la Piatra Neamt Lestes sieblosiformis. Communic. *Acad. R. P. R.*, vol. 5, No. 2, pp. 365–368.

Cotes, E.C. 1889. A catalogue of the moths of India, vol. 2, pp. 671–777.

Cowley, M.A. 1942. Descriptions of some genera of fossil Odonata. *Proc. R. Ent. Soc. London*, vol. 2, pt. 5, pp. 63–78.

Crampton, G.C. 1927. Eugereon and the Ancestry of the Hemiptera, Psocids and Hymenoptera. *Bull. Brookl. Entomol. Soc.*, vol. 22(1), pp. 1–17.

Cresson, E.T. 1887. Synopsis of families and genera of Hymenoptera of America north of Mexico. *Amer. Entomol. Soc.*, pp. 1–356.

Curtis, J. 1835. Insects, in James Clark Ross 'Appendix to John Ross' Narrative of a second voyage in Search of a Northwest Passage.

Dalla-Torre, C.G. 1893. Catalogus hymenopterorum, vol. 7, pp. 1–289.

Dalla-Torre, C.G. 1894. Catalogus hymenopterorum, vol. 9, pp. 1–181.

Dalla-Torre, C.G. 1898. Catalogus hymenopterorum, vol. 4, pp. 1–323.

Dalman, J.W. 1820. Forsok till Uppstallning ai Insect Familjen Pteromalini i synnerhet med afseende pa de i Sverige feume. *Svensk. arter Vetensk. Akad. Handl.*, vol. 41, pp. 1–96.

Damf, A. 1911. *Palaeopsylla lebsiana* n. sp. ein fossiler Floh aus dem baltischen Bernstein. *Schrift der Phys.-okon. Ges. Konigsberg*, vol. 51, pp. 248–259.

Davis, C. 1939. Taxonomic notes on the order Embioptera. XII. The genus *Haploembia* Verhoeff, No. 285–286, pp. 561–567.

Davis, C. 1940. Taxonomic notes on the order Embioptera. XIX. *Proc. Linn. Soc. N.S.W.*, vol. 65, pts. 5–6, No. 291–292, pp. 525–532.

Davis, C. 1940. Taxonomic notes on the order Embioptera. XX. *Proc. Linn. Soc. S.W.N.*, vol. 65, pp. 533–542.

Davis, C. 1942. Hemiptera and Copeognatha from the Upper Permian of New

South Wales. *Proc. Linn. Soc. N.S.W.*, vol. 67, pts. 3–4, pp. 111–122.

Deichmuller, J. 1881. Fossile Insecten aus den Diatomenschifer von Kutschlin bei Bilin. *Bohem. Abh. Nova Acta Leop. Carol.*, vol. 42, No. 6, pp. 293–331.

Deichmuller, J. 1882. Uber einige Blattiden aus den Brandschifern der Unteren. Leys von. Weissig. Sb. Ges. Isis.

Deichmuller, J. 1886. Die Insekten aus dem lithographischen Schiefer im Dresdener Museum. *Mitt. Kon. min-geol. praxist. Mus. Dresden*, vol. 7, p. 88.

Demoulin, G. 1954. *Aedoeophasma anglica* Scudder, Syntonopteroide meconnu. *Bull. Ann. Soc. Entomol. Belgique*, vol. 90, pp. 278–281.

Demoulin, G. 1954. Les Ephemeropteres jurassiques du Sinkiang. *Bull. Ann. Soc. Entomol. Belgique.*, vol. 90, pp. 322–326.

Demoulin, G. 1954. Quelques remarques sur les Archodonates. *Bull. Ann. Soc. Entomol. Belgique.*, vol. 90, jurassique bavarois. *Bull. Ann. Soc. Entomol. Belgique*, vol. 91, No. 1-2, p.33.

Demoulin, G. 1955. Contribution a letude morphologique, systematique et phylogenique des Ephemeropteres jurassiques d'Europe Central. II. Paedephemeridae. *Bull. Inst. R. Sci. Nat. Belgique*, t. 31, No. 55, pp. 1–10.

Desneux, J. 1904. A propos de la phylogenie des Termitides. *Ann. Soc. Entomol. Belg.*, vol. 48, No. 8, pp. 278–286.

Dodds, B. 1949. Mid. Triassic Blattoidea from the Mount Crosby insect Bed. *Pap. Dep. of Geol. Univ. Queensland*, vol. 3, No. 10, pp. 1–11.

Dohrn, A. 1866. Eugereon bockingi eine neue Insecten Form aus dem Rotliegenden. Palaeontographica, vol. 13, pp. 333–340.

Donisthorpe, H.St. J.K. 1920. British Oligocene ants. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 6, pp. 81–94.

Drake, C.J. 1950. Concerning the Contacaderiane of the World (Hemiptera-Fingidae),Buenos Aires, vol. 1, pp. 153–166.

Dunstan, B. 1924. Mesozoic insects of Queensland. pt. I, Introduction and Coleoptera. *Queensland Geol. Surw. Publ.*, No. 273, pp. 1–74.

Durrent, J.H. 1918. Comparison of Hübner's Tentamen and the Verzeichniss. *Entomol. Rec. London*, vol. 30, pp. 1–32.

Edwards, F.M. 1923. Oligocene mosquitoes in the British Museum, with a summary of our present knowledge concerning fossil Culcidae. *Journ. Geol. Soc. London*, vol. 79, pp. 139–154.

Emerson, A.E. 1942. The relations of a relict South African termite (Isoptera, Hodotermitidae, Stolotermes). *Amer. Mus. Novit.*, No. 1187. *Amer. Mus. Nat. Hist.*, pp. 1–2.

Emery, C. 1890. Le formiche dlll' ambra Siciliana nel museo mineralogico dell' universitadi Bologna. *Mem. R. Acad. Sci.* Ist Bologna, vol. 5, pp. 567–591.

Emery, C. 1905. Deux Tourmis de l'Ambre de la Baltique. *Bull. Soc. Entomol. France*, pp. 187–189.

Enderlein, G. 1903. Die Copeognathen des indoaustralischen Faunengebietes.

Ann. Mus. Nat. Hung., vol. 1, pp. 179–344.

Enderlein, G. 1905. Morphologie, Systematik und Biologie der Atropiden und Troctiden. *Res. Swed. Zool. Exped. Egypt*, No. 18, pp. 1–57.

Enderlein, G. 1908. Die Copergnathen-Fauna der Insel Formosa. *Zool. Anz.*, vol. 33, pp. 759–779.

Enderlein, G. 1909a. Die Klassifikation der Embiidihen nebst morphologischen und physiologischen Bemerkungen besonders uber das Spinnen derselben. *Zool. Anz.*, vol. 35, No. 6, pp. 166–191.

Enderlein, G. 1909b. Zur. Kenntnis fruhjurassischer Copeognathen und Coniopterygiden und uber das Schicksal der Archipsyiliden. *Zool. Anz.*, vol. 34, No. 26, pp. 770–776.

Enderlein, G. 1910a. Uber die Beziehungen der fossilen Coniopterygiden zu den rezenten und Archiconiocompsa prisca. *Zool. Anz.*, vol. 35, pp. 673–677.

Enderlein, G. 1910b. Uber die Phylogenie und die Klassification der Mecopteren unter Berucksichtigung der fossilen Formen. *Zool. Anz.*, vol. 35, pp. 385–399.

Enderlein, G. 1911. Die fossilen Copeognatha und ihre Phylogenie. *Palaeontographica*, vol. 58, pp. 339–342.

Enderlein, G. 1915. 2. *Psyllidologica* III. *Strophingia oligocaenica* nov. spec., eine fossile Psyllidae. *Zool. Anz.*, vol. 45, pp. 246–248.

Enderlein, G. 1920. Rhynchota in Brohmers Fauna. 2 Ed. (Fauna von Deutschland).

Enderlein, G. 1930. Die Klassifikation der Coniopterygiden auf Grund der rezenten und fossilen Gattungen. *Archiv. fur Klass. und Phyl. Entomol.*, vol. 1 (1929), No. 2, pp. 98–114.

Enderlein, G. and P. Petersen. 1927. New and little-known species of Neuroptera in British Coll. *Ann. Mag. Nat. Hist.*, set. 9, vol. 20, pp. 343–350.

Erichson, W.F. 1845–1858. Naturgeschichte der Insecten Deutschlands. Coleoptera. III. Berlin, pp. 1–968.

Essig, E.O. 1937. Insects and Arachnids from Canadian Amber. Reprinted from Univ. of Toronto Studies. Geol. ser. No. 40, pp. 7–21.

Essig, E.O. 1947. College Entomology, New York, pp. 1–900.

Evans, J.W. 1934. A revision of the Ipoinae. *Trans. Roy. Soc. South Australia*, vol. 58, p. 149.

Evans, J.W. 1934a. Upper Permian Homoptera from New South Wales. *Records Austr. Mus.*, vol. 21, No. 4, pp. 180–198.

Evans, J.W. 1943b. Two intersecting Upper Permian Homoptera from New South Wales. *Trans. Roy. Soc. South Australia*, Adelaida, vol. 67, pp. 7–9.

Evans, J.W. 1947. A new fossil Homopteron from Rimbles Hill, Belmont (Upper Permian). *Rec. Aust. Mus.*, Sydney, vol. 21, pp. 431–432.

Evans, J.W. 1948. Some observations of the classification of the Membracidae and on the ancestry, phylogeny and distribution of the Jassoidea, vol. 99, pt. 15, pp. 497–515.

Evans, J.W. 1950. A re-examination of an Upper Permian insect *Paraknightia magnifica* Ev. *Rec. Aust. Mus. Sydney*, vol. 22, pp. 246–250.

Evans, J.W. 1953. Les Cicadellidae de Madagascar (Homopteres). *Mem. l'Inst. Sci. de Madagascar* (ser. E), t. IV, pp. 87–137.

Evans, J.W. 1956. Palaeozoic and Mesozoic Hemiptere (Insecta). *Austr. Journ. Zool.*, vol. 4, No. 2, pp. 165–168.

Evans, J.W. 1958. New Upper Permian Homoptera from the Belmont Beds. *Rec. Austr. Mus.*, vol. 24, No. 9, pp. 109–114.

Ferris, G.F. 1941. A new species of *Slomacoccus* (Homoptera, Coccoidea, Margarodidae). Microentomology, Stanford Univ., vol. 6, pp. 29–32.

Fleury, F. 1937. Sur le carbonifere du Nord du Portugal a propos de sa faunule continental et specialement des insects. *Mem. Acad. Cien. Lisboa*, vol. 1, pp. 203–211.

Folsom, J.W. 1937. Collembela. In: Carpenter, F.M. Insects and Arachnids from Canadian Amber. *Univ. Toronto studies, geol.*, ser. No. 40, pp. 14–17.

Forbes, W.T.M. 1943. The origin of wings and venational types in insects. *Amer. Midl. Naturalist*, c. 29, pp. 381–405.

Forel, A. 1878. Etudes myrmecologiques en 1878-9 avec I'anatomie du gesier des formis. *Bull. Soc. Vaudoise Sci. Nat.*, vol. 15, No. 80, pp. 337–392.

Forster, A. 1856. Hymenopterologischen Studien, vol. 2, pp. 1–90.

Forster, B. 1891. Die Insekten des Pattigen Steinmergels Von Brunstatt. *Abh. Geol. Soc. spec.*, pp. 334–594.

Frasser, F.C. 1938. Additions to the family Amphipterygodae. *Proc. Roy. Entomol. Soc. London*, vol. 7, pp. 137–143.

Frasser, F.C. 1939. A reclassification of the order Odonata. *Austr. Zool.*, vol. 9, pp. 195–221.

Frasser, F.C. 1940. A note on the classification of *Zacallites balli* Cockerell. *Austr. Zool.*, vol. 9, pp. 62–64.

Fric, A. 1895. Vorl. Ber. uber die Arthropoden u. Mollusken der Bohm. Permformation. *Sb. Bolun. Ges.*, No. 36, pp. 1–4.

Fric, A. 1901. Fauna der Gaskohle und der Kalksteine der Permformation Bohmens, vol. 4.

Fric, A. 1912. Studie voboru ceskeho utvarce permskeho. Archiv pro prirodovedecky vyzkum Cech.

Froggat, W.W. 1896. Australian Termididae, pt. II. *Proc. Linn. Soc. N.S.W.*, vol. 21, pp. 510–552.

Geinitz, F.E. 1880. Der Jura von Dobbertin in Meklenburg und seine Versteinerunger. *Ztschr. Dtsch. geol. Ges.*, vol. 32, pp. 510–535.

Geinitz, F.E. 1884. Uber die Fauna des Dobbertiner Lias. *Ztschr. Dtsch. Geol. Ges.*, vol. 36, pp. 566–583.

Geinitz, F.E. 1887. Beitrag zur Geologie Mecklenburgs. *Arch. Ver. Naturg. Mecklenburg*, vol. 41, pp. 143–216.

Germar, E.F. 1810. Uber Classification der Insekten. *Neu. Schr. Halie. nat.*

Ges., 1, pp. 49–68.

Germar, E.F. 1813–1821. Magazin Des Entom. I–IV, Halle.

Germar, E.F. 1837. Fauna Insectorum Europae. 19. Insectorum Protogaeae specimen sistens insecta curbonum fossilum. Halle, pp. 1–25.

Germar, E.F.1839. Die versteinerten Insekten Solnhofens. *Nova Acta Acad. Leop. Carol.*, vol. 19, Abt. I. pp. 187–222.

Germar, E.F. 1842. Bescheibung einiger neuen fossile Insekten in den lithographischen Schiefern des Steinkohlengebirges von Wettin. Munster. Beitr. zur Petrefaktenkunde, No. 5, pp. 79–94.

Germar, E.F. and G. Berendt. 1856. Die im Bernstein befindlichen organischen Reste der Vorwelt. Bernst. Vorwelt, vol. 2.

Gerstaeker, A. 1855. Phipiphoridum Coleopterorum famillae Dispositio Systematica, pp. 1–36.

Giebel, C.G. 1852. Deutschl. Petrefakten. II. Leipzig, pp. 1–706.

Giebel, C.G. 1856a. Die Inskekten und Spinnen der Vorwelt. mit stater Berucksichtigung der lebenden Insekten und Spinnen; monographisch dargestellt. Leipzig, vol. 2, pp. 1–258.

Giebel, C.G. 1856b. Fauna der Vorwelt mit stater Berucksichtigung der lebenden Thiere. Leipzig, pp. 1–511.

Giebel, C.G. 1862. Wirbeltier und Insektenreste in Bernstein. *Zschr. Ges. Naturw.*, vol. 20, No. 8–9, pp. 313–314.

Goerin, F.E. 1823. Entomologie ou Histoire naturelle des crustaces, des arachnides et des insectes., t. 1.

Goldenberg, F. 1852. Prodrom einer Naturgeschichte der fossilen Insecten der Kohlenformation von saarbrucken. *Sb. Akad. Wiss. Wien.*, vol. 9, pp. 28–30.

Goldenberg, F. 1869. Zur Kenntniss der fossilen Insekten in der Steinkohlen. *Neues Jahrb. f. Miner.*, t. 3.

Grabau, A.W. 1923. Cretaceous fossil from Shantung. *Bull. Geol. Surv. of China*, pt. 2, No. 5, pp. 164–181.

Grote, A.B. 1886. Booknotice. *Can. Ent.*, vol. 18, p. 100.

Gutfleisch, V. 1859. Die Kaier Deutschlands. Vervollstandigt von. F. Ch. Box. Darmstadt, pp. 1–661.

Guthorl, P. 1930a. Eine neue Insektenart aus den Lebacher Schichten des Saarlandischen Rotliegenden. *Verh. Naturh. Ver Preuss. Rheinl.*, Bonn (1929), vol. 86, pp. 138–140.

Guthorl, P. 1930b. Neue Insektenfunde aus dem Saarcarbon. *Neues Jahrb. Min. Geol. Palaont. Stuttgart*, vol. 64, pp. 147–164.

Guthorl, P. 1933. Neue Insektenreste aus dem Rotliegenden von Ober-Franken und Thuringen. *Jahrb. u. Mitteil. d. Oberrh., Geol. Ver. N.F.*, vol. 22, pp. 44–49.

Guthorl, P. 1934. Die Arthropoden aus dem Carbon und Perm des Saar-Nahe-Pfalz Gebietes. *Abh. d. Preuss. Geol. Landesanst.*, No. 164, pp. 5–219.

Guthorl, P. 1936. Neue Beitrage zur Insekten-Fauna des Saar-Carbons, 5. Senckenbergiana, vol. 18, pp. 82–112.

Guthorl, P. 1939. Zur Arthropoden-Fauna des Karbons und Perm, 9. Palaeodictyoptera, Mixotermitoidea, Miomoptera und Blattaria. *Senkenbergiana*, vol. 21, No. 56, pp. 314–329.

Gyllenhal, L. 1808. Insecta svecica descripta a Leonardo Gyllenhal. Classis I. Coleoptera sive eleuterata, T. 1, pp. 1–572.

Gyllenhal, L. 1810. Insecta svecica descripta a Leonardo Gyllenhal. Classis, I. Coleoptera sive elcuterata. T. 2, pp. 1–660.

Hagen, H.A. 1854. Uber die Neutropteren der Bernsteinfauna. *Verh. Zool.-bot. Ges. Wien*, vol. 4.

Hagen, H.A. 1862. Uber die Neuropteren aus dem lithographischen Schiefers in Bayern. *Palacontographica*, X, pp. 96–145.

Hagen, H.A. 1866. Die Neuropteren Spaniens nach Ed. Pictet's Synopsis des Neuropters d'Espagne und Dr. StaudingersMitteilungen. *Stettin-Entomol. Zeitung Jahrg.*, 27, pp. 281–320.

Hagen, H.A. 1873. Beiträge zur Kenntnis der Phryganidae. *Verh. Zool.-bot. Ges. Wien.*, vol. 23, pp. 377–452.

Hagen, H.A. 1882. Über Psociden in Bernstein. *Stettiner Entomol. Leistung*, pp. 217–237, 265–300.

Hagen, H.A. 1883. Beiträge zur Monographie der Psociden. *Stettin. Entomol. Zeitung*, pp. 283–332.

Haliday, A.H. 1833. Essay on the classification of parasitic Hymenoptera. *Entomol. Mag.*, vol. 1.

Haliday, A.H. 1836. An epitome of the British genera in the order Thysanoptera, with indication of a few of the species. *Entomol. Mag.*, vol. 3, pp. 439–451.

Haliday, A.H. 1839. Hymenopterorum Synopsis ad methodum Fallenii utplurimum accommodata, London.

Haliday, A.H. 1840. Hymenoptera Britannica. London.

Handlirsch, A. 1904a. Uber enige Insektenreste aus der Permformation Russlands. *Zan. Nauk. akad. nauk. SPb. fiz. mat. otd.*, t. 16, No. 5, ctr. 1–7.

Handlirsch, A. 1904b. Les insectes houillers de la Belgique. *Mem. Mus. Royal d'Hist. nat. Belgique*, vol. 3, pp. 1–20.

Handlirsch, A. 1906a. Revision of American Palaeozoic insects. *Proc. U.S. Nat. Mus.*, vol. 29, No. 1441, pp. 661–820.

Handlirsch, A. 1906b. A new Blattoid from the Cretaceous Formation of North America. *Proc. U.S. Nat. Mus.*, vol. 29, pp. 655–656.

Handlirsch, A. 1906–1908. Fessilen Insekten und die Phylogenie der rezenten Formen. Leipzig, pp. 1–6, 1–1430.

Handlirsch, A. 1909. Uber Relikte. Verh. *Zool.-Bot. Ges. in Wien.*, vol. 59.

Handlirsch, A. 1909. Zur Kenntnis fruhjurassischer Copeognathen und

Coniopterygiden und uber das Schicksal der Archipsylliden. *Zool. Anz.*, vol. 35, pp. 233–240.

Handlirsch, A. 1909b. Uber die fossilen Inskekten aus dem Mittleren Oberkarbon des Konigreiches Sachsen. *Mitt. Geol. Ges. Wien.*, vol. 2, pp. 373–381.

Handlirsch, A. 1910. Die Bedeutung der fossilen Insekten fur die Geologic. *Mitt. Geol. Ges.*, vol. 3, pp. 503–522.

Handlirsch, A. 1911. New Paleozoic insects from the Vicinity of Mazon Creek. III. *Amer. Journ. Sci.*, vol. 31, art. 28, pp. 297–326, 353–377.

Handlirsch, A. 1919a. Eine neue Kalligrammidae (Neuroptera) aus dem Solnhofen Plattenkalke. *Senkenbergiana*, vol. 1, No. 3, pp. 61–63.

Handlirsch, A. 1919b. Revision der Palaozoischen Insekten. *Denkschr. Akad. Wiss. Wien. mathem-naturwiss. Klasse*, vol. 96, pp. 1–82.

Handlirsch, A. 1920. Beitrage zur Kenntnis der palaozoischen Blattarien. *Sb. Akad. Wiss. Wien.*, Abt. 1, vol. 129, No. 9, pp. 43–461.

Handlirsch, A. 1921. Palaeontologie. In *Schroders Handbuch der Entomologie*, vol. 3, Lief. 5.

Handlirsch, A. 1922. Insecta Palaeozoica-Fossilium catalogues. I. Animal, pars 16, pp. 1–230.

Handlirsch, A. 1925. Palaeontologie. *Systematische Ubersicht in Schroder's Handbucn der Entomologie.* pp. 117-229, 337-1140.

Handlirsch, A. 1926–1930. Insecta. In Kukental's Handbuch der Zoologie, vol. 4, pp. 403–892.

Handlirsch, A. 1938. Fossile Insekten aus Siebenburgen. *Mitt. Schweiz. entomol. Ges.*, vol. 17, pp. 25–29.

Handlirsch, A. 1937–1939. Neue Untersuchungen uber die fossilen Insekten mit Erganzungen und Nachtragen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. *Ann. Nat. Mus. Wien.*, vol. 48, pp. 1–140, and vol. 49, pp. 1–240.

Handschin, E. 1926a. Die Collembolen des baltischer Bernsteins. *Zool. Anz.*, vol. 65, pp. 179–182.

Handschin, E. 1926b. Revision der Collembolen des baltischen Bernsteins. *Entomol. Mitt.*, vol. 15, No. 2, pp. 161–185.

Handschin, E. 1926c. Revision der Collembolen des baltischen Bernsteins. *Entomol. Mitt.*, vol. 15, No. 3/4, pp. 211–223.

Handschin, E. 1926d. Revision der Collembolen des baltischen Bernsteins. *Entomol. Mitt.*, vol. 15, No. 5/6, pp. 330–342.

Handschin, E. 1929. Urinsekten oder Apterygota. *Die Tierwelt Deutschlands*, vol. 16, pp. 1–150.

Handschin, E. 1937. Fossile Insekten aus Siebengebirgen. Mitt. Schweiz. *Entomol. Ges.*, Berlin, vol. 17, pp. 25–29.

Hatch, H. 1925. Phylogeny and Phylogenetic Tendencies of Gyrinidae. *Mich. Acad. Sci.*, vol. 5.

Hatch, H. 1927. A revision of fossil Gyrinidae. *Bull. Brookl. Entomol. Soc.*, vol. 22, No. 2, pp. 89–97.

Hatch, H. 1927. Studies on the Silphinae. *Journ. N.Y. Entomol. Soc.*, vol. 35, pp. 331–370.

Haupt, H. 1940. Die altesten geflugelten Insekten und ihre Berichtungen zur Fauna der Jetztzeit. *Z.F. Naturwissenschaften*, vol. 94, pp. 60–121.

Haupt, H. 1950. Die Kafer aus der eozanen Braunkohle des Geiseltales. *Geologica*, Berlin, No. 6.

Haupt, H. 1956. Beitrag zur Kenntnis der eozanen Arthropodenfauna des Geiseltales. *Nova Acta Leopoldina*, vol. 18, No. 128, pp. 1–90.

Hebard, M. 1929. Studies in Malayan Blattidae. *Proc. Acad. Nat. Sci. Philad.*, vol. 81 (1930), pp. 1–109.

Heer, O. 1838–1841. Die Kafer der Schweiz mit besconderer Berucksichtigung ihrer geographischen Verbereitung. *Neues Denkscher. allgem. Schweizer. Ges. Naturwiss*, vol. 2–5.

Heer, O. 1838–1842. Fauna Coleopterorum helyetica. *Turici*, pp. 12–652.

Heer, O. 1843. Uber Trichopteryx Kirby. *Entomol. Zeitung. Stettin, Jahrg.*, 4, No. 2, pp. 39–62.

Heer, O. 1847. Die Insekten fauna der Tertiargebidae von Oeningen und von Radoboj in Kroatien. I Abt. Kafer. *Naouveaux memoires de la Soc. Helvetique des. Sc. nat.*, pp. 1–229.

Heer, O. 1849. Die Insektenfauna der Tertiargebidae von Oenigen und von Radoboj in Croatien, T. II. Leipzig, pp. 1–264.

Heer, O. 1852. Die Lias Insel im Aargau mit einer Tafel Lias-Insekten, Zurich.

Heer, O. 1853. Die Insektenfauna der Tertiargebilde von Oeningen und Radoboj in Kroatlen. III Abt. Rhynchoten. Zurich. *Neue. Denkschr. Allgem. Schweizer Ges. Naturwiss.*, vol. 13, pp. 1–138.

Heer, O. 1860. Untersuchungen uber das Klima und die Vegetationsverhaltnisse der Tertiarlandes, Winterthur.

Heer, O. 1862. Beitrage zur Insektenfauna Oeningens. *Verh. Holl. Moatsch. Wet.*, vol. 16, pp. 1–90.

Helmsing, L.W. and W.E. China. 1937. On the Biology and Ecology of *Hemiodoecus veithi* Hacker (Hemiptera, Peloridiidae). *Ann. Mag. Nat. Hist. London*, No. 113, pp. 473–489.

Henriksen, K. 1922. Eocene insects from Denmark. *Danm. Geol. Undersgel., Raekke*, pp. 5–36.

Henriksen, K. 1929. A new Eocene Grasshopper, *Tettigonia* (*Locusta*) *amoena* n. sp. from Denmark. *Medd. danm. geol. Foren.*, vol. 7, pp. 317–320.

Heslop–Harrison, G. 1956. TheAge and Origin of the Hemlptera with special reference to the suborders Homoptera. *Proc. Univ. Durham Phil. Soc.*, vol. 12, No. 15, pp. 150–169.

Heyden, C.H.G. 1859. Gliedtiere aus der Braunkohle des Niederrheins. *Palaeontographica*, vol. 8.

Heyden, C.H.G. 1866. Kafer und Polypen aus der Braunkohle des Siebengebirges. *Palaeontographica*, vol. 15.

Heyden, C.H.G. 1870. Fossile Dipteren aus der Braunkohle von Roth in Siebengebirge. *Palaeontographica*, vol. 17.

Heyden, L., E. Reiter and J. Weise. 1883. Catalogus Coleopterorum Europae et Caucasi, pp. 1–228.

Hickman, V.V. 1933. On Tasmanian Copeognatha (Corrodentia). *Occ. Pap. Proc. Roy. Soc. Tasmania*, pp. 77–89 (1934).

Hirst, S. and S. Maulik. 1926. On some Arthropod Remains from the Rhynie Chert (old red sandstone). *Geol. Mag.*, vol. 63, pp. 67–71.

Hoase, E. Bemerkungen zur Palaontologie der Insekten. *Neues Jahrb. Min.*, vol. 2, pp. 1–33.

Holmgren, N. 1911. Termitenstudien. 2. Systematik der Termiten. Die Familien Protermitidae and Mastotermitidae. *K. Svenska Vetensk. Akad. Handl.*, vol. 46, No. 6, pp. 1–88.

Hood, J.D. 1912. New genera and species of North American Thysanoptera from the south and west. *Proc. Biol. Soc. Washington*, vol. 25, pp. 61–76.

Hull, F.M. 1945. A revisional study of the fossil Syrphidae. *Bull. Mus. Compar. Zool. Harvard*, vol. 45, pp. 249–355.

Hunderford, H.B. 1932. Concerning a fossil water bug from the Florissant (Nepidae). *Univ. Kansas Sci. Bull. Lawrence*, vol. 20, pp. 327–331.

Hutchinson, G.E. 1942. Note on the occurrence of *Buenoa elegans* (Notonectidae) in the early postglacial sediment of Lyd-Hyt Pond. *Amer. Journ. Sci., New Haven*, No. 240, pp. 335–338.

Illies, J. 1955. Steinfliegen odor Plecoptera. In: *Die Tierwelt Deutschlands*, pt. 43, pp. 150, Jena.

Jaczewski, T. 1923. Uber die Fossilen Corixiden aus Boryslaw in Polen. *Vorlaufige Mitteilung. Rozpraw i Wiadomosci Zool. Mus. Dzieduszyckich.*, vol. 7–6 (1921–1922), str. 55–59.

Jakobi, A. 1938. Eine neue Bernsteincicada (Rhynchota-Homoptera). *Sitzungsber, der Ges. der Nat. Forsch. Freunde*, Berlin, vol. 15, pp. 188–189.

James, M.T. 1937–1939. A preliminary review of certain families of Diptera from the Florissant Miocene Beds. *Journ. Paleontol.*, vol. 11, No. 3, pp. 241–247, vol. 13, pp. 42–48.

Janse, A.J.T. 1917. Check-List of the South African Lepidoptera Heterocera. Pretoria.

Jessen, K. 1923. En undersosk Mosci Rundsted Harm og de senglacial Viceau Forandringer i Oresund. *Medd. Geol. Copenhagen*, vol. 14, pp. 1–18.

Jordan, H.E.K. 1944. *Oligocoris bidentata* n. gen. et n. sp., eine Miridae aus dem ostpreussischen Bernstein (Hem.-Het. Miridae). *Arb. Morph. Taxon. Entomol. Berlin*, vol. 2, No. 11, pp. 8–10.

Kaltenbach, J.H. 1843. Monographie der Familien der Pflanzenlause.

Karny, H.H. 1921. Zur Systematic der Orthropteroiden Insekten. *Treubia Buitenzorg*, pt. 1, pp. 207–210.

Karny, H.H. 1930. Zur Systematic der Orthropteroiden Insekten, pt. II. *Treubia*, vol. 12, Lief. 3–4, pp. 431–461.

Karny, H.H. 1932. Uber zwei angebliche Gryllacris-Arten aus dem Miocan von Radoboj. *Jahrb. geol. Bundesanst.* Wien, vol. 82, pp. 65–69.

Kawall, J.H. 1876. Organische Einschlusse im Bergkristall. *Byull. Mosk. ob-va ispyt prirody*, vol. 51, No. 3, pp. 170–173.

Keilbach, R. 1939. Neue Funde des Strepsipterons *Mengea tertiaria* Menge im baltischen Bernstein. *Bernst. Forsch.*, No. 4, pp. 1–7.

Kerville, H.G. 1893. Note sur les Thysanoures fossiles du genre *Machilis* et description d'une espece nouvelle du succin. *Ann. Soc. entomol. France*, vol. 62, pp. 463–466.

Kieffer, J.J. 1909a. Ceraphronidae. *Genera Insectorum*, fasc. 94, pp. 1–27.

Kieffer, J.J. 1909b. Hymenoptera. Fam. Serphidae. *Genera Insectorum*, fasc. 95, pp. 1–10.

Kieffer, J.J. 1916. Hymenoptera. Proctotrupoidea. *Das Tierreich.*, Lief. 44, pp. 1–627.

Kimmins, D.E. 1952. XL. Indian Caddis flies. VI. New species and a new genus of the subfamily Rhyacophilinae. *Ann. Mag. Nat. Hist.*, No. 52, pp. 313–346.

Kinsey, A.C. 1919. Fossil Cynipidae. *Pscyche*, vol. 26, pp. 44–49.

Kirby, W. 1837. Fauna Boreali-Americana, pt. 4, London.

Kirby, W. 1904. A synonimic catalogue of Orthoptera. I. London, I–X + 1–501.

Kirby, W. 1906. A synonymic catalogue of Orthoptera. *Brit. Mus.* (*Nat. Hist.*), *London*, vol. 1–3, p. 1737.

Kirkaldy, G.W. 1900. Bibliographical notes on the Rhynchota. *Entomologist* , vol. 33, p. 242.

Kirkaldy, G.W. 1907. Leaf-Hoppers supplement. *Bull. Hawaii Ass. Exp. Stu.*, vol. 3.

Kirkaldy, G.W. 1908. Catalogue of the genera of the Hemipterous family Aphidae. *Canad. Entomol.*, vol. 37 (1905–1908).

Klebs, R. 1910. Uber Bernsteinschlusse im allgemeinen und die Coleopteren meiner Bernsteinsammlung. Schr. phys.-okon. Ges., Konigsberg, vol. 51, pp. 217–242.

Kliver, M. 1886. Uber einige neue Arthropodenreste aus der Saarbrucken und der Wettin-Lobejuner Steinkohlen Formation. *Palaeontogr.*, vol. 32, pp. 99–115.

Klug, Fr. 1842. Versuch einer systematischen Bestimmung und Auseinandersetzung der Gattungen und Arten der Clerii, einer Insektenfamilie aus der Ordnung der Coleopteron. *Abh. Kon. Akad. Wiss. Berlin*, pp. 259–397.

Koch, L. 1854–1857. Die Pilanzenlause Aphiden. Nurnberg.

Kolbe, H. 1882. Neue Psociden der palaarktischen Region. *Entomol. Nachr.*, vol. 7, pp. 207–212.

Kolbe, H. 1883. Neue Beitrage zur Kenntnis der Psociden der Bernstein-Fauna. Stettin. *Entomol. Zeitung*, pp. 186–191.

Kolenati, F.A. 1848. Ueber den Nutzen und Schaden der Trichopteren. Stett. *Entomol. Zeitung*, vol. 9, pp. 50–52.

Kolenati, F.A. 1851. Uber Phryganiden im Bernstein. *Abh. Bohm. Ges. Wiss.* (5)6.

Kolenati, F.A. 1859. Genera et species Trichopterorum. *Pars Altera.*Moscow, pp. 143–296.

Kolsnitsyna, G.R. and O.M. Martynova. 1961. Novyi Yurskii rod *Ijapsyche* (Mecoptera, Paratrichoptera) iz Vostochnoi Sibiri [New Jurassic genus *Ijapsyche* (Mecoptera, Paratrichoptera) from East Siberia]. *Paleontol. zhurn.*, No. 4, pp. 162–164.

Konow, F.W. 1897. Zwei neue Striciden und einige palaarktische Tenthrediniden. *Entomol. Nachr.*, vol. 23, No. 24, pp. 372–376.

Krauss, H.A. 1902. Die Namen der altesten Dermapteren (Orthopteren) Gattungen und ihre Versendung fur Familien und Unterfamilion. Benennungen auf Grund der jetzigen Nomenklaturregeln. *Zool. Anz.*, vol. 25, pp. 530–543.

Kruger, L. 1913. Beitrage zu einer Monographie der Neuropteren Familie der Osmyliden. Stett. *Entomol. Zeitung*, 74 Jahrg., No. I, pp. 3–212.

Kruger, L. 1923. Neuroptera succinia baltica. Stett. *Entomol. Zeitung*, vol. 84, pp. 68–92.

Kuhn, O. 1938. Drei neue Insekten aus den Mesozoikum von Bayern. *Palaeontol. Ztsch.*, vol. 20, No. 3/4, pp. 318–320.

Kuhn, O. 1938. Neue Insektenreste aus der deutschen Lettenkohle (Ober Trias). *Beitr. Geol. Thuringen. Jena*, vol. 5, pp. 84–86.

Kukalova, J. 1955. Archimylacridae Handlirsch (Blattodea) of the Carboniferous of Bohemia. *Univ. Carolina Geologia*, vol. 1, No. 1, pp. 131–163.

Kukalova, J. 1955. Permoedischia n.g. Protorthoptera a Moraviptera n.g. (Palaeodictyoptera) z moravkeho permu. *Sbornik ustred. ustavu geologickeho*. sv. 31, oodd. paleontol., str. 541–575.

Kukalova, J. 1957. *Carpocoris hoberlandti* sp. nov. eine neue Wanzenart des Bohmischen Tertairs (Heteroptera). *Acta Entomol., Mus. Nat., Prague*, vol. 31, pp. 73–76.

Kukalova, J. 1958. Paoliidae Handlirsch (Insecta Protorthoptera) aus dem Oberschlesischen Steinkohlenbecken. *Geologie, Jahrg.* 7, No. 7, pp. 935–959.

Kukalova, J. 1959. On the family Blattinopsidae Bolton, 1925 (Insecta, Protorthoptera). *Rozpravy Ceskoslov, akad. ved., Rada met., a prir. ved.* R. 69, c. 1, str. 1–30.

Kusta, J. 1882. Uber eine Blattina aus der Lubhauer Gaskohle. *Sb. Bohm. Ges. Wiss.*, pp. 430–437.

Kusta, J. 1883. Uber einige neue bohmische Blattinen. *Sb. Bohm. Ges. Wiss.*, 211, az. 215.

Kuznetsov, N.N. 1926. O proiskhozhdenii pustynnoi fauny Turkestana (On the origin of desert fauna of Turkestan). *Russk. Zool. Zhurn.*, vol. 6, No. 1, pp. 61–82.

Kuznetsov, N.Y. 1928. *Oligamites martynovi* gen. et. sp. nn., a fossil Amatid Lepidopteron from the Oligocene beds of Central Asia. *Dokl. AN SSSR*, No. 20–21, pp. 431–436.

Kuznetsov, N.Y. 1941. Cheshuekrylye yantarya (Lepidoptera in amber). *Izd. AN SSSR*, pp. 1–104.

Lacordaire, T. 1854–1857. Histoire naturelle des insects genera des Coleopteres ou expose methodique et critique de tous les genres proposes jusquici dans cet ordre d'Insectes: t. 1, Paris, pp. 1–486; t. 2, pp. 1–548; r. 3, pp. 1–594 (1956); t. 4, pp. 1–579 (1957).

Lameere, M.A. 1917. Rrevision sommaire des insectes fossiles de Stephanien de Commentry. *Bull. Mus. Nat. d'Hist. Nat. Paris*, vol. 23, No. 3, pp. 141–200.

Lameere, A. and G. Severin. 1897. Les insectes de Bernissart. *Ann. Soc. Entomol. Belg.*, vol. 41, pp. 35–38.

Laporte, F.L. 1835–1840. (Castenau Delaporte). Histoire naturelle des animaux articules, vol. 1–2.

Laporte, F.L. 1840. Historie naturelle des animaux articules. *Ins. Col.*, vol. 1, pp. 1–297.

Latreille, P.A. 1802. Histoire naturelle crustaces et insectes, vol. 3, Paris, pp. 1–468.

Latreille, P.A. 1805. Histoire naturelle generale et particuliere des crustaces et des insectes, vol. 8, Paris.

Latreille, P.A. 1806–1809. Genera crustaceorum et insectorum, t. 1–4.

Latreille, P.A. 1809. In Humboldt and Bonpland. *Roy. Reg. Equin. Nouv. Continent.*, (2), vol. 2, p. 378.

Latreille, P.A. 1810. Considerations generales sur l'ordre naturel des animaux composant les classes des crustaces, des arachnides, et des insectes. Paris, pp. 1–444.

Latreille, P.A. 1825. Entomologie, ou histoire naturelle des crustaces, des arachnides et des insectes., r. 2. Paris.

Latreille, P.A. 1825. Familles naturelles due regne animal, Paris, pp. 1–570.

Latreille, P.A. 1829. Crustaces, arachnldes et ensectes. In: Cuvier G. Le regne animal, Paris, vol. 4, 5.

Laurentiaux, D. 1949. Ocorrenicia de Blatidios do genero Eneriblatta Telx. no Estefaniano do Saint-Eloyles-Mines (Franca). *Bol. Soc. Geol. Portugal Porto*, vol. 8, pp. 121–127.

Laurentiaux, D. 1950. Les insectes de bassins houillers du Gard et de la Loire. *Ann. Paleontol., Paris*, vol. 36, pp. 63–84.

Laurentiaux, D. 1952. Decouverte d'un Homoptere Prosboloide dans la Namurien Belge. *Ass. Paleontol. Stratigraphic Houilleres, Brussel*, vol. 14, p. 16.

Laurentiaux, D. 1953. *Traite de Paleontologie.* Paris, vol. 3, p. 487.

Laurentiaux, D. and L. Grauvogel. 1953. Insecta. In: *Traite de Paleontologie*, vol. 3, pp. 397–527.

Laurentiaux, D. and C. Teixeira. 1950. Novos Blatidios fosses das bacias de Valongo (Portugal) e Saint-Eloy-les-Mines (Franca). *Comm. Serv. Geol. Portugal*, No. 31, pp. 299–308.

Leach, W.E. 1810. On the genera and species of Eproboscideous insecta.

Leach, W.E. 1814–1817. The zoological miscellany; being descriptions of new, or interesting animals. London, vol. 1–3; vol. 1, 1814, pp. 1–144; vol. 2, 1815, pp. 1–154; vol. 3, 1817, pp. 1–152.

Leach, W.E. 1815. Article Entomology in Brewster's *Edinburgh Encyclopaedia*, vol. 9, pt. 1, pp. 52–172.

Leach, W.E. 1817. *Encycl. Brit.*

Leach, W.E. 1818. *Zool. Misc. Mag. Entomol.*, vol. 3, pp. 377–399.

Leach, W.E. 1819. Descriptions des nouvelles especes d'animaux decouvertes par le vaisseau Isabelle dans un voyage au pole boreae. *Journ. physique, de chimie et d'histoire naturelle*, vol. 88, pp. 462–467.

Lebedeve, I.V. 1950. Iskonaemye nasekomye iz yurskikh otlozhenii tsentralnogo raiona Kuzbassa (Fossil insects from the Jurassic beds of central districts of Kuzbas). *Izv. Tomsk. politekhn. in-ta*, vol. 65, vyp. 2, pp. 141–143.

Leconte, J.E. (Le Conte). 1853. Descriptions of twenty new species of Coleoptera inhabiting the United States. *Proc. Acad. Nat. Sci. Phylad.*, vol. 6, pp. 226–235. Classif. Col. North Amer. In: Smithson miscellaneous collections. III. 1862. art. III, 1861.

Leconte, J. and G.H. Horn. 1883. Classification of the Coleoptera of North America. Washington, Smithsonian miscellaneous collections, pp. 1–567.

Lefroy, H. 1842. *Cambridge Nat. Hist.*, vol. 5.

Lemche, H. 1940. The origin of winged insects. *Vindensk. Medd. Fra Dansk. Naturh. Fareu*, vol. 104, pp. 127–168.

Lepneva, S.G. 1956. Morfologicheskie cootnosheniya podsemeistv Psychomyinae, Ecnominae u Polycentropinae (Trichoptera, Annulipalpia) v preimaginalnykh fazakh [Morphological correlations of subfamilies Psychomyinae, Ecnominae and Polycentropinae (Trichoptera, Annulipalpia) in preimaginal stages]. *Entomol. obozr.*, vol. 35, No. 1, pp. 8–27.

Light, S.F. 1921. Note on Philippine termites, 11. *Philippine Journ. Sci.*, vol. 19, No. 1, pp. 23–63.

Linné, C. 1735. Systema naturae.

Linné, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, ed. X. t. 1.

Linné, C. 1767. Systema naturae, ed. 12.

Linsley, E.Y. 1942. A review of the fossil Cerambycidae of North America. *Proc. New Engl. Zool. C. Cambridge*, Mass., vol. XXI, pp. 17–42.

Luche, M. 1913. *Schr. phys.-okon. Ges Konigsberg*, vol. 54, pp. 288–291.

Mac Leay, W.S. 1819–1821. Horae Entomologicae. I. Paris.

Malaise, R. 1945. Tenthredinoidea of South-Eastern Asia with a general zoogeographical review. *Opusc. entomol., Lund suppl.*, vol. 4, pp. 1–288.

Maneval, H. 1938. Trois Serphoides de l'ambre de la Baltique. *Rev. franc. Entomol. Paris*, vol. 5, pp. 107–116.

Malyshev, S.I. 1947. Puti i usloviya evolyutsii pereponch-atokrylykh v svyazi s voprosom o proiskhozhgenii naesdnikov (Hymenoptera) (The paths and conditions of the evolution of Hymenoptera connected with problems of the origin of ichneumon wasps). *Dokl. AN SSSR*, vol. 58, No. 6, pp. 1207–1209.

Mani, M.S. 1944. Descriptions of some fossil Arthropods from India (fossil Aphidoid. Salt Marl. Punjab). *Indian Journ. Entomol.* New Delhi, vol. 6, p. 61.

Marsham, T. 1802. *Entomol. Brit. London*, vol. 1–2.

Martynov, A.V. 1923. O dvukh osnovnykh tipakh krylev nasekomykh i ikh znachenii dlya obshei klassifikatsii Nasekomykh (On the two main types of wings of insects and their importance in the classification of insects). Tr. 1. *Vseross sezda. Zool. anat. i gistol u. Petrograde*, 15–21, XII, 1922, pp. 88–89.

Martynov, A.V. 1924a. K ponimaniyu zhilkovaniya i trakheatsii krylev strekoz i podenok (Towards understanding the venation and tracheation of the wings of dragonflies and mayflies). Russk. *entomol. obozr.*, vol. 18, pp. 145–174.

Martynov. A.V. 1924b. Prakticheskaya entomologiya (Practical Entomology), Vyp. 5—Trichoptera, pp. 1–388.

Martynov, A.V. 1925a. O nekotorykh rezultatakh izucheniya nasekomykh slantsev Turkestana (On some results of the study of fossil insects from the shales of Turkestan). *Dokl. AN SSSR*, pp. 105–108.

Martynov, A.V. 1925b. Contributions to the knowledge of fossil insects from jurassic beds in Turkestan 1. Raphidioptera. *Izv. Ross AN*, No. 2, pp. 233–246.

Martynov, A.V. 1925c. Contributions to the knowledge of fossil insects from jurassic beds in Turkestan 2. Raphidroptera (cont.), Orthoptera (s. l.), Odonata, Neuroptera. *Izv. Ross. Akad. Nauk.*, pp. 569–598.

Martynov, A.V. 1925d. Contributions to the knowledge of fossil insects from jurassic beds in Turkestan. Hymenoptera, Mecoptera. *Izv. AN SSSR*, pp. 753–762.

Martynov, A.V. 1925e. Ober zwei Grundtypen der Flugel bei den Insekton und ihre Evolution. *Ztschr. Morph. Dokl. d. Tiere*, vol. 4, No. 3, pp. 465–501.

Martynov, A.V. 1925f. Ob odnoi novoi forme Orthopteroidea iz permskikh otlozhenii Yuzhno-Ussuriiskogo krya (On a new form of Orthopteroidea from the Permian beds of South Ussurian border). *Dokl. Ross. AN*, pp. 41–44.

Martynov, A.V. 1925g. Ob odnom interesnom iskopaemom zhyke iz yurskikh slantsev severnogo Turkestana (On an interesting fossil beetle from the Jurassic shales of North Turkestan). *Russk. entomol. obozr.*, vol. 19, pp. 73–78.

Martynov, A.V. 1926a. K poznaniyu iskonaemykh nasekomykh yurskukh slantsev Turkestana. 5. O nekotorykh formakh zhukov (Coleoptera). (Contributions to the knowledge of fossil insects from the Jurassic shales of Turkestan. 5. On some forms of beetles (Coleoptera). *Ezhegodn. Russk. Paleontol. ob-va* (1925), vol. 5, pt. 1, pp. 1–38.

Martynov, A.V. 1926b. Jurassic fossil insects from Turkestan, 6. Homoptera and Psocoptera. *Izv. AN SSSR*, pp. 1349–1366.

Martynov, A.V. 1927a. Jurassic fossil insects from Turkestan, 7. Some Odonata Neuroptera, Thysanoptera. *Izv. AN SSSR*, pp. 757–768.

Martynov, A.V. 1927b. O dvukh iskopaemykh tretichnykh strekozakh s Kavkaza (On two tertiary fossil dragonflies from the Caucasus). *Russk. entomol. obozr.*, vol. 21, No. 1–2, pp. 1–5.

Martynov, A.V. 1927c. Jurassic fossil Mecoptera and Paratrichoptera from Turkestan and Ust-Dalei (Siberia). *Izv. AN SSSR*, pp. 651–666.

Martynov, A.V. 1927d. Uber eine neue Ordnung der fossilen Insekten. Miomoptera nov. *Zool. Anz.*, vol. 22. No. 3/4, pp. 99–109.

Martynov, A.V. 1928a. A new fossil form of Phasmatodea from Galkino (Turkestan) and on Mesozoic Phasmids in general. *Ann. and Mag. Nat. History*, ser. 10, vol. 1, pp. 319–328.

Martynov, A.V. 1928b. Permian fossil insects of North-East Europe. *Tp. Geol. Muz. AN SSSR*, vol. 4, pp. 1–118.

Martynov, A.V. 1928c. O nekotorykh kharakternykh chertakh vymirayuschikh i ikh zameschayuschikh v mire nasekomykh (On some characteristic features of extinctions and successions in the world insects). Tr. III. Vseross. Sezda. Zool. anat. i gistol v Leningrade 14–20/XII (1927), pp. 143–144.

Martynov, A.V. 1929a. Ob iskopaemykh nasekomykh tretichnykh otlozhenii Ashutasa, Zaisanskogo uezda (On fossil insects from the tertiary beds of Ashutas, Zaisan district). *Tr. geol. muz. AN SSSR*, vol. 5, pp. 173–216.

Martynov, A.V. 1929b. Permian entomofauna of North Russia and its relation to that of Kansas. *4th Intern. Congr. of Ent.*, Ithaca, (1928), vol. 2, pp. 595–598.

Martynov, A.V. 1930a. O novykh iskopaemykh nacekomykh Tikhikh Gor.

Otdel. Neoptera (bez Miomoptera) [On New fossil insects of Tikhie Mountains. Division Neoptera (excluding Miomoptera)] . *Tp. Geol. Muz. AN SSSR*, vol. 8, pp. 149–212.

Martynov, A.V. 1930b. O dvukh novykh pryamokrylykh nasekomykh iz permskikh otlozhenii Kungurskogo uezda Permskoi gub. (On two new orthopteran insecta from the Permian beds of Kungurian district, Perm province). *Ezhegodn. Russk. Paleontol. ob-va*, vol. 8, pp. 35–47.

Martynov, A.V. 1930c. Permian fossil insects from Tikhie Gory. Order Miomoptera. Pt. I. The new fam. Atactophlebiidae and its relations. *Izv. AN SSSR*, No. 9, pp. 951–975.

Martynov, A.V. 1930d. Permian fossil insects from Tikhie Gory. Pt. II. The fam. Lemmatophoridae and Palaeomantidae. *Izv. AN SSSR*, No. 9, pp. 1115–1134.

Martynov, A.V. 1930e. New Permian insects from Tikhie Gory, Kazan Province, I. Palaeoptera. *Tr. Geol. Muz. Akad. nauk. SSSR*, vol. 6, pp. 69–86.

Martynov, A.V. 1931a. On some new remarkable Odonata from the Permian of Archangelsk district. *Izv. AN SSSR*, No. 1, pp. 141–147.

Martynov, A.V. 1931b. O podotryade Permanisoptera nom. nov. (Odonata) i ego polozhenii [On the suborder Permanisoptera nom. nov. (Odonata) and its systematic position]. *Dokl. AN SSSR*, pp. 246–257.

Martynov, A.V. 1931c. K poznaniyu yurskikh Palaeontinidae Handl., morfologiya sistematicheskoe polozheniya i opisanie novogo roda iz Ust-Baleya (Contributions to the knowledge of the Jurassic Palaeontinidae Handl., morphology, systematic position and description of a new genus from Ust-Balley). *Ezhegodn. Russk. Paleontol. ob-va*, vol. 9 (1930), pp. 93–122.

Martynov, A.V. 1931d. O paleozoiskikh nasekomykh Kuznetskogo basseina (On the Paleozoic insects of the Kuznetsk basin). *Izv. geol. razv. upr.*, vol. 49, No. 10, pp. 73–100.

Martynov, A.V. 1932a. On the wing venation in the family Meganeuridae (Meganisoptera). *Dokl. AN SSSR*, pp. 42–44.

Martynov, A.V. 1932b. New Permian Palaeoptera with the discussion of some problems of their evolution. *Tr. Palaeozol. in-ta AN SSSR* (1931), vol. 1, pp. 1–44.

Martynov, A.V. 1933a. K voprosy o vosraste paleozoiskikh nasekomonosnykh otlozhenii Kuznetskogo basseina (On the problem concerning the age of the Paleozoic insects in the deposits of Kuznetsk basin). *Dokl. AN SSSR*, No. 3, pp. 34–37.

Martynov, A.V. 1933b. On the Permian family Archescytinidae (Homoptera) and its relationships. *Izv. AN SSSR*, pp. 883–894.

Martynov, A.V. 1933c. Permian fossil insects from the Arkhangelsk district. The order Mecoptera. *Tr. Paleozol. in-ta. AN SSSR*(1932), vol. 2, pp. 23–62.

Martynov, A.V. 1933d. Permskie iskopaemye nasekomye Arkhangelskogo kraya. Ch. II. Setchatoknylye, visho-Krylye i zhuki s prilozhenien vpisaniya dvukh novykh zhukov iz Tikhikh gor (The Permian fossil Insects of Arkhangelsk Province. Pt. II. Neuroptera, Megaloptera and Coleoptera with a supplementary description of two new beetles from Tickhil mountains). *Tr. Paleozool. In-ta AN SSSR* (1932), vol. 2, pp. 63–96.

Martynov, A.V. 1934. Klass Insecta (Hexapoda). Nasekomye. [Class Insecta (Hexapoda)]. *Osnovy Paleontologii*. K. Tsittel. Pt. I. Besnozvonochnye, Moscow-Leningrad, pp. 986–1026.

Martynov, A.V. 1935a. Zemetka ob iskonaemykh Nasekomykh iz Mesozoiskikh otlozhenii Chelyabinskogo burougolnogo basseina. (Note on the fossil insects from the Mesozoic deposits of Cheliabinsk lignite basin). *Tr. Paleozool. in-ta AN SSSR*, vol. 4, pp. 37–48.

Martynov, A.V. 1935b. O nakhozhdenii tripsov (Thysanoptera) v permskikh otlozheniyakh [On the occurrence of thrips (Thysanoptera) in the Permian beds]. *Dokl. AN SSSR*, vol. 3, No. 7, pp. 333–336.

Martynov, A.V. 1935c. O neskolkikh nasekomykh iz Kolchudinskoi svity Kuznetskogo basseina (On a few insects from Kolichudin series of the Kuznetsk basin). *Izv. AN SSSR. ser. biol.*, No. 3, pp. 441–448.

Martynov, A.V. 1935d. Permian fossil insects from Arkhangelsk district. Pt. 5. Homoptera. *Tr. Paleozool. in-ta. AN SSSR*, vol. 4, pp. 1–35.

Martynov, A.V. 1936. O nekotorykh novykh materialakh chlenistonogikh zhivotnikh iz Kuznetskogo basseina (On some new data on the arthropods from Kuznetsk basin). *Izv. AN SSSR*, ser. biol., No. 6, pp. 1251–1264.

Martynov, A.V. 1937a. Liasovye nasekomye Shuraba i Kizil-kii (Liassic insects of Shuraba and Kizil-kii). *Tr. Paleontol. in-ta AN SSSR*, vol. 7, No. 1, pp. 5–232.

Martynov, A.V. 1937b. Permskie iskopaemye nasekomye Kargalu i ikh otnozheniya (Permian fossil insects of Kargala and their affinities). *Tr. Paleontol. in-ta*, vol. 7, No. 2, pp. 8–91.

Martynov, A.V. 1937c. O krylyakh termitov v svyazi s voprosom filogenii stoi i sosednikh grupp nasekomykh (On the wings of termites and the problem of their phylogeny with related group of insects). *Sb. v. chest N.V. Nasonova. Izd. AN SSSR*, pp. 83–150.

Martynov, A.V. 1938a. Mestonakhozhdeniya iskopaemykh nasekomykh v predelakh SSSR (Occurrence of fossil insects within the limits of USSR). *Tr. Paleontol. in-ta*, vol. 7, No. 3, pp. 6–28.

Martynov, A.V. 1938b. O novom permskom otryade pryamokrylykh nasekomykh Glosselytrodea (On a new order of Permian orthopterous insects, Glosselytrodea). *Izv. AN SSSR*. ser. biol., No. 1, pp. 187–206.

Martynov, A.V. 1938c. Permskie nasekomye Arkhangelskoi obl. Ch. V. Sem. Euthygrammidae i ego otnosheniya (s opisaniem odnogo novogo roda i semeistva iz Chekardy). [Permian insects of the Arkhangelsk district. Part V. Fam. Euthygrammidae and their affinities (with a description of a new genus and family from Chekarda)]. *Tr. Paleontol. in-ta AN SSSR*, vol. 7, No. 3, pp. 69–80.

Martynov, A.V. 1938d. Ocherki geologicheskoi istorii i filogenii otryadov nasekomykh (Pterygota). Ch. 1. Palaeoptera i Neoptera–Polyneoptera [Essays on geological history and phylogeny of orders of insects (Pterygota). Part I. Paleoptera and Neoptera—Polyneoptera]. *Tr. Paleontol. in-ta*, vol. 7, No. 4, pp. 5–149.

Martynov, A.V. 1940a. Permskie iskopaemya nasekoye Chekardy (Permian fossil insects of Chekarda). *Tr. Paleontol. in-ta*, vol. 11, No. 1, pp. 5–62.

Martynov, A.V. 1940b. Sravnitelnyi vozrast iskopaemykh po r. Soyane, u. Tikhikh gor i bliz Cherkady no r. Sylve (Comparative age of the fossils along river Soyana in Tikhie Gory and near Chekarda along the river Sylva). *Materialy po geologii permskoi sistemy Evropeiskoi chasti SSSR*, Gostoptekhizdat, pp. 86–89.

Martynova, O.M. 1939. *Miopsyche kaspievi* sp. n., novyi vid rucheinika iz miotsenovykh otlozhenii Ordjonikidzenskogo kraya. (*Miopsyche kaspievi* sp. n., a new species of Trichoptera from the Miocene beds of Ordjonikidzensk region). *Tr. Voroshil. Gos. ped. in-ta*, vol. 1, pp. 91–93.

Martynova, O.M. 1941. Permskie Mecoptera s.r. Soyany (Permian Mecoptera from river Soyana). *Referaty rabot uchr. otd. biol. nauk. AN SSSR*, za 1940g, p. 266.

Martynova, O.M. 1942. Permskie Mecoptera iz Cherkady i Kargaly (Permian Mecoptera from Cherkada and Kargala). *Izv. AN SSSR*, ser. biol., No. 1–2, pp. 133–149.

Martynova, O.M. 1943. Glasselytrodea iz yurzkikh slantsev kamennougolnogo mestorozhdeniya Cogyuty (Glosselytrodea from the Jurassic shales of Carboniferous formation of Sogyuta). *Dokl. AN SSSR*, vol. 39, No. 7, pp. 312–313.

Martynova, O.M. 1945. Turskie Mesoptera iz uglenosnykh slavtsen Sogyuty (Jurassic Mecoptera from the Carbonaceous shales of Sogyuta). *Ref. rabot uchr. otd. biol. nauk. AN SSSR*, za 1941–1943gg, p. 225.

Martynova, O.M. 1947a. Dve novye verblyudki iz yurskikh slantsev Karatau (Two new snakeflies from the Jurassic shales of Karatau). *Dokl. AN SSSR*, nov. ser., vol. 56, No. 6, pp. 635–637.

Martynova, O.M. 1947b. O prirode trubok *Pectinariopsis* Andr. (Trichoptera. non Polychaeta). [On the nature of cases of *Pectinariopsis* Andr. (Trichoptera. non Polychaeta]. *Entomol. obozr.*, vol. 29, No. 3, pp. 152–153.

Martynova, O.M. 1947c. Kalligrammidae (setchatokrylye) iz yurskikh slantsev Karatau [Kalligrammidae (Neuroptera) from the Jurassic shales of Karatau]. *Dokl. AN SSSR*, vol. 58, No. 9, pp. 2055–2058.

Martynova, O.M. 1948a. Dva novykh vida permskikh nasekomykh iz

Kuznetskogo basseina (Two new species of Permian insects from Kuznetsk basin). *Dokl. AN SSSR*, vol. 60, No. 1, pp. 113–114.

Martynova, O.M. 1948b. Individualnaya izmenchivost krylev Mecoptera (Individual variability in wings of Mecoptera). *Izv. AN SSSR*, No. 2, pp. 193–198.

Martynova, O.M. 1948c. Materialy po evolyutsii Mecoptera (Data on evolution of Mecoptera). *Tr. Paleontol. in-ta*, vol. 14, No. 1, pp. 1–76.

Martynova, O.M. 1949a. Mezozoiskie setchatokrylye SSSR (Mesozoic Neuroptera of USSR). *Tr. Paleontol. in-ta*, vol. 20, pp. 150–170.

Martynova, O.M. 1949b. Pervaya nakhodka yurskogo nesekomogo v Kuznetskom basseine (First discovery of Jurassic insect in Kuznetsk basin). *Dokl. AN SSSR*, vol. 66, No. 5, pp. 923–924.

Martynova, O.M. 1949c. Facetochnye organy na krylyakh skorpionnits (Mecoptera) [''Mirrors*'' on the wings of scorpionflies (Mecoptera)]. *Byull. Mosk. ob-va isnyt. prirody otd. geol.*, vol. 24, No. 4, pp. 93–95.

Martynova, O.M. 1951a. Dva novykh nizhneleiacorykh nasekomykh iz Kizil-kii (Two new Lower Liassic insects from Kizil-kii). *Dokl. AN SSSR*, vol. 78, No. 5, pp. 1009–1011.

Martynova, O.M. 1951b. Mestonakhozhdenie permskikh nasekomykh u derevni Sokolovoi v Kuznetskom basseine (Occurrence of Permian insects in ancient Sokolova in Kuznetsk basin). *Dokl. AN SSSR*, vol. 79, No. 1, pp. 149–151.

Martynova, O.M. 1952a. Nekotopye permskie nasekomye iz kyzbasskikh otlozhenii (Some Permian insects from the Kuznetsk Basin deposits). *Byull. Mosk ob-va isnyt. prirody otd. geol.*, vol. 27, vyp. 3, p. 92.

Martynova, O.M. 1952b. Otryad Glosselytrodea iz permskikh otlozhenii Kemerovskii oblasti (Order Glosselytrodea from the Permian beds of Kemerov region). *Tr. Paleontol. in-ta AN SSSR*, vol. 40, pp. 187–196.

Martynova, O.M. 1952c. Permskie setchatokrylye SSSR (Permian Neuroptera of USSR). *Tr. Paleontol. in-ta AN SSSR*, vol. 40, pp. 197–237.

Martynova, O.M. 1953a. Nastavlenie dlya sborov iskopaemykh nasekomykh (Directions for the collection of fossil insects). *Izd. Paleontol. in-ta AN SSSR*, pp. 1–14.

Martynova, O.M. 1953b. Sostav fauny skorpionnida iz mestonakhozhdenii nasekomykh bezugolnoi ili kuznetskoi svity uglenosnoi tolshchi Kuznetskogo basseina (The scorpionfly fauna from the insects in the noncarbonaceous or kuznetsk series of the carbonaceous layers of Kuznetsk basin). *Dokl. AN SSSR*, vol. 89, No. 4, pp. 727–729.

Martynova, O.M. 1954. Setchatokryloe nasekomoe iz melovykh otlozhenii Sibiri (Neuroptera from the Cretaceous beds of Siberia). *Dokl. AN SSSR*, vol. 94, No. 6, pp. 1167–1169.

Martynova, O.M. 1958. Novye nasekomye iz permskikh i Mezazoiskikh otlozhenii SSSR (New insects from the Permian and Mesozoic deposits of

USSR). Materialy K "*Osnovam* paleontologii", Vyp. 2, pp. 69–94.

Martynova, O.M. 1959. Filogeneticheskie vzaimootnosheniya nasekomykh mekopteroidnogo kompleksa (Phylogenetic interrelationships amongst insects of the Mecopteroid complex). *Tr. In-ta morfol. zhivotnykh AN SSSR*, vyp. 27, pp. 221–230.

Martynova, O.M. 1961. Sovremennye i vymershie verblyudki (Insecta, Raphidioptera) [The living and the extinct snakeflies (Insecta, Raphidioptera)]. *Paleontol. zhurn.*, No. 3, pp. 73–83.

Martynova, O.M. 1961a. See Rohdendorf, B.B., E.E. Bekker-Migdisova, O.M. Martynova, A.G. Sharov and A.A. Makhotin (1952). Vzaimootnosheniya osnovnykh grupp prygayushchikh pryamokrylykh i morfologiya ikh yaitseklada (Interrelationships of the major groups of saltatorial Orthroptera and morphology of their ovipositor). *Entomol. obozr.*, vol. 32, pp. 126–136.

Martynova, O.M. 1963. Filogeneticheskie vzaimootnosheniya osnovnykh grupp prygayushchikh pryamokrylykh i morfologiya ikh yaitseklada (Phylogenetic interrelationships of the major groups of saltatorial Orthoptera and morphology of their ovipositor). *Tr. in-ta morfol. zhivotnykh. AN SSSR*, Vyp. 8, pp. 5–61.

Mavr, G.L. 1855. Formicina Austriaca. Wien.

Mavr, G.L. 1867. Vorlaufige Studien uber die Radoboj-formiciden. *Jahrb. kon. k. Geol. Reichsanst.*, vol. 17, No. 1, pp. 47–62.

Mavr, G.L. 1868. Die Ameisen des baltischen Bernstein. *Schr. phys.-okon . Ges. Konigsberg*, vol. 1, pp. 1–1.02.

Mc Keown, K.C. 1937. New fossil insects wings (Protohemiptera. Family Mesotitanidae). *Rec. Australian Mus.*, vol. 20, pp. 31–37.

Melander, A.L. 1949. A report on some Miocene Diptera from Florissant, Colorado. *Amer. Mus. Novit. N.Y.*, No. 1407, pp. 1–63.

Menge, A. 1856. Lebensreichen verweltlicher im Bernstein eingeschlossener Thiere. *Progr. Petrisch. Danzig.*, pp. 1–32.

Menge, A. 1866. Uber ein Rhipidopteron und einige Helminthen im Bernstein. *Schr. Naturiorsch. Ges. Danzig*, N.F., vol. 1, pp. 1–8.

Menon, R. 1942. Studies on Indian Copeognatha. *Indian Journ. Entomol.*, vol. 4, pp. 23–42.

Meshkova, N.P. 1961. O lichinkakh Ephemeropsis trisetalis Eichwald (Insecta). [On the larvae of *Ephemeropsis trisetalis* Eichwald (Insecta)]. *Paleontol. Zhurn.*, No. 4, pp. 164–168.

Meunier, F. 1897. Revue critique de quelques insectes fossiles du Musee Teyler. *Arch. Mus. Teyler, Haarlem*, ser. 2, vol. 6, pp. 217–239.

Meunier, F. 1898a. Les insects des temps secondaires. *Arch. Mus. Teyler*, ser. 2, vol. 6, p. 85.

Meunier, F. 1898b. Revue critique de quelques insectes fossiles du Musee Teyler. *Arch. Mus. Teyler*, ser. 2, vol. 5, pt. 3, pp. 221–239.

Meunier, F. 1899a. Sur les Dipteres du Copal du Musee provincial de Konigsberg. *Miscellanea Entomol. Bruyelles*, vol. 7, No. 9, pp. 128–129.

Meunier, F. 1899b. Sur les Conopaires des l'ambre tertiare. *Bull. Soc. Entomol de France*, No. 9, pp. 145–146.

Meunier, F. 1899c. Revision des Dipteres fossiles types de Leon conserves au Musee provincial de Konigsberg. *Miscellanes Entomol.*, vol. 7, pp. 161–165–182.

Meunier, F. 1900. Revision des Dipteres fossilles types de low conserves au Musee provincial de Konigsberg. *Miscellanes Entomol.*, vol. 7, No. 12, pp. 1–17.

Meunier, F. 1903. Les Pipunculidae de l'ambre. *Rev. Sci. Bourbon*, pp. 148–154.

Meunier, F. 1904a. Monographie des Cecidomyidae, Sciaridae, Mycetophilidae et Chironomidae de l'ambre de la Baltique. *Ann. Soc. Sci. Bruxelles*, vol. 28, pp. 13–276, 16 Taf.

Meunier, F. 1904b. Contribution a la faune des Helomyzinae de Fambre de la Baltiques. *F. des Journ. Natur.*, 1 Dec., pp. 21–27.

Meunier, F. 1905. Monographic des Psychodidae de l'ambre de la Baltique. *Ann. Mus. Nat. Hungarici*, III, pp. 235–255.

Meunier, F. 1906a. Un nouvelle genere de Psychodidae et un nouvelle espece de *Dactylolabis* (Tipulidae) de l'ambre de la Baltique. *Naturaliste* , vol. 28, pp. 103–104.

Meunier, F. 1906b. Les Tipulidae de l'ambre de la Baltique. *Ann. Soc. Sci. Bruzelles*, vol. 36, pp. 213–215.

Meunier, F. 1906c. Monographie des Tipulidae et des Dixidae de l'ambre de la Baltique. *Ann. des sciences natur.* (*Zool*), (9)4, pp. 349–401, pls. 12–16.

Meunier, F. 1907. Monographie des Dolichopodidae de l'ambre de la Baltique. *Naturaliste*, 1 Sept., vol. 29, p. 197.

Meunier, F. 1908a. Monographie des Dolichopodidae de l'ambre de la Baltique. *Naturalists*. Paris, vol. 30, pp. 7–9, 21–23, 29–30, 57–59.

Meunier, F. 1908b. Monographie des Empidae de l'ambre de la Baltique. *Ann. Sci. Nat. Zoologie*, t. 7, pp. 81–129.

Meunier, F. 1908c. Les Asilidae de l'ambre de la Baltique. *Bull. Soc. Entomol. de France*, pp. 18–20.

Meunier, F. 1909a. Nouveles recherches sur les insectes du terrain houiller de Commentry. *Ann. Paleontol.*, vol. 4, pp. 125–152.

Meunier, F. 1909b. Uber einige Coleopteren-Flugeldecken aus der praglazialen Braunkohle und dem interglazialen Torflager von Lauenburg (Elbe). Ib. Preuss. Geol. Landesanst.

Meunier, F. 1910. Monographie der Leptiden und Phoriden des Bernsteins. *Jahrb. Geol. Landesanst.* Berlin, (2)30, pp. 64–90.

Meunier, F. 1911. Nouveaux insectes de houiller de Commentry. *Bull. Mus. Hist. Nat.*, vol. 17, pp. 117–198.

Meunier, F. 1911. Les Blattidae des houilleres de Commentry. Contr. *Rend. Acad. Sci.* Paris, vol. 153, pp. 845–847.

Meunier, F. 1912. Apercu sur les Protoblattinae et les Mylacrinae du houiller de Commentry, Bruxelles. *Ann. Soc. Sci.*, vol. 36, pp. 187–189.

Meunier, F. 1914a. Un Protoblattidae et ur Blattidae du houiller de Commentry. *Bull. Soc., entomol. France*, vol. 83, pp. 388–394.

Meunier, F. 1914b. Sur deux nouvelles especes de Blattidae du terrain houiller der Commentry, Bruxelles. *Ann. Soc. Sci.*, vol. 38, pp. 93–94.

Meunier, F. 1917. Un Pompilidae de l'ambre de la Baltique's. Gravenhage Tijdschr. *Entomol.*, vol. 60, pp. 181–184.

Meunier, F. 1920. Quelques insects de l'Aquitanien de Rott Sept.-Monts. *Proc. Akad. West Amsterdam*, vol. 22, pp. 727–737, 891–898.

Meunier, F. 1923a. Sur quelques insectes de l'Aquitanien de Rott (Sept.-Monst. Rhenanie). *Misc. Entomol. Castaner.*, Tolosan, vol. 26, pp. 82–87.

Meunier, F. 1923b. Eine Blattidae aus dem Kohlenbecken Baldur (Lippenmulde), Westfalen. *Jahrb. Preuss. Geol.* Landesanstalt zu Berlin (1921), vol. 42, pp. 511–512.

Meyrick, E. 1895. A handbook of British Lepidoptera, London, pp. 1–843.

Meyrick, E. 1912. Micropterygidae. *Genera Insectorum*, fasc. 132, pp. 1–9.

Mulsant, E. 1854. Hist. Nat. Col. France, Latigenes, pp. 1–396.

Mulsant, E. 1856. *Histoire naturelle des Coleopteres de France*, Paris, vol. 7a. Melandryidae, pp. 1–116; vol. 7b. Mordellidae, pp. 1–172; vol. 7c. Lagriidae, Pythidae, Pyrochroidae, pp. 1–45.

Mulsant, E. 1856. *Hist. Nat. Col. Fr.* Longipedes. 1856, pp. 16, 137–147.

Mulsant, E. and C.I. Rey. 1868. Floricoles. Paris, pp. 8–319.

Naora, N. 1933. Notes on some fossil insects from East Asiatic Continent, with description of three new species. *Entomol. World, Tokyo*, vol. 1, pp. 208–219.

Navas, L. 1915. Neuropteros nuevos o poco conocidos. *Cuarta ser. Mem. Rog. Acad. Cienc. Art. Barcelona*, vol. 2, pp. 373–398.

Navas, L. 1915. Neuropteros nuevos o poco conocidos. *Quinta ser. Mem. Roy. Acad. Cienc. Art. Barcelona*, vol. 2, pp. 455–480.

Navas, L. 1916. Notas sobre el orden de los Rafidiopteros. *Mem. Roy. Acad. Cienc. Art. Barcelona*, vol. 12, pp. 507–513.

Navas, L. 1918a. Monographia de l'ordre dels Rafidiopters. Barcelona, pp. 1–89.

Navas, L. 1918b. Neuropteros nuevos o poco conocidos. Decima ser. *Mem. Roy. Acad. Cienc. Art. Barcelona*, vol. 14, pp. 339–366.

Obenverger, J. 1957. Entomologie III. Nakladatelstyi ceskoslovenske Akademie Ved., Praha.

Oishi, K. 1931. Fossil lake deposits Shilobara. *Journ. Geol. Soc. Tokyo*, vol. 38, p. 91.

Oliers, E.W.M. 1907. Die Urinsekten (Thysanura und Collembola im Bernstein), *Schr. phys.-okon. Ges. Konigsberg*, vol. 48, pp. 1–40.

Oliers, E.W.M. 1912. Ein neuer Thysanur im Bernstein. Berliner. *Entomol. Ztschr.*, vol. 56, pp. 151–152.

Olivier, A. 1785. *Entomologie.* Paris, vol. 3, No. 54, pp. 1–557.

Oman, P.W. 1937. Fossil Hemiptera from the Fox Hills Sandstone of Colorado. *Journ. Paleontol.*, vol. 2, p. 38.

Oppenheim, P.B. 1885. Die Ahnen unserer Schmetterlinge in der Sekundar und Tertiarperiode Berliner. *Entomol. Ztschr.*, vol. 29, No. II, pp. 331–345.

Oppenheim, P.B. 1888. Die Insektenwelt des lithographische Schiefers in Bayern. *Palaeontographica*, vol. 34, pp. 215–247.

Oustalet, E. 1870. Recherches sur les insectes fossiles des terrains tertiairres da la France. 1. Insectes fossiles des l'Auvergne. *Ann. Soc. Geol.*, vol. 2, pp. 1–178.

Oustalet, E. 1874. Recherches sur les insectes fossiles des terrains tertiaires de la France II. Insectes fossiles d'Aix. Provence. *Ann. Soc. Geol.*, vol. 5, pp. 1–347.

Paramonov, S.Y. 1936. Doslidi nad entomofaunoyu yantariv (Enquiries on the entomofauna of ambers). *Instit. zool. ta biol. AN SSSR*, No. 18, pp. 53–64.

Paramonov, S.Y. 1939. Kritische Ubersicht der ge genwartigen und fossilen Bombay-liiden—Gattungen der ganzen Welt. *Instit. zool. ta biol. AN USSR*, No. 23, pp. 23–50.

Pasek, V. 1953. Prispevek ke klassifikaci sp. now a dva dalsi zajimavi zastupei celedi Lacynidae, (Hom. Aphidoideal. *Vestnik Cs. spol. zool.*, t. 17, pp. 140–1).

Passerini, J. 1863. Aphidae Italicae. *Arch. per la Zool.*, vol. 2, p. 129.

Paykull, G. 1811. Monographia Histeroidum. Upsaliae, pp. 1–112.

Pearman, J.V. 1936. The taxonomy of the Psocoptera. *Proc. Roy. Entomol. Soc. London*, ser. B, vol. 5, pp. 58–62.

Pesson, P. 1951. In: Grasse *Traite de Zoologie*, t. 10, fssc. 2, Paris.

Pierce, W.D. 1919. The comparative morphology of the order Strepsiptera together with records and descriptions of insects. *Proc. U.S. Nat. Mus.*, vol. 54, No. 2242, Washington, pp. 391–501.

Pierce, W.D. 1948. Fossile Arthropods of California. *Bull. S. Calif. Acad. Sci. Los Angelos* (1947), vol. 46; pp. 136–143; vol. 47, pp. 21–55.

Pierce, W.D. 1950. Fossil Arthropods of British Columbia. *Bull. S. Calif. Acad. Sci. Los Angelos*, vol. 49, pp. 101–104.

Pierce, W.D. 1951. Fossil Arthropods from onyx marble. Hot calcareous waters killing insects. *Bull. S. Calif. Acad. Sci. Los Angelos*, vol. 50, pp. 34–49.

Ping, C. 1928. Cretaceous fossil insects of China. *Palaeontologia Sinica*, ser. B, vol. 13, fac. 1, pp. 1–56.

Ping, C. 1931. On Blattoid Insects in the Fushun Amber. *Bull. Geol. Soc. China*, Peiping, vol. 2, p. 205.

Piton, L. 1933a. Insectes fossiles des cine rites et randannites d'Avvergne de Bussac, Clermont-Ferrand, pp. 1–4.

Piton, L. 1933b. Monographie de la perche tertiaire des schistes de Menat (P-de-D) suivie d'une note sur deax Hemipteres-Homopteres prouvenant du meme gisement. *Rev. Sci. Bourbonnais Moulins*, pp. 60–66.

Piton, L. 1936. Les Hemipteres-Homopteres de l'Eocene de Menant. (P-de-D). *Misc. Entomol.*, vol. 37, pp. 93–94.

Piton, L. 1939. Succinotettix chopardi Piton. Orthoptera (Tetriginae) medit de l'ambre de la Baltique. *Bull. Soc. Entomol. France*, Paris, vol. 43, pp. 226–227.

Piton, L. and A. Rudel. 1936. Sur des nouveaux gisements d'insectes fossiles dans l'oligocene des la Limagne. *Bull. Mens. Soc. Linn. Lyon* (*N.S.*), t. 5, pp. 78–81.

Piton, L. and V. Theobald. 1935a. La fauna entomologique des gisements miopliocene du Massif Central. *Rev. Sci. Nat. Auvergne. Clermont-Ferrand*, vol. 1, pp. 65–104.

Pongracz, A. 1928. Die fossilen Insekten von Ungarn, mit besonderer Berücksichtigung der Entwicklung der europäischen Insektenfauna. *Ann. Hist. Nat. Mus. Nat. Hung. Budapest*, vol. 25, pp. 91–203.

Pongracz, A. 1935. Die eozane Insektenfauna des Gieseltales. *Nova Acta Leop. Carol. Halle* (*N.F.*), vol. 2, pp. 483–572.

Ponomarenko, A.G. 1961. O sistematicheskom polozhenii Coptoclava longipoda Ping. (On the systematic position of *Coptoclava longipoda Ping*). *Paleontol. zhurn.*, No. 3, pp. 67–72.

Popov, V.V. 1933. Two new fossil ants from Caucasus (Hymenoptera, Formicidae). *Tr. Paleontol. in-ta AN SSSR*, vol. 2, pp. 17–21.

Priesner, H. 1920. Beitrag zur Kenntnis der Thysanopteren Oberosterreichs. *Jahr. Ber. oberost. Musealver. Linz*, vol. 78, pp. 50–63.

Priesner, H. 1924. Bernstein Taysanopteren. *Entomol.*, *Mitteil.*, vol. 13. No. 4/5, pp. 130–151.

Priesner, H. 1929. Bernstein Thysanopteren. II. Bernst.-Forsch. No. 1, pp. 3–138.

Priesner, H. and Quievreux. 1935. Thysanopteres des couches de potasse du Haut-Rhin. *Bull. Soc. Geol. France*, Ser. 5, t. 5, fasc. 6–7, pp. 471–477.

Priesner, H. and Quievreux. 1949. Genera Thysanopterorum. Keys for the identification of the genera of the order Thysanoptera. *Bull. Soc. Entomol. Egyp.*, Cairo, vol. 33, pp. 31–157.

Pruvost, P. 1912. Les insects houillers du Nord de France. *Ann. Soc. Geol. Nord*. Lille, vol. 41, pp. 323–380.

Pruvost, P. 1919. La faune continentale du terrain houiller du Nord de la France. Mem. pour servir a l'explication de la carte geologique detailee de la France. Paris, Insectes., pp. 97–321.

Pruvost, P. 1920. Nouvelle decourvertes d'insectes fossiles dans le terrain houiller du Nord et du Pas-de-Calais. *Ann. Soc. Geol. Nord*. Lille, vol. 43, pp. 282–295 (1914).

Rebel, H. 1901a. Neue Lepidopteren aus Bosnien und der Hercegovina. *Verh. Ges. Wien*, vol. 51, pp. 798–804.

Rebel, H. 1901b. Uber einige neue von Herrn. Max. Korb in Westasien gessammelte Lepidopterenformen. *Ann. Hofnus. Wien.*, vol. 16, pp. 165–169.

Rebel, H. 1934. Bernstein-Lepidopteren (aus der Sammlung Bachofen-Echt). *Palaeobiol.*, vol. 6, pp. 1–16.

Rebel, H. 1935. Bernstein-Lepidopteren. *Dtsch. Entomol. Ztschr. Iris*, vol. 40, pp. 162–186.

Rebel, H. 1935a. Description de trois especes nouvelles de microlepidopteres d'Ankara. *Mitteil. Schweiz. Entomol. Ges., Berne*, vol. 16, pp. 442–449.

Rebel, H. 1935b. Neue Microlepidopteren aus Kleinasien. *Mitteil. Munch. Entomol. Ges.*, vol. 25, pp. 39–41.

Rebel, H. 1936. Microlepidopteren aus dem baltischen, Bernstein. *Naturwiss.*, pp. 519–520.

Redtenbacher, L. 1845. Die Gattungen der deutschen Kaferfauna nach der analytischen Methode bearbeitet, nebst einem kurzgefassten Keitfaden zum Studium dieses Zwelges der Entomologie. Wien, pp. 1–177.

Redtenbacher, L. 1900. Die Dermapteren und Orthropteren von Oesterreich-Ungarn und Deutschland.

Rehn, J.W.H. 1903. Studies in American Blattidae. *Trans. Amer. Entomol. Soc.*, vol. 29, pp. 259–290.

Rehn, J.W.H. 1939. The genus *Ptilotentis foliatus* Gabb. *Notul. Nat. Philadelphia*, vol. 9, pp. 1–2.

Rehn, J.W.H. 1951. Classification of Blattaria. *Mem. Amer. Entomol. Soc.*, vol. 14, p. 134.

Ribaga, C. 1905. Descrizone di nuovi Copeognathi. *Redia*, vol. 2, fasc. 1, pp. 99–110.

Richardson, E.S. 1956. Pennsylvanian invertebrates of the Mazon Creek Area. *Illinois. Fieldiana geol.*, vol. 12, No. 1–4, pp. 3–76.

Reik, E.F. 1950. A fossil Mecopteron from the Triassic beds at Brookvale, N.S.W. *Rec. Australian Mus.*, vol. 22, No. 3, pp. 254–256.

Reik, E.F. 1953. Fossil Mecopteroid insects from the Upper Permian of New South Wales. *Rec. Australian Mus.*, vol. 23, No. 2, pp. 55–87.

Reik, E.F. 1954. Further Triassic insects from Brookvale, N.S.W. (Orders Orthoptera, Saltatoria, Protorthoptera, Perlaria). *Rec. Australian Mus.*, vol. 23, No. 4, pp. 161–168.

Reik, E.F. 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Australian Journ. Zool.*, vol. 3, No. 4, pp. 654–691.

Reis, O.M. 1940. Fauna rybnykh slantsev Zabaikalskoi oblasti (Fauna of the fish shales of the Trans-Baikal region). *Geol. issled i razved. raboty po linii sib. zh. d. s. pb.*, No. 29, pp. 1–68.

Rodeck, H.G. 1938. Type specimens of fossils in University of Colarodo.

Museum Univ. Color Stud., vol. 25, pp. 281–304.

Rikhter, A.A. 1935. O zhilkovanii nadkrylii zhukov (On venation in elytra of beetles). *Russk. Ent. obzr.*, vol. 26, No. 1–4, pp. 25–58.

Rikhter, A.A. 1947. Iskopaemye zlatki iz binagadinskikh kirovykh sloev (Fossil Buprestidae from Binagadinian Kirovian beds). *Dokl. AN Arm. SSR*, vol. 4, No. 5, pp. 147–150.

Roesler, R. 1950. Neue und wening bekannte Copeognathen Gattungen. I, II. *Zool. Anz. Leipzig*, vol. 129, pp. 225–242; 1940, vol. 130, pp. 1–25.

Rosen, K. 1913. Die fossilen Termiten. Eine kurze Zusammenfassung der bis jetzt Bekannten Funde. *Trans. Second Entomol. Congr.*, 1912, vol. 2, pp. 318–335.

Rohdendorf, B.B., E.E. Bekker-Migdisova, O.M. Martinova, A.G. Sharnov and L.S. Berg. 1928. Iskonaemaya babochka iz oligotsena Irtysha (Fossil Lepidoptera from the Oligocene of Irtysh). '*Priroda*', No. 10, p. 929.

Rohdendorf, B.B. 1938. Dvukrylye nasekomye Mezozoya Karatau (Dipteran insects of the Mesozoic of Karatau). *Tr. Paleontol. in-ta AN SSSR*, vol. 7, No. 3, pp. 29–67.

Rohdendorf, B.B. 1939a. O miotsenovoi faune nasekomykh okrestnostei g. Voroshilovska (On the Miocene insect fauna in the neighborhood of Voroshilovska). '*Priroda*', No. 2, pp. 85–98.

Rohdendorf, B.B. 1939b. Predstavitel otryada Protelytroptera iz Uralskoi permi (Representatives of the order Protelytroptera from the Permian of Urals). *Dokl. AN SSSR*, vol. 23, No. 5, pp. 505–507.

Rohdendorf, B.B. 1940a. Nakhozhdenie vtorogo roda semeistva Scytohymenidae v Uralskom permi (Discovery of a second genus of the family Scytohymenidae in the Permian of Urals). *Dokl. AN SSSR*, vol. 26, No. 1, pp. 106–107.

Rohdendorf, B.B. 1940b. Stroenie tela Archodonata i polozhenie etogo otryada v sisteme Palaeoptera (Body structure of Archodonata and the position of this order in the classification of Paleoptera). *Dokl. AN SSSR*, vol. 26, No. 1, pp. 108–110.

Rohdendorf, B.B. 1943. Ob evolyutsii poleta nasekomykh (On the evolution of flight in insects). *Dokl. AN SSSR*, vol. 40, No. 4, pp. 187–189.

Rohdendorf, B.B. 1944. Novoe semistvo zhukov iz permi Urala (A new family of beetles from the Permian of Urals). *Dokl. AN SSSR*, vol. 44, No. 6, pp. 277–279.

Rohdendorf, B.B. 1946. Evolyutsia kryla i filogenez dlinnousykh dvukrylykh Oligoneura (Evolution of wing and phylogeny of hematoceran dipteran Oligoneura). *Tr. Paleontol in-ta AN SSSR*, vol. 13, No. 2, pp. 5–108.

Rohdendorf, B.B. 1947a. Ob iskopaenykh nasekomykh iz Vorkutskogou-ugolnogo basseina (On fossil insects from the Vorkutsk coal field basin). *Dokl. AN SSSR*, vol. 57, No. 4, pp. 391–393.

Rohdendorf, B.B. 1947b. Fauna drukrylykh uasekomykh Karatau i znachenie ee dlya ponimaniya evolyutsii otryada (Fauna of dipteran insects of Karatau and their importance in understanding the evolution of the order). *Dokl. AN SSSR*, vol. 55, No. 8, pp. 757–760.

Rohdendorf, B.B. 1947c. O mestonakhozhdenii leiyasovykh nasekomykh Sogyutu (On the occurrence of Liassic insects of Sogyuta). *Dokl. AN SSSR*, vol. 57, No. 6, pp. 607–608.

Rohdendorf, B.B. 1948. Zhilkovanie krylev nasekomykh u ego znachenie dlya sistematiki (Venation of wings in insects and its importance in systematics). *Izv. AN SSSR*, ser. biol., No. 2, pp. 199–203.

Rohdendorf, B.B. 1949. Evolyutsiya i klassifikatsiya letatelnogo apparata nasekomykh (Evolution and classification of flight organs in insects). *Tr. Paleontol. in-ta AN SSSR*, vol. 16, pp. 1–176.

Rohdendorf, B.B. 1950a. Ob izuchenii konkretnykh putei evolyutsii nasekomykh (On the study of specific paths of evolution of insects). *Izv. AN SSSR, ser. biol.*, No. 1, pp. 78–97.

Rohdendorf, B.B. 1950b. Progressivnoe razvitie evolyutsii (Progressive developmental evolution). *Vestn AN SSSR*, No. 6, pp. 53–58.

Rohdendorf, B.B. 1951. Organy dvizheniya dvukrylykh nasekomykh i ikh nproiskhozhdenie (Organs of locomotion in Dipteran insects and their origin). *Tr. Paleontol. in-ta AN SSSR*, vol. 35, pp. 1–180.

Rohdendorf, B.B. 1952. Razvitie i znachenie palaeontomologicheskikh rabot v Kuznetskom basseine (Development and importance of paleontomological work in the Kuznetsk basin). *Byull. Mosk. ob-va ispyt. prirody., otd. geol.*, vol. 27, No. 3, p. 1.

Rohdendorf, B.B. 1954. Razvitie paleoentomologicheskikh issledovanii v kuznetskom basseine (Development of paleoentomological investigations in the Kuznetsk basin).*Tr. Tomskogo gos. universiteta*, vol. 132, pp. 126–128.

Rohdendorf, B.B. 1956. Paleozoiskie nasekomye yuzhnoi Sibiri (Paleozoic insects of Southern Siberia). *Entomol. obozr.*, vol. 35, No. 3, pp. 611–619.

Rohdendorf, B.B. 1957. Paleontomologicheskie issledovaniya v SSSR (Palaeoentomological investigations in the USSR). *Tr. Paleontol. in-ta*, vol. 66, pp. 1–102.

Rohdendorf, B.B. 1958a. Less Insectes Paleozoiques du Sud de la Siberie. *Proc. Tenth Int. Congress entomol.*, vol. 1, pp. 853–859.

Rohdendorf, B.B. 1958b. Paleontologieky vyzkum v SSSR. *Vesmir.*, 37, 10, pp. 341–343.

Rohdendorf, B.B. 1959. Voprosy paleozoologicheskoi sistematiki (Problems in paleozoological systematics). *Paleontol. zhurnal.*, No. 3, pp. 15–26.

Rohdendorf, B.B. 1961a. Osobennosti ontogeneza i ikh znachenie v evolyutsii nasekomykh (Peculiarities of ontogeny and their significance in the evolution of insects). *Acta symposii de evolutions insectorum*, Praha (1959). pp. 56–60.

Rohdendorf, B.B. 1961b. Paleoentomologicheskie issledovaniya v SSSR (Paleoentomological investigations in the USSR). *Sorok let sovetskoi Paleontologii. Tr. Chetvertoi sessii vses paleontol. ob-va*, pp. 23–30.

Rohdendorf, B.B. 1961c. Nasekomye paleozoya yuzhnoi Sibiri i ikh znachenie dlya paleogeografii i stratigrafii (Paleozoic insects of Southern Siberia and their importance for paleogeography and stratigraphy). Congresso Geologico Internation. XXa session, Section VII. *Paleontologia, Taxonomia y Evolution*. Mexico. D.E. pp. 37–54.

Rohdendorf, B.B. 1961d. Drevneishie infraotryady dvukrylykh iz Triasa Srednei Azii (Primitive infra orders of Diptera from the Triassic of Central Asia). *Paleontol. zhurn.*, No. 3, pp. 90–100.

Rohdendorf, B.B. 1961e. Opisanie pervogo krylatogo nasekomogo iz devonskikh otlozhenii Timana (Insecta, Pterygota) [Description of the first winged insect from the Devonian beds of Timan (Insecta, Pterygota)]. *Entomol Obozor.*, vol. 40, No. 3, pp. 485–489.

Rohdendorf, B.B. 1961f. Neue Anigeben uber das system der Dipteren. XI. Intern. Kongrez. f. Entomol. Verhandlungen, vol. 1, pp. 153–158.

Rohdendorf, B.B. 1961g. Die Palacentomologie in der UdSSR. *Tam. zhe*, pp. 313–318.

Rohdendorf, B.B. 1962. Tip Arthropoda. Chlenistonogie. Chelicerata. Picnogonides. Tracheata. (Phylum Arthropoda—Chelicerata, Picnogonides, Tracheata). *C. Paleontologiya* besnozvonochuykh pod redaktsei yu. A. Orlova, pp. 266, 306–328.

Rohdendorf, B.B., E.E. Bekker-Migdisova, O.M. Martynova and A.G. Sharov. 1961. Paleozoiskie nasekomye Kuznetskogo basseina (Paleozoic insects of Kuznetsk basin). *Tr. Paleontol. in-ta AN SSSR*, vol. 85, pp. 1–705.

Salt, G. 1931. Three Bees from Baltic Amber. Bernst.-Forsch., No. 2, pp. 136–147.

Saussure, H., de. 1864a. *Blattarum novarum* species aliquot. *Rev. Mag. Zool.* (2), XVI, pp. 305–326 (separ. 1–31).

Saussure, H., de. 1870. Melanges orthopterologiques. Genf. et Base.

Saussure, H., de. 1893. Revision de la tribu Heterogamieus. *Rev. Suisse Zool.*, 1, pp. 289–318.

Schiodte, J.M.C. 1849. Bidrag til den underjordiske Fauna. Kjobenhavn. pp. 1–39.

Schlechtendal, D.H.R. 1892. Uber das Vorkommen Fossilen Ruckenschwimmer (Notonecten) im Braunkohlengebirge von Rott. *Ztschr. Naturi.*, vol. 65, pp. 141–143.

Schlechtendal, D.H.R. 1894. Beitrage zur Kenntnis fossilen Insekten aus dem Braunkohlengebirge von Rott am Siebengebirge. *Abh. Naturi Ges.*, vol. 20, pp. 197–228.

Schlechtendal, D.H.R. 1912 (1913). Untersuchung uber die karbonischen

Insekten und Spinnea von Wettin unter Berucksichtigung von wandtern Faunen. Teil. I. Revision der Originale von Germar. Gieblel und Goldenberg. *Nova Acta Abh. Kais. Leop.-Carol. Dtsch. Akad. Naturi.*, vol. 98, Nr. I, pp. 99–162.

Schletterer, A. 1889. Die Hymenopteren-Gattungen *Stenophasmus*, *Monomachus*, *Pelecinus* und *Megalyra*. *Jahrb. Entomol. Zeitung.*, pp. 197–250.

Schneider, G.T. 1945. Verzeichnis der von Prof. Loew im Sommer 1842 in der Turkei und Kleiner Asien gesammelten Neuroptera nebst kurzer Beschreibung der neuen Arten. *Stett. Entomol. Zeitung*, vol. 6, pp. 110–116.

Scourfield, D.J. 1940. The oldest known fossil insect (*Rhyniella praecursor* Hist and Maulik)—further details from additional specimens. *Proc. Linn Soc. London*, vol. 152, pt. 2, pp. 113–131.

Scudder, S.H. 1868. *Geol. Surv. Illinois*, vol. 3, p. 568.

Scudder, S.H. 1875. Fossil Butterflies. In: *Mem. Amer. Assoc. Adv. Sci.*, vol. 1, pp. 12–99.

Scudder, S.H. 1876. Fossil Coleoptera from the Rocky Mountain Tertiaries. In: *Bull U.S. Geol. Geogr. Surv. Territ.*, vol. 2, pp. 77–87.

Scudder, S.H. 1878a. An account of some insects of unusual interest from the tertiary rocks of Colorado and Wyoming. *Bull. U.S. Geol. Surv.*, vol. 4, pp. 519–544.

Scudder, S.H. 1878b. The fossil. Insects of the Green River Shales. *Bull. U.S. Geol. Surv.*, vol. 4, No. 2, pp. 747–776.

Scudder, S.H. 1879. Paleozoic cockroach, a complete revision of the species of both Worlds, with an essay toward their classification. *Mem. Bost. Soc. Nat. Hist.*, vol. 3, pt. 1, No. 3, pp. 23–134.

Scudder, S.H. 1881. The Tertiary Lake Basin at Florissant, Colorado, between South and Hayden Parks. *Bull. U.S. Geol. Surv.*, vol. 4, pp. 279–300.

Scudder, S.H. 1882. A bibliography of fossil insects. *Bibliographical Contr.*, No. 13, Cambridge.

Scudder, S.H. 1883a. The Tertiary Lake Basin at Florissant, Colorado, between South and Hayden Parks. *Ann. Rep. U.S. Geol. Geogr. Surv. Territ.*, vol. 12, pp. 217–293.

Scudder, S.H. 1883b. A review of Mesozoic Cockroaches. *Mem. Boston Soc. Nat. Hist.*, vol. 3, No. 13, pp. 439–487.

Scudder. S.H. 1885a. Insecta. In: Zittel ''*Handbuch der Palaeontologie*'', I(II), pp. 747–831.

Scudder, S.H. 1885b. Winged insects from a palaeontological point of view. *Mem. Bost. Soc. Nat. Hist.*, vol. 3, No. 2.

Scudder, S.H. 1885b. New genera and species of fossil Cockroaches, from Older American Rocks. *Proc. Acad. Sci. Philadelphia*, pp. 34–49.

Scudder, S.H. 1886a. A review of mesozoic Cockroaches. In: *Mem. Bost. Soc.*

Nat. Hist., vol. 3, No. 13, pp. 430–485.

Scudder, S.H. 1886b. Systematic review of our present knowledge of fossil insects. *Bull. U.S. Geol. Surv.*, vol. 31, pp. 1–128.

Scudder, S.H. 1890a. Physiognomy of the American Tertiary Hemiptera. *Proc. Bost. Soc. Nat. Hist.*, vol. 24, pp. 562–580.

Scudder, S.H. 1890b. The Teritiary insects of North America. *Bull. U.S. Geol. Surv.*, vol. 13, pp. 1–734.

Scudder, S.H. 1892. Some insects of special interest from Florissant and other points in the tertiaries of Colorado and Utah. *Bull. U.S. Geol. Surv.*, vol. 93, pp. 11–25.

Scudder, S.H. 1893. Insect Fauna of the Rhode Island Coal Field. *Bull. U.S. Geol. Surv.*, vol. 101, pp. 1–27.

Scudder, S.H. 1894. Tertiary Tipulidae with special reference to those of Florissant, Colorado. *Proc. Amer. & Phil. Soc. Philad.*, vol. 32, pp. 163–245.

Scudder, S.H. 1895a. I. Canadian fossil insects. II. The tertiary Hemiptera of British Columbia, contributions to Canadian Palaeontology, pp. 5–26.

Scudder, S.H. 1895b. Revision of the American fossil Cockroaches, with description of new forms. *Bull. U.S. Geol. Surv.*, Territ, vol. 124, pp. 1–145.

Scudder, S.H. 1896. The European species of *Etoplattina*, with description of a new form. *Geol. Mag., N.S.*, Dec. IV, vol. 3, p. 12.

Seidlitz, G. 1875. Fauna Baltica. Die Kafer der Ostsceprovinzen Russlands.

Seidlitz, G. 1891. Fauna Baltica, Ed. II.

Sellards, E.H. 1903. Some new structural characters of Paleozoic cockroaches. *Amer. Journ. Sci.*, vol. 15, pp. 307–315.

Sellards, E.H. 1904. A study of the structure of Paleozoic Cockroaches with descriptions of new forms from the Coal Measures. *Amer. Journ. Sci.*, vol. 18, No. 103, pp. 112–134; No. 104, pp. 213–227.

Sellards, E.H. 1908. Cockroaches of the Kansas Coal Measures and the Kansas Permian. *Univ. Geol. Surv. Kansas.*, vol. 9, pp. 501–541.

Sellards, E.H. 1909. Types of Permian Insects, pt. 3, Megasecoptera, Oryctoblattinidae and Protorthoptera. *Amer. Journ. Sci.*, vol. 4, No. 25, pp. 154–173.

Selys-Longchamps, E.M. 1863. Synopsis des Agrionines, 4. Platycnemis. *Bull. Acad. Brux.*, vol. 16, pp. 147–176.

Sendelius, N. 1742. Historia Succinorum corpora aliena involventium, et. naturae opere pictorum etcaelatorum, ex Regiis Augustorum cimeliis Dresdae conditis aeri insculptorum conscripta, pp. 1–328.

Shaposhnikov, G.Kh. 1953. Zhivotnyi mir SSSR. (The animal world of the USSR), vol. 4, pt. 8, pp. 505–521.

Sharp, D. 1895, 1899. Lipsial, Insects. *The Cambridge Nat. Hist. London*, vol. 2.

Sharov, A.G. 1948. Triasovye Thysanura iz Priuralya (Triassic Thysanura from the Ural). *Dokl. AN SSSR*, vol. 61, No. 3, pp. 517–519.

Sharov, A.G. 1953. Pervaya nakhodka permskoi lichinki vislokrylogo nasekomogo (Megaloptera) iz Kargaly (First discovery of Permian larva of Megalopterous insects from Kargala). *Dokl. AN SSSR*, vol. 89, No. 4, pp. 731–732.

Sharov, A.G. 1957a. Nimfy miomopter iz permskikh otlozhenii Kuznetskogo basseina (Nymphs of Apterygota from the Permian beds of Kuznetsk basin). *Dokl. AN SSSR*, vol. 112, No. 6, pp. 1106–1108.

Sharov, A.G. 1957b. Svoeobraznye paleozoiskie beskrylye nasekomye novogo otryada Monura (Insecta, Apterygota) [Peculiar Paleozoic insects of the new order Monura (Insecta, Apterygota)]. *Dokl. AN SSSR*, vol. 115, No. 4, pp. 795–798.

Sharov, A.G. 1957c. Pervaya nakhodka melovogo zhalonosinogo pereponchatokrylogo (Hymenoptera, Aculeata) [First discovery of Cretaceous sting-bearing Hymenoptera (Aculeata)]. *Dokl. AN SSR*, vol. 112, No. 5, pp. 943–944.

Sharov, A.G. 1957d. Tipy metamorfoza nasekomykh i ikh vzaimootnosheniya (po sravnitelno ontogeneticheskim i paleontologicheskim dannym). [Types of metamorphosis in insects and their interrelationships (through comparative ontogenetic and paleontologic data)]. *Entomol. obozr.*, vol. 36, No. 3, pp. 569–576.

Sharov, A.G. 1960a. On the system of the orthopterous insects, Verh XI. Intern. Kongr. f. Entomologie, Wien 1960, vol. 1, pp. 295–296.

Sharov, A.G. 1960b. The origin of the order Plecoptera ibid, pp. 296–298.

Sharov, A.G. 1961. See Rohdendorf, B.B., E.E. Bekker-Migdisova, O.M. Martynova and A.G. Sharov (1962). Novoe permskoe semeistvo pryamokrylykh (Orthoptera). (New Permian family of Orthoptera). *Paleontol. zhurn.*, No. 2, pp. 112–116.

Shegoleva-Barovskaya, T. 1929. Der erste ventreter der Familie Mordellidae aus der Juraformation. Turkestans. *Dokl. AN SSSR*, pp. 27–29.

Shelford, R. 1910. On a collection of Blattidae preserved in Amber from Prussia. *Journ. Linn. Soc. London*, vol. 30, pp. 336–355.

Shelford, R. 1911. The British Museum collection of Blattidae enclosed in Amber. *Journ. Linn. Soc. London*, vol. 32, pp. 59–60.

Shtakel'berg, A.A. 1925. Novyi iskopaemyi predstavitel' roda *Tubifera* Mgn. (Diptera, Syrphidae) [New fossil representative of genus *Tubifera* Mgn. (Diptera, Syrphidae)]. *Russk. Entomol. obozr.*, vol. 19, pp. 89–90.

Silvestri, F. 1909. Isoptera. In: Michaelsen, W. and R. Hartmeyer. Die Fauna Sudwest Australia, vol. 2, Lief. 17, pp. 279–314.

Silvestri, F. 1913. Die Thysanuren des baltischen Bernsteins. *Schrift, Phys.-okon. Ges. Konigsberg.*, vol. 53, pp. 42–66.

Smith, F. 1851. List of the British animals in the collection of the British Museum. Pt. 4. Hymenoptera Aculeata, London, pp. 1–134.

Snyder, Th. E. 1925. New termites and hitherto unknown castes from the Canal Zone Panama. *Journ. Agr. Res.*, vol. 29, No. 4, pp. 179–193.

Snyder, Th.E. 1926. The biology of termite castes. *Quart. Rev. Biol. Baltimore*, vol. 1, pp. 522–552.

Snyder, Th.E. 1928. A new Reticulitermes from Baltic Sea amber (Isoptera). *Journ. Washington Acad. Sci.*, vol. 18, No. 19, pp. 515–517.

Snyder, Th.E. 1931. Iv. Isoptera. In: Carpenter, F.M. Insects from the Miocene (Latah) of Washington. *Ann. Entomol. Soc. Amer.*, vol. 24, No. 2, p. 317.

Snyder, Th.E. 1949. Catalogue of the termites (Isoptera) of the World. *Smiths. Miscell. Coll. Washington*, vol. 112, pp. 1–400.

Spinola, M. 1811. Essai d'une nouvelle classification generale des Diplolepaires. *Ann. Mus. Hist. Nat.*, vol. 17, pp. 138–152.

Spulder, A. 1910. Die Schemetterlinge Europas. Stuttgart, vol. 2, pp. 1–523.

Stach, J. 1922. Eine neue Sminthurusart aus der Bernsteinfauna. *Bull. Acad. Polon. Sci. et lettr.*, ser. B, p. 53.

Stainton, H.T. 1854. Insecta Britannica. Tineina. London, pp. 1–313.

Stal, C. 1874–1875. Recensio Orthopterorum Revue critique des Orthopteres. Stockholm, vol. 2, p. 121; vol. 3, p. 105.

Statz, G. 1937. Tertiary fossil water-insects of Lower Rhine. *Nat. am Niederthein*, vol. 13, pp. 1–16.

Statz, G. 1938. Neue Funde parasitische Hymenopteren aus dem Tertiar von Rott am Sibengebirge. *Decheniana*, vol. 98A, No. 1, pp. 71–154.

Statz, G. 1939, 1940. Geradefluger und Wasserkafer der oligocanen Ablagerungen von Rott. *Decheniana*, vol. 99A, pp. 1–102.

Statz, G. 1940. Neue Dipteren (*Brachycera* et *Cyclorhapha*) aus dem Oberoligozan von Rott. *Palaeontographica*, vol. XCI, Abt. A, Lief, 3–6, pp. 120–174.

Statz, G. 1943, 1944. Neue Dipteren (Nematocera) aus dem Oberoligocan von Rott. *Palaeontographica*, vol. 95, Abt. A, Lief, 1–6, pp. 1–185.

Statz, G. 1950. Alte und neue Hydrocorisae (Wasserwanzen) aus dem Oberoligocan von Rott. *Palaeontographica*, vol. 98, Abt. A, Lief. 1–4, pp. 47–94.

Statz, G. 1950. Cicadariae (Zikaden) aus dem oberoligocanen Ablagerung von Rott. *Palaeontographica*, vol. 98, Abt. A, Lief. 1–4, pp. 1–44.

Statz, G. 1952. Fossil Mordellidae und Lamellicornia aus dem Oberoligozan von Rott. *Palaeontographica*, vol. 102, Abt. A, Lief. 1/2, pp. 1–17.

Statz, G. and E. Wagner. 1950. Geocorisae (Landwanzen aus den Oberoligocanen Ablagerungen von Rott). *Palaeontographica*, vol. 98, Abt. A., Lief. 5–6, pp. 97–134.

Stephens, J.F. 1828, 1832. Illustrations of British Entomology. Coleoptera, I–V. London.

Stephens, J.F. 1829, 1835. Family Perlidae Leach. In: Illustrations of British Entomology, pp. 144–145. London.

Stephens, J.F. 1836–1837. Illustrations of British Entomology, vol. 5.

Stephens, J.F. 1836–1837. Illustrations of British Entomology, vol. 6, pp. 146–239.

Strand, E. 1928. Miscellanea nomenclatorica zoologica et palaeontologica (A). *Arch. Naturgesch.*, vol. 92, No. 6, pp. 30–75.

Strand, E. 1929. Zoological and paleontological nomenclatorial notes. *Acta Univ. Latv., Riga*, vol. 20, p. 129.

Strand, E. 1942. Miscellanea nomenclatorica zoologica et paleontologica. X–XII. *Folia Zool. Hydrobiol., Riga*, vol. 2, pp. 386–402.

Sturm, J. and J.H.C.F. Sturm. 1805–1806. Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. V. Die Insekten. Kafer. I–XXIII. Nurnberg, T. 12, pp. 29–88.

Ter-Minasyan, M.E. 1947. Novyi iskopaemyi vid roda Rhynchites iz binagadinskikh kirovykh sloev (New fossil species of the genus Rhynchites from the Binagadinian-kirovian beds). *Dokl. AN Arm. SSR*, vol. 7, No. 5, pp. 227–229.

Teixeira, C. 1939. Insectes de Estefaniano do Doure. *Litoral Publ. Mus. Lab. Min. Geol. Fac. Ci. Porto*, vol. 9, pp. 1–20.

Teixeira, C. 1941. Nouveaux insects du Stephanien portugaes. *Bol. Soc. Geol., Portugal*, Porto, vol. 1, pp. 13–32.

Teixeira, C. 1941. Sur quelques insectes lossiles de Carbonifere de l'Alentejo. *Ann. Fac. Cienc.*, Porto, vol. 26, pp. 117–120.

Teixeira, C. 1944. Sur les insectes du genre Lusitanomylacris. *Bol. Spc. Esp. Hist. Nat.* Madrid, vol. 42, pp. 411–415.

Teixeira, C. 1947. Nota sobre um Blatidio fossil do Retiano de Coimbra. *Bol. Soc. Geol., Portugal*, Porto, vol. 6, pp. 243–244.

Theobald, C.R. 1934. Fossil insects of limestone of camoins (Marseills), Cereste (Basses-Alpes) and Aix en Province. *Acad. Sci. Tr.*, vol. 199, pp. 1057–1058.

Theobald, N. 1937. Les insectes fossiles des terrains oligocene de France. Nancy, pp. 1–473.

Thomson, C.P. 1859–1868. Skandinaviens Coleoptera, synoptiskt bearbetade. I–X. Lund, pp. 2–420.

Thomson, C.P. 1864a. Scand. Col., t. 6, Lund, pp. 1–385.

Thomson, C.P. 1864b. System cerambycidarum ou expose de tous les genres compris dans la famille des Cerambycides et familles limitrophes. Liege, Paris, pp. 1–352.

Tillyard, R.J. 1916. Mesozoic and Tertiary insects of Queensland and New South Wales. *Queensland Geol. Surv.*, No. 253, pp. 1–49.

Tillyard, R.J. 1917. Mesozoic insects of Queensland, No. 1. Planipennia, Trichoptera and the new order Protomecoptera. *Proc. Linn. Soc. N.S.W.*, vol. 42, pt. 1, pp. 175–200.

Tillyard, R.J. 1918 (1917). Permian and Triassic insects from New South Wales in the collection of Mr. John Mitchell. *Proc. Lin., Soc. N.S.W.*, vol. 42, pt. 4, No. 168, pp. 720–756.

Tillyard, R.J. 1918a. A fossil insect-wing from the roof of the coalseam in the Sydney harbour colliery. *Proc. Linn. Soc. N.S.W.*, vol. 43, pt. 2, pp. 260–264.

Tillyard, R.J. 1918b. Mesozoic insects of Queensland, No. 3. *Proc. Linn. Soc. N.S.W.*, vol. 43, pt. 3, pp. 417–436.

Tillyard, R.J. 1918c. On the affinities of two interesting fossil insects from the Upper Carboniferous of Commentry, France. *Proc. Linn. Soc. N.S.W.*, vol. 43, pp. 123–134.

Tillyard, R.J. 1918d. Permian and Triassic insects in the Collection of Mr. John Mitchell. *Proc. Linn. Soc. N.S.W.*, vol. 42, pt. 4, No. 168, pp. 720–756.

Tillyard, R.J. 1918–1919. The panorpoid complex. *Proc. Linn. Soc. N.S.W.*, vol. 48, pp. 286–319, 626–657; vol. 44, pp. 533–718.

Tillyard, R.J. 1919. A fossil insect wing belonging to the new order Paramecoptera, ancestral to the Trichoptera and Lepidoptera, from the Upper Coal Measures of Newcastle. N.S.W. *Proc. Linn. Soc. N.S.W.*, vol. 44, pt. 2, No. 174, pp. 231–256.

Tillyard, R.J. 1919. Mesozoic insects of Queensland, No. 5. Mecoptera, the new order Paratrichoptera, and additions to Planipennia. *Proc. Linn. Soc. N.S.W.*, vol. 44, pt. 1, pp. 194–212.

Tillyard, R.J. 1921. Two fossil insect wings in the collection of Mr. John Mitchell from the Upper Permian of Newcastle, belonging to the order Hemiptera. *Proc. Linn. Soc. N.S.W.*, vol. 46, No. 4, p. 413.

Tillyard, R.J. 1922a. Mesozoic insects of Queensland, No. 9. Orthoptera and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proc. Linn. Soc. N.S.W.*, vol. 47, pt. 4, pp. 447–470.

Tillyard, R.J. 1922b. Some new Permian insects from Belmont. N.S.W., in the collection of Mr. John Mitchell. *Proc. Linn. Soc. N.S.W.*, vol. 47, pt. 3, No. 187, pp. 279–292.

Tillyard, R.J. 1924a. On a tertiary fossil insect wing from Queensland (Homoptera, Fulgoroidea) with description of a new genus and species. *Proc. Roy. Soc. Queensland*, Brisbane, vol. 35, pp. 16–20.

Tillyard, R.J. 1924b. Upper Permian Coleoptera and a new order from the Belmont beds. N.S.W. *Proc. Linn. Soc. N.S.W.*, vol. 49, pp. 429–435.

Tillyard, R.J. 1925. Alleged Rhaetic craneflies. *Nature*, vol. 116, pp. 676–677.

Tillyard, R.J. 1926. Kansas Permian insect. Pt. 7, The order Mecoptera. *Amer. Journ. Sci.*, vol. 2, pp. 133–164.

Tillyard, R.J. 1926a. Kansas Permian insects. Pt. 8. *Amer. Journ. Sci.*, vol. 2, No. 5, pp. 315–349.

Tillyard, R.J. 1926. Kansas Permian insects. Pt. 9. Hemiptera. *Amer. Journ. Sci.*, vol. 2, ser. 5, pp. 381–395.

Tillyard, R.J. 1926d. The Rhaetic Craneflies from South America not Diptera but Homoptera. *Amer. Journ. Sci.*, vol. 2, ser. 5, pp. 265–272.

Tillyard, R.J. 1926e. Upper Permian insects of New South Wales. Pt. I.

Introduction and the order Hemiptera. *Proc. Linn. Soc. N.S.W.*, vol. 51, pp. 1–30.

Tillyard, R.J. 1926f. Upper Permian insects of New South Wales. Pt. II. The order Mecoptera, Paramecoptera and Neuroptera. *Proc. Linn. Soc. N.S.W.*, vol. 51, pt. 3, pp. 265–282.

Tillyard, R.J. 1927. The Ancestry of the order Hymenoptera. *Trans. Entomol. Soc. London*, pp. 307–317.

Tillyard, R.J. 1928a. Kansas Permian insects. Pt. 10. The new order Protoperlaria: A study of the typical genus *Lemmatophora* Sellards. *Amer. Journ. Sci.*, vol. 16, pp. 185–220.

Tillyard, R.J. 1928b. Kansas Permian insects. Pt. II. Order Protoperlaria: family Lemmatophoridae. *Amer. Journ. Sci.*, vol. 16, No. 93, pp. 313–348.

Tillyard, R.J. 1928c. Kansas Permian insects. Pt. 12. The family Delopteridae, with a discussion of its ordinal position. *Amer. Journ. Sci.*, vol. 16, No. 96, pp. 469–484.

Tillyard, R.J. 1928d. Some remarks on the Devonian fossil insects from the Rhynie Chert Beds, old red sandstone. *Trans. Entomol. Soc., London*, vol. 76, pp. 65–71.

Tillyard, R.J. 1929. Permian Diptera from Warner's bay. N.S.W. *Nature*, vol. 123, pp. 778–779.

Tillyard, R.J. 1932. Kansas Permian insects. Pt. 14. The order Neuroptera. *Amer. Journ. Sci.*, vol. 23, No. 133, pp. 1–30.

Tillyard, R.J. 1933. Fossil insects. No. 3. The Panorpoid complex in the British Rhaetic and Lias. *Brit. Mus. Nat. Hist.*, pp. 7–79.

Tillyard, R.J. 1935a. The evolution of the Scorpion-flies and their derivatives (Order Mecoptera). *Ann. Entomol. Soc., America*, vol. 28, No. 1, pp. 1–45.

Tillyard, R.J. 1935b. Upper Permian insects of New South Wales. Pt. 3. The Order Copeognatha. *Proc. Linn. Soc. N.S.W.*, vol. 60, pt. 3/4, pp. 265–279.

Tillyard, R.J. 1936a. A new Upper Triassic Insect Bed in Queensland. *Nature*, vol. 138, p. 719.

Tillyard, R.J. 1936b. Kansas Permian Insects. Pt. 17. The order Megasecoptera. *Amer. Journ. Sci.*, vol. 33, No. 194, pp. 435–453.

Tillyard, R.J. 1937a. Kansas Permian Insects. Pt. 17. The order Megasecoptera and additions to the Palaeodictyioptera, Odonata, Protoperlaria, Copeognatha and Neuroptera. *Amer. Journ. Sci.*, vol. 33, No. 195, pp. 81–110.

Tillyard, R.J. 1937b. Kansas Permian Insects. Pt. 18. The order Embiaria. *Amer. Journ. Sci.*, vol. 33, No. 196, pp. 241–251.

Tillyard, R.J. 1937c. Kansas Permian Insects. Pt. 19. The order Protoperlaria. The family Probnisidae. *Amer. Journ. Sci.*, vol. 33, No. 198, pp. 401–425.

Tillyard, R.J. 1937d. Kansas Permian Insects. Pt. 20. The order Blattaria. *Amer. Journ. Sci.*, No. 201, vol. 34, pp. 169–202, 249–276.

Tillyard, R.J. 1937e. A small collection of fossil cockroach remains from the

Triassic beds of Mount Crosby, Queensland. *Proc. Roy. Soc., Queensland* (1936), vol. 48, pp. 35–40.

Tillyard, R.J. 1937f. The ancestors of the Diptera. *Nature*, vol. 139, No. 3506, pp. 66–67.

Tillyard, R.J. and F.C. Fraser. 1938. A reclassification of the order Odonata. Pt. 1. *Australian Zool.*, vol. 9, pp. 125–169.

Tiraboschi, C. 1904. Les rats, les. souris et leurs parasites cutanes dans leurs rapports avec la propagation de la peste bubonique. *Arch. parasit.*, vol. 8, pp. 161–349.

Torquist, A. 1910. Die in der Koniglichen Universitats Bernsteinsammlung eingefuhrte Konservierungsmethode fur Bernsteinschlusse.. *Schrift. Phys.-okom. Ges. Konigsberg*, vol. 51, pp. 217–297.

Toussaint de Serres, M. 1829. Geognosie des terrains Monpellies et Paris, pp. 1–277.

Tullgren, A. 1909. Aphidologische Studien. I. *Arch. zool.*, (14), p. 190.

Uhler, P.R. 1864. Orthopterological contributions. *Proc. Entomol. Soc., Philadelfia*, vol. 2, pp. 543–555.

Ulmer, G. 1903a. Beitrage zue Metamorphose der deutschen Trichopteren. XI–XIV. *Allgem. Ztschr. Entomol.*, vol. 8, pp. 11–14, 70–73, 90–93, 209–211.

Ulmer, G. 1903b. Ueber die Metamorphose der Trichopteren. *Abh. Naturw. Ver. Hamburg.*, vol. 18, pp. 1–154.

Ulmer, G. 1905. Ueber die geographische Verbreitung der Trichopteren. *Ztschr. Wiss. Insekt.-Biol.*, vol. I, pp. 16–32.

Ulmer, G. 1906. Neuer Beitrag zur Kenntnis Aussereuropaischer Trichopteren. *Notes Leyden Mus.*, vol. 28, pp. 1–116.

Ulmer, G. 1912. Die Trichopteren des baltischen Bernsteins. *Schrift. phys.-pkon. Ges. Konigsberg*, No. 10, pp. 1–380.

Ulrich, W. 1927. Uber das bisher einzige Strepsipteron aus dem baltischen Bernstein und uber eine Theorie der Mengenien Biologie. *Ztschr. Morph. u. Okol. der Tiere*, vol. 8, pp. 45–65.

Usinger, R.L. 1939. *Protepiptera*, a new genus of Achilidae from Baltic amber. *Psyche. Cambridge Mass.*, vol. 46, pp. 65–67.

Usinger, R.L. 1940. Fossil Lygaeidae from Florissant. *Journ. Paleontol.*, vol. 14, No. 1, pp. 79–80.

Usinger, R.L. 1941. Two new species of Aradidae from Baltic amber (Hemiptera). *Psyche.*, vol. 48, pp. 95–100.

Usinger, R.L. 1942. An annectent Genus of Cimicoidea from Baltic amber. *Psyche.*, vol. 49, pp. 41–46.

Verhoeff, K.W. 1902. Ueber Dermapteren. I. Versuch eines neuen naturlichen Systems. *Zool. Anz.*, vol. 25, pp. 181–208.

Viereck, H.L. 1916. Chalcidoidea. *Bull. Connecticut St. Geol. Nat. Hist. Survey*, vol. 22, pp. 443–528.

Walker, F. 1833. Monographia Chalciditum. *Entomol. Mag.*, vol. 1.

Walker, F. 1835. Monographia Chalciditum. *Entomol. Mag.*, vol. 3.

Walker, F. 1867–1873. Catalogue of the specimens of Hemiptera and Heteroptera.

Walker, F. 1868. Catalogue of the specimens of Blattariae in the collections of the British Museum, London.

Walker, F. 1869–1871. Catalogue of the specimens of Dermaptera and Saltatoria of the British Museum, vol. 1–5. *Brit. Mus.* (*Nat. Hist.*), *London.*

Wallengren, H.D.J. 1891. Skandinaviens Neuroptera. *Andra afdelningen. Svenska Akad. Handbook*, vol. 21, No. 10, pp. 1–73.

Wallis, F.S. 1939. New Blattoid Insects from the South Wales Coalfield. *Geol. Mag.*, vol. 76, No. 895, pp. 23–35.

Wallis, F.S. 1945. Note on a fossil insect from the Barren Red Measures Yockie's Syke Cumberland. *Trans. Geol. Soc. Glasgow*, vol. 20; pp. 341–342 (1943–1944).

Walther, J. 1904. Die Fauna der Solnhoefener Plattenkalke. Festschrift zum sichzigsten Geburtstage von Ernst Haeckel. Jena., pp. 135–214.

Wasmann, E. 1932. Eine ameisenmordende Gastwanze (*Proptilocerus dolosus* n. g. n. .sp.) im baltischen Bernstein. *Bernst-Forsch*, No. 2, pp. 1–3.

Waterlot, G. 1934a. Etude de la Faune continental du terrain houilier Sarrolorain. *Etud. Cites. Min. France, Lille*, pp. 111–221; 269–273.

Waterlot, G. 1934b. Paleozoic insects of the Saare Basin. *Ann. Soc. Geol. Nord.*, vol. 59, pp. 205–208.

Weissberg, St. 1925. *Mesoleuctra gracills* Br. R.G. Kosmos. Lwow, vol. 50, p. 114.

Westwood, J.O. 1828–1829. History of insects, London.

Westwood, J.O. 1839. Introduction to modern classification of insects, vol. 1, London.

Westwood, J.O. 1840. Introduction to modern classification of insects, vol. 2, London, pp. 5–17.

Westwood, J.O. 1845. In Brodie, P.B.: A history of fossil insects in the secondary rocks of England, London, pp. 1–130.

Westwood, J.O. 1854. Contributions to fossil entomology. *Quart. Journ. Geol. Soc. London*, vol. 10, pp. 378–396.

Weyenbergh, H. 1869. Sur les insectes fossiles du calcaire lithographique de la Baviere, qui se trouvent an Musee Teyler. *Arch. Mus. Teyler.*, vol. 5, No. 2, pp. 247–294 (22–24).

Wheeler, W.M. 1910. Ants, their structure, development and behavior. *Physche.*, vol. 17.

Wheeler, W.M. 1915. The Ants of the Baltic amber. *Schrift phys.-okon. Ges. Konigsberg*, vol. 55, pp. 1–142.

Wickham, H.F. 1909. New fossil Coleoptera from Florissant. *Amer. Journ. Sci.*, vol. 28, ser. 4, No. 164, pp. 126–130.

Wickhan, H.F. 1912. On some fossil rhynchophorous Coleoptera from

Florissant, Colorado, N.Y. *Bull. Amer. Mus. Nat. Hist.*, vol. 31, pp. 41–55.

Wickham, H.F. 1912. A report on some recent collections of fossil Coleoptera from the Miocene Shales of Florissant. *Bull. State Univ. Iowa*, vol. 6, No. 3, pp. 3–38.

Wickham, H.F. 1913. Fossil Coleoptera from Florissant in the U.S. National Museum. *Proc. U.S. Nat. Mus., Washington*, vol. 45, pp. 283–303.

Wickham, H.F. 1914. Twenty new Coleoptera from the Florissant shales. *Trans. Amer. Entomol. Soc. Philadelfia*, vol. 40, pp. 257–270.

Wickham, H.F. 1914. New Miocene Coleoptera from Florissant. *Bull. Mus. Compar. Zool. Harvard Coll.*, vol. 48, pp. 423–494.

Wickham, H.F. 1916. The fossil Elateridae of Florissant. *Bull. Mus. Compar. Zool. Harvard Coll.*, vol. LX, pp. 493–527.

Wickham, H.F. 1917. Some fossil beetles from the Sangamon peat. *Amer. Journ. Sci. New Haven*, vol. 44, pp. 137–145.

Wickham, H.F. 1917. New species of fossil beetles from Florissant. *Proc. U.S. Nat. Mus.*, vol. 52, pp. 463–472.

Wickham, H.F. 1920. Catalogue of fossil North American Coleoptera. In Leng's Catal. Coleopt. North Amer. pp. 347–365.

Wieland, G.R. 1925. Rhaetic Crane Flies from South America. *Amer. Journ. Sci.*, vol. 9, No. 5, pp. 21–28.

Winkler, A. 1925. Catalogus Coleopterum regeonis Palaearticae. Vienna, vol. 3, 4, 5, pp. 241–624.

Woodward, H. 1879. On the occurrence of *Branchipus* (or *Chirocephalus*) in a fossil state, associated with *Eosphaeroma* and with numerous insects-remains in the Eocene freshwater (Cambridge) limestone of Gurnet Bay, Isle of Wight. *Quart. Journ. Geol. Soc. London*, vol. 35, pp. 342–350.

Wygodzinsky, P. 1959. A new Hemiptera (Dipsocoridae) from the Miocene amber of Chiapas. *Mexico Journ. Paleontol.*, vol. 33, No. 5, pp. 853–854.

Zalessky, M.D. 1926. Observation sur un nouvel insecte fossile du permien de Kargala. *Bull. Soc. Geol. France*, Ser. 4, vol. 26, pp. 75–84.

Zalessky, M.D. 1928a. O novom iskopaemom nasekomom iz permskikh otlazhenii Kargaly (On new fossil insect from the Permian formations of Kargala). *Izv. Geol. Kom-ta.*, vol. 46, No. 7, pp. 693–699.

Zalessky, M.D. 1928b. Sur un nouvel insecte neuropteroide du permien du bassin de Kama. *Bull. Soc. Entomol. France*, Ser. 4, vol. 28, pp. 381–385.

Zalessky, M.D. 1929a. O novykhiskonaemykh iz permskikh otlozhenii basseinov rek Kamy, Vyatki i Beloi (On the new fossil finds from the Permian deposits of Kama, Viatka and Bela river basins). *Tr. ob-va estestvoion pri Kazansk*. ya-te, vol. 52, No. 1, pp. 3–50.

Zalessky, M.D. 1929b. Sur un nouveau Prothorthoptera du permien de Kama. *Ann. Soc. Geol. Nord.*, vol. 54, pp. 20–26.

Zalessky, M.D. 1930. Sur deux representants nouveaux des Paleohemipteres du permien de la Kama et du Perebore dans le bassin de la Petchora. *Izv. AN SSSR* ser. biol., pp. 1017–1027.

Zalessky, M.D. 1931. O Nasekomykh naidennykh v uglenosnykh otlozheniyakh Kuznetskogo basseina i o vozraste etikh otlozhemi na osnovanii entomofauny. (On the insects discovered from the Carboniferous deposits of Kuznetsk Basin and on the age of these formations on the basis of their entomofauna). *Byull. Mosk. Ob-va ispyt prirody otd. biol.*, No. 3–4, pp. 399–406.

Zalessky, M.D. 1932a. Observation sur les nouveaux insectes permiens de l'Europe orientale. *Bull. Soc. Geol. France.*, ser. 5, vol. 2, pp. 183–210.

Zalessky, M.D. 1932b. Observation sur les insectes trouves dans les depots a charbon u du bassin de Kousnetsk et. sur lage de ces derniers d'apres la faune entomologique. *Bull. Soc. Geol. France*, ser. 5, t. 2, pp. 209–218.

Zalessky, Yu.M. 1931a. Observation sur un nouvel insecte libelluloide du permien du bassin du fleuve Kama. *Ann. Soc. Geol. Nord.*, vol. 56, pp. 36–41.

Zalessky, Yu.M. 1931b. O novom strekozopodobnom nasekomom iz permskikh otlozhenii basseina r. Kamy (On a new dragonfly-like insect from the Permian deposits of the Kama river basin). *Iz. AN SSSR, ser. bil.*, pp. 855–861.

Zalessky, Yu.M. 1932. O zhilkovanii krylev strekoz i podenok i ikh filogeneticheskom razvitii (On the wing venation of dragonflies and mayflies and their phylogenetic links). *Izv. AN SSSR*, ser. biol., pp. 713–733.

Zalessky, Yu.M. 1933. Sur deux nouveeux insectes permiens. *Ann. Soc. Geol. Nord.*, t. 57, pp. 135–144.

Zalessky, Yu.M. 1934. Sur deux representants permiens nouveaux de l'ordre des Protorhthopteres. *Ann. Soc. Entomol. France*, t. 103, pp. 149–157.

Zalessky, Yu.M. 1935. Sur deux restes d'insectes fossiles provenant du bassin de Kouznetsk et sur l'âge géologique des dépots qui les renferment. *Bull. Soc. Géol. France*, ser. 5, t. 5, pp. 687–695.

Zalessky, Yu.M. 1937a. Ancestors of some groups of the present-day insects. *Nature*, vol. 140, pp. 847–849.

Zalessky, Yu.M. 1937b. Nouveaux representants des Protohymenopteres et des Archoclonates provenant du terrain permien du bassin de la riviere Kama et leurs liens de parente. *Ann. Soc. entomol. France*, vol. 106, pp. 101–114.

Zalessky, Yu.M. 1937c. Permskie nasekomye r. Sylvy i voprosy evolyutsii v klasse nasekomykh (Permian insects of Sylva river region and problems in evolution of class Insecta). Pt. I. "*Probl. paleontologii*", vol. 2–3, pp. 601–607.

Zalessky, Yu.M. 1937d. Pt. II. *Probl. paleontologii*, vol. 2–3, pp. 609–613.

Zalessky, Yu.M. 1937e. Sur un representant d'un nouvel ordre d'insectes permiens. *Ann. Soc. Geol. Nord.* (1936), vol. 60, pp. 50–71.

Zalessky, Yu.M. 1938. Nouveaux insectes permiens de l' ordre des Embriodea. *Ann. Soc. Geol. Nord.*, vol. 63, pp. 62–81.

Zalessky, Yu.M. 1939. Novye predstavitel Protohymenoptera, Homoptera, Hemipsocoptera, Psocoptera, Protoperlaria, Isoptera i Protoblattoidea (New representatives of Protohymenoptera, Homoptera, Hemipsocoptera, Psocoptera, Protoprelaria, Isoptera and Protoblattoidea). "*Probl. Paleontologii*", vol. 5, pp. 33–91.

Zalessky, Yu.M. 1940. O Nekotopykh novykh nakhodkakh iskonaemykh nasekomykh iz bardinskogo yarusa permskikh otlozhenii Urala (On some new finds of fossil insects from Bardinian stage of the Permian formations of the Urals). *Tr. XVII sessii Mezhdunar. geol. kongress*, Moscow, vol. 6, pp. 193–196.

Zalessky, Yu.M. 1943a. Kratkoe izlozhenie osnovanii k izmeneniyu terminologii zhilkovaniya krylev Nasekomykh (A short summary of the main changes in terminology of wing venation of Insects). *Zool. Zhurn.*, vol. 22, No. 3, pp. 154–169.

Zalessky, Yu.M. 1943b. Predstavitel novogo otryada nasekomykh, nesyshchikh elitry (A representative of the new order of Insects, with elytra). '*Priroda*', No. 3, pp. 70–71.

Zalessky, Yu.M. 1944. Predstavited novoi gruppy naukomykh iz permskikh otlozhenii Urala (A representative of a new group of insects from the Permian formations of the Ural). *Dokl. AN SSSR*, vol. 44, No. 8, pp. 370–372.

Zalessky, Yu.M. 1946a. O novom predstavitele Palaeodictyoptera iz verkhnego paleozoya Kuznetskogo basseina (On a new representative of Palaeodictyoptera from the upper Paleozoic of Kuznetsk Basin). *Byull. Mosk. ob-va isnyt. prirody. otd. biol.*, vol. 51, No. 4–5, pp. 58–62.

Zalessky, Yu.M. 1946b. Ob odnom predstavitele novogo otryada polustrekoz (Hemiodonata) iz permi Urala (About a representative of the new order Hemiodonata from the Permian of Urals). *Bycull. Mosk. ob-va isnyt prirody. otd. biol.*, pp. 63–70.

Zalessky, Yu.M. 1946c. O novoi nodenke iz permskikh otlozhenii Urals (On a new mayfly from the permian formations of the Ural). *Dokl. AN SSSR*, vol. 54, No. 4, pp. 353–355.

Zalessky, Yu.M. 1946d. Novyi predstravitel permskikh setchatokrylykh (A new representative of the Permian Neuroptera). *Dokl. AN SSSR*, vol. 51, No. 7, pp. 543–547.

Zalessky, Yu.M. 1947. O dvukh novykh permskikh zhykak (On two new Permian beetles). *Dokl. AN SSSR*, vol. 6, No. 8, pp. 857–860.

Zalessky, Yu.M. 1948a. O Novoi vesnyanke iz permskikh otlozhenii Urala (On a new stonefly from the Permian deposits of the Ural). *Dokl. AN SSSR*, vol. 60, No. 6, pp. 1041–1043.

Zalessky, Yu.M. 1948b. O predstavitele novogo otroyada nasekomykh obladayuschikh elitrami (On a representative of a new order of insects with elytra). *Dokl. AN SSSR*, vol. 59, No. 2, pp. 317–320.

Zalessky, Yu.M. 1948c. Nasekomye iz permskikh otlozhenii Solikamskogo i Cherdyanskogo raionov (Insects from the Permian deposits of the Solikamian and Cherdenian districts). *Vopr. Tecr. i prikl. geol.*, No. 5, pp. 44–52.

Zalessky, Yu.M. 1949. Novyi tretichnyi muravei (A new tertiary ant). *'Sovetsk-geol.'*, No. 40, pp. 50–54.

Zalessky, Yu.M. 1950a. Permskie Nasekomye basseina r. Sylvy i voprosy e'volyutsii v klacce nasekomykh. IV. Novye predstaviteli gruppy Epiembiodea i e'volyutsiya embii (Permian insects of Sylva river basin and problems of evolution in class Insecta. New representatives of the Epiembiodea and evolution of Embioptera). "*Voprocy paleontologii*", vol. 1, pp. 41–60.

Zalessky, Yu.M. 1950b. K voprocy O vozraste svity solikamskikh plitnyakov (On the problem of age of the Solikamian flagstones). *Dokl. AN SSSR*, vol. 70, No. 4, pp. 683–685.

Zalessky, Yu.M. 1950c. Novye predstaviteli iskopaemykh nacekomykh otrayda Protodonata (New representatives of fossil insects of order Protodonata). *Byull. Mosk. ob-va. inpyt. prirogy, otel. geol.*, vol. 25, No. 4, pp. 98–108.

Zalessky, Yu.M. 1951a. Novyi predstavitel arkhodonat. (A new representative of archodonates). *Dokl. AN SSSR*, vol. 81, No. 2, pp. 269–271.

Zalessky, Yu.M. 1951b. Novye permskie nacekomye otryada predpryamokrylykh Protorthoptera (New Permian insects of the order of primitive orthoptera—Protorthoptera). *Dokl. AN SSSR*, vol. 78, No. 5, pp. 1005–1007.

Zalessky, Yu.M. 1951c. Novyi predstavitel permskikh nacekomykh otryada predvesnyanok—Protoperlaria (A new representative of the Permian insects of the order of primitive stoneflies—Protoperlaria). *Dokl. AN SSSR*, vol. 81, No. 1, pp. 81–84.

Zalessky, Yu.M. 1952. O predvesnyankakh iz permskikh otlozhenii Urala (On primitive stoneflies from the Permian formations of the Ural). *Dokl. AN SSSR*, vol. 82, No. 6, pp. 985–989.

Zalessky, Yu.M. 1953a. Novye mestonakhozhdeniya melovykh nasekomykh v Povolzhe, Kazakhstane i Zabaikale (New sites of Cretaceous insects in Povolzh, Kazakhstan and Baikal). *Dokl. AN SSSR*, vol. 89, No. 1, pp. 163, 166.

Zalessky, Yu.M. 1953b. Novye predstavitel permskikh nasekomykh otryada Protoperlaria (New representatives of Permian insects of the order Protoperlaria). *Byull. Mosk. ob-va. ispyt. prirody otd biol.*, vol. 58, No. 2, pp. 42–47.

Zalessky, Yu.M. 1954. Stroenie golovy permskogo nasekomogo Perielytron mirabile G. Zalessky (Structure of the head of the Permian insect

Perielytron mirabile G. Zalessky). *Geol. Ob. Lvovsk. Geol. ob-va.*, No. 1, pp. 194–197.

Zalessky, Yu.M. 1955a. Novye predstaviteli otryada Protoblattoidea i Protorthoptera iz permskikh otlozhenii Urala (New representatives of orders Protoblattoidea and Protorthoptera from the Permian formations of the Ural). *Dokl. AN SSSR*, vol. 101, No. 2, pp. 347–350.

Zalessky, Yu.M. 1955b. Novye predstaviteli paleoentofonfaun Urala i ikh geologicheskii vosrast (New representatives of paleoentomofauna of Urals and their geological age). *Ezhegodnu Bses, paleontol. ob-va*, vol. 15, pp. 274–304.

Zalessky, Yu.M. 1955c. O dvukh novykh permskikh strekozopodobnykh nasekomykh otryada Permodonta (On two new Permian dragonfly-like insects of the order Permodonta). *Dokl. AN SSSR*, vol. 101, No. 4, pp. 630–633.

Zeuner, F. 1933. Die Stammesgeschichte der Kafer. Uber die Beziehungen der Form der Organe zu ihrer Funktion. I. *Palaeontol. Ztschr.*, vol. 15, No. 4, pp. 280–311.

Zeuner, F. 1935. The recent and fossil Prophalangopsidae (Saltatoria). *Stylops.*, vol. 4, pt. 5, pp. 102–108.

Zeuner, F. 1936. The recent and fossil Tympanophorinae (Tettig.). *Trans. Roy. Entomol. Soc. London*, vol. 85, pt. 12, pp. 287–302.

Zeuner, F. 1937. Descriptions of new genera and species of fossil Saltatoria. *Proc. Roy. Entomol. Soc. London*, (B), vol. 6, pp. 154–159.

Zeuner, F. 1938. Die Insektenfauna des Mainzer Hydrobienkalks. *Palaeontol. Ztschr.*, vol. 20, No. 1, pp. 104–154.

Zeuner, F. 1939. Fossil Orthoptera Ensifera. *British Mus. (Nat. Hist.) London*, pp. 1–321.

Zeuner, F. 1940. Biology and evolution of fossil insects. *Proc. Geol. Assoc.*, vol. 51, pp. 44–48.

Zeuner, F. 1941. The Eocene insects of the Ardtun Beds, Isle of Mull. Scotland. *Ann. Mag. Nat. Hist. London*, vol. 7(11), pp. 82–100.

Zeuner, F. 1942. The Locustopsidae and the phylogeny of the Acridodea (Orthoptera). *Proc. Roy. Entomol. Soc. London*, (B), vol. 11, pt. 1, pp. 1–19.

Zeuner, F. 1944. Notes on Eocene Homoptera from the Isle of Mull, Scotland. *Ann. Mag. Nat. Hist. London*, vol. 2, No. 74, pp. 110–117.

Zeuner, F. 1955. A fossil Blattoid from the Permian of Rhodesia. *Ann. Mag. Nat. Hist. London*, vol. 8, No. 93, pp. 685–693.

Zittel, C. 1885. *Handbuch der Palaeontologie*, pp. 789–796.

SUBPHYLUM CHELICEROPHORA

Chelicerate Arthropods

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Chelicerate Arthropods

V.B. Dubinin

Arthropods are characterized by the absence of a separate cephalic division and a reduction of the tergum of the anterior segment and its appendage, the antennule. The second pair of appendages are modified into grasping organs—chelicerae. The appendages of the third through sixth segments arise close to the oral aperture, and their basal segments primarily function as mouthparts or gnathobases. The anterior segments of the body (one to six) usually form a special division of the body or tagma (prosoma) and bear walking legs.

Two superclasses, Chelicerata and Pycnogonides (sea spiders) belong to this subphylum.

Superclass CHELICERATA

General Characteristics

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Bending of the longitudinal axis of body was an important morphological process in the evolution of chelicerate arthropods. This resulted in a shifting of the cephalic segments to the dorsal region and in the reduction of the anterior pair of cephalic appendages, namely the antennules. Chelicerates are distinguished from other arthropods by the absence of antennae and antennules and by the presence, in adults, of six pairs of well-developed appendages. The two anterior pairs (chelicerae and pedipalpi) play a vital role in grasping and breaking up of food; they are also tactile in function. The remaining four pairs are locomotary (walking legs). The body of the chelicerates is, in most cases, divided into a cephalothorax (prosoma) and abdomen (opisthosoma). The cephalothorax comprises the acron, which represents the cephalic lobe (prostomium) of the annelids, and six body segments with corresponding six pairs of cephalothoracic appendages. The four anterior segments are larval. They represent the four segments of the protaspis larvae of trilobites. The homology of the appendages and body segments is shown in Table 1 (p. 581).

Morphology and Development. Cephalothorax or prosoma: in most chelicerates such as Merostomata, Arachnida and many Scorpionomorpha, the prosoma is covered with a shield which consists of fused terga of six segments. Sometimes the dorsal shield is divided into a larger anterior part—the propeltid—homologous with the head shield of the Trilobites and two posterior parts, the meso- and metapeltid (Palpigradi, Solifugae and others). In all ticks and mites (Acaromorpha), a fusion of the segments bearing the chelicerae and pedipalpi into a distinctly separate region (gnathosoma) or capitulum is observed. The proboscis is, therefore, dorsal or propodosomal. Shields of all Acromorphs are not homologous with the dorsal shields of other chelicerates.

The segmentation of the opisthosoma (abdomen) is most complete in Scorpionida and Eurypterida, where there are 12 segments and one anal lobe or teslon. Moreover, in many Merostomata and Scorpionomorpha the opisthosoma is characteristically divided into two separate parts: a wide

Table 1. Scheme of distribution of the appendages and their derivatives according to segments and regions of the body of the major subclasses and classes of arthropods

Segments of body	Superclass Trilobitomorpha		Superclass Chelicerata														Superclass Pycnogonida		Superclass Tracheata, Class Insecta	
			Class Merostomata			Class Scorpionomorpha		Class Arachnida		Class Solifugomorpha		Class Acaromorpha								
I_a	Pre-antennal segment	Head	–	Cephalothorax (Prosoma)		–	Cephalothorax (Prosoma)	–	Cephalothorax (Prosoma)	–	Proterosoma	–	Gnathosoma			Proterosoma	–	Proterosoma	Antennae	Head
I	Antennal segment		Chelicerae			Chelicerae		Chelicerae		Chelicerae		Chelicerae					Chelicerae		–	
II	Postantennal 1st		Pedipals			Pedipals		Pedipals		Pedipals		Pedipals					Palps		Mandibles	
III	Postantennal 2nd		Legs I			Legs I		Legs I		Legs I		Legs I	Podosoma	Pro prodosoma	Idiosoma		Egg carriers		Maxillae I	
IV	Preoccipital		Legs II			Legs II		Legs II		Legs II		Legs II					Legs I	Mesosoma	Maxillae II	
V	Occipital		Legs III			Legs III		Legs III		Legs III	Mesosoma	Legs III		Meta-podosoma		Hysterosoma	Legs II		Legs I	Thorax
VI	Legs	Body	Legs IV			Legs IV		Legs IV		Legs IV		Legs IV					Legs III		Legs II	
VII	Legs		–	Metasoma	Opisthosoma	–	Messoma (ante-abdomen)	–	Abdomen (Opisthosoma)	–	Abdomen (Opisthosoma)	–	Opisthosoma				Legs IV (Legs V)		Legs III	
VIII	Legs		Genital operculum			Genital operculum		Lungs or genital operculum		Half opening		–					–		Abdominal limbs of protura	Abdomen
IX	Legs		Gills			Pectinate organ				Stigmas		–					(Legs IV)		Jumping fork of Apterygota, styli and cerci of cockroaches, ovipositors of numerous Insecta	
X	Legs		Gills			Lungs		Lungs		Stigmas		–					–	Abdomen (Opisthosoma)		
XI	Legs		Gills			Lungs		Spinnerets		Stigmas		–					–			
XII	Legs		Gills			Lungs		Spinnerets		–		–					–			
XIII	Legs		Gills			Lungs		–		–		–					–			
XIV	Legs		–			–		–		–		–					–			
XV	Legs		–			–		–		–		–					–			
XVI	Legs		–	Metasoma		–	Metasoma (Postabdomen)	–		–		–					–			
XVII	Legs		–			–		–		–		–					–			
XVIII	Legs		–			–		–		–		–					–			
XIX																				

mesosoma (anterior body), and a narrow metasoma (posterior body). In Merostomata the segments of the metasoma are partly fused with the telson and form a long caudal spine. In Eurypterida and Scorpionida the metasoma comprises the maximum number of segments (five); in other orders of the class Scorpionomorpha the metasoma is much reduced. In the representatives of the class Solifugomorpha and Arachnida the metasoma is normally absent. Among chelicerates the class Arachnida and the class Acaromorpha in part exhibit a further reduction of the posterior segments of the body, resulting in a complete disappearance of six segments of the metasoma. In some sarcoptid forms of the order Acariformes the number of segments of the mesosome is also reduced to one to three.

380 The attachment between the opisthosoma an prosoma varies. In most forms these two divisions are joined along the entire width of body segments six and seven. Only in spiders are they connected by a narrow pedicel. Segmentation of the abdomen is characteristic of all representatives of the classes Merostomata and Scorpionomorpha. Among Arachnida, in most spiders the segments of the abdomen are fused together. Disappearance of body segmentation is also observed in most representatives of the class Acaromorpha.

Along with the changing character of segmentation the appendages also become specialized and partially reduced. In general we notice that in all chelicerates, when they emerge on to dry land the appendages of the prosoma remain oral and locomotory and those of mesosoma become respiratory. Appendages of the metasoma, which are well developed in Trilobitomorpha, are absent in Chelicerata. Secondly, in Chelicerata there is a transformation of the primarily aquatic branchiate appendages of mesosomal segments of Merostomata and Eurypterida into air-breathing organs, as seen in most Scorpionomorpha, some Arachnida and Solifugomorpha. Finally, the general trend is toward retension of prosomatic appendages as mouthparts. In Merostomata the oral aperture is surrounded by gnathobases (endites) of all appendages of the prosoma except the chelicerae. In Eurypterida and scorpions the preoral region has been formed by endites of pedipalpi and first two pairs of walking legs. In Opiliones and Pedipalpides a similar function is performed by the endites of the pedipalpi and coxae of the legs of the first and, rarely, of the second pair. In most other chelicerates, only the endites of the coxae of the pedipalpi perform this function. The functions of chewing, and often of grasping food are performed by the two- to four-segmented chelicerae. In most Chelicerata these are claw-shaped, with serrated edges on the claw-digits. In Araneae and Anthracomarti the chelicerae are hook-shaped; in these chelicerates digestion is external. In these, a special filtration apparatus is developed on the coxal endites of pedipalpi, through which the liquified food is processed. Strong development of pedipalpi is observed in almost all Merostomata and Scorpionomorpha. These pedipalps are claw-shaped and help in grasping and breaking up food. In other chelicerates pedipalpi are leg-shaped and are sensory. Pedipalpi are known to be homologous with the mandibles of insects and crustaceans. A similar function is partly performed in primitive Chelicerata. In male spiders pedipalpi transport sperms into genital opening of females and are modified for this function.

Other appendages of the prosoma are the 'walking legs'. Often the first pair of legs are structurally differently from other legs and function as sensory organs. In many Pedipalpides, for example, they look like flagella. Walking legs in some acarines are reduced; in some prosomatic appendages are reduced to one pair (in some Tarsonemini) or to two pairs (in Eriophyidae). It is interesting that this reduction is brought about only in the posterior pairs of legs. The posterior appendages occur on larval segments in all Chelicerates.

The division of the limbs is relatively constant. Coxae are fused with the body integument in one group and remain free and mobile in others. Moreover, the free limb (endopodite) is divided into a trochanter, femur, patella, tibia and tarsus. Often, the femur and trochanter are subdivided into two independent segments, such as the basi- and telofemur. The tarsus is divided into metatarsus and a tarsus of five segments. Two claws, or pretarsus, are attached to the tip of the tarsus. The pretarsus is often modified into a claw-shaped appendage or feathery empodium. Various sensory organs may be located on the segments of appendages. A sternal shield is often formed between the coxae of the legs on the ventral region of the cephalothorax.

The appendages of the mesosoma in the primarily aquatic chelicerates (Merostomata, Eurypterida and Silurian scorpions Apoxypodes) comprise four pairs of branchiate appendages located on segments IX–XIII, and a pair of genital opercula on the eighth sternum. In terrestrial chelicerates the entire series of mesosomal appendages is seen in scorpions where there is a pair of genital opercula on segment eight, four pairs of pulmonary sacs on the sterna of segments X–XIII, and a pair of comblike sensory organs on the ninth segment. The pulmonary sacs represent invaginated skin of the branchiate appendages of ancestors that lived in water. Reduction in size of mesomatic appendages is observed in other chelicerates. Only two pairs of pulmonary sacs on the ninth and tenth segments are preserved in Uropygi, Amblypygi, Palpigradi, Ricinulei and others and in spiders there are either one or two pairs. In spiders of the subclass Araneae the posterior pair of mesosomatic appendages are converted
381 into two pairs of spinnerets. The third pair of spinnerets in its development is not associated with any segment of the body.

The characteristic peculiarity in the organization of many chelicerates is the sternal skeleton of the mesosoma, absent in Trilobites, Merostomata and many primitive Scorpionomorpha, Solifugomorpha and Arachnida. This was necessary for strengthening the legs for a life on land and for hardening the covering of the ventral region of the thorax. Coxae either fused with exoskeleton of the body to form peculiar coxal shields, or they first develop as metameric structures and then fused into the special sternal shields.

Genital opening in all Chelicerata is located on sternum VIII of body (second opisthosomal segment). Invariably it lies at the same level as or behind the coxae of legs IV. In certain mites, particularly in Opiliones, the genital opening is shifted to the front and lies at the level of the coxae of legs 1.

A gradual concentration of abdominal ganglia is seen in the evolution of the nervous system in Chelicerata. In recent Merostomata the ganglia of the prosoma fuse in the proximity of the esophagus into a nerve mass, and the ganglia of the mesosoma remain separate. The metasoma has a single ganglion. In scorpions all ganglia of the prosoma and the four ganglia of the mesosoma are fused together. The remaining two mesosomal ganglia and six metasomal ganglia remain free. In Uropygi and Solifugae all the ganglia of the abdominal nerve cord fuse into one subpharyngeal mass. Only at the posterior end of the body are three separate ganglia present, innervating the three last segments of body. In all remaining Chelicerata, all the ganglia are fused into a continuous nerve mass (brain) surrounding the esophagus.

The digestive system is similar to that of other Arthropods. It is characterized by the constant presence of long lateral diverticuli in the midgut. At the junction of the mid and hind guts the excretory organs open; they consist of the blindly ending malpigian tubes. Of the other excretory organs, the coxal glands are peculiar in certain Chelicerata. They are better developed in embryos and young, but are often reduced in the adults.

All Chelicerata are dioecious. Sexual dimorphism is usually weakly developed and normally pertains to differences in body size of the sexes and in the structure of some organs. Almost all Chelicerata are oviparous. Very rarely they are viviparous (scorpions and some mites). Sometimes the eggs are encased in cocoons, covered by threads of cobweb (spiders) carried below the abdomen of females (pseudoscorpions) or attached to the dorsal region of the body of females (some mites, Oribatai). Eggs of Chelicerata are comparatively large and rich in yolk, and as a result segmentation of the egg is incomplete and superficial. As a rule, the embryos show distinct metamerism. There are rudiments of appendages on five abdominal segments in spiders and on seven abdominal segments in scorpions. In scorpion embryos the pretarsi originally bear only a single claw. This helps in determining phylogeny. Postembryonic development is direct, but in the mites there is a fairly complex metamorphosis. It is interesting that in some Chelicerata (mites, Ricinulei) the larva emerging from the egg has only six legs, whereas in other chelicerates it has eight.

Ecology and Geographical Distribution. Chelicerates are extremely varied in their ecology. The Merostomata and their descendants such as Eurypterida and the Silurian scorpions of the suborder Apoxypodes, are primarily aquatic. Already, in the Devonian, chelicerates had left the aquatic environment and became terrestrial. This influenced the subsequent evolution of these animals. Representatives of the order Palpigradi, living in water-saturated soil, preserved the maximum primitive structural features of all the land chelicerates. Later, a few representatives of various systematic groups returned to an aquatic mode of life (water spiders of the family Argyronetidae, the freshwater and marine mites Hydrachnellae and Halacarae). However, this was not accompanied by any essential change in their organization. The terrestrial chelicerates, particularly oribatid and sarcoptid mites and spiders are now encountered everywhere on land. A majority of groups in the Recent epoch are primarily inhabitants of tropical and subtropical countries. Most Chelicerata are predators, but there are also herbivorous forms, saprophages and parasites.

A very large number of chelicerates are crepuscular or nocturnal which is probably associated with difficulties in thermoregulation and water exchange. 382 Still, there are some species that hunt in broad daylight, such as wolf spiders, some phalangids etc.

SYSTEMATIC POSITION AND PHYLOGENY. It is now an acknowledged fact that Recent land chelicerates originated from primitive aquatic chelicerates which, in turn, originated from Trilobitomorpha. Still, the precise line of evolution remains obscure and disputed. It is not certain whether all known chelicerates evolved only from Merostomata, Eurypterida and Apoxypodes. Independent evolution of various groups of land chelicerates from various little-known groups of aquatic chelicerates has been suggested (Beklemishev, 1952). This assumption undoubtedly arose because classification of Chelicerata was based on the erroneous principle of dividing them into two, essentially ecological groups: aquatic (Merostomata) and terrestrial (Arachnida). The suggestion of a polyphyletic origin for all Recent orders is contradicted by the following features in all Chelicerata: complete reduction of antennules and their replacement by the chelicerae, constancy of number of segments of prosoma and mesosoma, presence of rudimentary seventh segment of the body, and the universal bending of the longitudinal axis of the body, first in the region of head and then in the tail part. Such coincidence of structural changes can hardly be expected during polyphyletic evolution of the group. The above-mentioned features also support the origin of terrestrial chelicerates indirectly from Trilobites, besides some aquatic chelicerates.

Undoubtedly there is a direct phylogenetic relationship between the representatives of the former class of chelicerate organisms, Merostomata, with Trilibitomorpha. This is evident from a study of comparative anatomy and embryology, such as: structure and function of biramous abdominal appendages with branchial appendages, formation of cephalothorax by fusion of larval and postlarval regions, the structure of excretory and circulatory organs. Similarly, there is no doubt as to the direct phylogenetic link between Merostomata and Eurypterida, which more than once have been combined into a single class, the Palaeostraca.

Considerable difficulties and discrepancies were encountered in establishing the relationship of terrestrial chelicerates with the above groups. Grouping the terrestrial spiders of the class Arachnoidea with myriapoda of subclass Tracheata on the basis of parallel evolution of trachea and malpigian tubules in all these groups is obviously erroneous.

Phylogenetic affinity or similarity of Merostomata with other Chelicerata, is confirmed by the similarity of formation of main divisions of the body, and the nature of metamerism and a host of other characters such as: identical number of appendages on cephalothorax, homology of abdominal branchiate appendages of Merostomata and eurypteroids with lung sacs of terrestrial chelicerates, absence of antennae and antennules in both groups, homology of coxal glands, blind diverticulae of intestines, structure and position of eyes, etc. Hence, there is ample evidence to support the origin of terrestrial chelicerates from aquatic chelicerates and evidently from some eurypteroidal organisms with the general appearance and morphology of various organs not very different from those of present-day scorpions.

While examining fossil and Recent chelicerates, the most striking fact which comes to light is the presence in them of extensive groupings of orders with a straight longitudinal axis of the body. Representatives of these orders usually have a long body and an abdomen subdivided into a broad anterior part—mesosoma—and a narrower tail-like posterior part—metasoma, which may be considerably shortened. These organisms are characterized by invariable presence of large, chelate, prehensile pedipalps. Similar structures are observed in Eurypterida, Scorpiones, Palpigradi, Uropygi, Amblypygi, Ricinulei, Pseudoscorpionoidea and Kustarachnida. All these orders are here grouped under the class Scorpionomorpha, which has its direct origin from the primitive Merostomata, resembling the Cambrian Aglaspida. Among Chelicerata, representatives of Scorpionomorpha are the most primitive.

Other orders of Chelicerata are formed into three distinct groups on the basis of differences in the basic plan of structure, peculiarities of the secondary bending of longitudinal axis of body, structure of pedipalpi, etc.

The first group, the class Solifugomorpha includes the order Solifugae. In members of this group three segments of the anterior part of the body are fused to form a proterosoma and the remaining free segments III and IV bear paired appendages. The longitudinal axis of body remains straight. The pedipalpi are retained as large leg-like appendages, without chelate tibiae and tarsi.

The second group, the class Acaromorpha, contains three orders of mites 383 (Acariformes, Parasitiformes and Opilioacarina), which were once incorrectly classified into two superorders (Zakhvatkin, 1952). In these mites a separate prosoma is absent and, unlike in all other chelicerates, the first two segments always constitute a special division, the gnathosoma, distinct from the rest of the body. The last segments of mites are divided into either three (propodosoma, metapodosoma and opisthosoma: some Endeostigmata); or two divisions (podosoma and opisthosoma; or propodosoma and histerosoma: most Acariformes); or all the segments of the body are fused together to form an unsegmented idiosoma (many Parasitiformes) (cf. Table 1). Respiration in these chelicerates is carried out with the help of trachea; in some forms the respiratory organs are absent. The longitudinal axis of the body is bent in the posterior part, resulting in a substantial reduction of opisthosomatic segments. The classes Solifugomorpha (more primitive) and Acaromorpha (more specialized) exhibit features revealing their origin from the very primitive forms of the subclass Pedipalpides, class Scorpionomorpha, in particular from organisms closely allied to the Recent Palpigradi and Schizopeltidia. Divergence of these classes took place not later than the Upper Silurian. In the Devonian mites related to the Recent families are already encountered.

A third group of orders contrasts with the two above-mentioned classes of terrestrial chelicerates. The representatives of this group are characterized by the presence of a well-shaped prosoma, retention of lung-type respiration, presence on the abdomen of appendages modified to form paired genital operculum, spinnerets, etc. Another distinctive feature is the sharp bending of the longitudinal axis of body caudally, which leads to displacement of some segments toward the abdominal region and consequent reduction of their sterna. These diagnostic characters are observed in four extinct orders (Haptopoda, Phalangiotarbi, Anthracomarti and Trigonotarbi) and two Recent orders (Opiliones and Araneae), which have been placed in an independent class, Arachnida. The class Arachnida had their origin from a group of highly specialized Scorpionomorpha, particularly the primitive forms of orders Amblypygi and Ricinulei. Divergence of these groups from Scorpionomorpha took place only in the Upper Devonian and Carboniferous.

Figure 1152 illustrates the proposed phylogenetic relations of different orders and classes of Chelicerata. On the basis of this scheme, which differs from the existing classification, we undertake the classification of the entire superclass Chelicerata. Until recently all chelicerates were grouped under the subphylum Chelicerata, which was divided into three independent classes: Eurypterodea, Xiphosura (many workers included these two under a single class—Merostomata) and Arachnoidea (or Arachnida). Such a scheme, for example, is presented in the multivolume manual 'Traite de Zoologie' (Vol. VI, p 217) edited by Grasse (Grasse, 1949), and in 'Treatise on Invertebrate Paleontology' (Petrunkevitch, 1955).

Many workers have repeatedly raised the question of revising the classification on Chelicerata, noting the assorted nature of this grouping. In 1949, the American paleontologist Petrunkevitch made his first attempt to improve the existing classification of Chelicerata. He retained the division of the subphylum Chelicerata into two classes—aquatic Merostomata and terrestrial Arachnida. He suggested a subdivision only of the class Arachnida into four subclasses: Latigastra (orders Scorpiones, Pseudoscorpiones, Opiliones, Architarbi and Acari), Stethostomata (orders Haptopoda and Anthracomarti), Soluta (with one order, Trigonotarbi) and Caulogastra, split into five branches: Latisterna (Palpigradi), Camrostomata (Uropygi and Kustarachnae), Labellata (Phrynichida and Arneae), Rostrata (Solifugae) and Cucullifera (Ricinulei).

This scheme of classification was adopted by the author in later works (Petrunkevitch, 1950, 1953, 1955) and was followed by Waterlot (1953). The most striking defect of this classification is the separation of phylogenetically close orders as, for example, Opiliones and Haptopoda, Anthracomarti and

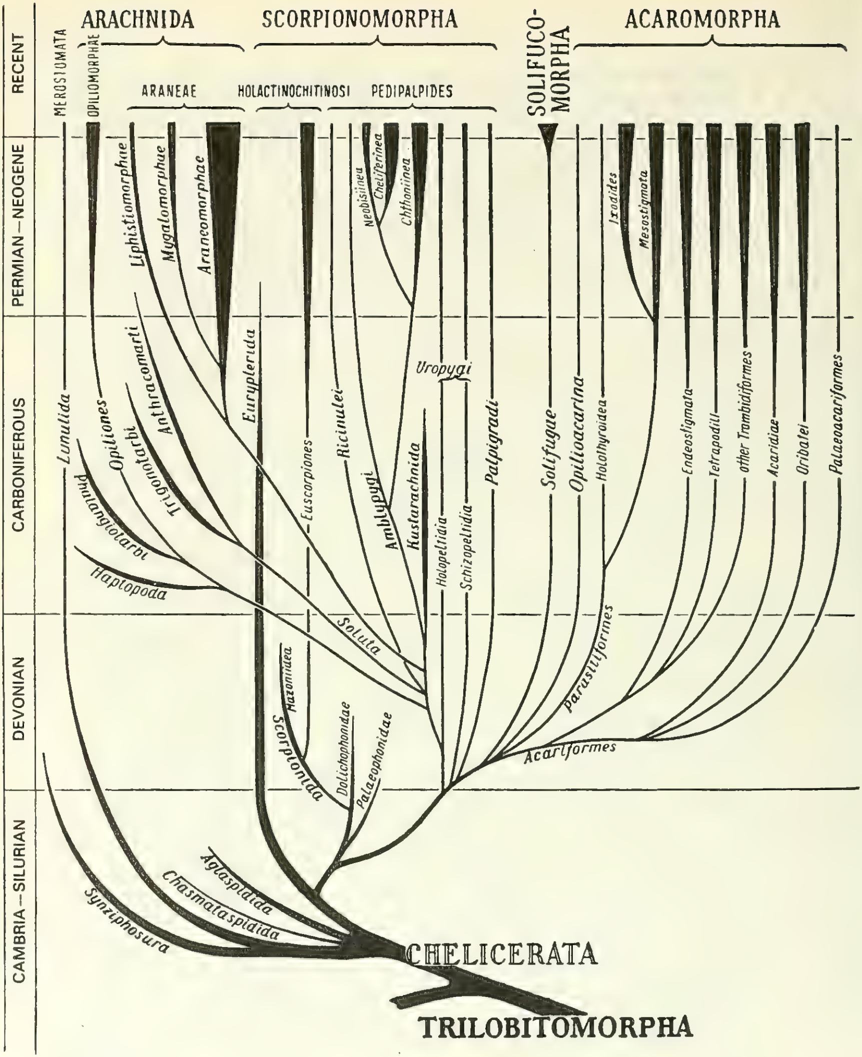


Fig. 1152. Phylogenetic relationships of classes, subclasses and orders of Chelicerata (Dubinin, 1959). Time of appearance, development and distribution of different classes, subclasses and orders are shown against the background of the geological column.

Trigonotarbi, or Acarina and Solifugae, etc. in the various subclasses. But a greater drawback of Petrunkevitch's classification is the fact that it is based on the structure of the abdomen and the general structure of mouth parts, ignoring the more important data from comparative anatomy and embryology of living and fossil forms.

The second attempt to introduce order in the classification of Chelicerata was undertaken by A.A. Zakhvatkin (1952 a, b). On the basis of a study on the localization of optically anisotropic substances in the exoskeleton of various chelicerates and using data on comparative anatomy (mainly in mites), the Chelicerata was divided into four superorders. A significant improvement was the inclusion of the orders Eurypterida (= Gigantostraca), Scorpiones, and Telyphones (= Holopeltidia) in one superorder—Holactinochitinosi Zachvatkin. This superorder (subclass in our classification) of the class (superclass) Chelicerata immediately follows the superorder (class) Merostomata. According to Zakhvatkin, two other superorders of Chelicerata, Actinochaeta and Actinoderma, still remained assorted because the orders of Arachnida were assigned to them on the basis of just one formal condition: the presence or absence of optically anisotropic substances only in the exoskeleton or in the axial core of the setae. Because of this the order Acarina is grouped into three independent orders by Zakhvatkin, namely Acariformes, Parasitiformes and Opilioacarina, which are actually related to different superorders.

In his studies the present author has recognized the chief differences between the distinctly shaped prosoma of the Recent Arachnida and Scorpionomorpha and the pseudoprosoma (prosoma without gnathosome) of the mites or proterosomes of the phalangids.

V.N. Beklemishev (1952) adopted Zakhvatkin's classification and has published his views on this topic in his interesting book.

The proposed new system of classification of the chelicerates of the superclass Chelicerata detailed below is free from the defects of the earlier classifications and more fully reflects their phylogenetic relationship (Dubinin, 1959).

- Subphylum Chelicerophora
  - Superclass Chelicerata
    - Class Merostomata
      - Order Aglaspidida
      - Order Chasmataspidida
      - Order Synziphosura
      - Order Limulida
    - Class Scorpionomorpha
      - Subclass Holactinochitinosi
        - Order Eurypterida
          - Suborder Eurypterina
          - Suborder Stylonurina
        - Order Scorpionida
          - Suborder Apoxypodes
          - Suborder Dionychopodes
      - Subclass Pedipalpides
        - Order Uropygi
          - Suborder Schizopeltidia
          - Suborder Holopeltidia
        - Order Amblypygi
        - Order Kustarachnida
        - Order Palpigradi
        - Order Pseudoscorpionodea
          - Suborder Chthoniinea

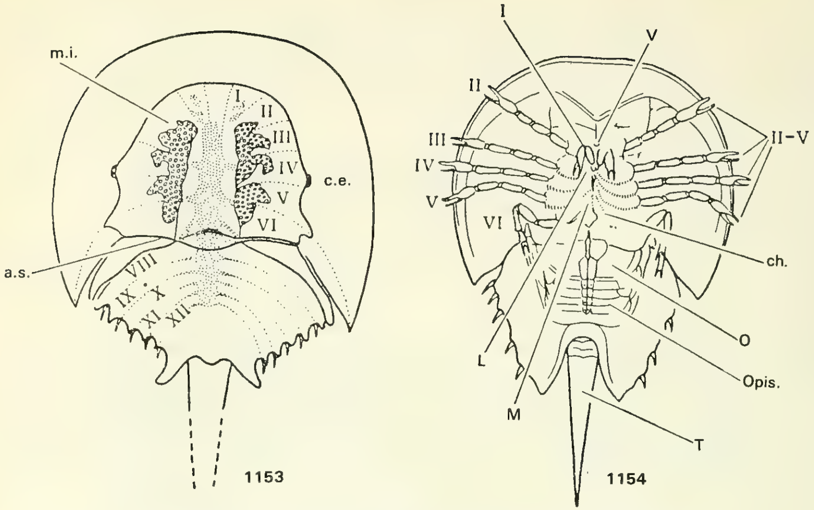
- Suborder Neobisiinea
- Suborder Cheliferinea
- Order Ricinulei
- Class Solifugomorpha
  - Order Solifugae
- Class Acaromorpha
  - Order Acariformes
    - Suborder Palaeacariformes
    - Suborder Oribatei
    - Suborder Acaridiae
    - Suborder Trombidiiformes
    - Suborder Tetrapodili
  - Order Parasitiformes
    - Suborder Holothyroidea
    - Suborder Mesostigmata
    - Suborder Ixodides
  - Order Opilioacarina
- Class Arachnida
  - Subclass Opiliomorphae
    - Order Haptopoda
    - Order Phalangiotarbi
    - Order Opiliones
      - Suborder Cyphophthalmi
      - Suborder Laniatores
      - Suborder Palpatores
  - Subclass Soluta
    - Order Trigonotarbi
    - Order Anthracomarti
  - Subclass Araneae
    - Order Liphistiomorphae
    - Order Arachnomorphae
    - Order Mygalomorphae
      - Suborder Nelipoda
      - Suborder Hypodemata
      - Suborder Pycnotheloides
    - Order Araneomorphae
      - Suborder Ecribellatae
      - Suborder Cribellatae

Class MEROSTOMATA. Xiphosura

(Nestor Novozhilov)

Aquatic chelicerates. Size of body in the smallest Paleozoic forms ranges from 1 to 3 cm; Recent forms measure up to 60 cm. Body subdivided into an anterior, usually very large prosoma (or cephalothorax); and a posterior opisthosoma (or abdomen), with possibly a sword-shaped telson. Opisthosoma sometimes divided into mesosoma (anterior part, with appendages) and metasoma (posterior part, without appendages). Prosoma more or less round, helmet-shaped in profile, generally with postero-lateral projections (genal spines) directed posteriorly. Rarely, these appendages are absent (Liomesaspididae). Prosoma bears median eyes and compound eyes (very rarely, they are absent—Synziphosura) and six pairs of appendages of which the first pair, chelicerae, bear chelae, consisting of three or four segments. Other appendages of the prosoma, including the pedipalps (second pair), serve as walking legs. Their proximal segments (coxae) partly perform functions of jaws, like breaking up food. Opisthosoma with varying number of segments. They may be reduced or fused. Fusion of opisthosomatic segments is most complete in Limulida. Appendages of the partly reduced first segment of opisthosoma are located on the ventral side of prosoma. They form a pair of plates called the chilaria (metastoma). The first pair of appendages of opisthosoma, representing the eighth segment of body, is known as operculum and bears the genital aperture. Other appendages of opisthosoma platelike and biramous, each consisting of many, reduced, median and lateral flattened exopodites carrying gills.

Morphology. Body of present-day Merostomata are covered with firm, more or less mineralized chitinous cuticle (exoskeleton). Thickness of cuticle of extinct representatives was also considerable. Prosoma more or less semicircular or helmet-shaped, flat and convex. Dorsal surface of prosoma (Fig. 1153) with a median primary lobe (glabellar part, axis) with a median crest on which, in the young of present-day Merostomata, spines are developed. Median eyes located in front of primary lobe. Compound lateral eyes located close to the border of prosoma. Both in front and behind each compound eye there is sometimes a crest or ridge (ocular crest or ocular ridge). In certain forms, as in Euproopidae, or in



1153 **1154**

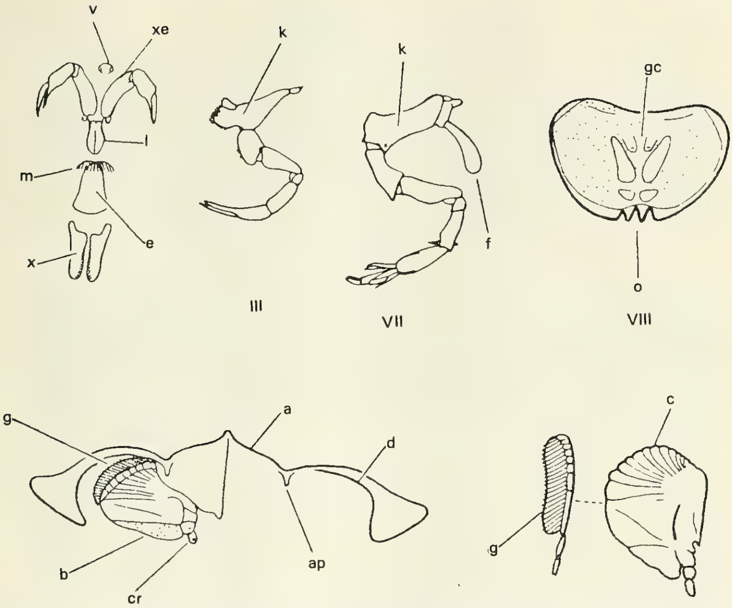
387 Figs. 1153–1154. Morphological features of Recent Merostomata (Stormer, 1955).

1153. *Tachypleus gigas* (Müller); dorsal surface of young individual showing segmentation. 1154. *Limulus polyphemus* (Linnaeus); ventral view. I–IV—segments of prosoma; VII–XII—segments of opisthosoma; m.i.—muscle impression; c.e.—compound eyes; a.s.—movable articulation between prosoma and opisthosoma; T—telson; II–V—first through fourth walking legs; VI—fifth pair of walking legs; Ch—Chilaria (belongs to sixth segment of prosoma); O—operculum ; M—mouth; L—labrum; V—ventral olfactory organ; Opis—Opisthosoma (much reduced).

the young stages they bear backwardly directed spines. The space between the ocular ridges is called cardio-ophthalmic area, and the space between the primary lobe and each ocular ridge interocular area, which coincides with the glabellar square. Arrangement of muscles in the interocular region and to some extent in the primary lobe reflects the segmentation of the prosoma.

Prosoma and opisthosoma divided dorsally by a transverse suture. This suture morphologically crosses the seventh segment which is considerably reduced. The wide rim or limb of prosoma surrounding the cardio-ophthalmic area, in all probability, belongs to the first segment.

387 From the ventral side of the prosoma (Fig. 1154) along its margins there is a fold which is the inflected margin of dorsal exoskeleton of prosoma. A narrow upper lip (labrum) fringes the mouth in front. Base of labrum with a small rounded olfactory organ. Bordering mouth from behind is a small inner plate (endostoma). Appendages of the prosoma (Fig. 1155) slender and segmented. Chelicerae small. Pedipalps and the four pairs of walking legs basically similar.



388 Fig. 1155. Appendages of segments III, VII and VIII of prosoma and opisthosoma of recent Merostomata *Limulus polyphemus* (Linnaeus) (Stormer, 1955).

xe—chelicerae; m—mouth; v—ventral olfactory organ; e—endostoma; k —coxa; l—labrum; f—flabellum; x – chilaria; gc – openings of genital canal; a – axis; d – inflected margin; o – operculum; ap – apodema; g – gills; c – articulation of lateral branches of abdominal appendage; b and cr – lateral and middle branches of opisthosomatic appendages; much reduced.

The large elongate coxae of these appendages are provided with spines along the median line and assist to push food particles into the mouth. The crest or tubercles on coxae of the fourth pair of legs assist in pulverizing food. In Limulidae the pedipalps and legs III–V are chelate. Legs VI bear spines adapted for digging, lateral margin of coxae of legs VI with unsegmented lateral appendages (flabellum).

Structure of opisthosoma varies in different Merostomata. In Limulidae it forms a continuous and moderately convex shield. Sometimes longitudinal furrows divide the opisthosoma into three lobes. In Limulidae these furrows are replaced by six pairs of the depressions which correspond to attachment points for muscles. The long dagger-shaped telson of Limulidae is articulated to the abdomen by means of a special T-shaped process obviously representing the tergum of the posterior rudimentary segment. Telson mobile. In modern Limulidae it helps in locomotion and in burying eggs in sand.

Development. Ontogeny of the Recent Merostomata is of great interest for the elucidation of their phylogeny. In the early development stages of Limulidae only four primary segments (like the protaspis of trilobites) appear. Here we see the close phylogenetic similarity between the chelicerates and trilobites. In the later stages of development, Merostomata pass through a stage wherein the telson is not elongated and the general form of the animal reminds us of a trilobite. Hence this stage is often called the 'trilobite stage', though in fact there is a closer resemblance to the Paleozoic Merostomata, Euproopidae.

388 At the time of molting the exoskeleton, possessing a marginal prosomal suture, is cast off.

Ecology and Geographical Distribution. Recent Merostomata are all marine. Adults crawl on the bottom and bury themselves in silt or sand. For reproduction they crawl ashore. Young larvae (and some adults) are capable of swimming on their backs with the help of their abdominal appendages. Most early Merostomata were not inhabitants of the sea, as is evident from the fossil remains which occur mainly in fresh water and brackish water sediments. The discovery of remains of Merostomata are rare and hence the number of species as compared to the known genera is relatively small. Within the limits of the USSR the remains of primitive Merostomata to date have been found in small numbers. Representatives of all the four families are known. Paleomeridae and Aglaspididae of the order Aglaspidida are found in the Middle Devonian and Upper Silurian (Rivers Angara and Lena). Bunodidae of the order Synziphosura are known from the Upper Silurian of Estonia, and Belinuridae, of the order Limulida, from the Upper Devonian of Liptsky region.

Most known species are from the Paleozoic (Table 2). Mesozoic forms in small numbers are known from the Triassic, Jurassic and Cretaceous. Remains of representatives of the present-day genus *Tachypleus* Leach, are found in the Neogene. Extant Merostomata are represented by three genera with five species inhabiting small bodies of water along the eastern shores of North America and Asia.

Classification, Phylogeny and Systematic Position. The general shape of the body, structure of prosoma, eyes, appendages of opisthosoma (appendages of the prosoma in part), structure of the nervous system, genital
389 glands and other morphological peculiarities of Merostomata are similar to those of the primitive Trilobitomorpha. Still, in the evolution of Merostomata there are distinctive features: formation of chelicerae, reduction of antennule, modification of prosoma, induced bending of anterior part of longitudinal axis of body, addition of a fifth and a sixth segment of opisthosoma to the original four larval segments of trilobites, and absence of pygidium. It is obvious that Merostomata originated from the most primitive trilobites whose organization was at the level of development of the superfamily Olenelloidea. Merostomata were the first chelicerates. During their evolution bending of the anterior part of

TABLE 2. CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION OF MEROSTOMATA

Merostomata	Assigned geological age
Order Aglaspidida	
Family Paleomeridae	
Paleomerus	Upper and Middle Cambrian
Angarocaris	Middle Ordovician
Family Aglaspididae	
Aglaspis	Upper Cambrian
Girardevia	Middle Ordovician
Aglaspella	Upper Cambrian
Aglaspoides	Upper Cambrian
Glypharthrus	Upper Cambrian
Uarthrus	Upper Cambrian
Cyclopites	Upper Cambrian
Craspedops	Upper Cambrian
Setaspis	Upper Cambrian
Family Strabopidae	
Strabops	Upper Cambrian
Neostrabops	Upper Ordovician
Family Beckwithiidae	
Beckwithia	Middle Cambrian
Order Chasmataspidida	
Family Chasmataspidae	
Chasmataspis	Lower Ordovician
Order Synziphosura	
Family Limuloididae	
Limuloides	Upper Silurian
Family Bunodidae	
Bunodes	Upper Silurian to Downtonian
Bunaia	Downtonian
Family Neolimulidae	
Neolimulus	Upper Silurian to Lower Devonian
Family Pseudoniscidae	
Pseudoniscus	Upper Silurian
Cyamocephalus	Upper Silurian
Family Weinberginidae	
Weinbergina	Lower Devonian
Order Limulida	
Superfamily Belinuridea	
Family Belinuridae	
Belinurus	Upper Devonian to Upper Carboniferous
Protolimulus	Middle Devonian
Family Austrolimulidae	
Austrolimulus	Middle Triassic
Family Euproopidae	
Euproops	Upper Carboniferous to Lower Permian
Family Elleriidae	
Elleria	Upper Devonian to Upper Carboniferous
Family Kiaeriidae	
Kiaeria	Downtonian
Superfamily Liomesaspididea	
Family Liomesaspididae	
Liomesaspis	Upper Carboniferous
Prolimulus	Lower Permian
Superfamily Limulidea	
Family Paleolimulidae	
Paleolimulus	Carboniferous to Permian
Family Mesolimulidae	
Psammolimulus	Lower Triassic
Limulitella	Lower to Upper Triassic
Mesolimulus	Jurassic to Cretaceous
Family Limulidae	
Tachypleus	Miocene to Recent

longitudinal body axis took place. This led to the modification of mouth parts. Evolution of this class was accompanied by cephalization which attained an extreme stage. Primitive Merostomata (order Aglaspidida), with complete separation of opisthosoma and the somewhat separate meso- and metasoma, were obviously direct ancestors of the so-called 'Eurypterida', which in all probability must be taken as the ancestral group of the all terrestrial Chelicerata. As observed by Stormer (Stormer, 1944, 1955) *Paleomerus* Stormer apparently represents a transitional form between Aglaspididae (Merostomata) and Eurypterida. The transitional form between these groups is well represented by *Angarocaris* Chermyshev.

Classification of Merostomata was usually based not only on morphological characteristics but also on life history. Stormer (1944, 1955) included under Merostomata two subclasses: Xiphosura (strictly Merostomata) and Eurypterida. Zakhvatkin (1952) and Dubinin (1959) included Eurypterida (treating it as an order) under the order Scorpionida, which was placed under the subclass Holactinochitinosi, on the basis of morphological studies. Thus the two orders are combined and grouped under one subclass Holactinochitinosi. Dubinin placed them together with the subclass Pedipalpida in a special class Scorpionomorhpa.

Dubinin did considerable work on the classification of Chelicerata but his suggested separation of Eurypterida from Xiphosura has not met with success.

In accordance with the classification followed in this volume, Merostomata (in the narrow sense) and Eurypterida are placed in different classes. The class Merostomata comprises four orders: Aglaspidida, Chasmataspidida, Synziphosura and Limulida.

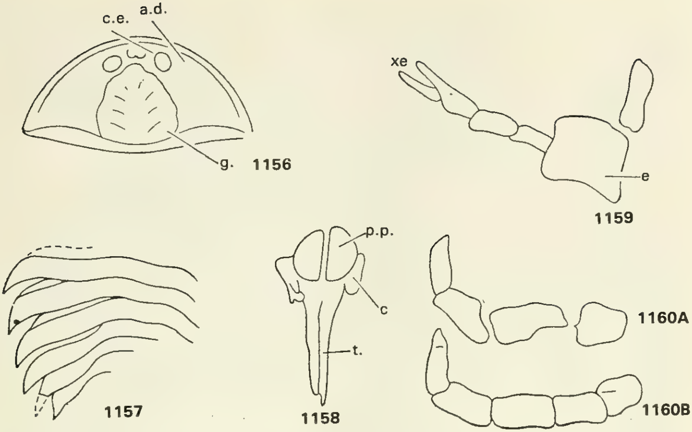
390

Order AGLASPIDIDA

(Aglaspida)

This order includes merostomata with an oblong and more or less convex body. Prosoma always shorter than one-half of opisthosoma, with markedly convex compound eyes. Opisthosoma with 11 or 12 segments, almost all movably articulated. Rarely, three posterior segments are fused (Beckwithiidae). Opisthosoma either indistinctly three-lobed or smooth. Ventral side of opisthosoma with post-ventral plates. Telson with broad basal part. Chelicerae four-segmented. All appendages of prosoma and apparently of opisthosoma also are in the form of short walking legs. Surface of exoskeleton granular to varying degrees.

Morphology. Aglaspidida mainly includes small forms. The average length varies from 2 to 6 cm, though individuals of 21 cm long are also known. Body oblong, more or less oval, without true axial furrows, but with the more or less distinct three-lobed condition observed due to the bulging of axial and lateral regions. Prosoma comparatively large and broad, with weakly developed genal angles. Compound eyes are usually located close to anterior margin of middorsal



Figs. 1156–1160. Morphological peculiarities of order Aglaspidida, Upper Cambrian, North America (Størmer, 1955).

1156. *Craspedops modesta* Raasch; prosoma: a.d.—anterior depression; c.e.—compound eyes; g – glabellar lobe, × 2 (reconstruction). 1157. *Aglaspis spinifer* Raasch; movable segments of opisthosoma with pleurae at ends. 1158. *Uarthrus instabilis* Raasch; p.p.—post-ventral plates; c—11th segment; t—telson, × 2. 1159. *Aglaspis spinifer* Raasch; anterior appendage of prosoma, × 1.3; e—episthosoma; xe—chelicerae. 1160. *Aglaspis spinifer* Raasch; A—last appendage of prosoma; B—first appendage of opisthosoma.

line. Eyes may be developed but not always visible. Glabellar area between eyes and posterior margin corresponds to inter-ophthalmic area of later forms. This area is raised above the flatter part of prosoma. Glabellar area may be lobed (Fig. 1156), more or less triangular and broad posteriorly. Pleurae usually have pleural appendages which partly overlap. Bent pleural ribs often do not reach the transverse articular line, which confirms the primitive articulation of segments whose terga may move relative to one another (Fig. 1157). Subdivision of opisthosoma into meso- and metasoma not observed with the exception of Beckwithiidae, where the posterior semicircular shield is separated, corresponding to the pygidium of trilobites or metasoma. A quadrilateral plate is developed on the ventral surface of prosoma behind doublure, corresponding to episthosoma. Behind the last opisthosomatic segment and base of telson there are special postventral plates (Fig. 1158). The morphological nature of these is not clear.

391 Limited information regarding the appendages is known only from the genus *Aglaspis* Hall (Figs. 1159, 1160). The four-segmented chelicerae are

equipped with chelae; all other appendages of the prosoma are ambulatory, simple and four-segmented. First pair of appendages of opisthosoma are ambulatory and five-segmented. This shows the primitive character of Aglaspididae as compared with later Merostomata, in which appendages of opisthosoma are not ambulatory and are modified into gills. Exoskeleton of aglaspidids ornamented with tubercles of different sizes, sometimes in the form of pustules or wrinkles resembling the ripple marks on sand.

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. Aglaspidids and trilobites, are similar in their body form particularly with regard to a few merostoma like forms of Trilobitomorpha, such as Leanchoillidae and Emeraldellidae. Still, in these forms the head division has only four pairs of appendages behind the mouth, whereas in Aglaspidida there are six. The absence of antennules in Aglaspidida and their presence in trilobites and merostoma like forms distinguish Aglaspidida from the latter two groups and others. Among merostomata and Aglaspidida there are many genera such as Synziphosura, and Pseudoniscidae, which are distinguished by their larger prosoma, absence of eyes, and in the structure of opisthosoma. The Aglaspidida, such as Strabopidae (Upper Cambrian) and especially Paleomeridae (Lower Cambrian), exhibit a close similarity in the body form with Eurypterida such as Hughmilleridae (Middle Ordovician to Lower Devonian). The presence of 12 segments in the opisthosoma of Aglaspidida links them with Eurypterida. A still greater resemblance is exhibited by Hughmilleridae with the later representative of Paleomeridae, genus *Angarocaris*, from the Middle Ordovician. In these forms the opisthosoma is narrower and fusiform, recalling Eurypterida rather than Merostomata.

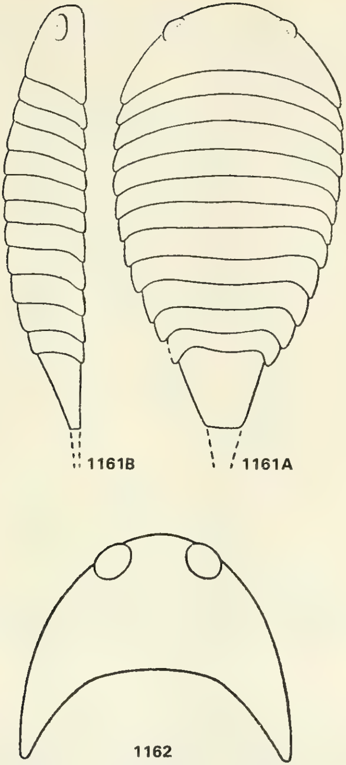
ECOLOGY AND GEOGRAPHICAL DISTRIBUTION. Remains of known aglaspidids are found along with trilobites, brachiopods, molluscs. In all probability Aglaspidida were inhabitants of more or less shallow-water seas. Lower Cambrian to Ordovician. Families: Paleomeridae, Aglaspididae, Strabopidae and Beckwithiidae.

Family PALEOMERIDAE Størmer, 1955

Medium sized animals (6–10 cm). Opisthosoma of 12 free segments, 12th segment trapezoidal. Telson and appendages indistinct. Lower Cambrian to Middle Ordovician. Two genera.

392 *Paleomerus* Størmer, 1955. Genotype—*P. hamiltoni* Størmer, 1955; Lower Cambrian, Sweden. Prosoma and Opisthosoma together are oval, relatively convex. Prosoma short, with bulging compound eyes located close to anterolateral margins. 12th segment of abdomen elongate and trapezoidal (Fig. 1161). One species. Lower Cambrian of Sweden.

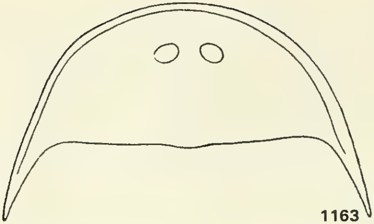
Angarocaris Chernyshev, 1953. Genotype—*Eurypterus* ? *tschekanowskii* Schmidt, 1886 (homotype described by Chernyshev); Middle Ordovician, East Siberia (Krivolutan stage, Inteian horizon). Prosoma more or less flattened and



Figs. 1161–1162. Family Paleomeridae.

1161. *Paleomerus hamiltoni* Størmer: A—lateral view; B – dorsal view, × 0.8. Lower Cambrian, Sweden (Størmer, 1955). 1162. *Angarocaris tschekanowskii* (Schmidt); prosoma, × 1.2. Middle Ordovician, East Siberia (original drawing).

parabolic. With long genal processes or with only genal angles. Compound eyes strongly bulging, rounded, located close to the anterior lateral margins of prosoma. Exoskeleton with wrinkles, resembling aeolian ripples on sand, and with small pits. Opisthosoma of 12 free segments, elongate and narrow. 12th segment oblong, telson dagger-shaped (Fig. 1162). Eight species. Middle Ordovician of East Siberia.



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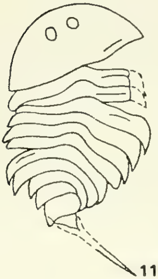

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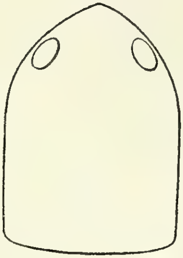

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Figs. 1163–1165. Family Aglaspididae.

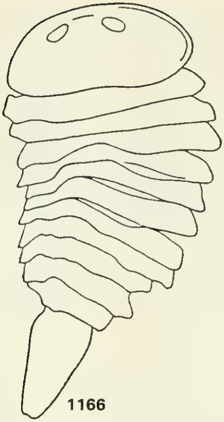
1163. *Aglaspis spinifer* Raasch; prosoma, × 2. Upper Cambrian, North America (Størmer, 1955). 1164. *Aglaspis simplex* Raasch; × 0.7. Upper Cambrian, North America (Størmer, 1955). 1165. *Girardevia musculus* Andreeva; prosoma, × 1.5. Middle Ordovician, East Siberia (original drawing).

Family AGLASPIDIDAE Miller, 1877

Medium sized forms (4–16 cm), opisthosoma of 11 free segments, moderately elongate. Eight genera. Upper Cambrian–Middle Ordovician.

Aglaspis Hall, 1862. Genotype—*A. barrandi* Hall, 1862; Upper Cambrian, North America. Prosoma parabolic with long genal processes or only genal angles. Posterior margin of prosoma almost straight and convex. 393 Interophthalmic area elongate and convex, convexity extends upto occipital margin. Terga with paired postaxial projections (Figs. 1163–1164). More than three species. Upper Cambrian of North America.

Girardevia Andreeva, 1957. Genotype—*G. musculus* Andreeva, 1957; Middle Ordovician, East Siberia (Krivolutan stage, Kirenian horizon, river Lena). Prosoma markedly convex, anterior half triangular with rounded anterior angles; posterior half rectangular. Occipital margin of the prosoma straight. Compound eyes markedly bulging, oval and located a little forward from the middle of prosoma. Sculpturing of exoskeleton in the form of wrinkles,



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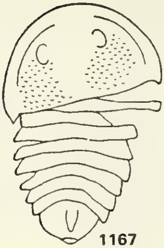

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Figs. 1166–1167. Families Strabopidae, Beckwithiidae.

1166. *Strabops thacheri* Moysey; × 0.7. Upper Cambrian, North America (Stϕrmer, 1955). 1167. *Beckwithia typa* Resser; × 1. Middle Cambrian, North America (Stϕrmer, 1955).

resembling aeolian ripples on sand. Prosoma 9–13 mm long (Fig. 1165). Two species. Middle Ordovician of East Siberia.

Outside the USSR: Seven genera from the Upper Cambrian of North America; *Aglaspella* Raasch, 1939. *Aglaspoides* Raasch, 1939; *Glypharthrus* Raasch, 1939; *Uarthrus* Raasch, 1939; *Cyclopites* Raasch, 1939; *Craspedops* Raasch, 1939 and *Setaspis* Raasch, 1939.

Family STRABOPIDAE Gerhardt, 1932

Medium sized forms (12–13 cm). Opisthosoma of 11 free segments, without epimers. Prosoma short and elliptical. Compound eyes located in the middle of prosoma or close to the anterior margin. Opisthosoma elongate and oval. Telson broad. Upper Cambrian to Middle Ordovician. Two genera.

Strabops Beecher, 1901. Genotype—*S. thacheri* Beecher, 1901; Upper Cambrian, North America. Terga with indistinct lamellae close to posterior margin. Body elongate. Eyes located close to the anterior margins of prosoma (Fig. 1166). One species. Upper Cambrian of North America.

Also, *Neostrabops* Caster and Meek, 1952 is known from the Upper Ordovician of North America. Opisthosoma oval, eyes at the middle of prosoma.

Family BECKWITHIIDAE Raasch, 1939

The three posterior segments of opisthosoma form a continuous shield. Middle Cambrian. One genus.

Beckwithia Resser, 1931. Genotype—*B. typa* Resser, 1931; Middle Cambrian, North America. Prosoma almost semicircular with a flat rim. Eyes located on the anterior half of prosoma. Eight free segments of prosoma exhibit tubercular ornamentation. The more or less semicircular posterior part of opisthosoma is formed of fused segments and with dorsal spines. Telson narrow and dagger-shaped (Fig. 1167). One species. Middle Cambrian of North America.

Aglaspidida Incertae sedis

Three genera from the Middle Ordovician of East Siberia, described by B.I. Chernyshev, are *Obrutschewia* Chernyshev, 1953; *Intejocaris* Chernyshev, 1953 and *Chacharejocaris* Chernyshev, 1953. Although the shape of the prosome of these three genera resemble that of Aglaspidida, all structures of the body remain unknown.

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Order CHASMATASPIDIDA

[nom. corr. Novojilov, hic (pro Chasmataspida Caster and Brooks, 1956)]

Prosoma semioval, flattened, with small genal processes. Compound eyes large, bulging and rounded. Opisthosoma clearly divided into mesosoma and metasoma. Mesosoma of three fused segments forming a single flat shield with serrations along lateral margins. Mesosoma flat, the three-lobed character is expressed by two lateral plates; with prominent epimers on second and third segments. Ventral region of mesosoma compact except for the lateral slitlike opening of the gill chamber. Metasoma long and narrow and consists of nine segments with epimers. Telson not movable and shaftlike. Exoskeleton with prominent ornamentation consisting of tubercles and pustules on dorsal and ventral surfaces. One family: Chasmataspididae Caster and Brooks, 1956 with

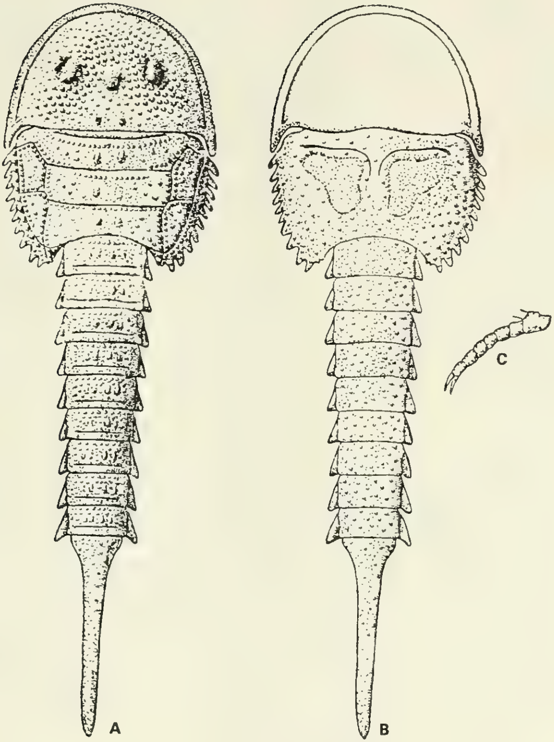

Fig. 1168. Order Chasmataspidida.

Chasmataspis laurenci Caster and Brooks; A—dorsal view; B—ventral view; C—appendage, × 1.5. Ordovician, Canada (Carter and Brooks, 1956).

one genus, *Chasmataspis* Caster and Brooks, 1956 (Fig. 1168). Lower Ordovician of Canada.

Order SYNZIPHOSURA

Prosoma without compound eyes and with or without a primary lobe. Opisthosoma made up of nine or 10 free segments, sometimes sixth and seventh segments are fused. Appendages with flat distal processes in place of claws.

Morphology. Synziphosura are of small size—about 5 cm long, including telson. Body elliptical. Structure of body in representatives of the genus *Pseudoniscus* Nieszkowski, shows that Synziphosura could roll into a ball. Prosoma large, almost semicircular or helmet-shaped. In some forms prosoma with slightly oblong genal angles (*Pseudoniscus* Nieszkowski and *Weinbergina* Richter and Richter). In other genera prosoma smaller and rounded in varying degrees and ornamented. Primary lobe prominent in Bunodidae, particularly in Neolimulidae. Ocular ridges usually surrounded by glabellar area (Limuloididae and Neolimulidae), in most Recent forms. Segmentation of peripheral zone of primary lobe sometimes indicated by radial furrows (Bundodidae) or by radial ribs (Limuloides). Usually no trace of compound eyes found, bút probably they
395 were present in *Neolimulus* and *Pseudoniscus*. In earlier reconstructions of the Baltic species of *Pseudoniscus* large compound eyes were shown. In the American species of this genus no trace of eyes was detected except for some structures that Rudeman interpreted as small eyes and facial sutures. Stormer (1956) observes that the specimens were badly deformed in argillaceous shales. The small starlike formations on the ocular ridges of Limuloides, as noted by Stormer, may have been sensory organs apparently homologous with the dorsal organs in the embryos of Recent Merostomata.

The opisthosoma consists of nine or 10 distinct segments. Often the opisthosoma shows sharp division into a broad mesosoma and a narrow metasoma. Mesosoma six- or seven-segmented. Moreover, the sixth and seventh terga sometimes fuse. Rarely, subdivision of opisthosoma indistinct (Neolimulidae and Pseudoniscidae). The three-lobed condition prominent in Pseudoniscidae and Neolimulidae and less so in other forms lacking dorsal furrows. Pleura may be grooved and extend as short pleural outgrowths.

Prosomal appendages are known only in Weinberginidae—as five pairs of walking legs, Chelicerae absent. Structure of legs very closely akin to structure of leg IV of the Recent Limulida. Claws absent, but with characteristic outgrowths on distal segments. Absence of traces of appendages of opisthosoma in well-preserved specimens precludes the possibility of existence of platelike appendages like those in Limulida and Eurypterida. Exoskeleton usually smooth, rarely heavily ornamented.

Classification, Phylogeny and Systematic Position. The differences in the distinctive features of Pseudoniscidae and Weinberginidae on the one hand and the remaining known families on the other makes it possible to separate them into two groups (? superfamilies). Such a subdivision may be possible in light of more definite data. Phylogenetic relations of Synziphosura have been little studied so far. The presence, in some groups of the order, of sharply demarcated metasoma and highly ornamented exoskeleton brings these Merostomata close to Chasmataspididae. On the other hand, the large, broad prosoma and little differentiated, shortened opisthosoma suggest obvious affinities with Limulida, which are probably descendants of some synziphosurs still not known.

Ecology and Geographical Distribution. Synziphosura in all probability were benthic forms and did not constitute the typical marine fauna. Known Silurian and Downtonian species were part of eurypterid fauna and apparently populated saline or freshwater basins. Only the Lower Devonian *Weinbergina*, found together with trilobites, was a typical marine form. Upper Silurian through Lower Devonian. Families: Limuloididae, Bunodidae, Neolimulidae, Pseudoniscidae and Weinberginidae.

Family LIMULOIDIDAE Størmer, 1952
(Hemiaspididae Zittel, 1881)

Small, forms. Prosoma with primary lobe, ocular ridges, radial ribs and marginal spines. Opisthosoma divided into a six-segmented trapezoidal mesosoma and a narrow three-segmented metasoma. Sixth segment of mesosoma formed by fusion of sixth and seventh segments. Mesosoma with broad axial region (primary area). Opisthosoma with rows of large tubercles on axial and lateral parts of first four tergites of mesosoma. One genus: *Limuloides* Størmer, 1952 [= *Hemiaspis* Woodward, 1864 (non Fitzinger, 1861)] (Fig. 1169). Upper Silurian of Western Europe.

Family BUNODIDAE Packard, 1886

Prosoma semioval, wide and radially lobate. Opisthosoma subdivided into broad six-segmented mesosoma, with movable pleural spines, and four-segmented narrow metasome without pleural spines. First segment of metasoma narrow. Terga of mesosoma bear median row of tubercles. Metasoma has none. Axial lobe (primary lobe) on opisthosoma not demarcated. Upper Silurian through ? Lower Devonian (Downtonian)[1]. Two genera.

396 *Bunodes* Eichwald, 1860. Genotype—*Exapinurus lunula* Nieszkowski, 1859; Upper Silurian, USSR (Estonia). Prosoma almost semicircular with distinct radial lobes and no genal projections. Mesosoma broad with foliaceous pleural spines. Metasoma narrow cylindrical. Telson dagger-shaped. Surface of

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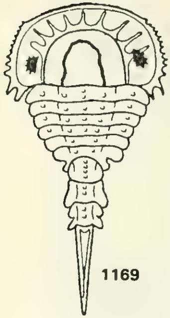
[1] Downtonian represents the uppermost (fourth according to estimate) stage of the upper division of the Silurian, directly over the Ludlovian stage (*Dictionary of the Geology of Oil*, Gostoptekhizdat, 1952).For some time, the independent status of this stage has been disputed by some stratigraphers. Obviously, this is why the Downtonian stage has not been accommodated in the stratigraphic scheme adopted in "Principles of Paleontology" (see p. 6) and in general has not found any mention in this scheme. In the *Treatise on Invertebrate Paleontology*, Pt. P, Arthropoda 2, the Downtonian is cited with a question mark (?) in the Lower Devonian as "? Lower Devonian (Downtonian)". Many Eurypterida and some Merostomata described in *Principle of Paleontology* occur both in the Ludlovian and Downtonian stages as also in the strictly Lower Devonian. To avoid confusion and errors of usage in *Principles of Paleontology*, throughout this text the Downtonian stage is cited as in the American treatise, that is, " ? Lower Devonian (Downtonian)". In cases where the distribution of a particular genus in the Downtonian is itself doubtful another question mark is given in brackets: "(?) ? Lower Devonian (Downtonian)". This involves differentiating Downtonian forms from Ludlovian (Upper Silurian) and from the strictly Lower Devonian ones.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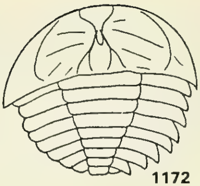
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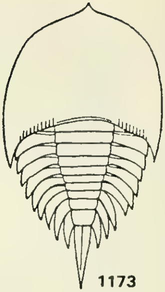
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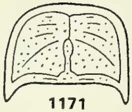
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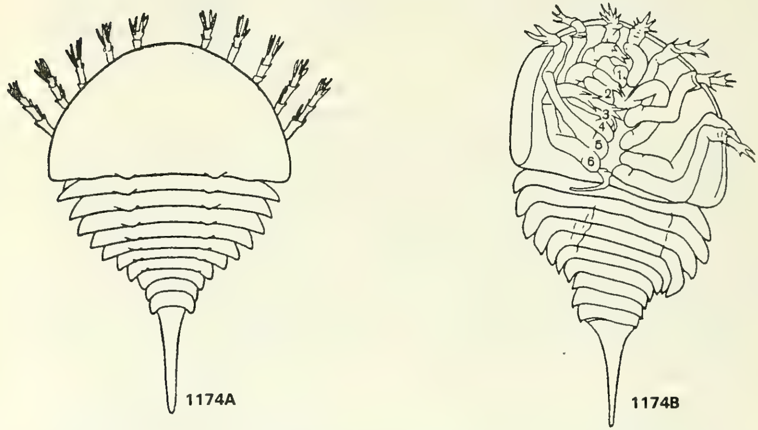
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396 Figs. 1169–1174. Order Synziphosura (families Limuloididae, Bunodidae, Neolimulidae, Pseudoniscidae, Weinberginidae).

1169. *Limuloides limuloides* (Woodward); × 1. Upper Silurian, England (Størmer, 1955). 1170. *Bunodes lunula* (Nieszkowski); × 1.3. Upper Silurian, Estonia (Størmer,1955). 1171. *Bunaia heintzi* Stormer, × 1. Lower Devonian (Downtonian), Norway (Swalbard) (Størmer, 1955). 1172. *Neolimulus falcatus* Woodward; × 3. Lower Devonian, Scotland. 1173. *Pseudoniscus roosevelti* Clarke; × 2. Upper Silurian, North America (Størmer, 1955). 1174. *Weinbergina opitzi* Richter and Richter; × 0.7. Lower Devonian, Germany; A—dorsal view (reconstruction) (Størmer, 1955); B—ventral view (X-ray photograph) (Lehmann, 1956).

prosoma and telson granular (Fig. 1170). Two species. Upper Silurian of USSR; ? Lower Devonian (Downtonian), Norway.

Also, *Bunaia* Clarke, 1919 (Fig. 1171). Downtonian of North America and Norway.

Family NEOLIMULIDAE Packard, 1886

Small forms. Prosoma broad, parabolic with a primary lobe and with acute 397 genal angles; ocular ridges united anteriorly. Opisthosoma broad, more or less semicircular, with axial furrows bordering primary lobe. Metasoma distinct. Telson short. Body smooth, without ornamentation (Fig. 1172). One genus: *Neolimulus* Woodward, 1863. Upper Silurian to Lower Devonian of Western Europe.

Family PSEUDONISCIDAE Packard, 1886

Small forms. Prosoma large, constitutes about one-half of the entire body length. Body smooth and flat with acute or rounded genal angles. Opisthosoma of nine or 10 free segments, with sharp axial furrows and with pointed pleural spines. Metasoma not distinct. Two genera from Western Europe and North America: *Pseudoniscus* Nieszkowski, 1859 (Fig. 1173) and ?*Cyamocephalus* Currie, 1927.

Family WEINBERGINIDAE Richter and Richter, 1929

Medium sized forms. Prosoma large, semicircular, smooth, equal in size to opisthosoma; opisthosoma of 10 segments. Metasoma indistinct and consists of three segments. Axial (primary) area demarcated on mesosoma by rows of tubercles. Chelicerae very short; five pairs of walking legs with spines. On genus: *Weinbergina* Richter and Richter, 1929 from the lower Devonian of Western Europe (Fig. 1174A, B).

Synziphosura Incertae sedis

The genera *Bembicosoma* Laurie, 1899 (Silurian of Scotland) and *Bunodella* Matthew, 1889 (Lower Silurian of North America) have been very incompletely described from fragmentary remains.

Order LIMULIDA

(Limulina)

Prosome large with primary lobe, ocular ridges, ocelli, and lateral compound eyes. Opisthosoma nine-segmented, segments well-developed, movable and, to some extent, joined. Telson dagger-shaped, longer than opisthosoma.

MORPHOLOGY. Prosoma large, more or less semicircular with genal spines. Genal spines rarely absent (Liomesaspididae). Primary lobe wedge-shaped, usually carinate, occasionally with projecting nodules on anterior margin. Primary lobe bordered in front by converging occular ridges. These ridges extend along the lateral region of primary lobe through the lateral eyes and terminate at the anterior margin of prosoma. Inter-ophthalmic ridges may be developed in cardio-ophthalmic area. They border a rectangular plate which encompasses primary lobe and narrow belts. If inter-ophthalmic ridges are present the cardio-ophthalmic area is subdivided into five parts instead of three. Opisthosoma semicircular, more or less triangular or an irregular hexagon, not divided into mesosoma and metasoma. Segmentation of opisthosoma in the Paleozoic forms is indicated clearly by pleural ribs. Rarely, opisthosoma forms complete shield. Segmentation of opisthosoma indicated only by rows of pits in axial furrows and pleural spines (Limulidea). Sometimes, opisthosoma without trace of segmentation (Liomesaspididae) or has one free segment in front of telson (Paleolimulidae). In genera of superfamily Euproopidea the circular axis has conical spines. Appendages of prosoma found only in a few forms which closely resemble those of Recent Limulidae. The appendages in Liomesaspididae are peculiar: the walking legs are of different sizes. The surface of the shield smooth or with tubercles of different shapes and sizes.

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. Phylogeny of Limulida traces back to the Silurian Sinziphosura, Neolimulidae and then to Belinuridae, thence to Mesozoic and Recent Limulidae. Their evolution is characterized by shortening of opisthosoma and fusion of segments, and also by a gradual increase in size. On the whole oligomerization of the entire skeleton is clearly exhibited. ? Lower Devonian (Downtonian) to Recent. Three superfamilies: Belinuridea, Liomesaspididea and Limulidea.

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SUPERFAMILY BELINURIDEA

[nom. transl. Novojilov. hic (ex Belinuracea Stormer, 1965; Belinuridae Zittel and Eastman, 1913)]

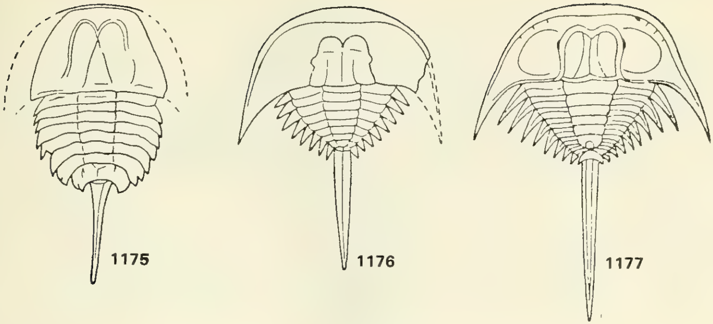
Opisthosoma well segmented and with a prominent axial lobe. Prosoma invariably with long genal angles. Middle Devonian to Permian. Five families: Belinuridae, Austrolimulidae, Euproopidae, Elleriidae and Kiaeriidae.

Family BELINURIDAE Zittel and Eastman, 1913

(Bellinuridae Packard, 1886)

Opisthosoma trapezoidal; consists of eight sharply separated segments provided with movable pleural spines along the margins. Opisthosoma as long as or longer than prosoma. Middle Devonian to Upper Carboniferous. Three genera.

Neobelinurus Eller, 1938. Genotype—*Bellinuroopsis rossicus* Chernyshev, 1933; Upper Devonian, Liptsk province (near Lebedyani). Prosoma with a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Figs. 1175—1177. Order Limulida, Superfamily Belinuridea, family Belinuridae (Størmer, 1955).

1175. *Neobelinurus rossicus* (Chernyshev); × 0.5. Upper Devonian, Liptsk province. 1176. *Belinurus baldwini* Woodward; × 2. Upper Carboniferous, England. 1177. *Belinurus regina* Baily; × 2. Upper Carboniferous. Ireland.

wedge-shaped primary lobe. Opisthosoma oblong, somewhat tapering posteriorly and with eight mobile segments. Last segment paired. Segments with pleural spines (Fig. 1175). One species from the Upper Devonian of the USSR.

Also, *Belinurus* Konig, 1820, Upper Devonian to Upper Carboniferous of Western Europe and North Africa; *Protolimulus* Packard, 1886, Middle Devonian of North America (Figs. 1176, 1177).

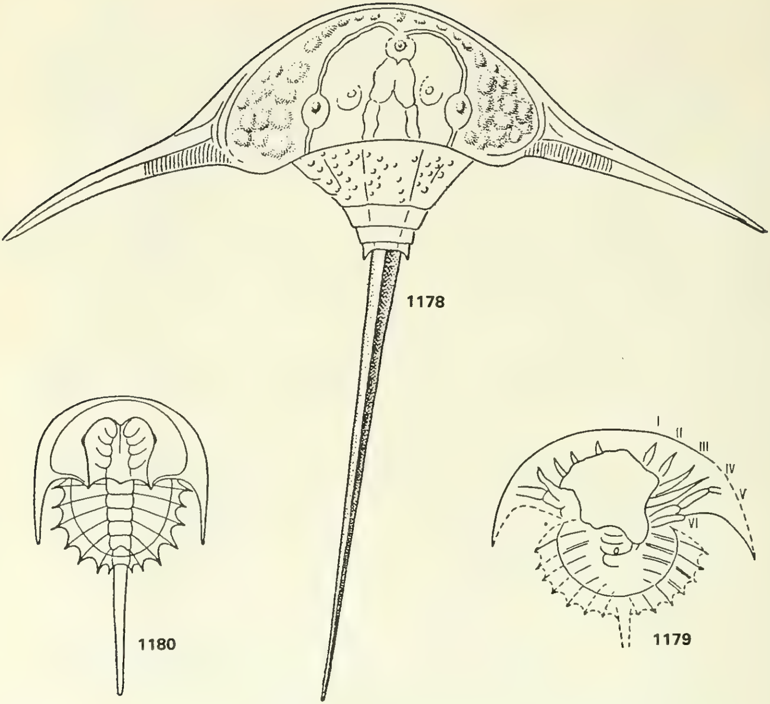
Family AUSTROLIMULIDAE Riek, 1955

Opisthosoma small, shorter than prosoma, distinctly converges distally and consists of three fused anterior and three movable posterior segments. Genal spines of prosoma large, widely divergent toward different regions. Triassic. One genus.

Austrolimulus Riek, 1955. Genotype—*A. fleetcheri* Riek, 1955. Middle Triassic, Australia. Prosoma short, broadly rounded. The tips of long genal spines reach level of last segment of opisthosoma. Compound eyes located in posterior part of prosoma. Prosoma with irregular tubercles and, in some places, ribbed. Opisthosoma with six segments, axial region very narrow. Anterior three segments jointed to form a trapezoidal shield. Three posterior segments taper to the rear, narrow and mobile. Telson three-sided and half as long as prosoma and opisthosoma put together (Fig. 1178, Pl. XVII). One species. Middle Triassic of Australia.

Family EUPROOPIDAE Eller, 1938

Small forms with wedge-shaped primary lobe fringed by furrows. Cardio-



399 Figs. 1178–1180. Families Austrolimulidae and Euproopidae.

1178. *Austrolimulus fleetcheri* Riek; × 1.5. Middle Triassic, Australia (drawing by N. Novozhilov from photograph). 1179. *Euproops anthrax* Woodward; dorsal view with appendages spread, × 0.7. Carboniferous, England (Stormer, 1945). 1180. *Euproops thompsoni* Raymond; × 1. Upper Carboniferous, North America (Stormer, 1955).

ophthalmic area well-developed. Ocular ridges converge behind eyes. Opisthosoma wide, rounded and comprises six or seven distinct and closely connected segments with pointed lateral appendages. Axis annulate and with high prominences on its last segments. One genus: *Euproops* Neek, 1867 (Figs. 1179, 1180). Upper Carboniferous of Western Europe; Upper Carboniferous to Permian of North America; Lower Permian of East Asia.

Family ELLERIIDAE Raymond, 1944

This group is insufficiently known. Segmentation of axis of opisthosoma and
399 pleural plates distinct. Each segment of the axis with three tubercles. Posterior part of opisthosoma deeply notched. Telson and prosoma not known. One genus, *Elleria* Raymond, 1944. Upper Devonian to Carboniferous of North America.

Family KIAERIIDAE Størmer, 1952

This group is not well described. Opisthosoma large, with axial furrows and smooth axis. Segmentation and a wide posterior incision indicate the possibility of movable segments. Telson and prosoma not known. One genus, *Kiaeria* Stormer, 1934. ? Lower Devonian (Downtonian), Scandinavia.

Belinuridea Incertae sedis

The following poorly preserved genera have also been described: *Pringlia* Raymond, 1944 (Upper Carboniferous of Western Europe and North America); *Anacontium* Raymond, 1944 (Permian of North America); *Pincombella* Chapman, 1932 (Upper Carboniferous of Western Europe); and *Belinuropsis* Matthew, 1909 (Upper Silurian of North America).

SUPERFAMILY LIOMESASPIDIDEA

[nom. transl. Novojilov, hic (ex Liomesaspididae Raymond, 1944)]

Opisthosoma complete, without trace of segmentation along margin. Prosoma and opisthosoma similar in form and size, rounded, without spines, with a close doublure along the margin. Genal angles absent. Upper Carboniferous to Lower Permian. One family: Liomesaspididae.

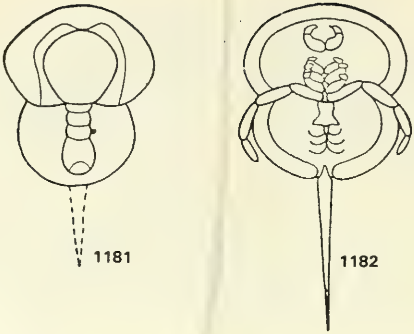
Family LIOMESASPIDIDAE Raymond, 1944

Prosomal primary lobe convex. Genal spines absent. Opisthosoma without
400 pleural spines and pleural ribs. Posterior axial segment without projections. Two genera: *Liomesaspis* Raymond, 1944 (Upper Carboniferous of North America) and *Prolimulus* Fritsch, 1899 (Permian and Western Europe) (Figs. 1181, 1182).

SUPERFAMILY LIMULIDEA

[nom. transl. Novojilov, hic (ex Limulidae Zittel, 1885; Limulacea Raymond, 1944)]

Opisthosoma shield-like. Only one segment before telson is occasionally mobile. Segmentation of opisthosoma determined from position of pleural spines or teeth and presence of pits in axial furrows. Prosoma with parallel posterior



Figs. 1181–1182. Superfamily Liomesaspididea, Family Liomesaspididae.

1181. *Liomesaspis laevis* Raymond; × 1.7. Upper Carboniferous, North America (Stormer, 1955).
1182. *Prolimulus woodwardi* Fritsch; ventral view, × 2. Lower Permian, Czechoslovakia (Stormer, 1955).

branches of ocular ridges and moderately elongate genal processes (sometimes, as observed by Stormer, due to peculiar concealment the ventral structure leaves traces on dorsal surface, which gives an incorrect picture of the structure of prosoma). Permian to Recent. Families: Paleolimulidae, Mesolimulidae and Limulidae.

Family PALEOLIMULIDAE Raymond, 1944

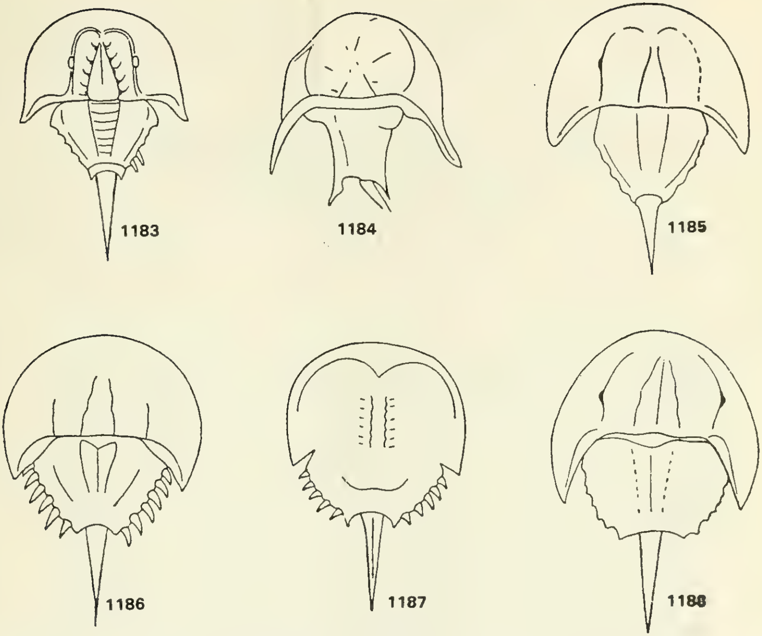
Small forms. Ocular ridges converge in front of primary lobe. Axial part of opisthosoma distinctly annular. With a mobile segment in front of telson. One
401 genus: *Paleolimulus* Dunbar, 1923 (Fig. 1183). Carboniferous to Permian of Western Europe and North America.

Family MESOLIMULIDAE Størmer, 1952

Small to medium sized forms. Ocular ridges do not converge in front of primary lobe. Genal angles extend somewhat posteriorly. Axial furrows distinct. Axis of opisthosoma is not distinctly annular. First pair of marginal spines lies within the limits of anterior third of opisthosoma. Three genera: *Psammolimulus*Lange, 1923 (Lower Triassic of Europe); *Limulitella* Størmer, 1952 (Lower through Upper Triassic of Europe and North America); and *Mesolimulus* Størmer, 1952 (Jurassic, ? Cretaceous of Western Europe and ? Asia) (Figs. 1184–1187).

Family LIMULIDAE Zittel, 1885
(Xiphosuridae Pocock, 1902)

Medium to large sized forms. Ocular ridges do not converge in front of primary



400 Figs. 1183–1188. Family Paleolimulidae, Mesolimulidae and Limulidae (Størmer, 1955).

1183. *Paleolimulus avitus* Dunbar; × 1. Permian, Canada. 1184. *Psammolimulus gottingensis* Lange; × 0.5. Lower Triassic, Europe. 1185. *Limulitella bronni* (Schimper); × 0.5. Lower Triassic, France. 1186. *Mesolimulus walchi* (Demarest); × 0.5. Jurassic, Germany. 1187. *Mesolimulus syriacus* (Woodward); × 0.2. Middle Cretaceous, Central Asia. 1188. *Tachypleus decheni* (Zinken); × 0.13. Miocene, Germany.

lobe. Genal angles considerably extended backward. Opisthosoma more or less hexagonal. Axial furrows indistinct. First pair of marginal spines nearly halfway between anterior and posterior margins of opisthosoma. Neogene to Recent. Three genera in the Recent fauna, of which *Tachypleus* Leach, 1819 (Fig. 1188) is known from fossil record (Miocene of Western Europe).

Class SCORPIONOMORPHA.
Scorpion-like Forms

(V.B. Dubinin)

402 Body sharply subdivided into an anterior division, cephalothorax or prosoma, consisting of the first six segments carrying segmented appendages; and posterior division or opisthosoma, consisting of 12 segments and the telson or anal lobe without appendages. Opisthosoma, sometimes divided into mesosoma and metasoma. All terga of prosoma fused, together to form one cephalothoracic shield, homologous with the head-shield of trilobites. Appendages of prosoma have lost their respiratory function, and this is expressed morphologically in the reduction of preepipodites. They help in locomotion and mastication. In typical aquatic Scorpionomorpha, Paleozoic eurypterids and Silurian aquatic scorpions of the suborder Apoxypodes, the appendages of the prosoma are devoid of respiratory organs. Conversely, the appendages of the mesosoma have lost telopodites and masticating structures (basendites) of the primitive appendage. They preserve only preepipodites, which here carry out the respiratory function (gills in Eurypterida, lungs in Scorpiones and others) and have acquired other functions connected with external genital openings (genital opercula).

The more primitive representatives of the class (subclass Holactinochitinosi) retained the comparatively sharp division of opisthosoma into two separate divisions—meso- and metasoma. In the subclass Pedipalpides these two units are fused together, and only in some representatives of the order Uropygi are the last segments of opisthosoma morphologically distinct. Still, in the class Scorpionomorpha the maximum coalescence of body segments characteristic of the Arachnida is absent.

Respiratory organs are of three types. In the aquatic representatives of the class (Eurypterida and Apoxypodes), there is branchial respiration carried out with the help of the podobranches of segments III–VI of the mesosoma. In the terrestrial forms (scorpions of the suborder Dionychopodes and majority of the subclass Pedipalpides), the primary podobranches are modified into pulmonary sacs or lung books, which are located in the mesosomal segments and open to the outside through four (scorpions) or two (pedipalpids) pairs of narrow spiracles. Finally, in Pseudoscorpionidea trachea-type respiration is developed with the loss of lungs. In all representatives of this class two large median eyes are present in the middle of the dorsal region of the head-shield and three to six pairs of small, simple eyes are located near the antero-lateral angles of the prosoma.

SYSTEMATIC POSITION AND PHYLOGENY. A series of anatomical peculiarities testify to the great phylogenetic primitiveness of various representatives of class Scorpionomorpha, which appear as the first terrestrial organisms of the subphylum Chelicerata and perhaps of Arthropoda. Their archaic nature is revealed in the preservation of comparatively homonomous segmentation of body with the maximum number of segments—19 (Scorpiones), 18 (Uropygi, Amblypygi and Pseudoscorpionidea) or 16 (Palpigradi). Other indications include retention of primitive, aerial respiration with the help of podobranches—pulmonary sacs enclosed within the integument (tracheae appeared only in most specialized forms, Pseudoscorpionidea); and the preservation in the adults of many groups of seven segments located between prosoma and mesosoma, and well-developed in Merostomata. The seventh segment is best developed in Palpigradi, where it retains its identity and serves as a connecting stalk between the prosoma and mesosoma. In Uropygi it is fused with the eighth segment but the terga and sterna are retained among groups of dorsoventral muscles. In Amblypygi the seventh segment is weakly developed. In Pseudoscorpionidae its terga is retained. In other Scorpionomorpha and all remaining chelicerates there is extreme reduction of the seventh segment (Petrunkevitch, 1922): sometimes it is discernible only during development. Another feature is the preservation in some Scorpionomorpha (for example, in a few Scorpiones and in all Palpigradi) of the stomatic cone, at the apex of which the mouth opens. Also characteristic is the presence in the Recent scorpions of maxillary appendages on the coxae of all appendages of the prosoma, which form the preoral cavity (pedipalpi and two anterior pairs of legs). The progressive dissimilarity of appendages of the prosoma in Chelicerata is reflected by the fact that in Arachnida only chelicerae gather food, whereas in Scorpionomorpha this is done by the pedipalpi, which are homologous with the mandibles of Crustacea, Insecta and Myriopoda. In the class Scorpionomorpha, only in members of the order Palpigradi, do pedipalps not help in holding food.

Until recently the order Chelicerata, included here under the class Scorpionomorpha, had been assigned by one group of workers to different classes (Merostomata and Arachnoidea; Grasse, 1949), and by another in different superorders (Zakhvatkin, 1952; Beklemishev, 1952) or to the class Eurypterida and two subclasses of Arachnida (Petrunkevitch, 1949, 1953). A similar situation occurred in the times of Lanchester (1911) and Pocock (1910), when two artificial groups of chelicerates were recognized in the class Arachnida and subclass Eurachnida: aquatic and terrestrial. Later the artificial groups of terrestrial chelicerates were placed under the class Arachnoidia. Such a separation of terrestrial chelicerates from the remaining group based only on purely ecological principle led to the most confused, complicated classification within this class. It did not take into account their highly intricate and complex anatomy and obviously did not reflect the natural interrelationships among these arthropods (Petrunkevitch, 1949, 1953). Zakhvatkin (1952) did not correct these shortcomings and suggested a new classification of the class Chelicerata. He established the phylogenetic relationship of aquatic Eurypterida with the terrestrial scorpions and Thelyphonida, which were included under an independent superorder, Holactinochitinosi. Zakhvatkin's classification was adopted by Beklemishev (1952) with certain reservations.

Arachnoidea is subdivided into three independent classes. First of these three classes, the class Scorpionomorpha—scorpion-like, leg-feeding or lung-breathing chelicerates—is represented by two subclasses: Holactinochitinosi (orders Eurypterida and Scorpiones) and Pedipalpides (orders Uropygi, Amblypygi, Palpigradi, Kustarachnida and Pseudoscorpionoidea).

Subclass Holactinochitinosi

Body greatly elongate, and subdivided into two divisions: the prosoma, covered by the headshield and comprising the first seven segments; and the long opisthosoma, with 13 segments. Opisthosoma often subdivided into a broad six- or seven-segmented mesosoma and a narrow six-segmented metasoma. Last segment of metasoma articulates with telson and is in the form of a bent claw, straight spine or fin. Chelicerae three-segmented, short, rarely elongate (Pterygotidae) and pincer-shaped. Pedipalpi variously modified. In Eurypterida they are either short or long, filamentous (*Slimonia*) or of a prehensile type (as in *Mixopterus*). In all Scorpiones they are in the form of large, powerful prehensile pincers. All appendages of the prosoma (except chelicerae) have a masticatory lobe on the coxae. Gills absent. In Eurypterida and aquatic
404 scorpions the genital operculum is located on the eighth segment and the podobranches on the eight-ninth. These appendages were modified into pulmonary sacs of terrestrial scorpions when they migrated to dry land.

In the superorder Holactinochitinosi, despite radical shift in ecology (from aquatic to terrestrial mode of life) the characteristic division of body with its complex appendages and also the general scorpionid appearance are distinctly preserved in all groups. Terrestrial fossils and the Recent scorpiones are rightly called terrestrial eurypterids by many workers.

Ecology and Biogeography. This subclass is known from the Ordovician to the Recent. Being primarily aquatic, they trace their ancestry to the Merostomata. Representatives of the order Eurypterida lived throughout the Paleozoic. Separation of Scorpiones from Eurypterida occurred in the Silurian. At first the scorpions were aquatic (suborder Apoxypodes), but during the Carboniferous they became terrestrial (suborder Dionychopodes). In the Recent epoch only the order Scorpiones is represented, with species widely distributed in all tropical and subtropical countries (cf. p. 423).

Order EURYPTERIDA

(Nestor Novozhilov)

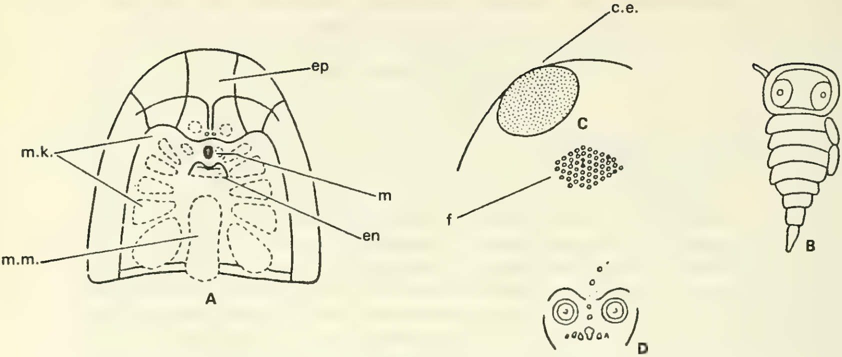
These are chelicerates that resemble some primitive Merostomata like Aglaspidida. Body elongate, more or less lancet-shaped, rarely three-lobed (as in a few scorpionoids and Mycteropidae: *Borchgrevinkium*). Prosoma highly variable, almost rounded, with a notch at the posterior end, or with a semicircular, semioval, square trapezoidal, pentagonal or helmet-shaped outline. Opisthosoma of 12 movable segments, the anterior seven comprise the mesosoma (preabdomen) and the posterior five, the metasoma (postabdomen). Telson attached to the last segment of metasoma, dagger-shaped, or ring-, blade- or claw-shaped, as in the Scorpiones. Chelicerae three-segmented and pincer-shaped. Pedipalpi and four posterior pairs of appendages modified as walking legs. Sometimes pedipalpi and third pair of appendages of prosoma are of grasping type. Posterior pair (VI) of appendages often modified into swimming legs. Mouth medium, confined behind by two plates, endostome and metastome. Genital appendage with a postgenital plate (operculum). Appendages of opisthosoma plate-like and with undivided gills.

MORPHOLOGY. Most known Eurypterida are not more than 10–20 cm long, though a few forms are indeed large, 100–180 cm in length. Such are the Ordovician Megalograptidae, the Silurian *Slimonia* Page and *Pterygotus* Agassiz, and some Devonian Stylonuridae (*Tarsoptrella* Størmer, and *Ctenopterus* Clarke and Ruedemann). Exoskeleton of varying thickness, often with many-segmented tactile hairs or their persisting basal pits, particularly on the plate-like appendages of the opisthosoma. Short cylindrical tubes, set one inside the other, are sometimes developed on the terga of mesosoma along the median line (in *Tylopterella* Størmer). Their significance is not known. Ornamentation of chitinous exoskeleton of Eurypterida varied. It may be similar in representatives of different families and, on the other hand, dissimilar in forms that are related. The following types of ornamentation are observed:

1. Tubercular or shagreen type: small or large tubercles developed on different parts of the body; or with flattened tubercles of different sizes and shapes. Entire surface has a shagreen appearance.

2. Scaly type: Ornamentation takes form of closely-spaced or dispersed scalelike markings, with broad more or less semicircular (so-called 'crescent' shaped); tonguelike; modified into acute-angled prominences resembling feathers of birds.

3. Pitted type: With pits of different sizes and shapes on different parts of the body (for example, on the segments of the opisthosoma of *Megalograptus ohioensis* Caster and Kjellesvig-Waering), together with the scale pattern; accentuated ribs are also found.



405 Fig. 1189. Morphological peculiarities of the prosoma in representatives of the order Eurypterida (Størmer, 1955).

A—Prosoma of *Hughmilleria*; ventral view. B—Larva of *Stylonurus myops* Clarke; × 11. Silurian, North America. C—Compound eyes (c.e.) and facets (f) of *Pterygotus* sp. Silurian, Estonia. D—Median eyes of *Eurypterus fischeri* Eichwald; × 4. ep—epistoma; m—mouth ; en—endostoma; m.k.—points of attachment of appendages; m.m.—point of attachment of metastome; c.e.—compound eyes; f—facets of compound eyes.

Prosoma (Fig. 1189A) somewhat convex, varied in form in widely different families. Anterior part or prosoma, rarely the posterior (*Melbournopterus* Caster and Kjellesvig-Waering) with rounded, oval or kidney-shaped compound 405 eyes of different sizes (Fig. 1189B, C). Besides the compound eyes on the prosoma there are simple eyes—ocelli. Ocelli are close together, sometimes touching, on a small plate along the median line (Fig. 1189D).

Doublure of prosoma borders the points of attachment of six pairs of appendages of prosoma surrounding the mouth (Fig. 1189A). First pair form pincer-shaped three-segmented chelicerae, which function as prehensile or piercing organs (Fig. 1190). In Pterygotidae they are very strongly developed and both segments of claw have pointed, fairly thick teeth. Next five pairs (II–VI) of appendages usually locomotory or all are of walking type (Stylonurina); or appendages of last pair (pair VI of prosomal appendages) modified for swimming as oar-shaped appendages (Eupterina). Usually pair II or pedipalpi form the first pair of locomotory appendages. Sometimes pedipalpi represent pair III appendages and are modified into grasping organs of complex structure (Megalograptidae and Mixopteridae).

Walking legs more or less of similar structure and consist of cylindrical segments with or without spines. First segment of every leg forms more or less broad coxa with small epicoxae at base of toothed oral margin of coxa (Fig. 1190 B, D). In *Eurypterus* coxa of leg V has small openings which are apparently

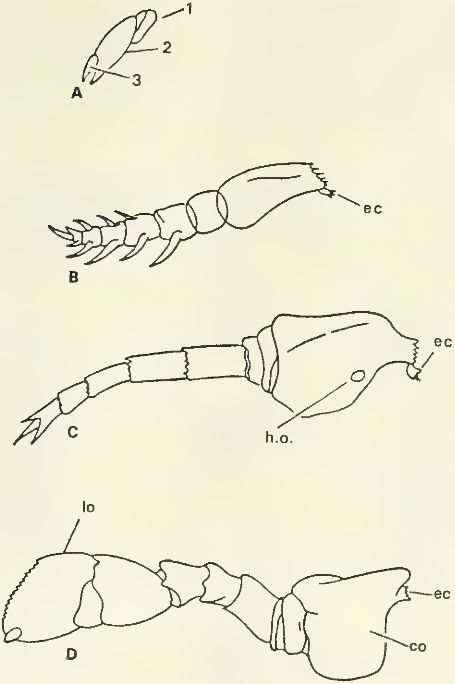


Fig. 1190. Appendages of prosoma (I, IV, V, VI) of *Eurypterus fishcheri* Eichwalk, Silurian, Estonia.

A—three-segmented chelicera; B—fourth pair of walking leg; C—walking leg of fifth pair; D—swimming leg; ec—epicoxites; h.o.—auditory organ; co—coxa; lo—paddle lobe; × 1. (Størmer, 1955).

406 auditory organs (Fig. 1190C). Beside coxa, walking legs consist of seven or eight segments: the trochanter, which is double in leg V, a double femur (femur and prefemur), patella, tibia, and tarsus with distal claws corresponding to pretarsus of insecta. Legs with movable or relatively movable spines on ventral surface. Absence of spines on legs of some forms is evidence of primitiveness of structure. In some genera spines modified into special long needles, probably capable of venomous secretion (as in Megalograptidae and Mixopteridae).

In Eurypterina sixth pair of prosomal appendages is modified for swimming. Last two segments of this appendage are more or less broad to form

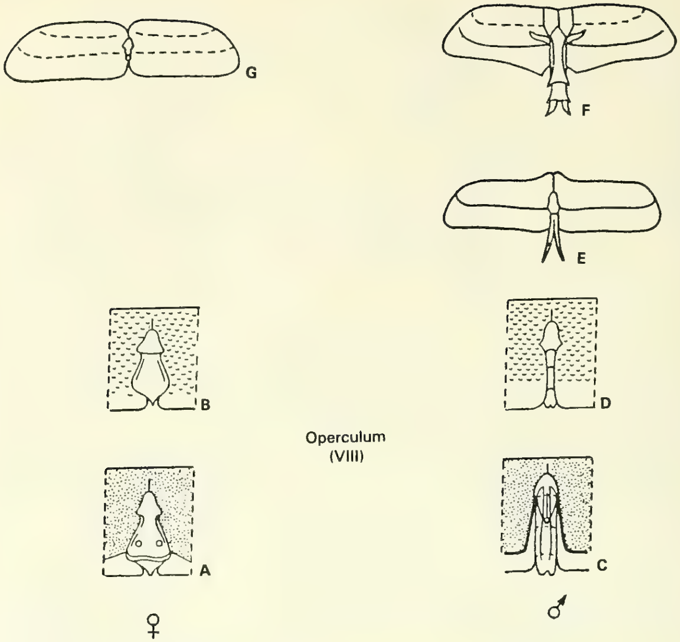


Fig. 1191. Operculum and genital appendages of females and males of order Eurypterida (Størmer, 1955).

Pterugotus (Pterugotus) rhenaniae Jaekel, Devonian, Germany; A—female, dorsal view; B—female, ventral view; C—male, dorsal view; D—male, ventral view; *Eurypterus fischeri* Eichwald, Silurian, Baltic; E and F—male, ventral view; G—female, ventral view.

an earlike lobe or paddle (Fig.1190D). In Dolichopteridae the paddles are little developed and exhibit the transition from walking to swimming appendages (or conversely, gradually lose their swimming function?).

Behind the mouth there are two plates one behind the other—the endostome and metastome. The latter is homologous with the chilaria of Xiphosura and belongs to first segment of opisthosoma.

Operculum (Fig. 1191) represents eighth genital segment of body and forms second segment of opisthosoma. Genital appendages short in females, long and broadened distally in males. It is interesting to note that it is not yet clear to which of the sexes these structures should be attributed.

Mesosoma best developed in families Eurypteridae, Hughmilleriidae, Dolichopteridae and, particularly, in Mixopteridae, whereas in Stylonuridae (particularly in the genus *Stylonurus* Page) mesosoma narrow and takes the form of a wedge. The last segment of metasoma (pretelson) with lateral outgrowths (epimers). Epimers may develop on other segments of meta- and mesosoma.

407 Telson usually dagger-shaped, narrow, or more or less wide, sometimes constricted in the middle (as in representatives of certain families: Stylonuridae—*Drepanopterus* Laurie, *Eurypteridae—Onychopterella* Stormer, and Hughmilleriidae—*Salteropterus* Kjelleswig-Waering). Rarely, as in Pterygotidae, telson more or less bladelike, with a wedge-shaped keel along dorsal side of the plate. Keel represents normal sword-shaped telson, and the broad plate represents strongly developed epimers of telson. In *Slimonia* this plate resembles the head of a spear. The telson of the scorpionlike Carcinosomatidae and Mixipteridae is a narrow, long, bent spine with clawlike, flattened base.

ECOLOGY AND GEOGRAPHICAL DISTRIBUTION. Eurypterida are absent in typical marine deposits. The occurrence of their remains in continental deposits indicates that these chelicerates inhabited fresh or brackish water. Most of them obviously were benthic forms in spite of having well-developed swimming legs. Pterygotids were rather immobile forms of nektons. Lack of locomotory powers was compensated by their thick, mobile pincers, which they used to catch prey. The most active predators were obviously Mixopteridea, with forwardly located compound eyes and well developed anterior legs with stout spines, which were obviously organs of offence.

Ordovician to Permian. Distributed almost all over the world, but were not numerous (Table 3).

Table 3. CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION OF GENERA OF THE ORDER EURYPTERIDA

Eurypterida	Assigned geological age
Suborder Eurypterina	
Superfamily Eurypteridea	
Family Hughmilleriidae	
Hughmilleria	Upper Ordovician–Middle Devonian
Salteropterus	Lower Devonian
Grossopterus	Lower and Middle Devonian
Lepidoderma	Upper Devonian and Upper Permian
Family Slimoniidae	
Slimonia	Upper Silurian
Family Eurypteridae	
Eurypterus	Ordovician to Lower Devonian
Erieopterus	Ordovician to Devonian
Tylopterella	Upper Silurian to Lower Devonian
Onychopterella	Upper Silurian

Family Dolichopteridae	
Dolichopterus	Silurian
Strobilopterus	Lower Devonian
Superfamily Pterygotidea	
Family Pterygotidae	
Pterygotus	Silurian to Upper Devonian
Superfamily Mixopteridea	
Family Mixopteridae	
Mixopterus	Upper Sulurian to Downtonian
Family Megalograptidae	
Megalograptus	Ordovician
Echinognatus	Ordovician
Family Carcinosomatidae	
Carcinosoma	Ordovician to Silurian
Rhinocarcinosoma	Silurian
Suborder Stylonurina	
Superfamily Stylonuridea	
Family Stylonuridae	
Subfamily Stylonurinae	
Stylonurus	Silurian to Middle Devonian
Drepanopterus	Upper Silurian to Upper Devonian
Brachyopterus	Middle Ordovician to Downtonian
Ctenopterus	Silurian to Middle Devonian
Tarsopterella	Lower and Upper Devonian
Subfamily Marsupipterinae	
Marsupipterus	Downtonian
Polystomurum	Upper Devonian
Family Hibbertopteridae	
Hibbertopterus	Upper Devonian to Lower Carboniferous
Campylocephalus	Upper Carboniferous to Upper Permian
Family Rhenopteridae	
Rhenopterus	Lower Devonian
Superfamily Mycteropidea	
Family Mycteropidae	
Mycterops	Upper Carboniferous
Borchgrevinkium	Lower Devonian
Family Woodwardopteridae	
Woodwardopterus	Lower Carboniferous

Classification, Phylogeny and Systematic Position. Eurypterida are related on the one hand, to other aquatic chelicerates—merostomates—and on the other, to the terrestrial chelicerates—the scorpionids. Eurypterida were capable not only of walking but also of swimming (suborder Eurypterina). Most probably they were descendants of merostomates—Aglaspidida. Almost contemporaneous simultaneously with them were Eurypterida which only had walking legs (suborder Stylonurina). The scorpion-like Mixopteridea of the suborder Eurypterina were very close ancestors of terrestrial scorpions. Thus the evolution of both phylogenetic branches—walking and swimming and only walking—proceeded in parallel fashion. But the walking phylogenetic clans were somewhat later forms. Suborders: Eurypterina and Stylonurina.

408

Suborder Eurypterina

[nom. transl. Novojilov, hic (ex Eurypteridae Burmeister, 1845)]

Last pair of appendages of prosoma as swimming and rowing legs. Their terminal segments broad and form propelling lobes. Ordovician to Permian, Superfamilies: Eurypteridea, Pterygotidae and Mixopteridea.

SUPERFAMILY EURYPTERIDEA BURMEISTER, 1845

[nom. corr. Novojilov, hic (ex Eurypteraceae Størmer,1951)]

Chelicerae short and weakly developed. Mesosoma and metasoma poorly differentiated. Ordovician to Permian. Families: Hughmilleriidae, Slimoniidae, Eurypteridae and Dolichopteridae.

Family HUGHMILLERIIDAE Kjellesvig-Waering, 1951

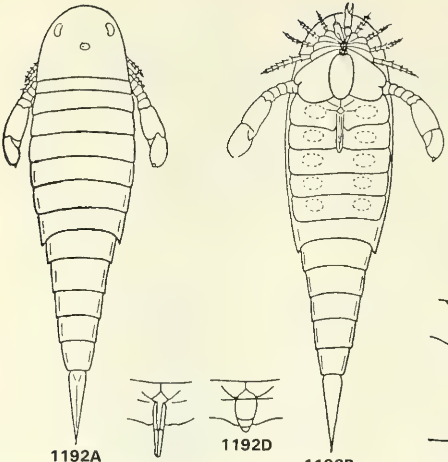
Length 7 to 30 cm. Exoskeleton with transverse folds or semicircular 'scales', large or small. Compound eyes small, located on deeper part of sides or close to the middle of prosoma. Doublure with epistome. Metastoma oval. Genital appendage of males narrow, without lateral pointed ends. Chelicerae lack serration. Walking legs with spines or serrations. Swimming appendages narrow. Opisthosome divided into a somewhat broad mesosoma and a wedge-shaped metasoma. Telson lancet-shaped or broad at base. Four genera. Ordovician to Permian.

Hughmilleria Sarle, 1903. Genotype—*H. socialis* Sarle, 1902; Lower Silurian, North America. Prosoma semi-elliptical to semicircular. Compound eyes close to the anterolateral margin of prosoma. Doublure with distinct epistosomal sutures and less distinct anterolateral sutures. Genital appendage of females short and wide. Mesosoma barrel-shaped, with only slightly convex lateral margins. Last segment of mesosoma with posterolateral angles. Metasoma broad, tapering like a wedge. Telson wedge-shaped. Ornamentation of exoskeleton in the form of a series of plates resembling those of *Pterygotus*; but often it takes the form of 'terraced' lines (Fig. 1192; Pl. XVIII, Figs. 1 – 4). Fifteen species. Upper Ordovician of Canada; Lower and Upper Silurian of North America, Scotland and England; ? Lower Devonian (Downtonian) of Scandinavia; ? Lower and Middle Devonian of Asia (Krasnoyar district, Tuva).

Outside the USSR: *Salteropterus* Kjellesvig-Waering, 1951 (Lower
410 Devonian of Europe); *Grossopterus* Stormer, 1934 (Lower and Middle
Devonian of Western Europe and North America); and *Lepidoderma* Reuss, 1855 (Upper Devonian through Upper Permian of Western Europe, North America, Asia)(Figs. 1193–1195).

Family SLIMONIIDAE Novojilov, fam. nov.

Length about 10 cm. Exoskeleton smooth. Compound eyes rounded at corners

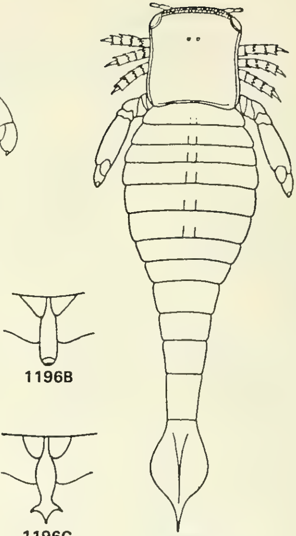


1192A

1192C

1192D

1192B



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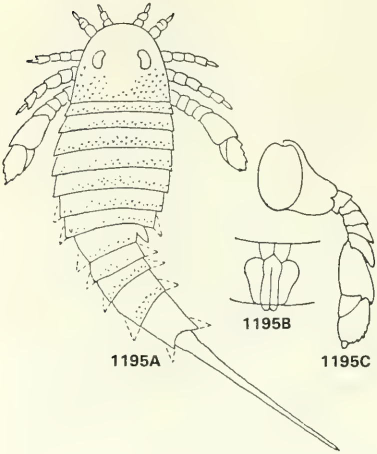

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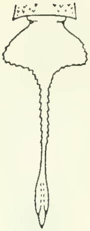

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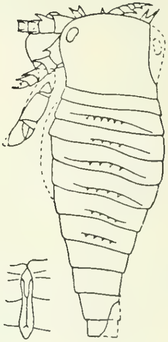

1194B

1194A

of anterior margin. Prosoma more or less rectangular. Metasome narrow heart-shaped. Genital appendage of males with lateral pointed ends. Pedipalpi thin, without spines. Telson broad and finlike. One genus: *Slimonia* Page, 1856. Upper Silurian of Western Europe (Fig. 1196).

Family EURYPTERIDAE Burmeister, 1845

Length 10–30 cm, with distinct scaly or feathery ornamentation; or only ribbed. Prosoma almost semicircular or rectangular. Compound eyes more or less kidney-shaped and located close to middle of prosoma. Telson wedge-shaped, rarely with a minor constriction. Doublure without epistome. Metastoma oval or heart-shaped in front. Walking legs increase in length from front to back; with or without spines. Paddles of swimming appendages with or without short spurs. Genital appendage very short with lateral lobes in females, but long with diverging distal spines in males. Ordovician to Upper Carboniferous. Four genera.

Eurypterus De Kay, 1825. Genotype— *E. remipes* De Kay, 1825; Upper Silurian, North America. Prosoma with narrow marginal rings. Doublure of prosoma with a median suture. Metastome oval with deep dentate incision in front. Anterior three pairs of walking legs relatively short, with spines on all segments. Fourth pair of walking legs longer, spines only on the distal segment. Paddles of swimming appendages markedly broad, with weakly developed spurs. Exoskeleton usually with feathery ornamentation (Fig. 1197). Eight species and seven subspecies. Upper Silurian (Ludlovian Stage) of Estonia, Norway and North America; ? Lower Devonian (Downtonian) of Scotland; Lower Devonian of the USA (Wyoming), Ukraine, Kazakhstan, Siberia, Scotland, France, Belgium, Germany and Czechoslovakia; and Permian of Portugal, China and North America.

Erieopterus Kjellesvig-Waering, 1958. Genotype—*Eurypterus microphthalmus* Hall, 1859; Silurian, North America. Prosoma with narrow or broad ring. Doublure of prosoma without the median suture, grooved on inner margin. Walking legs similar in structure, without spines or have immovable spines on distal segments. Paddles of swimming appendages broad, with distinct spur at

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409 Figs. 1192–1196. Families Hughmilleriidae and Slimoniidae (Størmer, 1955).

1192. *Hughmilleria norvegica* (Kiaer)?; Lower Devonian (Downtonian), Norway; A – dorsal view; B—ventral view showing location of gills of opisthosoma (dotted), × 0.5; C—genital appendage of male; D—genital appendage of female, × 1. 1193. Telson of *Salteropterus abbreviatus* (Salter); × 1. ? Lower Devonian (Downtonian), England. 1194. *Grossopterus overathi* (Gross); A – dorsal view, × 0.25; B—genital appendage of male, × 0.3; Lower Devonian, Germany. 1195. *Lepidoderma* Reuss: A— *L. mansfieldi* (C.E. Hall), dorsal view, × 1.3; Upper Carboniferous, North America; B, C— *L. masonense* (Meek and Worthen). × 1; B—genital appendage of female; C—metasoma with swimming leg; Upper Carboniferous, North America. 1196. *Slimonia acuminata* (Salter); A—dorsal view, × 0.1; B—genital appendage of female (?); C—genital appendage of male (?), × 0.13; Silurian, Scotland.

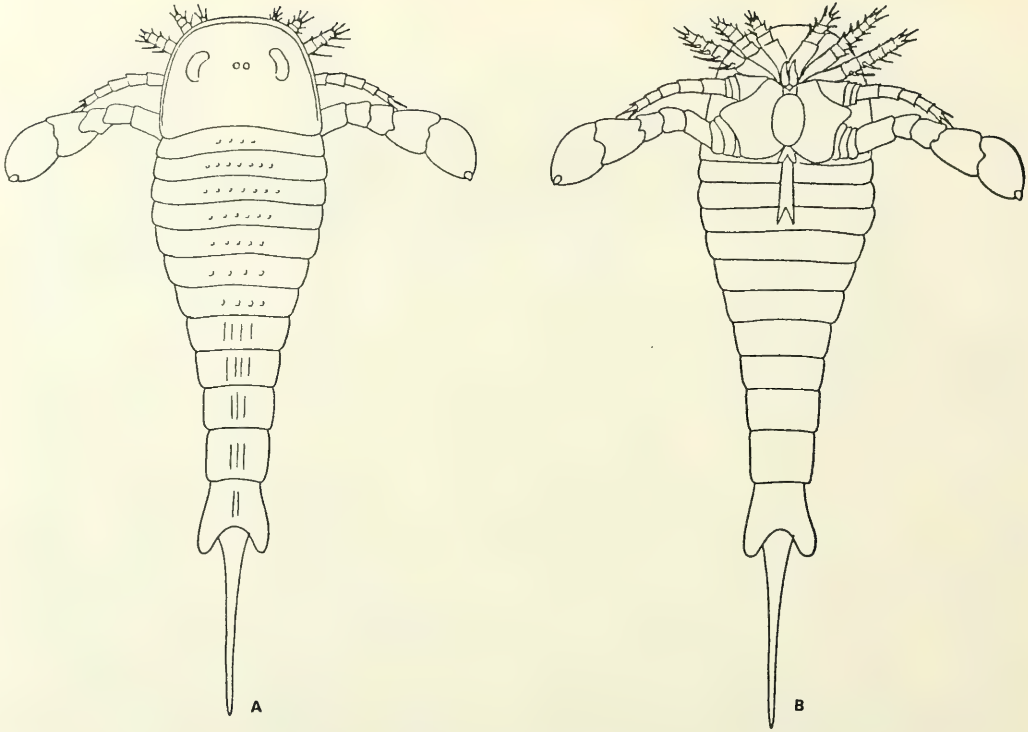
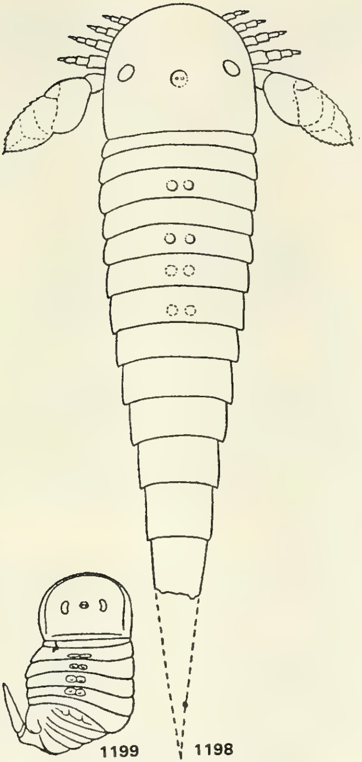


Fig. 1197. Family Eurypteridae.

Eurypterus fischeri Eichwald; A—dorsal view; B—ventral view (reconstruction), × 0.5. Middle Silurian, Estonia (Stormer, 1955)



Figs. 1198–1199. Family Eurypteridae.

1198. *Tylopterella boyli* (Whiteaves): × 0.17. Silurian, North America (Størmer, 1955). 1199. *Tylopterella mennri* (Novojilov); × 4.2. Lower Devonian, North Siberia (Novojilov, 1958).

distal cleft. Border between meso- and metasoma sharper than in Eurypterus; telson wedge-shaped. Exoskeleton smooth or vesicular (Pl. XX, Fig. 2). Ten species. Ordovician of North America; Silurian of Estonia and North America; and Devonian of Scotland and North America.

Tylopterella Størmer, 1951 (= *Tylopterus* Clarke and Ruedemann, 1912). Genotype—*Eurypterus boyli* Whiteaves, 1884; Upper Silurian, North America (Ontario). Prosoma more or less rounded, with a notch at occipital margin; or rounded-quadrate. Compound eyes kidney-shaped or oval, located more or less close to the lateral margins at level of median line of prosoma. Ocelli located between compound eyes or a little behind. Walking legs short, narrow and without spines. Swimming appendages with fairly broad paddles. Opisthosoma long, wedge-shaped; mesosoma slightly broad. With paired, cylindrical, short pores or round plates on some terga of mesosoma along the median line. Telson wedge-shaped (Figs. 1198, 1199; Pl. XVIII, Fig. 5). Two species. Upper Silurian of North America; Lower Devonian of North Siberia (SW Taimur).

Also, *Onychopterella* Størmer, 1951 (Upper Silurian, North America).

Family DOLICHOPTERIDAE Kjellesvig-Waering and Størmer, 1952

Length about 30 cm. Opisthosoma poorly delineated, mesosoma wide and narrow metasoma. Telson wedge-shaped. Compound eyes large, convex, widely spaced, located close to the anterior margin of prosoma. First three pairs of walking legs (appendages of segments II–IV of prosoma) comparatively stout, short, with large spines. Last two pairs of appendages of prosoma longer, without spines but with terminal outgrowths. Posterior pair bears broad paddles representing the enlarged last three segments. These paddles differ in structure from those of other families. Metasoma narrow, concave in front. Genital appendage of males long. Exoskeleton wrinkled or with vesicular tubercles or
411 semicircular 'scales'. Two genera: *Dolichopterus* Hall, 1859 (Fig.1200 A, B), Silurian, North America; and *Strobilopterus* Ruedemann, 1935 (Fig. 1201 A, B), Lower Devonian of North America.

SUPERFAMILY PTERYGOTIDEA CLARKE AND RUEDEMANN, 1912

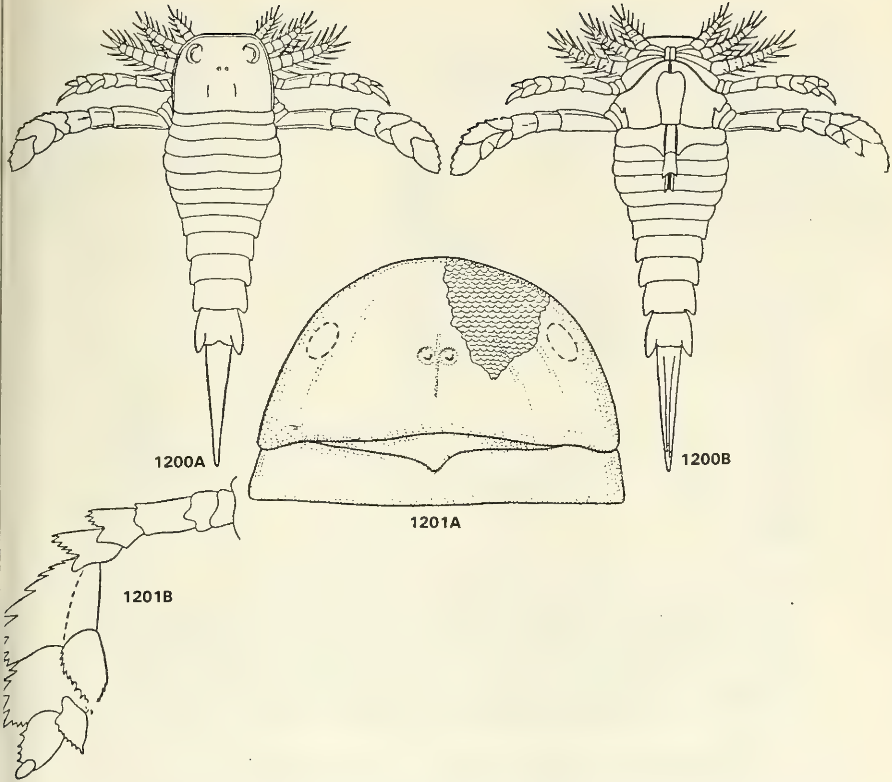
[nom. transl. Novojilov, hic (ex Pterigotidae Clarke and Ruedemann, 1912)]

Chelicerae very large, considerably longer than entire prosoma, with well developed expansions, on both branches of which there are long, broad serrations. Last pair of prosomal appendages in form of swimming legs with paddles similar to those in Eurypteridae and Hughmilleriidae. With large compound eyes on the anterolateral margins of prosoma. Opisthosoma not distinctly divided into mesosoma and metasoma. ? Ordovician to Devonian. One family.

Family PTERYGOTIDAE Clarke and Ruedemann, 1912

Small to very large forms (large ones measure 80–200 cm). Opisthosoma more or less undivided, no sharp border between meso- and metasoma. Telson rounded or in form of oval plates with keel on dorsal surface. Walking legs slender, composed of cylindrical segments without spines or spurs. Genital
412 appendage short, pear-shaped in females, long and blunt-tipped in males. Exoskeleton with scaly ornamentation. One genus. ? Ordovician to Devonian.

Pterygotus Agassiz, 1844. Genotype—*P. anglicus* Agassiz, 1844; Lower Devonian, Scotland. Prosoma semi-oval, more or less trapezoidal or



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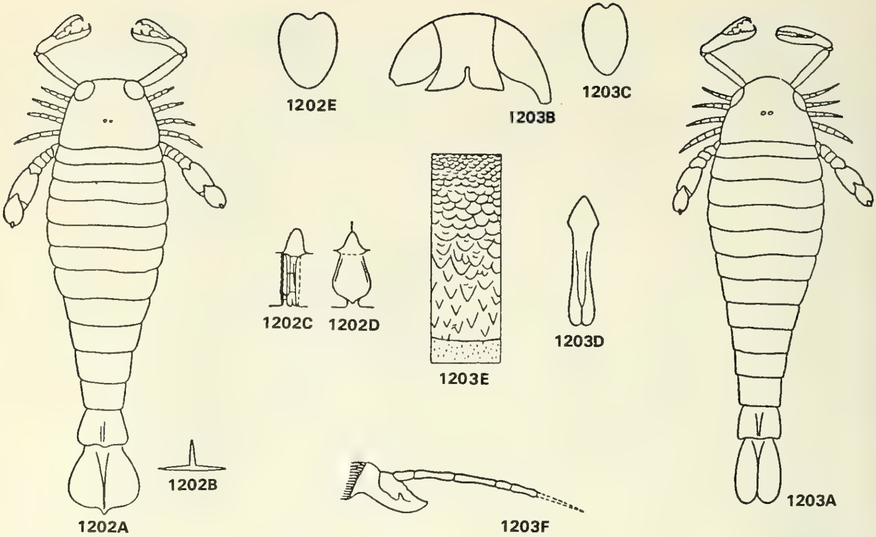
Figs. 1200–1201. Family Dolichopteridae.

1200. *Dolichopterus macrocheirus* Hall; A—dorsal view; B—ventral view (reconstruction), × 0.3. Silurian, North America. 1201. *Strobilopterus princetoni* Ruedemann; A—prōsoma with first tergum; B—swimming leg, × 0.75. Lower Devonian, North America (Størmer, 1955).

rectangular, its rounded anterior corners bearing the large compound eyes. Doublure with epistome. Metasome more or less oval to heart-shaped (Figs. 1202–1204; Pl. XVIII, Figs. 6–7). About 30 species. Silurian of Estonia, Scotland, North America and ? Australia; ? Lower Devonian (Downtonian) of Scotland, Norway, North Siberia (SW Taimur), Germany and North America; Middle Devonian of Canada; Upper Devonian of Scotland, North America; and Devonian of Czechoslovakia.



414 Figs. 1202–1203. Family Pterygotidae (Størmer,1955).

1202. *Pterygotus* (*Pterygotus*) *rhenaniae* Jaekel; A—dorsal view; B—cross section of telson, × 0.14; C—genital appendage of male; D—genital appendage of female, × 0.2; Lower Devonian, Germany; E—metastome of *P.* (*P.*) *anglicus* Agassiz, × 0.3; Lower Devonian, Scotland. 1203. *Pterygotus* (*Erettopterus*) *osliensis* Schmidt; A—dorsal view, × 0.1; B—prosomal doublure with epistome, × 0.3; C—metastome, × 0.2; D—genital appendage of (?) male; E—ornamentation on ventral surface of first segment of opisthosoma, × 0.7; Silurian, Estonia; F—*P.* (*P.*) *bilobus* (Salter); walking leg, × 1; Silurian, Scotland.

SUPERFAMILY MIXOPTERIDEA CASTER AND KJELLESVIG-WAERING, 1955

[nom. transl. Novojilov, hic (ex Mixopteridae Caster and Kjellesvig-Waering,1955)]

Resemble Eurypterid scorpions. With a movable metasoma bearing a bent, clawlike or straight telson. Chelicerae pincerlike and very short. Opisthosome sharply divided into broad mesosoma and narrow cylindrical metasoma.

Classification, Phylogeny and Systematic Position. This group of eurypterids is charactrerized by well developed adaptations for active predation i.e., thorny organs; telson and clasping appendages. The phylogenetic affinities of these forms with other eurypterids are still not clear. The presence of swimming appendages brings them close to Eurypteridea, the primitive forms of

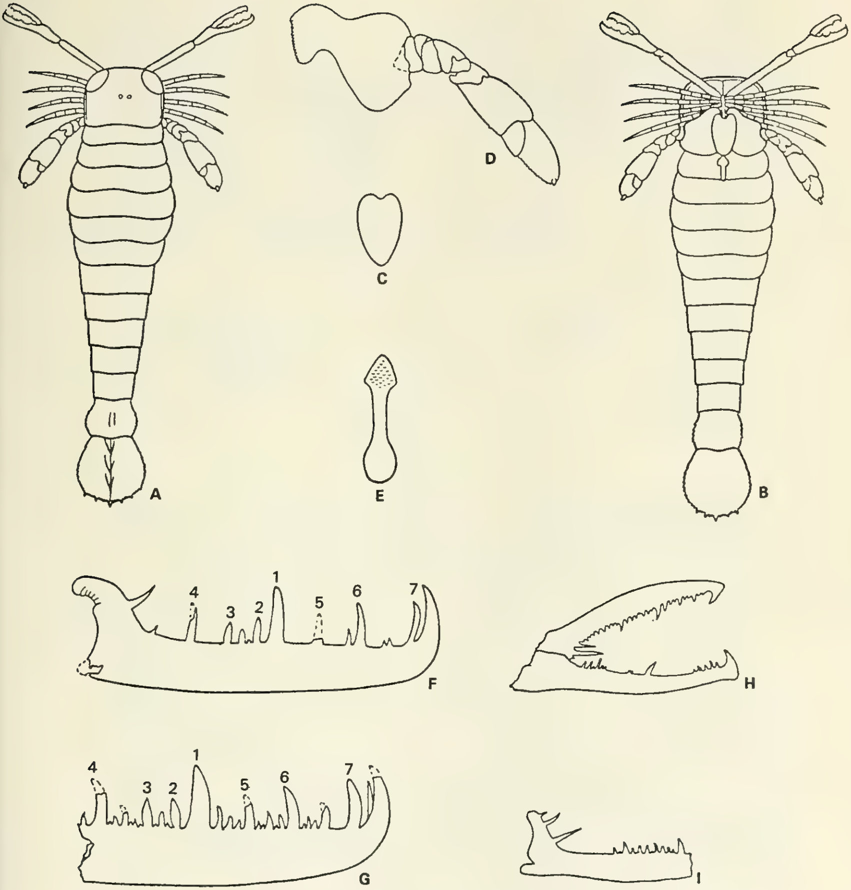


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Fig. 1204. Family Pterygotidae.

Pterygotus (*Acutiramus*) *buffalcensic* (Pohlman); A—dorsal view; B—ventral view, × 0.045; C—metasoma; D—swimming appendage, × 0.3; E—genital operculum (?) of male, × 0.17; Silurian, North America (Størmer, 1955); F and G—*P.* (*Acutiramus*)*waylandsmithi* Kjellesvig-Waering and Caster; movable finger of chela with crushing teeth (1–7); H—*P.* (*Acutiramus*) *floveri* Kjellesvig-Waering and Caster; chela, I—movable finger of chela, × 2. Silurian (Werkon shales), North America (Kjellesvig-Waering and Caster, 1955).

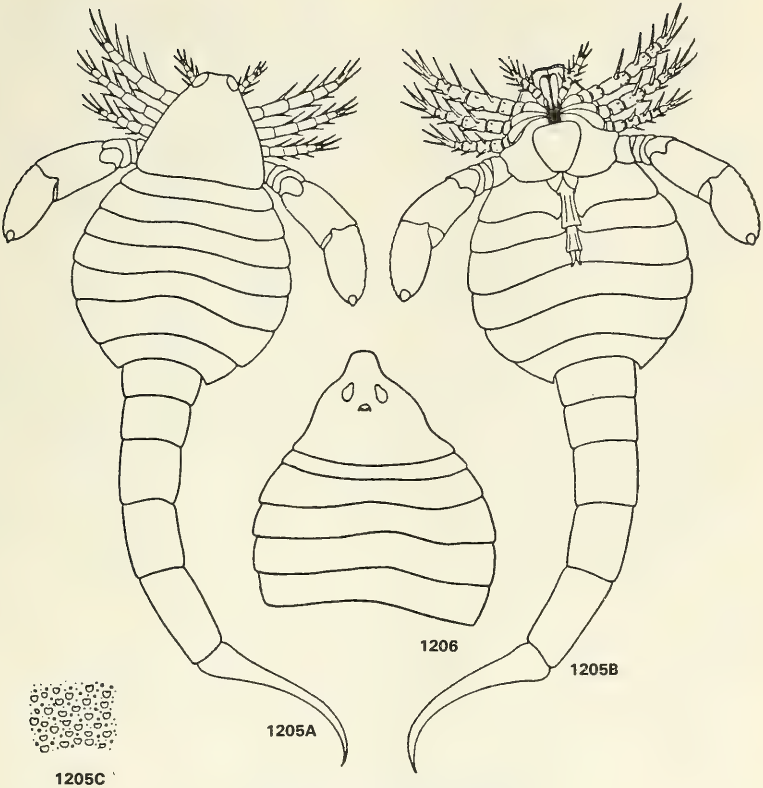
which were probably close to their ancestors, Mixopteridea. The long, paired spines on the distal four (in *Mixopterus*) or five (in *Megalograptus*) segments of appendages of these forms are very unique. In all probability they were poisonous, stinging and prehensile organs. Modification of the appendages as well as the general form of body in both these families are very similar. The more ancient Megalograptidae differ from Mixopteridae only in the form of the narrow, straight, needlelike telson. On the other hand, Carcinosomatidae have a telson similar to that of Mixopteridae but differ from them (as well as from Megalograptidae!) in the absence of the enlarged prehensile organs and in the better developed swimming appendages. The close similarity of the third pair (similar also to the second—pedipalpi) of appendages of prosoma in Megalograptidae and Mixopteridae obviously points to the phylogenetic affinity of these families.

ECOLOGY AND GEOGRAPHICAL DISTRIBUTION. Members of this group were possibly, benthic inhabitants of water bodies and lived as predators, always on the look-out for prey. The grasping organs served as catching nets, resembling seaweed. Ordovician to ? Lower Devonian (Downtonian). Families: Carcinosomatidae, Mixopteridae and Megalograptidae.

Family CARCINOSOMATIDAE Størmer, 1934

Small to large sized animals (4–60 cm in length). Prosoma trapezoidal, tapering 413 to the front. Compound eyes small, oval and lodged on anterior part of prosoma. Opisthosoma sharply demarcated, very broad, rounded, with convex mesosoma and a narrow cylindrical metasoma. Telson has the form of a long bent claw-shaped spine. Doublure with short narrow epistome. Chelicerae thin, short with strong spines, as also the succeeding three pairs of walking legs. Pedipalpi short, strong, a little longer than chelicerae. Swimming appendages stout. Metasoma trapezoidal with rounded corners, narrow posteriorly. Genital appendage short and broad (? in females), long with distal spines (? in males). Exoskeleton with thin tubercles or with scale-like markings. Two genera: *Carcinosome* Claypole, 1890, Ordovician to Silurian, North America (Fig.1205) and *Rhinocarcinosoma* Novojilov, gen. nov., Silurian, North America.

Rhinocarcinosoma Novojilov, gen. nov. Genotype—*Carcinosoma vaningeni* Clarke and Ruedemann, 1912; Silurian, North America. Prosoma helmet-shaped, lateral margins convex in anterior part and concave behind. Prosoma with a short blunt projection in front. Eyes compound, small, oval, and converge to the front; located in the anterior part of prosoma and project at the level of lateral regions. Mesosoma truncated-rounded, with a shorter anterior segment. Metasoma trapezoidal. Exoskeleton with tubercles. Appendages, metasoma, telson and genital appendages not known (Fig. 1206). One species from the Silurian of North America.



416 Figs. 1205–1206. Family Carcinosomatidae.

1205. *Carcinosoma scorpionis* (Grote and Pitt), male (reconstruction); A—dorsal view; B—ventral view, × 0.2; C—ornamentation on appendage of opisthosoma, × 2. Silurian, North America (Størmer, 1955). 1206. *Rhinocarcinosoma vaningebi* Clarke and Ruedemann; prosoma and five terga of opithosoma, × 2. Silurian, North America (Størmer, 1955).

414 Family MIXOPTERIDAE Caster and Kjellesvig-Waering, 1955

Length of body 20–70 cm. Prosoma almost quadrate, with projecting median anterior margin. Compound eyes small, kidney-shaped and located at the anterior margin. Mesosoma somewhat broad with axial furrows. Metasoma

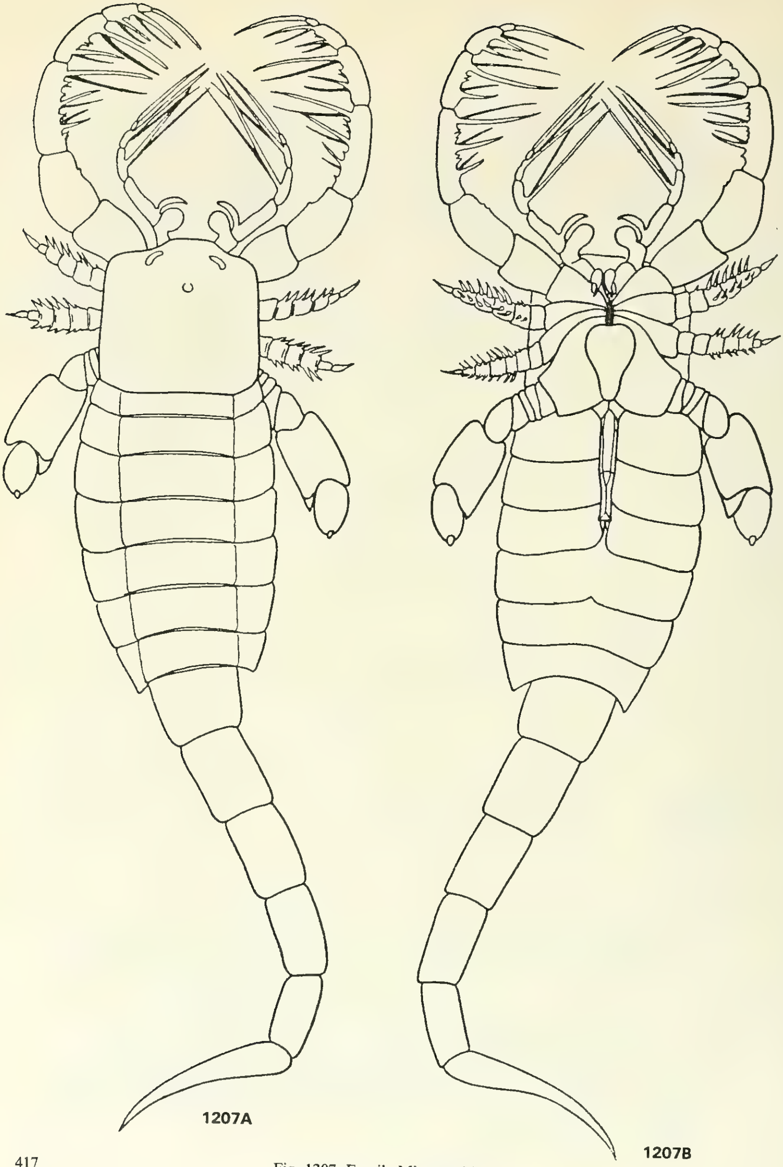


Fig. 1207. Family Mixopteridae.

Mixopterus kiaeri Stormer; A—dorsal view; B—ventral view (reconstruction), × 0.2. ? Lower Devonian (Downtonian), Norway (Størmer, 1955).

narrow with cylindrical segments. Telson clawlike. Pedipalpi and third pair of appendages of prosoma long, and with long paired spines. Appendages of third pair particularly large, fourth and fifth pairs short. Swimming legs well developed, with long, broad seventh and less-developed eighth segment. Metasoma heart-shaped, tapering to the rear. Genital appendage of females long. Exoskeleton with long tubercles or semicircular scale pattern. One genus: *Mixopterus* Ruedemann, 1921. Four species (Fig. 1207). Upper Silurian (Wenlockian stage), Scotland and ? Lower Devonian (Downtonian) of Scandinavia.

Family MEGALOGRAPTIDAE Caster and Kjellesvig-Waering, 1955

Body 60 – 70 cm long. Prosoma helmet-shaped and broad in front. Compound eyes anterolateral. Mesosoma slightly broad with axial furrows, last segment without pleurae. Metasoma narrow, with cylindrical segments, last segment broad and with flat, clawlike appendages. Telson slender and needlelike. Doublure of prosoma with a short, wide epistome. Second and third pairs of appendages of prosoma grasping type with long, paired spines. Third pair stouter and three times as large as pedipalpi (pair II). Fourth and fifth pair of appendages slender and with protruding spines. Swimming legs with very large fourth and seventh segments. Metastome oval to heart-shaped. Exoskeleton of opisthosoma with oval- or triangular-scaly pattern, and with longitudinal ridges
415 on posterior part of segments. Genital appendage short, club-shaped in females, long and narrow in males. Two genera from the Ordovician of North America: *Megalograptus* Miller, 1874 (Fig. 1208) and *Echinognatus* Walcott, 1882.

Suborder Stylonurina

[nom. transl. Novojilov, hic (ex Stylonuridae Diener, 1924; Stylonuracea Størmer, 1951)]

Appendages of prosoma starting from second pair in form of long walking legs. Ordovician to Lower Permian. Superfamilies: Stylonuridea and Mycteropidea.

416 SUPERFAMILY STYLONURIDEA DIENER, 1924

[nom. corr. Novojilov, hic (ex Stylonuridae Diener, 1924; Stylonuracea Størmer, 1951)]

In this superfamily all segments of mesosoma more or less equal sized. Ordovician to Lower Permian. Families: Stylonuridae, Rhenopteridae and Hibbertopteridae.

Family STYLONURIDAE Diener, 1924

Length 5–50 cm. Prosoma with widely varying outline: more or less quadrate with smooth anterior surface (in *Drepanopterus* Laurie, 1892 and

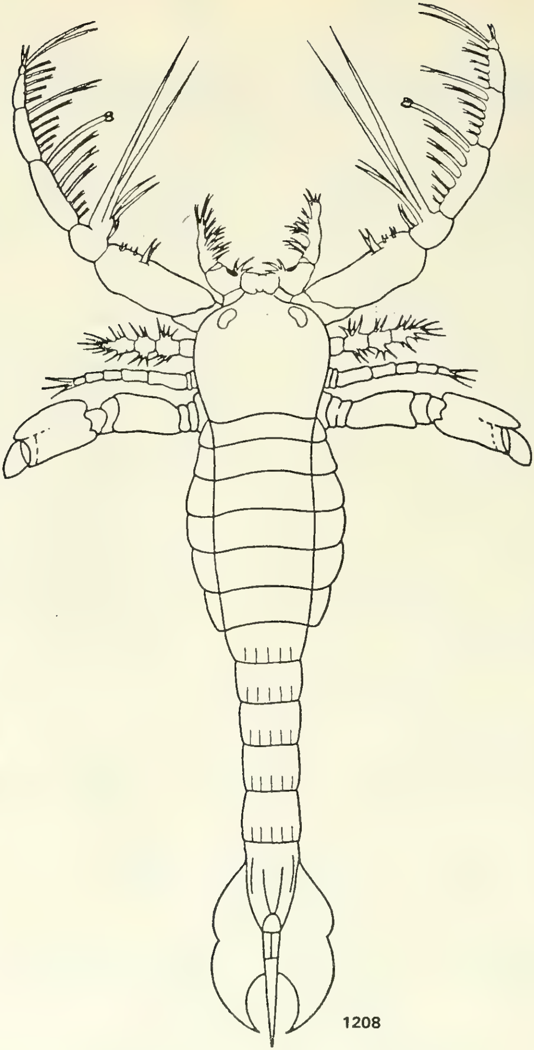


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Fig. 1208. Family Megalograptidae.

Megalograptus ohioensis Caster and Kjellesvig-Waering; dorsal view (reconstuction), × 0.2. Upper Ordorivi, North America (Størmer, 1955).

Tarasopterella Størmer, 1951), oval and rounded-truncated at rear (in *Stylonurus* Page, 1856), trapezoidal-rounded (in *Ctenopterus* Clarke and Ruedemann, 1912), pentagonal (in *Brachyopterus* Størmer, 1951) or almost round (in *Campylocephalus* Eichwald, 1860). Compound eyes round or kidney-shaped, located in anterior half of prosoma. Opisthosoma more or less narrow, with division into meso- and metasoma, with or without lateral epimers. Telson wedge-shaped, even or constricted, with or without openings on dorsal surface and a cavity on the ventral. Doublure of prosoma narrow; with epistome.
418 Appendages long, of walking type, increasing in size from front to rear, with or without spines. Metasoma has the form of elongate narrow plate. Genital appendage short and broad in females, long in males. Exoskeleton with scalelike markings, changing to tubercles and spines. Ordovician to Lower Permian. Subfamilies: Stylonurinae and Marsupipterinae.

Subfamily Stylonurinae Diener, 1924

[nom. transl. Novojilov, 1958 (ex Stylonuridae Diener, 1924)]

Telson without opening on dorsal surface, without cavity on ventral surface. Ordovician to Lower Permian. Six genera.

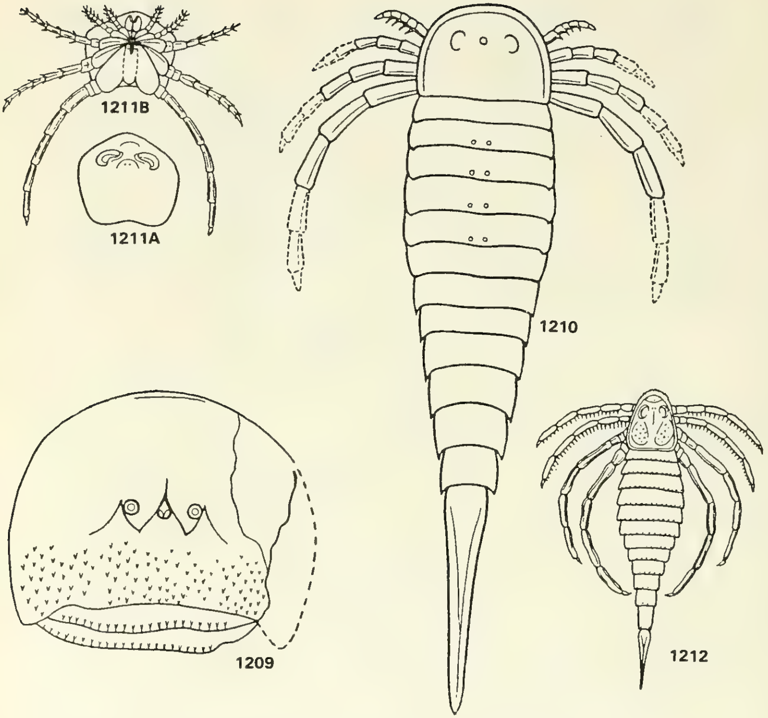
Stylonurus Page, 1856. Genotype—*S. powrieri* Page, 1856; Devonian, Scotland. Prosoma semioval or oval, truncated posteriorly. Compound eyes kidney-shaped, located close to lateral margins of prosoma in anterior half. Ocelli present between compound eyes. Appendages long with narrow, oblong segments. First three pairs of legs equal to opisthosoma or longer. Genital appendage of males stout, long with broad lobes at base and bifurcated at distal end. In outline they resemble an anchor. Opisthosoma narrow with poorly differentiated meso- and metasome. Telson dagger-shaped, with wrinkled surface (Pl. XIX, Figs. 1–4). Ten species. Silurian of England and Scotland; ? Lower Devonian (Downtonian) of Scandinavia; Devonian of Scotland; ? Middle Devonian of South Siberia and North America.

Other known forms: *Drepanopterus* Laurie, 1892 (Fig. 1210), Upper Silurian of Scotland and North America (Indiana) and Upper Devonian of Ireland; *Brachyopterus* Størmer, 1951 (Fig. 1211), Middle Ordovician of England, ? Lower Devonian (Downtonian) of Norway; *Ctenopterus* Clarke and Ruedemann, 1912 (Fig. 1212), Silurian and Middle Devonian of the USA (New York State); and *Tarsopterella* Størmer, 1951, Upper and Lower Devonian of Scotland.

Subfamily Marsupipterinae Novojilov, 1958

Telson with openings on dorsal surface and with a cavity on ventral region. ? Lower Devonian (Downtonian) to Upper Devonian. Two genera.

Polystomurum Novojilov, 1958. Genotype— *P. stormeri* Novojilov, 1958; Upper Devonian, Voronezhian province. Telson nail-shaped, with keel and

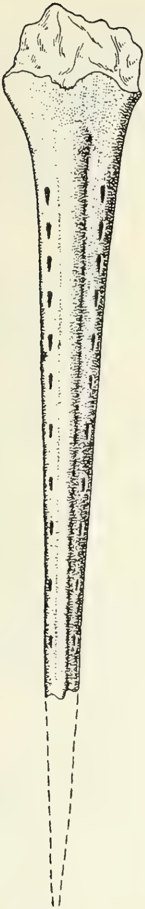


419 Figs. 1209–1212. Family Stylonuridae and Hibbertopteridae.

1209. *Hibbertopterus scouleri* (Hibbert); prosoma with two terga, × 0.25. Lower Carboniferous, Scotland (Størmer, 1955). 1210. *Drepanopterus abonensis* Simpson (reconstruction); × 0.23. Upper Devonian, England (Simpson, 1951). 1211. *Brachyopterus* ? *pentagonalis* Stormer; A—prosoma dorsal view; B—prosoma with appendages, ventral view, × 0.4. ? Lower Devonian (Downtonian), Norway. 1212. *Ctenopterus cestrotus* Clarke; dorsal view, × 0.5. Silurian, North America (Stormer, 1955).

paired openings on dorsal surface. Ventral surface of telson not known. Presence of cavity on ventral surface as in genus *Marsupipterus* is suggested. Cavity of telson in all probability contained poisonous glands whose secretion oozed out through dorsal openings (Fig. 1213).

419 Also, *Marsupipterus* Kjellesvig-Waering, 1955 (Fig. 1214). ? Lower Devonian (Downtonian) of England.



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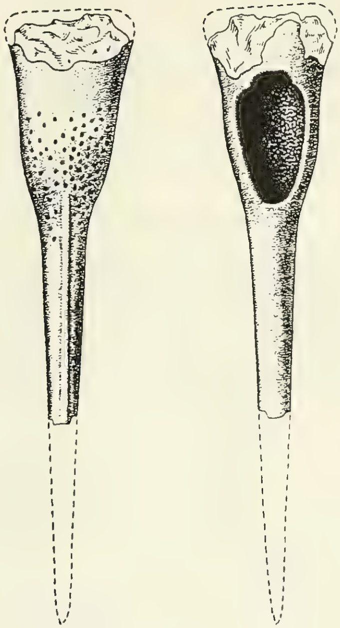

1214A

1214B

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Figs. 1213–1214. Family Stylonuridae.

1213. *Polystomurum stormeri* Novojilov; telson × 12. Upper Devonian, USSR (Voronezhian province) (Novojilov, 1958). 1214. *Marsupipterus sculpturatus* Kjellesvig-Waering; telson; A—dorsal view; B—ventral view, × 0.5. Upper Silurian, England (Kjellesvig-Waering, 1955).

Family HIBERTOPTERIDAE Kjellesvig-Waering, 1959

Large forms (about 50 cm); prosoma rounded; compound eyes rounded or kidney shaped; located in the median part of prosoma with ocelli between them; coxae of hind extremities of prosoma without serrated appendages; metasoma trapezoidal—heart-shaped, project forward from caudal part of median suture; genital operculum in males not known, in females with short clavate appendage and anterior ovate plate. Segments of opisthosoma narrow, telson not known. Exoskeleton of prosoma consists of small feathery scalelike pattern, hind margins of terga with similar scale pattern in the shape of fringe. Upper Devonian (?) – Lower Carboniferous. Two genera.

Campylocephalus Eichwald, 1860 [*Eidothea* Scouler, 1831 (non Risso, 1826, nec Chambers, 1873)]. Three genera—*Limulus oculatus* Kutorga, 1838; Upper Permian, Bashkiya (basin of Belaya river, Durasovskii Oredum). Prosoma roundish with a notch on the posterior margin and a narrow border; compound eyes kidney-shaped, located in the middle part of prosoma; ocelli in front of compound eyes; terga straight, narrow. Remaining body parts not known (Pl. XXI). One species.

420 In addition, *Hibbertopterus* Kjellesvig-Waering, 1959 (Fig. 1209), Upper Devonian (?) of Ireland, Lower Carboniferous of Scotland.

Family RHENOPTERIDAE Størmer, 1951

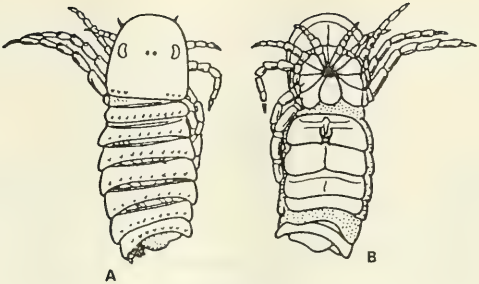
Small sized forms (5–10 cm long). Prosoma semioval, with kidney-shaped compound eyes on middle of its lateral margins. Doublure with median suture but without epistome. First two (or three ?) pairs of legs with spines. Last two pairs without spines. Metasoma pear-shaped, with concave anterior margin. Genital appendage of males short, with two distal spines. Exoskeleton with varied tubercles (Pl. XIX, Fig. 5). One genus: *Rhenopterus* Størmer, 1936 (Fig. 1215). Lower Devonian of Germany.

SUPERFAMILY MYCTEROPIDEA COPE, 1886

[nom. transl. Novojilov, hic (ex Mycteropidae Cope, 1886)]

First segment of opisthosoma very large, only slightly shorter than prosoma. Last segments short and gradually decrease in width toward the wedge-shaped telson. Appendages narrow, short or long as in Stylonuridae.

Eurypterida with large first segment of opisthosoma are known from incomplete specimens of four species: *Mycterops ordinatus* Cope, 1886 (Carboniferous of Pennsylvania), *Eurypterus scabrosus* Woodward, 1887 (Lower Carboniferous of Scotland), *Glavcodes mathieui* Pruvost, 1923 (Upper Carboniferous of Belgium) and *Borchgrevinkum taimyrense* Novojilov, 1958 (Lower Devonian of North Siberia). The segmentation characteristics seen in these forms as shown by the large anterior segment (or two segments ?) of the opisthosoma, sharply distinguished these from Stylonurina and generally from



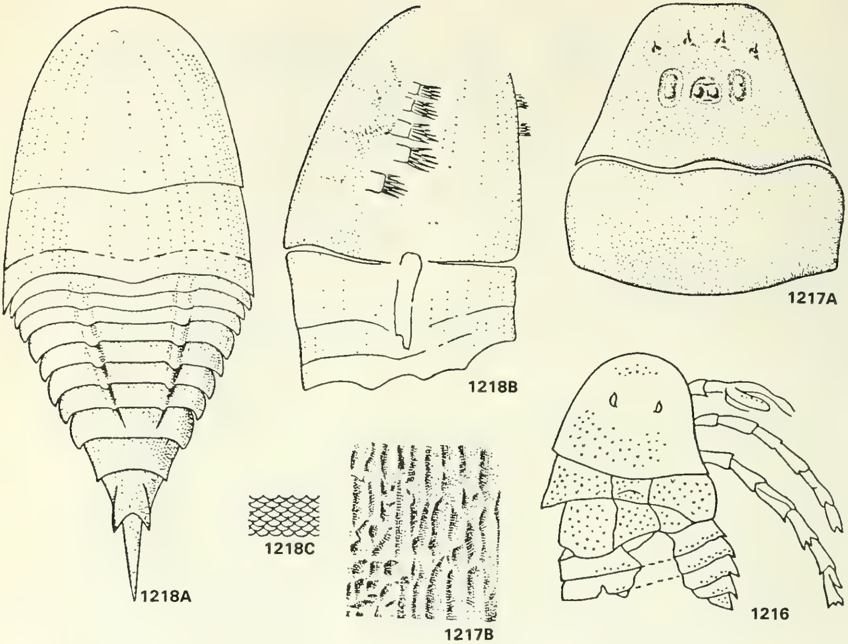
421 Fig. 1215. Family Rhenopteridae.

Rhenopterus diensti Størmer; prosoma and mesosoma of male; A—dorsal view; B—ventral view, × 1. Lower Devonian, Germany (Størmer, 1955).

all other Eurypterida. This morphological peculiarity points to an affinity with other chelicerates. Absence of reliable data on the structure of the body as a whole and its appendages precludes any final conclusion on the systematic position of Mycteropidea. Ranking this group as a separate superfamily is only preliminary. Eventually these forms may have to be ranked much higher.

It should be mentioned that the remains of representatives of Eruypterida studied were rather scanty for us to concede that the opisthosoma had a large first segment. In *Mycterops ordinatus* (Pl. XXII), on which the genus and family
421 are based, only the trapezoidal prosoma, narrow in front, and the first tergum of opisthosoma, with the right side broken off, are preserved (at first these remains were believed to belong to primitive vertebrates). A peculiar, irregular cellular-reticulate ornamentation covers the surface of the entire prosoma and first tergum. Similar remains (prosoma and first tergum) but in a somewhat better state of preservation were discovered in the Upper Carboniferous of Belgium. They were described as *Glaucodes mathieui* (Pl. XIX, Fig. 6), though they should be included under the genus *Mycterops*.

Because of breaks and displacement of terga, identification of remains recovered from the Lower Carboniferous of Scotland first described as *Eruypterus scabrosus* is not possible. One or two large segments form the anterior part of the opisthosoma. The subsequent segments can be judged only from the remains of the four preceding ones. They are uniformly narrow with pleural angles. The three right appendages preserved are long and narrow, as in Stylonuridea. Ornamentation consists of small feathery 'scales' covering the prosoma and the large tergum. Størmer included (1951, 1955) this species in the
422 genus *Mycterops* on the basis of the large (two ?) prosomal segments. Kjellesvig-Waering (1959) established it as a new genus *Woodwardopterus* and included it in a new family, Woodwardopteridae. He placed this family under the superfamily Eurypteridea on the basis of certain similarities of appendages.



421 Figs. 1216–1218. Superfamily Mycteropidea, families Mycteropidae and Woodwardopteridae.

1216. *Woodwardopterus scabrosus* (H. Woodward); prosoma with six terga of mesosoma and three right appendages, × 0.5. Lower Carboniferous, Scotland (Størmer, 1955). 1217. *Mycterops mathieui* (Pruvost); A—prosoma with large segment of mesosoma, × 0.38; B—ornamentation on prosoma and terga, × 3. Upper Carboniferous, Belgium (Pruvost, 1923). 1218. *Borchgrevinkium taimyrense* Novojilov; A—dorsal view (reconstruction); B—appendages on fused part of prosoma and vestige of genital appendage; × 3.4; C—scaly ornamentation on terga of opisthosoma, × 10. Lower Devonian, North Siberia (Novojilov, 1959).

A more complete morphological picture of the large segmented Eurypterida is furnished by the nearly complete specimen of the genus *Borchgrevinkium*, though it is poorly preserved (Fig. 1218). Its ornamentation is reticulate-cellular as in *Mycterops* but is truly scaly. On the fused central part narrow appendages are visible, as in Stylonuridae, but all the appendages are short (Fig. 1218B; Pl. XIX, Fig. 7).

On the basis of the presence of one (or two) large segments of the opisthosoma with typical ornamentation in all the four above-mentioned forms, they are included here under one superfamily, Mycteropidea, with two families: Mycteropidae and Woodwardopteridae. Lower Devonian to Upper Carboniferous.

Family MYCTEROPIDAE Cope, 1886
(= MYCTEROPIDAE Størmer, 1951)

Small to more or less large sized forms. Prosoma parabolic or trapezoidal. Compound eyes small, granular, round, sometimes indistinct, placed at anterior half of prosoma. First segment of opisthosoma very large, sharply isolated from others and forms its anterior part. Lateral margins of the large anterior segment are continuation of lateral sides of the prosoma. Telson narrow and wedge-shaped. Appendages slender, either short or long. Ornamentation of exoskeleton scaly or irregularly cellular. Lower Devonian to Carboniferous. Two genera.

Borchgrevinkium Novojilov, 1958. Genotype—*B. taimyrense* Novojilov, 1958; Lower Devonian (uppermost horizon), SW Taimur (River Imaigda). Prosoma parabolic, constitutes one-third (or more) of the entire length. Anterior part of opisthosoma forming one large segment (or two ?), comprises a little less than one-third of the whole. The succeeding segments of the opisthosoma form its posterior triangular part. Last segment of opisthosoma with bifid dorsal projection. Telson narrow and wedge-shaped. Radial folds converging posteriorly are seen on the terga of the posterior part of the opisthosoma. They extend only up to the middle of the tenth tergum. Appendages slender and homonomous with spines on distal segments. Exoskeleton with reticulate cells in the form of semicircular 'scale' pattern. Eyes indistinct (Fig. 1218; Pl. XIX, Fig. 7). One species. Lower Devonian of North Siberia.

Also, *Mycterops* Cope, 1886 (= *Glaucodes* Pruvost, 1923) (Fig. 1217; Pl. XIX, Fig. 6; Pl. XXII), Upper Carboniferous of the USA (Pennsylvania) and Belgium.

Family WOODWARDOPTERIDAE Kjellesvig-Waering, 1959

Length 20–30 cm. Prosoma parabolic. Small, more or less kidney- or grain-shaped compound eyes located in anterior part of prosoma, divide the middle third of its width at this point. Ocelli not known. Appendages of prosoma slender and increase in length from front to back. Segments without spines. One (or two ?) anterior segments of opisthosoma large and the rest short with lateral lobes. Surface of prosoma and terga with feathery or tubercular (?) ornamentation. One genus: *Woodwardopterus* Kjellesvig-Waering, 1959 (Fig. 1216) from the Lower Carboniferous of Scotland.

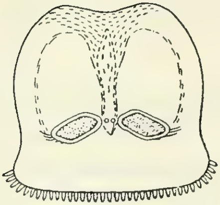


Fig. 1219. Order Eurypterida. Systematic position not clear.

Prosoma of *Melbournopterus crossotus* Caster and Kjellesvig-Waering, × 1.5. Upper Silurian, Australia (State Victoria) (Størmer, 1955).

Eurypterida Incertae sedis

Melabournopterus Caster and Kjellesvig-Waering, 1953 (Fig. 1219); Upper Silurian, Australia (Victoria). Only the prosoma of this genus is known. It differs from those of other known Eurypterida in its concave anterior and lateral margins and toothed fimbriae of the posterior margin. Another peculiarity is the
423 shape and location of the compound eyes which resemble rhombic, automobile headlights. They are located in the posterior part of the prosoma. These features and the absence of appendages obscure the true taxonomic position of this Australian form in one of the two suborders of Eurypterida.

Unionopterus Chernyshev, 1948; Lower Carboniferous, Kazakhstan.

Prosoma almost quadrate-rounded, with small compound eyes located at anterior margin; ocelli centrally placed. Walking legs (only the second right, complete third left and a few segments of fourth preserved) with spines, but their mobility could not be ascertained. Swimming appendages with narrow lobes and a small spur on distal margin of lobe. Opisthosoma with broad mesosoma and narrow metasoma. Telson not known. The poor illustrations do not clearly present the morphological characteristics of the form described by Chernyshev from the Karagandinian series of Kazakhstan. Collection number and place where it is deposited are not known.

* * *

In his recently published paper, E.N. Kjellesvig-Waering—"The Silurian Eurypterida of the Welsh borderland", *Journ. Paleont.*, v. 35, No. 4, pp. 789–835, Kjellesvig-Waering establishes a new genus, *Parahughmilleria*, in the family Hughmilleriidae and elevates it to the rank of genus the subgenus *Erettopterus* Salter, 1839 (Genus *Pterygotus*, family Pterygotidae). Eleven new species belonging to various genera are established, mainly those of the previously described forms.

Order SCORPIONIDA. Scorpions

(V.B. Dubinin)

Scorpions, the primitive terrestrial chelicerates, are known from the Silurian. Recent scorpions are the largest terrestrial representatives of the superclass, with lengths up to 20 cm. Moreover, they are the lone Recent chelicerates with maximum number of body segments—19.

Body convex and sharply divided into three sections: small cephalothorax (prosoma), broad anterior part of abdomen (mesosoma—seven segments) and narrow posterior part of abdomen (metasoma—five segments), terminating at telson in claw-shaped stinging organ in dorsal region.

As in other Chelicerata (cf. p. ...*), the prosoma is constituted by acron and six segments of cephalothoracic appendages: chelicerae, pedipalpi and four pairs of walking legs. The seventh segment, a part of the abdomen is vestigial in adults, and their existence is revealed by presence of a pair of corresponding lateral arteries and ligaments of heart.

Cephalothorax of present-day scorpions constitutes only one-eighth of the body (Figs. 1220, 1257). The dorsal shield of the cephalothorax (carapace) is composed of acron fused with terga of the six following segments. The surface is uneven and ornamented with pits, furrows and rows of tubercles and scattered hairs. The presence of large median eyes in the middle of carapace is of taxonomic importance (Fig. 1221A). Two to five small lateral eyes are (Figs. 1228, 1235) located at about the anterolateral angles of carapace. Ventral surface of cephalothorax almost entirely covered by coxae of pedipalpi and walking legs (Fig. 1226 A, F). With a small triangular plate, metastoma or sternum (Fig. 1226 A, F), behind and between the coxae of legs III and IV, formed by the fusion of sterna of fifth and sixth segments. Posterior to sternum lie paired genital opercula (Figs. 1223, 1226 A, F). Position of genital opercula of taxonomic importance. Coxae of pedipalpi and legs I and II on inside have lobes called gnathobases, which, are absent on coxae of legs III and IV (Fig. 1226 A, F). Mouth cavity with a fairly large oral cone, at base of which lies the mouth opening. Morphologically it lies between pedipalp bearing segments and legs I. Claw-shaped three-segmented chelicerae lie in front and dorsal to mouth opening (Figs. 1232, 1244). Movable finger of chelicerae, in some species, is bifurcated at apex. Pedipalpi of scorpions stouter and longer than other appendages, clawshaped and adapted to capture, hold and bring prey to chelicerae. Pedipalpi consist of six segments: movable coxae, trochanter, femur, patella, tibia and terminal segments of tarsus. Walking legs very short in the Silurian aquatic forms. They gradually increase in size from first to extreme 424 posterior pair, particularly in the Recent forms. All legs eight segmented: first five segments same as in pedipalpi, sixth and seventh referred to as first and

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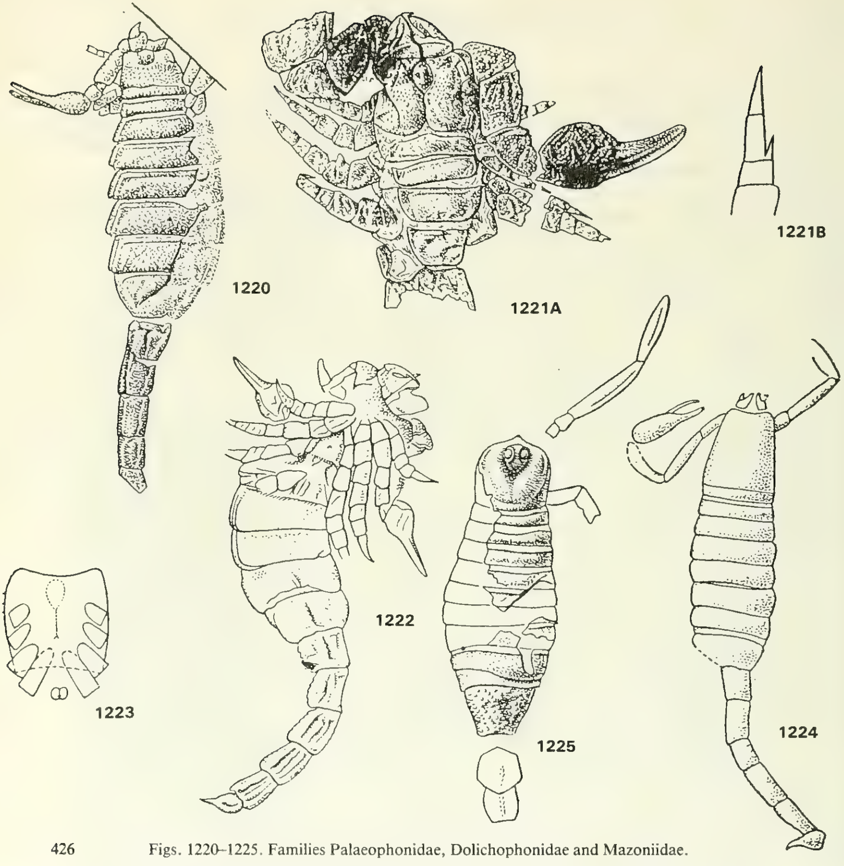
* Not given in the Russian original. Obviously the reference is to p. 580 ff – General Editor.



426 Figs. 1220–1225. Families Palaeophonidae, Dolichophonidae and Mazoniidae.

1220. *Proscorpius osborni* Whitfield; general view, × 2.5. Silurian, North America (Werner, 1934). 1221. *Palaeophonus nuncius* Thorell and Lindstrom; A—anterior part of dorsal surface of body, × 3.5; B—tarsi of second leg with spine at tip of tibia, × 30. Silurian, Sweden (Petrunkevitch, 1949, 1953). 1222. *Palaeophonus caledonicus* Hunter; general view, × 3.5. Silurian, Western Europe (Petrunkevitch, 1949). 1223. *Palaeophonus nuncius* Thorell and Lindstrom; schematic representation of coxosternal region, × 3.5. Silurian, Sweden (Petrunkevitch, 1953). 1224. *Dolichophonus loudonensis* Laurie; general view, × 2.5. Carboniferous, Western Europe, Scotland (Petrunkevitch, 1953). 1225. *Mazonia woodiana* Meek and Worthen; general view, × 3.5. Carboniferous, North America (Petrunkevitch, 1953).

second segments of metatarsus, and the eighth and last segment bears claws. Coxae of walking legs of scorpions immovably fused with body. Legs with sparse hairs on major divisions and numerous setae and spurs on terminal segments. All adults of present-day scorpions with two claws (Dionychopodes) on their tarsi, whereas the Silurian scorpions were one-clawed (Apoxypodes) (Figs. 1220, 1222), as seen in the early developmental stages of present-day forms (Pavlovsky, 1917).

The first six segments of the mesosoma (VIII–XIII) have greatly modified appendages (genital operculum, pectines, lung-books). In Silurian scorpions (Apoxypodes), there were other vestiges of telopodites of legs in the region of the pectines (Fig. 1222). The last segment of the broad anteroabdomen (XIV) and similarly all segments of the metasoma are without appendages, or their vestiges. The broad flat segments of the mesosoma are covered dorsally by terga (Fig. 1220), which are distinct from the small pleural plates. Segments of mesosoma covered with sterna on ventral side (Fig. 1244). Sternum of segment IX (second segment of mesosoma) is a small triangular plate—metasternum—located between pectines (Fig. 1244). Sterna of remaining segments of mesosoma are broad. On segment VIII of scorpions, as in all other chelicerates lies the genital aperture covered by two genital opercula homologous with appendages of first abdominal segment. The peculiar sensory organs characteristic only of scorpions—the comblike pectines (Fig. 1243)—represent vestigial appendages of second abdominal segment. Within the next four segments (X–XIII) paired pulmonary sacs are located. Near posterior margin of these segments there is a transverse slit—the spiracle. The lungs of scorpions are homologous with gills of Eurypterodea. It is interesting that Silurian aquatic scorpions had no lungs (Fig. 1222), and in *Isobuthus* Fritsch and *Microlabis* Corda there were other large semicircular 'gill' shields (Fig. 1245). The last segment of the mesosoma (XIV or VII of body) is considered part of the metasoma and essentially forms its first segment. It is devoid of appendages but possesses longitudinal cylinders typical of metasomal segments (Figs. 1222, 1258B). A complete fusion of tergum and sternum is observed on the fifth segment of metasoma. The metasomal segments are in the form of chitinous rings. The metasoma is very flexible and can curve over the dorsal side of the animal. The anal opening is located on the ventral surface between the last segment of metasoma and telson. The telson is somewhat swollen at base and is curved toward dorsal side, terminating in a curved needle—the sting (Figs. 1222, 1243, 1254). There are two poison glands in telson, and their ducts open at tip of sting.

Ecology and Biogeography. Currently scorpions are distributed all over the world, primarily in the tropical and subtropical zones. They inhabit dry deserts, steppes and hilly tracts and also forests. Scorpions are mainly nocturnal and predatory. In the Silurian scorpions probably were aquatic like the eurypterida. Terrestrial forms similar to the Recent scorpions appeared during the Carboniferous.

Classification and Phylogeny. Scorpions are closely related to eurypterids (Eurypterida—cf. p.407) and are their descendants. The anatomical similarity of these two orders is so striking that scorpions are called terrestrial eurypterids (Beklemishev, 1952). The similarity of scorpions to eurypterids is considerably greater than to other orders of terrestrial arachnoids.

Classification of fossil scorpions and their interrelations with the Recent forms have not been established for certain. First, Thorell (Thorell and Lindstrom, 1885) included the Silurian scorpion *Palaeophonus nuncius* Thorell and Lindstrom, 1885 in the special suborder Apoxypodes, as different from all other scorpions with two trasal claws, which were grouped under the suborder Dionychopodes. Workers in the field later showed that Apoxypodes lived only in the Silurian, while the typical terrestrial Dionychopodes flourished in the Carboniferous. This division was adopted by Werner (1935), Wateriot (1949), Bekelmishev (1952) and others. Thorell (1885) included the Carboniferous scorpions in the group Anthracoscorpi, rather than include them under the Recent Neoscorpi, which are morphologically different from the Carboniferous forms. Later Pocock (1911), on the basis of the differences in the structure of the ventral region of cephalothorax, divided all scorpions into a group of more primitive species—Lobosterni—and a group of scorpions resembling present-
425 day ones—Orthosterni. Still later, Biyalmitsky-Birulya (1917) included all Carboniferous scorpions in two groups, Palacoscorpiones and Neoscorpiones, improving on Pocock's classification. Finally, Petrunkevitch (1949, 1953) suggested a new classification of fossil scorpions, dividing them into two suborders: Protoscorpiones, with eight mesosomatic segments; and Euscorpiones, with seven mesosomatic segments and with two tarsal claws. This book follows the above classification but the suborders described by Petrunkevitch are treated as two superfamilies of the suborder Dionychopodes Thorell.

Distribution through Time. Scorpions are known from the Silurian (Apoxypodes). In the Carboniferous, they were represented by many genera of Dionychopodes, of which only Palaeoscorpiidae differed somewhat from the Recent forms. The remaining genera are typical Neoscorpiones resembling the Recent scorpions (Biyalynitsky-Birulya, 1917; Beklemishev, 1905).

Suborder Apoxypodes. Pointed-foot scorpions

Body divided into small cephalothorax, seven-segmented mesosoma and metasoma. Prosoma with median eyes located on median tubercle, rarely absent (Dolichophonidae). Along posterior margin of prosoma there is a transverse depression homologous with the suture between terga VI and VII (Fig. 1221A). Chelicerae short and claw-shaped. Pedipalpi long, five-segmented, with large chela. Walking legs with seven short homonomous segments; last segment simple and pointed (Fig. 1221B). Metasoma located behind legs IV, with the result appendages group around mouth, as in Eurypterodea. Mesosoma of usual seven segments. Genital opening on first segment. The comb-shaped organs of second segment bear traces of division of preepipodites (telopodites) of abdominal appendages observed in Trilobites (Fig. 1222). Spiracles absent on remaining four segments, apparently the podobranches were located here but have never been preserved. Metasoma consists of five segments and the telson (Fig. 1222).

ECOLOGY AND BIOGEOGRAPHY. The Silurian scorpions, Apoxypodes, were aquatic like eurypterids, probably inhabited shallow parts of bodies of water. All the observed peculiarities of structure are related to the aquatic environment. Upper Silurian deposits of Europe (Sweden, England) and North America.

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. The nature of the division of body and appendages, the absence of pulmonary sacs and other characteristics of present-day scorpions point to the close affinity of Silurian aquatic scorpions to eurypterids. Silurian. Two families: Palaeophonidae and Dolichophonidae.

Family PALAEOPHONIDAE Thorell and Lindstrom, 1885

All segments of legs short and approximately of same length (Fig. 1221B). Pedipalps with short segments. Two genera.

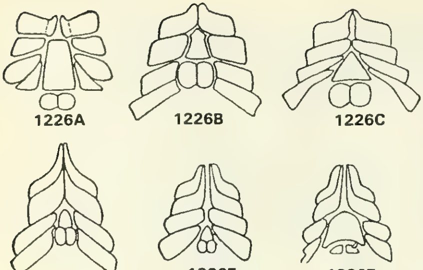
Palaeophonus Thorell and Lindstrom, 1885. Genotype—*P. nuncius* Thorell and Lindstrom, 1885; Silurian, Sweden. Cephalothorax almost square, slightly convex in front. Chela of pedipalpi very stout, with a raised base and comparatively short digits. Length of chela equal to that of raised base. Femur of pedipalp nearly as long as tibia. Large species: carapace 7.5–8 mm long. Length of body up to 35.5 mm (Figs. 1221–1223). Three species. Silurian of Western Europe.

Proscorpius Whitfield, 1885. Genotype – *P. osborni* Whitfield, 1885; Silurian, North America. Carapace broader, convex in front. Chela of pedipalpi longer than base, with narrow, bent digits. Femur of pedipalp twice as long as tibia. Small species: length of carapace 4 mm (Fig, 1220). One species. Silurian of North America.

Family DOLICHOPHONIDAE Petrunkevitch, 1953

Leg segments of varying lengths, as in the Recent scorpions. Pedipalp long, with slender segments. One genus. Silurian of Western Europe.

Dolichophonus Petrunkevitch, 1949. Genotype—*Paleophonus loudonensis* Laurie, 1889; Silurian, Scotland. Carapace markedly long, concave on anterior margin. Digits of pedipalp with concave inner margins. Base of chela longer than digits. Carapace 9.25 mm long and 6.4 mm wide posteriorly (Fig. 1224). One species. Silurian of Western Europe.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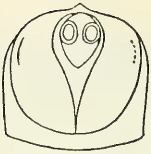
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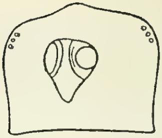
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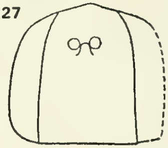
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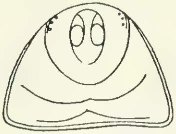
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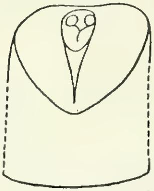
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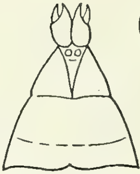
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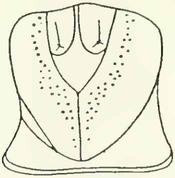
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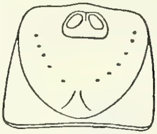
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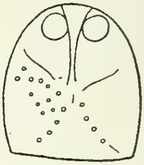
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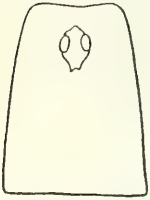
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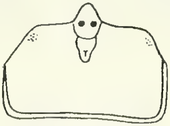
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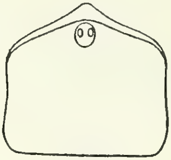
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Figs. 1226–1240. Structure of prosoma of different scorpions.

1226. Structure of coxosternal region in scorpions of different families of suborder Dionychopodes. A—Archaeoctonidae, B—Centromachidae, C—Mesophonidae, D—Isobuthidae, E—Cyclopthalmidae, F—Eoscorpionidae (Petrunkevitch, 1953). 1227. *Mazonia woodiana* Meek and Worthen; prosoma, dorsal view, × 9. Carboniferous, North America (Petrunkevitch, 1953). 1228. *Isobathus kralupensis* Thorell and Lindstrom; prosoma, dorsal view, × 7. Carboniferous, Western Europe (Petrunkevitch, 1953). 1229. *Eoctonus miniatus* Petrunkevitch; prosoma dorsal view, × 8. Carboniferous, North America (Petrunkevitch, 1953). 1230. *Alloscorpius tuberculatus* (Peach);

Suborder Dionychopodes. Two-clawed scorpions

426 Mesosoma seven, rarely eight-segmented (eight segments only in Mazoniidae). Prosoma with large median eyes located at or near center of anterior margin of carapace. Usually with a few small ocelli at anterolateral angles (Fig. 1227). Tarsi of legs terminate in two claws (Fig. 1241). Metasoma located behind legs II (Fig. 1226 A–E). As a result the posterior pairs of legs appear to have been shifted from mouth opening. Pectines well developed. Their telopodites not delimited (Fig. 1243). Four median abdominal segments of mesosoma (X–XIII) with slitlike respiratory stigmata (Fig. 1243).

Ecology and Biogeography. This suborder is represented from the Carboniferous to Recent. These typical dry-land organisms respire by means of
427 lungs. Remains occur in continental deposits. Recent distribution of scorpions shows their confinement to tropical and subtropical areas (cf. p. 647).

Classification, Phylogeny and Systematic Position. The two-clawed scorpions stand out as example of the subsequent adaptation of descendants of primary aquatic Eurypterida and Apoxypodes to a terrestrial way of life (cf.
428 p. 585.. *Mazonia woodiana* Meek and Worthen, 1868 (Figs. 1225, 1227) has been reported from the remains of fossil scorpions in the Carboniferous of the USA (Pennsylvania State). It combines features of both the suborders. Classification of Carboniferous, Permian, and other fossil scorpions, with the interrelationships with the Recent forms, is still uncertain. In this edition we adopt the latter scheme of classification suggested by Petrunkevitch (1949). Moreover, the various orders are treated only as superfamilies.

SUPERFAMILY MAZONIIDEA

Mesosoma segmented. Carapace small, terminating in a conical tip. Posterior margin crescentic, forms a narrow strip. It is separated from the convex anterior part of carapace by a furrow. This border is probably a vestige of sixth tergum of prosoma. Around the anterolateral angles of carapace there are semilunar

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prosoma, dorsal view, × 7.5. Carboniferous, Western Europe (Petrunkevitch, 1953). 1231. *Palaeopisthacanthus Schucherti* Petrunkevitch; prosoma, dorsal view, × 8.5. Carboniferous, North America (Petrunkevitch, 1913). 1232. *Trigonoscorpio americanus* Petrunkevitch; prosoma, dorsal view, × 7. Carboniferous, North America (Petrunkevitch, 1913). 1233. *Buthioscorpius buthiformis* (Pocock); prosoma, dorsal view, × 8.6. Carboniferous, Western Europe (Petrunkevitch, 1953). 1234. *Cyclophthalmus senior* (Corda); prosoma, dorsal view, × 10. Carboniferous, Europe (Petrunkevitch, 1953). 1235. *Compsoscorpius elegans* Petrunkevitch; prosoma, dorsal view, × 10. Carboniferous, Western Europe (Petrunkevitch, 1953). 1236. *Europhthalmus longimanus* Petrunkevitch; prosoma, dorsal view, × 3.5. Carboniferous, Western Europe (Petrunkevitch, 1953). 1237. *Typhloscorpius distinctus* Petrunkevitch; prosoma, dorsal view, × 6. Carboniferous, Western Europe (Petrunkevitch, 1953). 1238. *Lichnophthalmus pulcher* Petrunkevitch; prosoma, dorsal view, × 2.6. Carboniferous, Western Europe (Petrunkevitch, 1953). 1239. *Mesophonus perornatus* Wills; prosoma, dorsal view, × 3. Carboniferous, Western Europe (Petrunkevitch, 1953). 1240. *Garnettius hungerfordi* (Elias); prosoma, dorsal view, × 3. Carboniferous, North America (Petrunkevitch, 1953).

helmet-shaped depressions. Along with these primitive features, the Carboniferous Mazoniidae also had structural features similar to extinct and Recent scorpions of the suborder Dionychopodes. Pedipalpi slender, long, with very short trochanters and femurs and a very long tubular patella and tibia. Structure of legs, respiratory system and other organs is not yet known. Length of prosoma 11 mm, width about 10 mm. Carboniferous. One family, Mazoniidae, with genus *Mazonia* Meek and Worthen, 1868 from Middle Carboniferous of North America (Figs. 1225, 1227).

SUPERFAMILY SCORPIONIDEA. Recent scorpions

Mesosoma segmented. Legs long, with eight equal sized segments. Pedipalpi long, five-segmented and with well-developed claws. Carboniferous to Recent. Six families: Buthidae, Scorpionidae, Diplocentridae, Chactidae, Vejovidae, Bothriuridae, of which the first two are known from the Paleogene. Besides these, the following nine extinct families from the Devonian, Carboniferous and Triassic are known: Palaeoscorpiidae, Archaeoctonidae, Centromachidae, Isobuthidae, Cyclophthalmidae, Eoscorpiidae, Trigonoscorpionidae, Garnettiidae and Mesophonidae.

Family PALAEOSCORPIIDAE Lehmann, 1944

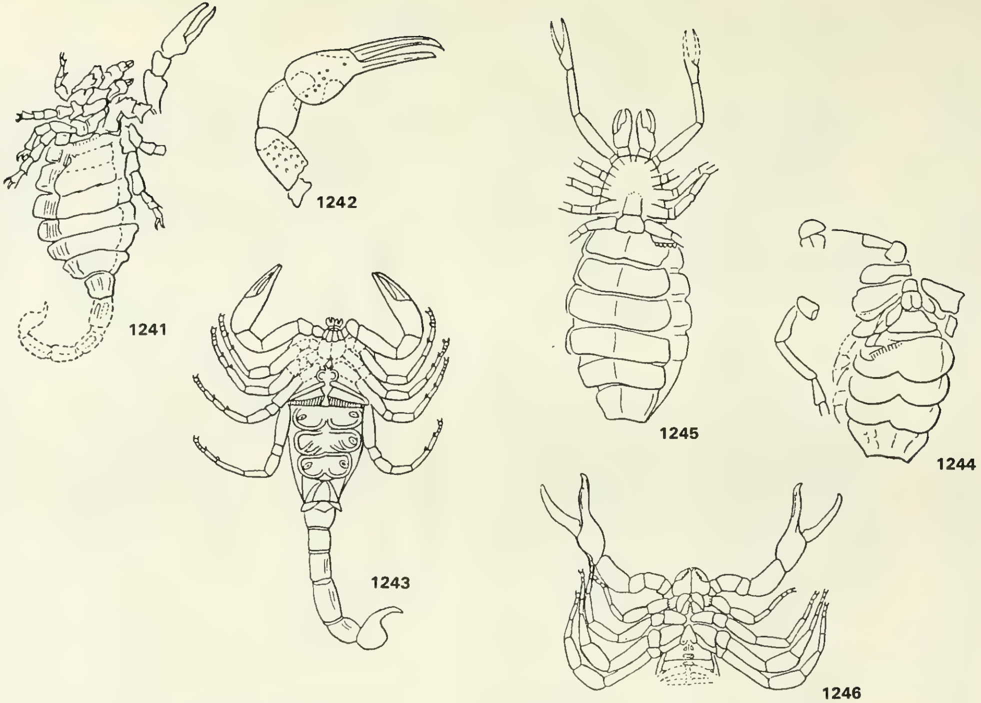
Segments of metasoma with central longitudinal or cylindrical thickening. Median eyes located at posterior part of carapace. Structure of coxosternal area not known. One genus, *Palaeoscorpius* Lehmann, 1944 from the Lower Devonian of Western Europe.

Family ARCHAEOCTONIDAE Petrunkevitch, 1949

Segments of metasoma without median cylinder but resemble recent scorpions (Fig. 1241). Sternum large, rectangular, and occupies entire middle part of thorax. Coxae of three posterior pairs of legs located along sides of it. Inner surface of coxae of legs I, with maxillary lobes that extend to median line of body. They are located in front of sternum (Fig. 1226A). Genital opening lies posterior to level of coxae of legs IV. Legs comparatively short, with spines on venter of tibial apex and with two large claws. Pedipalpi twice as stout and long as walking legs. Chelae large, with long digits (Fig. 1241). Length of prosoma about 9 mm. Carboniferous. Two genera: *Archaeoctonus* Pocock, 1911 from the Carboniferous of Western Europe and *Eoctonus* Petrunkevitch, 1913 from the Carboniferous of North America.

Family CENTROMACHIDAE Petrunkevitch, 1953

Folds of genital opening located between inner surfaces of coxae of legs III and IV. In front lies a triangular sternum extending up to coxae of legs I. Coxae of legs II are located on sides of sternum (Fig. 1226B). Coxae of legs I with wide



Figs. 1241– 1246. Families Archaeoctonidae, Centromachidae, Isobuthidae and Cyclophthalmidae.

1241. *Archaeoctonus glaber* (Peach); general view, × 1.5. Carboniferous, Western Europe (Werner, 1934). 1242. *Centromachus euglyptus* Peach; pedipalpi, × 6. Carboniferous, Western Europe (Petrunkevitch, 1953). 1243. *Isobuthus kralupensis* Thorell and Lindstrom; ventral view, × 3. Carboniferous, Czechoslovakia (Werner, 1934). 1244. *Isobuthus holti* Pocock; general view of fossil, × 5.5. Carboniferous, Czechoslovakia (Petrunkevitch, 1953). 1245. *Microlabis sternbergii* (Corda); ventral view, × 3.5. Carboniferous, Czechoslovakia (Pocock, 1911). 1246. *Cyclophthalmus senior* (Corda); prosoma and appendages, × 1.5. Carboniferous, Czechoslovakia (Werner, 1934).

gnathobases which are in close contact with one another along median line of body. Pedipalpi with short, stout segments covered with conical tubercles. Pedipalpi about 9 mm long. Digits of chelae long, slender and pointed (Fig. 1242). One genus: *Centromachus* Thorell, 1885 from the Carboniferous of Western Europe.

Family ISOBUTHIDAE Petrunkevitch, 1913

Folds of genital opening located between coxae of legs IV. In front of coxae lies a small triangular sternum which separates only coxae of legs III. Coxae of legs I and II meet along median line of body (Fig. 1226D). Carboniferous. Three genera: *Isobuthus* Fritsch, 1904 (Figs. 1243, 1244) and *Microlabis* Corda, 1839 (Fig. 1245) from the Carboniferous of Western Europe and *Palaeobuthus* Petrunkevitch, 1913 from the Middle Carboniferous of America.

429 Family CYCLOPHTHALMIDAE Petrunkevitch, 1913

Folds of genital opening located behind coxae of legs IV. Coxae of first and second legs with long gnathobases arranged along median line of body and parallel to one another. Sternum small, triangular and lies between coxae of legs IV (Fig. 1226E). Carapace broad, rectangular, somewhat tapering in front. Median eyes lie on small rhomboid tubercle located in anterior one-third of carapace (Fig. 1233). One genus: *Cyclophthalmus* Corda, 1835 from the Carboniferous of Western Europe.

Family EOSCORPIIDAE Scudder, 1884

Folds of genital opening very small, lie behind coxae of legs IV. Sternum wide, pentagonal and located between coxae of legs III and IV, pushing them apart to sides. Gnathobases of coxae of legs I and II long and straight, extend forward and are parallel (Fig. 1226F). Pedipalpi comparatively long and slender (Fig. 1247). Legs smooth and devoid of spinelike growths. Metasoma large, stout and as long as rest of body. Anterior margin of prosoma broad and blunt. Carboniferous. Seven genera.

Eoscorpius Meek and Worthen, 1868. Genotype—*E. carbonarius* Meek and Worthen, 1868; Carboniferous, North America. Prosoma and metasoma nearly of same length. Carapace more or less straight, with parallel sides. Eye tubercle shifted toward anterior half of the carapace. Eyes small, located on anterior margin of carapace (Fig. 1247). Legs long and slender. Pedipalpi long and only half as thick again as walking legs. Their patella same length as claw. Length of body up to 130 mm. Four species, of which two are from the Carboniferous of Europe.

Alloscorpius Petrunkevitch, 1949. Genotype—*Eoscorpius granulosus* Petrunkevitch, 1913; Carboniferous, North America. This resembles the preceding genus, but differs in the semicircular furrow dividing the anterior part of carapace, by the large pear-shaped eye tubercle almost reaching the anterior margin of carapace (Fig 1236). Eyes hemispherical. Chelae as long as or longer than patella of pedipalpi (Fig. 1248). Length of body up to 130 mm. Length of 431 chelae of pedipalpi 29 mm. Four species. Two species from the Carboniferous of North America and two from the Carboniferous of Europe.

Anthracoscorpius Kusta, 1888 (= *Lichnoscorpius* Petrunkevitch, 1949) Genotype—*Cyclophthalmus* (*Anthracoscorpius*) *juvenis* Kusta, 1885 (= *C senior* Kusta, 1884, pars); Carboniferous, Czechoslovakia. Metasoma comparatively stout and nearly as long as prosoma (Figs. 1249, 1250). Carapace with convex sides and convex surface, widely rounded in front and semidiscoid with length nearly equal to width (Fig. 1249). Eyes located close to anterior margin. Pectines long (Fig. 1250). Length of body 9–11 mm. Length of carapace 0.95–1.41 mm and width at posterior part 1.5–1.71 mm. Two species from the Carboniferous of Europe.

Europhthalmus Petrunkevitch, 1949. Genotype—*E. longimanus* Petrunkevitch, 1949; Carboniferous, England. Carapace elliptical and truncated at posterior end. Median eyes large, located at anterior margin of carapace. Eyes separated by small triangular eminence (Fig. 1236). Surface of carapace with numerous small tubercles. Pedipalpi very long: tips reach third segment of postabdomen when the pedipalps are bent. Chelae with long, straight digits (Fig. 1254). Length of body 60 mm. Length of carapace 10.5 mm. Length of chela of pedipalp 18.7 mm. One species. Carboniferous of Western Europe.

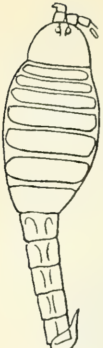
Other forms from the Carboniferous of Western Europe: *Typhloscorpius* Petrunkevitch, 1949 (Fig. 1237); *Lichnophthalmus* Petrunkevitch, 1949 (Fig. 1238) and *Buthiscorpius* Petrunkevitch, 1953 (Fig. 1252).

Family TRIGONOSCORPIONIDAE W. Dubinin, fam. nov.

Metasoma much reduced. It is one-third to one-half the length of rest of body. Metasomal segments very slender (Figs. 1232, 1251, 1256). Carapace narrows anteriorly; neither blunt nor widened in front. Four genera from the Carboniferous of Europe and North America.

Trigonoscorpio Petrunkevitch, 1913. Genotype—*T. americanus* Petrunkevitch, 1913; Carboniferous, North America. Carapace triangular, margins narrowing toward the front, rounded or truncated in front, considerably longer than broad, with a straight transverse furrow dividing surface into two parts (Figs. 1232, 1251). Eyes located on narrow triangular area around anterior margin of carapace. Metasoma very narrow and approximately as stout as walking legs (Fig. 1251). Pedipalpi long and twice as stout as walking legs; their patella shorter than length of chela. Carapace 1.7 mm long, and 3.2 mm wide at rear. Two species from the Carboniferous of North America (Fig. 1251) and Western Europe.

Compsoscorpius Petrunkevitch, 1949. Genotype—*C. elegans* Petrunkevitch, 1949; Carboniferous, England. Carapace semitriangular, widely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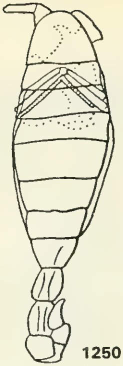
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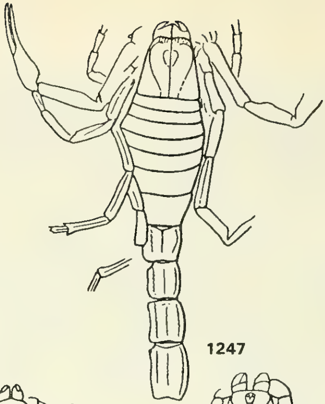
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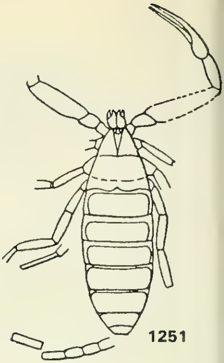
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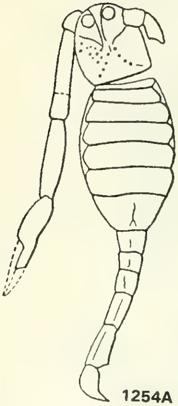
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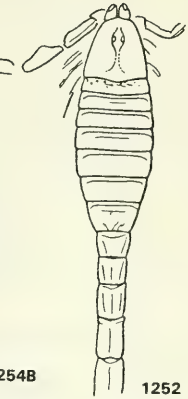
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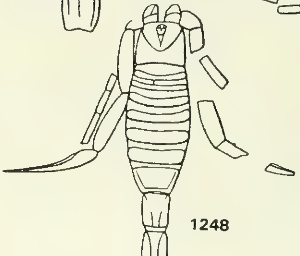
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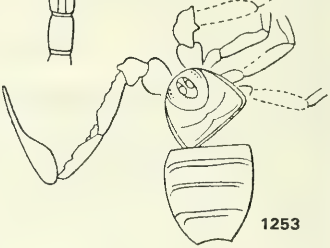
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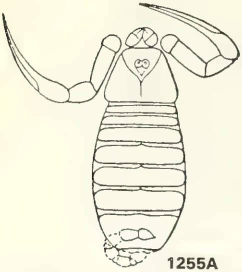
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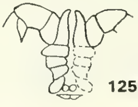
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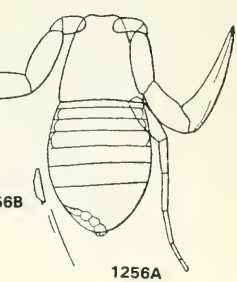
1256A

rounded at anterior end and truncated at the rear (Fig. 1235). Posterior and lateral margins of carapace with a long, slender furrow, separating a narrow lenticular margin. Of the other three furrows, the two posterior ones run across body and the anterior furrow forms a semicircle around a smooth oval prominence and the small marginal ocelli (Figs. 1235, 1253). Large pedipalpi are one and one-half times as stout as walking legs. Inner margins of segments wavy. Chela narrow with long, slender digits. Length of claw one and one-half to two times the length of patella and somewhat larger than femur. Length of carapace 2.57 mm. Two species. Carboniferous of Western Europe.

Typhlopisthacanthus Petrunkevitch, 1949. Genotype—*Palaeopisthacanthus mazonensis* Petrunkevitch, 1913; Middle Carboniferous, North America. Metasoma very short, slender, curved anteriorly. Its telson not reaching the posterior border of sixth segment (Fig. 1256A). Carapace long, apparently smooth, trapezoidal, with slightly convex sides. Eyes absent. Pedipalpi very stout and long (Fig. 1256B). Fig. 1256B shows the positions of coxae of legs, sternum and valves of genital openings. Length of body 23 mm. Carapace 6.6–6.3 mm wide at level of posterior margin. Besides the genotype there is one more species from the Carboniferous of Western Europe.

Also known from the Carboniferous of North America is *Palaeopisthacanthus* Petrunkevitch, 1943 (Fig. 1231).

432 Family GARNETTIIDAE W. Dubinin, fam. nov.

Coxosternal area as in Eoscorpiidae and all Recent scorpions. Mesosoma long, oval, with a small prosoma in front. Terga of mesosoma narrow in front but gradually broaden toward posterior end. Tergum of seventh segment longest, and narrowest, and almost quadrate. Metasoma comparatively thick. Telson narrow with straight process (Fig. 1257A). Carapace almost square at base with

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Figs. 1247–1257. Family Eoscorpiidae, Trigonoscorpionidae, Garnettiidae.

1247. *Eoscorpius dunlopi* Pocock; general view, × 1. Carboniferous, Western Europe (Pocock, 1911). 1248. *Alloscorpius granulosus* (Petrunkevitch); general view, × 0.75. Carboniferous, North America (Petrunkevitch, 1913). 1249. *Anthracoscorpius minutus* Petrunkevitch; general view, × 0.75. Carboniferous, Czechoslovakia (Petrunkevitch, 1953). 1250. *Anthracoscorpius juvenis* Kusta; general view, × 0.75. Carboniferous, Czechoslovakia (Petrunkevitch, 1953). 1251. *Trigonoscorpio americanus* Petrunkevitch; general view, × 1. Carboniferous, North America (Petrunkevitch, 1913). 1252. *Buthiscorpius buthiformis* Pocock; general view, × 1. Carboniferous, Western Europe (Pocock, 1911). 1253. *Compsoscorpius elegans* Petrunkevitch; general view of fossil, × 5. Carboniferous, Western Europe (Petrunkevitch, 1949). 1254. *Europhthalmus longimanus* Petrunkevitch; A—general view, × 1.7; B—pedipalpi, × 2.3; Carboniferous, Western Europe (Petrunkevitch, 1940). 1255. *Palaeopisthocanthus schucherti* Petrunkevitch; A—general view; B—coxosternal area; × 4. Carboniferous, North America (Petrunkevitch, 1913). 1256. *Typhiopisthacanthus mazonensis* (Petrunkevitch); A—general view; B—coxosternal area, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1257. *Garnettius hungerfordi* (Elias); A—general view, × 2.5; B—leg III, × 18. Carboniferous, North America (Petrunkevitch, 1913).

a triangular process in front whose extreme anterior margin is divided by a furrow. Eye tubercle very small, oval and located near anterior margin of body (Fig. 1240). Tibia and metatarsus of legs III with numerous dorsal spinal outgrowths (Fig. 1257A). Legs slender and comparatively short. Pedipalpi comparatively short, with stout chelae (Fig. 1257A, B). One genus:*Garnettius* Petrunkevitch, 1953 from the Upper Carboniferous of North America.

Family MESOPHONIDAE Wills, 1910

Genital operculum located posterior to coxae of legs IV. Sternum large, triangular or pentagonal and fits into angle between coxae of legs III and IV. Gnathobases are limited to the coxae of legs I. Coxae of legs II straight and extend to median line of body in front of sternum (Fig. 1226C). Segments of mesosoma and particularly of metasoma sharply separated from one another. Segments of postabdomen have a longitudinal row of tubercles, as in Recent scorpions (Fig. 1258A, C). Carapace rectangular, with a median outgrowth projecting forward on which eyes are located (Fig. 1239). Legs long and slender. Pedipalpi large, with stout chela (Fig. 1258A, B). Two genera from the Triassic of Western Europe.

Mesophonus Wills, 1910. Genotype— *M. perornatus* Wills, 1910; Triassic, England. Sternum pentagonal. Surface of segments smooth or with equal sized granules. Carapace a transverse rectangle with diagonally incised anterior corners and a projecting central part which bears eyes. Posterior and lateral margins of carapace bordered by furrow (Fig. 1239). Six species from the Triassic of England.

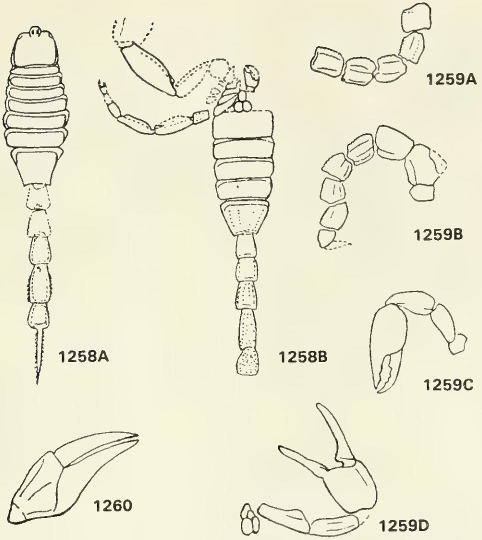
Spongiotarsus Wills, 1947. Genotype— *S. pustulosus* Wills, 1947; Triassic, England. This differs from preceding genus in its triangular sternum and reticular ornamentation of exoskeleton (Fig. 1226C). One species from the Triassic of Western Europe.

Family BUTHIDAE C.L. Koch, 1837

Sternum triangular. Two spines on inter-segmental membrane between metatarsus and tarsus. Lateral eyes 3 or 5 pairs. Paleogene to Recent. There are 34 Recent genera, of which *Tityus* C.L. Koch, 1837 is from the Paleogene of Europe (Baltic amber).

Family SCORPIONIDAE Leach, 1815

Sternum pentagonal, single spine on inter-segmental membrane between metatarsus and tarsus of legs I and II. Without tarsal spur on legs III and IV. Lateral eyes 3 or 5 pairs. Paleogene to Recent. Twenty living genera of which *Scorpio* Linnaeus, 1758 from the Paleogene of Europe (Baltic amber) and the Miocene of Germany.



Figs. 1258–1260. Family Mesophonidae and Scorpionidae Incertae sedis.

1258. *Mesophonus* sp. (reconstruction); A—dorsal region; B—ventral region, × 1.5. Triassic, Western Europe (Werner, 1934). 1259. *Palaeomachus anglicus*(Woodward); A—middle segments of metasoma; B—metasoma and last segment of mesosoma; C—pedipalp; D—pedipalp with chela open, × 1. Carboniferous, Western Europe (Pocock, 1911). 1260.*Palaeomachus* sp.; chela of pedipalp, × 1. Carboniferous, Western Europe (Petrunkevitch, 1949).

433 Scorpionida Incertae sedis

Palaeomachus Pocock, 1911. Genotype—*Eoscorpius anglicus* Woodward, 1876, nec Petrunkevitch, 1949; Carboniferous, England. Two pedipalps (Figs. A, B 1259, 1260) and two fragments of metasoma (Fig. 1259) have been described.

Liassoscorpionides Bode, 1951. Genotype—*L. schmidti* Bode, 1951; Lower Jurassic, Germany. Poorly preserved and briefly described scorpion. Length of body 14.4 mm, width 4.8 mm. One species. Jurassic of Western Europe.

SUPERORDER PEDIPALPIDES

V.B. Dubinin

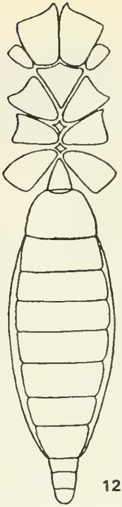
Body long or short oval, subdivided into two divisions: prosoma covered by carapace, opisthosoma with distinct segmentation. Opisthosoma not divided into a large, broad anterior and a narrow posterior part, as in subclass Holactinochitinosi. Posterior part of opisthosoma sharply tapered, and its last three segments (XVI–XVIII) constitute short, slender metasoma which in certain species terminates in a long segmented flagellum (Figs. 1262, 1263, 1265). Only in a few Pseudoscorpiones, is mesosoma blunt posteriorly and without trace of metasoma. Pedipalps very large (some Uropygi), claw-shaped (Pseudoscorpionodea), prehensile (Amblypygi, Uropygi) or leglike (Palpigradi, Ricinulei). Gnathobases only on coxae of pedipalpi or legs I in some species (Fig. 1263). Walking legs are long and thin. They usually have thickened femurs and long, thin distal segments. Tarsi of legs with two claws (Figs. 1262, 1270). Legs I usually attain a great length and become flagellate. They are locomotory in function but serve as sensory organs (Figs. 1262, 1270). Legs I differentiated from others only in pseudoscorpions and Ricinulei.

Ventral side of mesosoma with modified appendage in the form of a fold of genital opening on second abdominal sternum (Fig. 1264); two pairs of pulmonary sacs or stigma (Pseudoscorpionodea) on segments III and IV, of opisthosoma. Structure of coxosternal area typically of 'scorpionoid' type with the only difference that in Amblypygi, particularly in Kustarachnida, coxae of all prosomatic appendages are radial, their apices pointing towards the center (Figs. 1262B, 1271, 1273). Among some Pedipalpides the development of a true thoracic shield–sternum is noticed for the first time among chelicerates. The sternum develops due to sclerotization of ventral tegumen of thorax extending to all segments of walking legs. In Uropygi and Amblypygi, development of a small rhomboid thickening of chitin along median line of body is evident between inner surfaces of coxae of legs. The formation of distinct thoracic sterna on all segments of the prosoma and mesosoma in the fossil *Sternarthron zitteli* Haase (Fig. 1276) is interesting. Similar independent sterna are seen on the segments of the chelicerae and the three posterior pairs of legs in Recent palpigradi (Koeneniidae). Sterna of pedipalpi and legs I fused into a common plate. Most species are of small size. Length of body varies from 0.8–2.8 mm (Palpigradi) to 75 mm (Uropygi).

ECOLOGY AND BIOGEOGRAPHY. Terrestrial chelicerates distributed primarily in tropical and subtropical countries. Only the Pseudoscorpiones are found far north, where they live in nests and burrows of animals and human dwellings. Many species live in surface layers of soil, in moist plant litter. Most species are predators.

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. The superorder Pedipalpides comprises a group of scorpionoid chelicerates that undoubtedly originated along with the scorpions from a common ancestor. The presence in Pedipalpides of pulmonary sacs, probably derived from the branchiate appendages of aquatic Chelicerate, points to the aquatic life history of their ancestors. In other, more specialized Pedipalpides, for example in represen-

1263B



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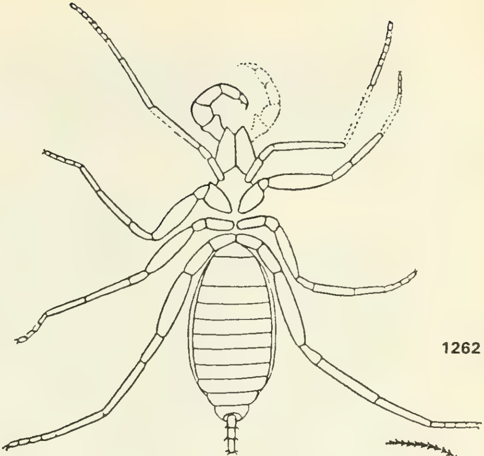

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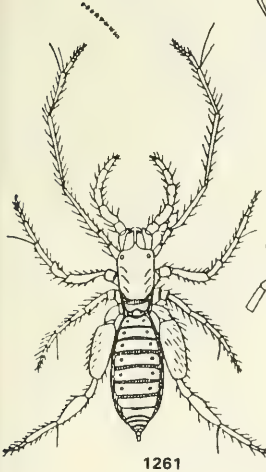

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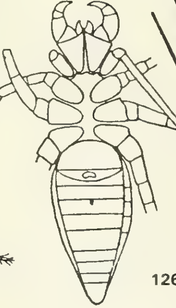

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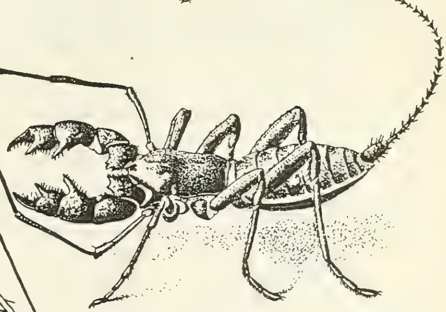


1265

Figs. 1261–1265. Order Uropygi.

1261. *Schizomus tenuicaudatus* (Cambridge); general view, × 5. Recent (Roewer, 1934). 1262.*Calcito fisheri* Petrunkevitch; general view, × ?. Neogene, North America (Petrunkevitch, 1955). 1263. *Prothelyphonous brithannicus* (Pocock); A—female, abdominal region, × 3.5 (Petrunkevitch, 1949); B—female, dorsal view, × 2.5. Carboniferous, Western Europe (Pocock, 1911). Carboniferous of Western Europe. 1264. *Prothelgyphonus giganteus* (Petrunkevitch); ventral view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1265. *Thelyphonus caudatus* Linnaeus; male, general view, × 2.5 Recent (Millot, 1949).

tatives of the order Pseudoscorpionodea, reduction of the pulmonary sacs and development of trachea on their base is observed. Carboniferous to Recent. Six orders: Uropygi, Amblypygi, Kustarachnida (extinct), Palpigradi, Pseudoscorpionodea and Ricinulei.

434 Order UROPYGI. Whip scorpions

(Thelyphonida)

Body elongate, with narrow extended prosoma and twelve-segmented oval opisthosoma. Posterior segments taper to form short, slender metasoma to which is attached a long whip-like tail (Figs. 1263B, 1265). Legs long, slender, 435 segments very slender, long ending in long threadlike sensory organs (Fig. 1265). The remaining three pairs of walking legs eight-segmented, with stout femurs. Coxae of legs located along the margins of thoracic segment of prosoma. Some species develop individual small sternal plates between the coxae, which do not move coxae to the sides of cephalothorax. Chelicerae short, claw-shaped and three-segmented. Pedipalpi very large, stout and form pincers in front of head (Fig. 1264). Two pairs of openings of pulmonary sacs located on sterna of second and third abdominal segments. In front of them lie folds of the genital aperture at middle of first segment. Two large eyes are located on raised oval tubercle near anterior margin of carapace; and three small ocelli located near anterolateral angles. Size of body ranges from 3 to 75 mm.

Ecology and Biogeography. The pedipalpid scorpions or Thelyphonida inhabit rain forests of tropical and subtropical zones of America, Africa and Southeast Asia. They ascend high altitudes up to 1,200 m above sea level. Carboniferous to Recent. There are about 100 species in recent fauna.

Classification, Phylogeny and Systematic Position. Order Uropygi is close to the order Amblypygi (cf. p. 436), to which is sometimes added the order 436 Pedipalpi. Still, Millot (1942, 1949) pointed out the need to divide Thelyphonida and Amblypygi into independent orders. Two suborders: Schizopeltidia and Holopeltidia.

Suborder Schizopeltidia

(Tartarides, Schizomida)

Carapace divided into a large propeltidium and two small terga lying behind it. Tail-whip with only one or three segments. Pedipalpi slender and leglike, segments devoid of spines on inner surface. Femurs of posterior legs are swollen like a barrel. Other segments of legs slender (Fig. 1275). Length of body 2.5 to 6 mm. Paleogene to Recent. Two families: Recent Schizomidae and Tertiary Calcitronidae.

Suborder Holopeltidia

(Oxypoel, Urotricha, Thelyphonida)

Carapace not differentiated. Tail-whip long and many-segmented. Pedipalpi very stout, segments with large teethlike projections on inner surface (Fig. 1265). Rarely are they without these, but then pedipalpi are shorter than carapace (Fig. 1264). Legs long and slender, femurs of all legs of uniform thickness, but not swollen as in the species of the suborder described above. Large sized forms. Length of body ranges from 18 to 75 mm. Carboniferous to Recent. One family.

Family THELYPHONIDAE Lucas, 1882

(Geralinuridae Scudder, 1884)

This family is characterized by features of suborder. Carboniferous to Recent. Ten Recent genera, two from the Carboniferous.

Prothelyphonus Fritsch, 1904. Genotype—*Thelyphonus bohemicus* Kusta, 1884; Carboniferous, Western Europe. Carapace extended and hexagonal. Eyes well developed. Along the sides of eyes from anterior margin of body backwards run two weakly curved furrows, at the ends of which are small oval thickenings. Length of carapace 10 mm and width 6 mm. Length of abdomen 20 mm (Figs. 1263, 1264). Two species from the Carboniferous of Western Europe and one from the Middle Carboniferous of North America.

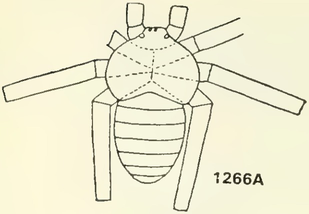
Also, the genus *Geralinura* Scudder, 1884 from the Middle Carboniferous of North America and the Recent genus *Thelyphonus* Laterille, 1802 from the Neogene of North America.

Order AMBLYPYGI. Tailless whip scorpions

(Phrynida, Phrynichida)

Body short-oval with almost disk-shaped prosoma and small oval twelve-segmented adbomen. Last segments do not form narrow cylindrical appendage. Only in certain species is there one small segment at the tip of body (Fig. 1270). Surface of prosoma with numerous radial depressions, its anterior part somewhat raised, with two large median eyes at the extreme anterior margin and two groups of ocelli along their sides with three eyelets in each (Fig. 1270). Coxae of walking legs and pedipalpi radially arranged on ventral side of cephalothorax. Chelicerae large, claw-shaped and three-segmented. Pedipalpi reach huge size—occasionally four times as large as length of body (*Phrynichus* Karsch). Pedipalp six-segmented, with numerous slender needlelike processes along inner surface (Figs. 1268, 1270). Legs long, slender with long femurs and tibiae. Segments of legs I highly elongate, rodlike with long, slender, flagellate and many-segmented sensory tarsus (Fig. 1270). Tarsi of all legs with two claws and soft cushion-like area at their base. Respiratory organs consist of two pairs of pulmonary sacs opening as slit-like spiracles on sterna of segments II and III of abdomen. Length of body ranges from 7 to 35 mm.

Ecology and Biogeography. Inhabit rain forests of tropical and subtropical countries of America, Africa and Southeast Asia. Carboniferous to Recent.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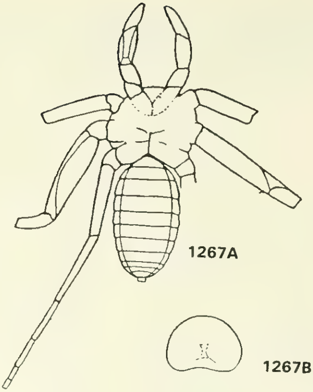
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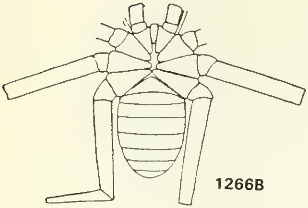
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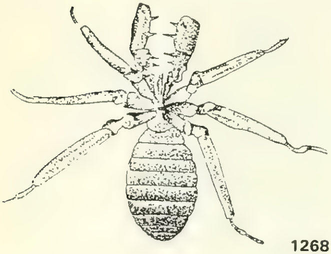
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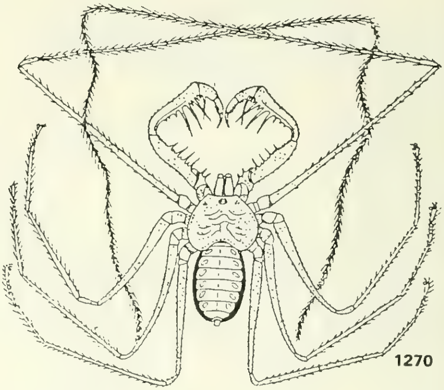
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Figs. 1266–1270. Order Amblypygi.

1266. *Protophrynus carbonarius* Petrunkevitch; general view; A – dorsal view, B – ventral view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1267. *Thelynhrynus elongatus*Petrunkevitch; A—general view from ventral side, × 13; B – prosoma, dorsal view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1268. *Graeophonus anglicus* Pocock; ventral view side, × 2.5. Carboniferous, Western Europe (Pocock, 1911). 1269. *Graeophonus anglicus* Pocock; dorsal view, × 2.5. Carboniferous, Western Europe (Pocock, 1911). 1270. *Stygophrynus dammermani* Roewer; general view, × 3. Recent (Werner, 1935).

Classification, Phylogeny and Systematic Position. The order Amblypygi is close to the order Uropygi, with which it is often combined in the heterogenous 'order' Pedipalpi. Although these two groups superficially resemble each other and possess an undoubted common ancestry, Amblypygi differs from Uropygi principally in the structure of coxosternal area and loss of 437 the tendency to form the scorpionoid narrow metasoma and, more so, the flagellum. Millot (1942, 1949) showed that differences between these two groups involve the structure of the genital, circulatory, nervous and digestive systems, coxal and anal glands, etc. It is interesting that the supra-pharyngeal ganglia (procephalon) of Recent Amblypygi are similar to those in the thelyphonids of the order Uropygi, while the subpharyngeal ganglia resemble spiders of the suborder Liphistiomorphae (cf. p. 751). The similarity of Amblypygi to primitive Araneae is also confirmed by the structure of coxosternal area and other organs. Hence the orders Amblypygi and Uropygi are recognized as separate groups, despite their common origin. Attempts of certain workers (Werner, 1935) to discover ancestral Protopalpigradi that unite the two orders together do not seem to have met with success. One family: Tarantulidae.

Family TARANTULIDAE Karsch, 1897

(Phrynidae Pocock, 1902; Cnarontidae Simon, 1936)

This family is divided into four subfamilies. Carboniferous to Recent. There are 14 genera in the Recent fauna. Moreover there are three genera from the Carboniferous of Western Europe and North America: *Graeophonus* Scudder, 1890 (Figs. 1268, 1269), *Protophrynus* Petrunkevitch, 1913 (Fig. 1266) and *Thelyphrynus* Petrunkevitch, 1913 (Fig. 1267).

Order KUSTARACHNIDA

Body oval with disk-shaped prosoma and a narrower egg-shaped or conical abdomen. Carapace discoidal (Fig. 1273A) or semicircular (Fig. 1272). At the center or a little closer to the broad anterior rounded edge is a small oval tubercle with two eyes. Lateral eyes absent (Figs. 1272, 1273A). Coxae of legs extended triangularly and closely pressed together. Coxae converge radially toward center of ventral surface of the thorax. Coxae of pedipalpi fused together to form a single triangular plate (Figs. 1271, 1273B). Pedipalpi short, four to five-segmented and claw-shaped. Legs very long and slender (Figs. 1271, 1273B). Abdomen twelve-segmented, gradually narrowing posteriorly; last segments (one or two) very slender and forming a short metasoma (Fig. 1273B). Chelicerae and respiratory organs not known. Probably the Kustarachnida as well as the related Amblypygi had two pairs of pulmonary sacs opening onto third and fourth sterna of abdomen. Length of body ranges from 11 to 15 mm.

Ecology and Biogeography. These pedipalpids probably lived in rain forests of tropical and subtropical America in the Carboniferous.

Classification, Phylogeny and Systematic Position. Representatives of the order Kustarachnida are related to the order Amblypygi from which they probably originated. Melanger's (1903) and Pocock's (1910) suggestion as to the relationship of Kustarachnida to Ricinulei is erroneous and is not confirmed by data from comparative anatomy. Most probably the order Kustarachnida represents a small blind branch of pedipalpids of the order Amblypygi which branched off and soon became extinct in the Carboniferous of North America. One family: Kustarachnidae.

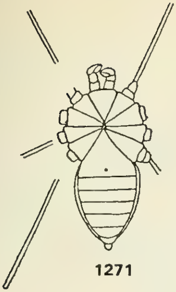
Family KUSTARACHNIDAE Petrunkevitch, 1913

One genus *Kustarachne* Scudder, 1890 from Middle Carboniferous of North America (Figs. 1271, 1273).

Order PALPIGRADI

(Microthelyphonida, Palpigradida)

This order includes very small chelicerates (length of body 0.8 – 2.8 mm) with an elongate body narrowing at the junction of the prosoma and opisthosoma and long segmented flagellum (Fig. 1274). Prosoma an extended oval. Carapace divided into large head shield—a propeltidium lying behind the small metapeltidium and two small shields (mesopeltidia) on sides of cephalothorax over bases of legs III (Fig. 1275A). Median eyes absent. Ocellus present on anterolateral angles of carapace. A large trapezoidal plate-sternum (dentosternum) present on ventral side of thorax at the level of coxae of legs I and
438 pedipalpi in Recent Palpigradi. Behind this, at the level of the coxae of the hind legs lie small quadrangular sterna (tritosternum, pentasternum and metasternum). In the Upper Jurassic *Sternathron zitteli* Haase, six small separate sternal plates have been observed on all thoracic segments (Fig. 1276). This shows that the dentosternum of Recent forms has been formed as a result of the fusion of three sternal plates (chelicerals, pedipalpal and that of leg I). The presence of these separate plates remained unexplained for a long time, and Jurassic Palpigradi (genus *Sternarthion* Haase) were erroneously included in the 'order' pedipalpi. Only Verslyus and Demoll (1922) established the correct systematic position of this group. Opisthosoma with twelve clearly differentiated segments separated from prosoma by considerably constricted seventh segment. Terga and sterna absent on ventral segments. Posterior three segments of abdomen (XV–XVII) slender and cylindrical and form short narrow metasoma, the last segment of which is attached to a long, segmented hairy flagellum (Figs. 1274–1276). Chelicerae large, claw-shaped, three-segmented, projecting considerably forward with the claws curved towards ventral side (Fig. 1275A). Pedipalpi long, slender, nine-segmented and leg-like (Fig. 1274). The peculiarity of the structure of the pedipalpi and other organs bring the Palpigradi close to the suborder Schizopeltidia of the order Uropygi.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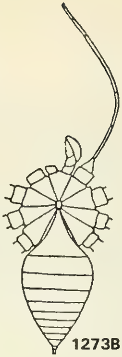
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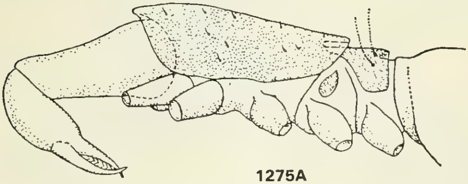
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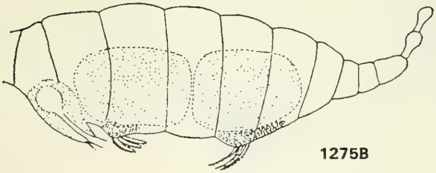
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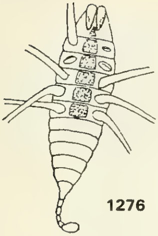
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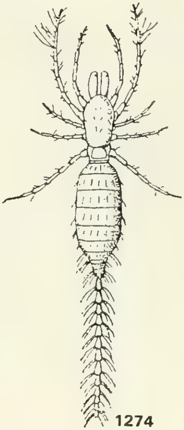
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Figs. 1271–1276. Orders Kustarachnida and Palpigradi.

1271. *Kustarachne conica* Petrunkevitch; ventral view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1272. *Kustarachne tenuipes* Scudder; prosoma, dorsal view, × 4. Carboniferous, North America (Petrunkevitch, 1913). 1273. *Kustarachne extincta* Melander; A—prosoma, dorsal view, × 4. B—ventral view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1274. *Koenenia mirabilis* Grassi; dorsal view, × 3.5 Recent (Boewer, 1934). 1275. *Koenenia mirabilis* Grassi; A—cephalothorax of female (lateral view), × 7. B—abdomen of female (lateral view), × 7. Recent (Millot, 1949). 1276. *Sternathron zitteli* Haase; ventral view, × 5. Jurassic. Western Europe (Werner, 1935).

Legs are long, slender with numerous homonomous small segments. In the Jurassic legs impression of *Sternasthron* indicate presence of slender straight furrows (Fig. 1276). Respiratory system represented, as in some other Scorpionomorpha, by four pairs of thick pulmonary sacs located on ventral side of third to sixth segments. Deep inside these sacs are primitive tracheae embedded in muscles. Genital opening located on ventral side of second opisthosomal segment. The three-lobed genital cone arising from the gonapophyses of the II and III abdominal segments is observed here (Fig.
439 1275B). Genital cone in both sexes nearly alike.

Ecology and Biogeography. Recent palpigradi inhabit damp soils of tropical and subtropical regions of north and south America, Africa, Europe and southeast Asia. Most of the finds were from sea shores and some freshwater bodies. *Koenenia* was obtained from East Africa (Kijabe) at a height of 2,100 meters above sea level. Fossil forms are known from the Upper Jurassic of Bavaria.

Classification, Phylogeny and Systematic Position. Palpigradi is a separate order of Scorpionomorpha related to order Uropygi (suborder Schizopeltidia) of the primitive pedipalpid scorpionomorpha. Combining these two orders is not justified. Palpigradi and Schizopeltidia branched off from a common stem of Scorpionomorpha at the very beginning of evolution of terrestrial chelicerates. Recent palpigradi probably retained, up to a certain stage, the ancestral aquatic biology. The common ancestral forms which initiated the evolution of members of the superorder Pedipalpides were probably ancestors of some groups of Arachnida—primarily the order Solifugae and the class Acaromorpha (cf. pp. 679, 681).

Order Palpigradi is represented by two families: Recent Eukoeneniidae and Jurassic Sternarthronidae.

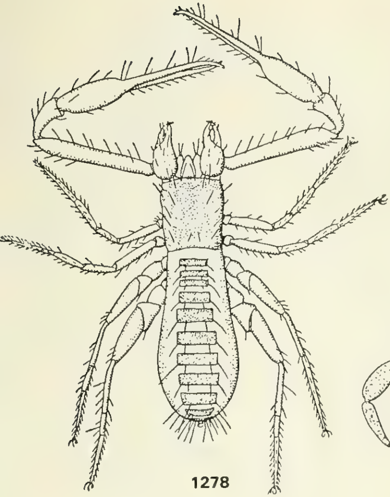
Family STERNARTHRONIDAE Haase, 1890

Body oval, segmented; terminal segments tapered and with a flagellum. Segments at junction of prosoma and opisthosoma not constricted. Six separate sternal shields on ventral side of cephalothorax metamerically corresponding to the six pairs of appendages. Legs slender and long (Fig. 1276). Length of the body 13 mm. Jurassic. One genus *Sternathron* Haase, 1890 (= *Halometra* Oppenheim, 1887) from Upper Jurassic of Germany.

Order PSEUDOSCORPIONODEA

(Pseudoscorpiones, Chelonethi, Chelonethida)

Body broadly oval or elongate and flat dorsoventrally; either broadly rounded or with one small cylindrical segment (suborder Neobisiinea) at posterior end. Dorsal surface of body sharply subdivided into a narrow, usually triangular prosoma and larger abdomen; these two divisions are immovably joined



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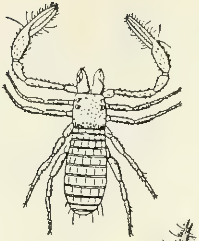

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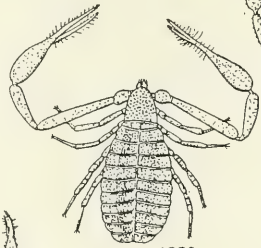

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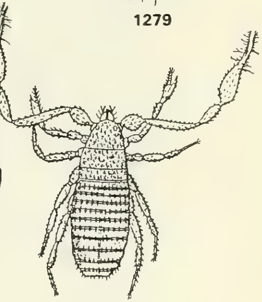

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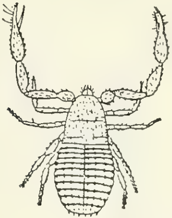

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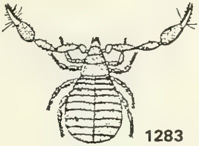

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Figs. 1277–1283. Order Pseudoscorpionodea.

1277. *Heterolophus kochii* (Menge); dorsal view, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1278. *Chtnonius troglodites* Redikortsev; dorsal view, × 15. Recent (Redikortsev, 1928). 1279. *Neobisium rathkei* (Koch and Berendt); dorsal view, × 18. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1280. *Pseudogarypus hemprichii* (Koch and Berendt); dorsal view, × 30. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1281. *Oligochernes weigandi* (Menge); dorsal view, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1282. *Oligochelijer berendti* (Menge); dorsal view, × 37. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1283. *Cheliridium hartmanni* (Menge); dorsal view, × 33. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955).

together. Prosoma covered by a thick carapace with two furrows which divide it into three parts (propeltidium, mesopeltidium and metapeltidium); or with only two transverse folds demarcating the border of fusion of these primary shields. Two or four large eyes located on anterior margin of carapace or on its sides. Eyes rarely absent or variably reduced. A narrow rectangular tergum of the first abdominal segment present along posterior margin of carapace; first tergum is not divided into two halves. Rest of terga (II–X) and sterna (III–X) usually divided along median line by soft membrane into left and right half. Tergum and sternum of segment XI usually entire and undivided (Figs. 1277–1283). Terga and sterna in the primitive pseudoscorpions of the suborder Chthoniinea and most Neobisiinea entire, not divided by a longitudinal furrow of soft membrane (Figs. 1278, 1279). Rudimentary anal (XII) segment present at posterior end of abdomen in many species. It is sometimes in the form of a narrow and short tube reminiscent of metasoma of ancestral forms (Amblypygi). Sternal region of cephalothorax entirely covered by closely fitting coxae of pedipalpi and walking legs. Chelicerae small, claw-shaped and three-segmented. Pedipalpi very large and five-segmented with large claws reminiscent of pedipalpi of scorpions but less strongly chitinised and with long sensory hairs. At the tip of the chela are located the open ducts of the spinnerets, whose secretions envelop the prey as well as egg mass. Walking legs of medium length, five-segmented (tarsus not divided). Femurs of legs somewhat stout. Tarsi with two claws and an arolium. Genital opening located at middle of sternum of second abdominal segment. It is covered in front by an operculum. Along sides of sterna III and IV at the location of the pulmonary sacs of other Scorpionomorpha there are two pairs of stigmata from which extend branching tracheal tubes inside the body. Length of body 0.8 to 6 mm.

Ecology and Biogeography. Pseudoscorpions live in the soil, in mosses, in plant debris, nests of animals and in places where small mites, insects and other organisms, which constitute their prey, are encountered. Stray species live exposed on the leaves of plants and as ectoparasites on animals. Found in all continents with the exception of the polar regions. They are most numerous in tropical and subtropical zones. Nocturnal and predatory. More than a thousand Recent species. Fossil forms are recorded from Baltic amber.

Classification, Phylogeny and Systematic Position. The phylogenetic relations of the order Pseudoscorpionodea remain unclarified because of the absence of fossil remains of primitive pseudoscorpions. Most investigators place this order close to the group Pedipalpi (Amblypygi + Uropygi) (Schelkanobtsev, 1899-1910; Kastner, 1928; Beier, 1932–1939) and partly the spiders of the order Araneae (Chamberlin, 1924). Data from comparative anatomy and embryology confirm the affinities of the order Pseudoscorpionodea to the group 'Pedipalpi' 441 (probably Amblypygi), which were the ancestors not only of pseudoscorpions but also of the order Araneae (cf. p. 586).

The order Pseudoscorpionodea is known in fossil form from the Paleogene of Europe (Baltic amber). Recent Pseudoscorpionodea are represented by 20 families and 200 genera. Three suborders: Chthoniinea, Neobisiinea, Cheliferinea.

Suborder Chthoniinea

Carapace with parallel margins or slightly narrowed posteriorly with four eyes, rarely reduced. Chelicerae large, stout, extending beyond base of anterior margin of the shield. Jagged process at tip of mobile digit (galea) absent. Pectinate plate (serrula) on galea free and attached only at base. Tufts of setae (flagella) on inner margin of base of chela long; chelicra usually with serrate setae on one side. Pedipalpi comparatively short. Tibia raised and bowl-shaped. Anterior two pairs of legs with undifferentiated (single segmented) tarsi. Tarsi of posterior two pairs of legs two-segmented (Fig. 1279). Coxae of legs I, II and III with spines. Femurs of legs IV stouter. Claws of tarsus simple, long. Secondary sexual characters not distinctly developed. Paleogene to Recent. Two families: Dithidae and Chthoniidae.

Family DITHIDAE Chamberlin, 1931

Stigmata disposed obliquely. Genital area of female thickened. Paleogene to Recent. Seven genera in the Recent fauna including *Heterolophus*Tomosvary, 1884 (Fig. 1277) from the Paleogene of Europe (Baltic amber).

Family CHTHONIIDAE Hansen, 1894

Stigmata arranged transversely. Genital area of female soft (Fig. 1278). Paleogene to Recent. 14 genera in Recent fauna including *Chthonius* from the Paleogene of Europe (Baltic amber) *Chthonius* C.L. Koch, 1843.

Suborder Neobisiinea

Carapace with more or less parallel sides, occasionally slightly concave. Eyes two or four, absent in cave species. Chelicerae large, stout and partly projecting beyond margin of the shield. Galea present or absent. Serrula of mobile digit only partly free at distal margin. Tibia of pedipalpi extended. Tarsi of fourth pair of walking legs usually two-segmented. Femurs of all legs developed nearly uniformly. Secondary sexual characters well developed. Paleogene to Recent. Three superfamilies: Neobisiidea, Garypidea and Feaellidea.

SUPERFAMILY NEOBISIIDEA

Tarsi of all legs two-segmented. Mobile digit of chela of chelicera serrate. Paleogene to Recent. Three families in Recent fauna: Neobisiidae, Syarinidae, Ideoroncidae. First described from the Paleogene of Europe (Baltic amber).

Family NEOBISIIDAE Chamberlin, 1930

Basi- and telofemur of legs IV are delimited by a furrow. Poison glands present only in the immobile digit of pedipalp. Pleural area of opisthosoma with tubercles. Paleogene to Recent. Eleven genera in the Recent fauna including *Neobisium* Chamberlin, 1930 (Fig. 1279) from the Paleogene of Europe (Baltic amber).

SUPERFAMILY GARYPIDEA

Tarsi two-segmented. Mobile digit of chelicera smooth. Paleogene to Recent. Three families in the Recent fauna: Menthidae, Olpiidae, Garypidae; the last two are described from fossil forms.

Family OLPIIDAE Chamberlin, 1930

Opisthosoma slightly broader than prosoma. Both digits of chela of pedipalpi with poison glands. Pleurae of opisthosoma smooth. Paleogene to Recent. Eighteen genera in the Recent fauna including *Garypinus* Daday, 1889, from the Paleogene of Europe (Baltic amber).

Family GARYPIDAE Hansen, 1894

Opisthosoma significantly broader than prosoma. Both digits of pedipalpi with poison glands. Pleurae of opisthosoma with tubercles on surface. Paleogene to Recent. Six genera in the Recent fauna including *Garypus* C.L. Koch, 1873 and *Geogarypus* Chamberlin, 1930 from the Miocene of South Asia and Paleogene of Europe (Baltic amber).

SUPERFAMILY FEAELLIDEA

Tarsi of legs single-segmented. Prosoma often with lobes or processes. Paleogene to Recent. Three families in the Recent fauna: Synsphyronidae, Feaellidae, Pseudogarypidae. The last one described from fossil forms.

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Family PSEUDOGARYPIDAE Chamberlin, 1923

Prosoma with projections in the form of short horns. Opisthosoma without pleural plates. Paleogene to Recent. Recent fauna represented by*Pseudogarypus* Ellingsen, 1909 (Fig. 1280), also from the Paleogene of Europe (Baltic amber).

Suborder Cheliferinea

Head shield with convex sides, rectangular or triangular with straight margins narrowing anteriorly. Eyes two, or may be absent. Surface of the shield smooth or with pointed spine-like setae (Fig. 1282). Terga and sterna of opisthosoma subdivided longitudinally along median line (Figs. 1280, 1281, 1283). Chelicerae small, with more or less well developed galea at tip of movable digit. Serrula fused to chelicerate finger along its entire length. Pedipalpi long with very large, stout chela. Tarsi of legs single-segmented. Tertiary to Recent. Two superfamilies: Cheliferidea and Cheiridiidea.

SUPERFAMILY CHELIFERIDEA

Carapace with one or two transverse furrows (Figs. 1281, 1282) or furrows absent. Immovable digit of chela with eight, and the movable one with four sensory hairs. Femurs of legs in I and II subdivided by a furrow differently than in legs III and IV. Chitinous plate of pseudosternum absent between coxae of legs. Paleogene to Recent. Four families in the Recent fauna: Antemnidae, Chernetidae, Myrmochernetidae, Cheliferidae, which are primarily tropical and subtropical pseudoscorpions. Only the last two families have fossil representatives.

Family CHERNETIDAE Menge, 1855

Carapace elongate, longer than wide, anterior margin more or less rounded; with one or two faint transverse lines on the posterior half of the shield (Fig. 1281). Eyes well developed, rarely absent. Setae on body and pedipalpi show normal development and not spatulate. Tuft of flagellum on chelicerae consists of two to four setae. Ducts of poison glands located only in the immovable digit of chelae of pedipalpi. A second more or less rare row of teeth projecting slightly from margin present on both digits of chela of pedipalp besides row of teeth on the serrate margin. Tarsi of legs IV with dorsal sensory seta. Paleogene to Recent. Fortythree genera in the Recent fauna. One species—*Oligochernes* Beier, 1937 (Fig. 1281) is from the Paleogene of Europe (Baltic amber).

Family CHELIFERIDAE Hagen, 1879

Carapace elongate or triangular or a square. Transverse furrows and eyes well developed. In some species eyes reduced to mere eye spots. Carapace and terga usually coarse punctate. Setae on body and pedipalpi serrate or thickened at base. Flagellum of chelicerae consists of three to five setae. Ducts of poison glands open on both digits of pedipalpi. Lateral rows of teeth on digits of chelae of pedipalpi absent. Sensory seta present on tarsi of legs IV, rarely absent (Fig. 1282). Paleogene to Recent. More than 30 genera in the Recent fauna. The four genera described from the Paleogene of Europe (Baltic amber) are *Electrochelifer* Beier, 1936; *Oligochelifer,* 1937; *Oligowithius* Beier, 1937; *Pycnochelifer* Beier, 1937

SUPERFAMILY CHEIRIDIIDEA

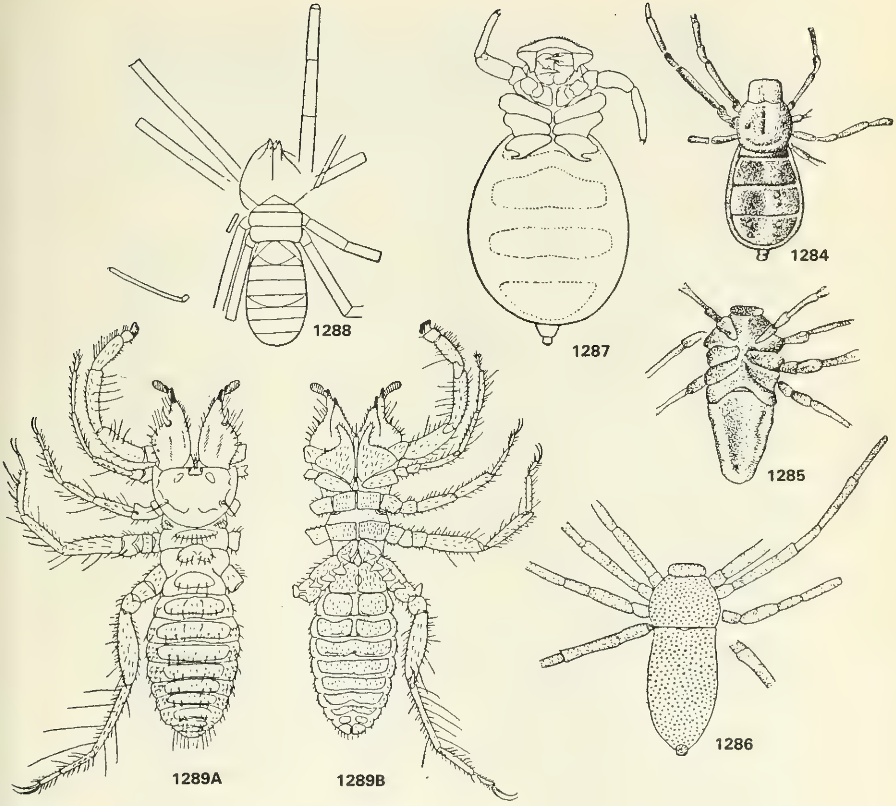
Carapace with two transverse furrows (Fig. 1283). Surface of shield thick and coarsely ornamented. Only one or two sensory hairs on movable digit. Femora of all legs with vestigial, nonfunctional, rudimentary articulation or a furrow. Pseudosternum present between coxae of legs. Paleogene to Recent. Two families in Recent fauna: Cheiridiidae and Sternophoridae; the first family is from the Paleogene of Europe (Baltic amber).

Family CHEIRIDIIDAE Chamberlin, 1931

Anterior margin of carapace with depression. With two transverse furrows on posterior part of the shield. Eyes two, or may be absent. Shield covered with fine or coarse granules. Chelicerae with two or three setae. Ducts of poison glands open only at tip of immovable digit. Walking legs five-segmented (Fig. 1283). Paleogene to Recent. Genus *Cheridium* Menge, 1855, is from the Paleogene of Europe (Baltic amber).

443 Order RICINULEI

Small arthropods with short, stout, oval body consisting of 17 segments. Body divided into prosoma and opisthosoma. Eyes absent. Cephalothorax small, oval or prismatic. Shield covering body usually with longitudinal median depression or transverse furrow along posterior margin and separating the narrow part of the shield (apparently homologous with metapeltidium). Anterior margin of the shield with a mobile, oval plate (cucullus) bent downwards and protecting the mouth parts. Opisthosoma nine- to ten-segmented of which only four are distinct due to the presence of overlapping terga and sterna (Figs. 1284–1287). At the posterior end of the body the last two to three segments become extremely slender and are tube-like, with a short metasoma (Figs. 1284, 1287), a
444 characteristic feature of the subclass Pedipalpides. Mouth parts comprise short two-segmented, claw-shaped chelicerae and comparatively long six-segmented pedipalpi. With short trochanter and femur, stout, long patella, long tubular tibia with a hook-shaped process in front; subterminal to this is located a small claw-like mobile tarsus forming a chela at apex of tibia (Fig. 1287). Basal segment of pedipalp-coxa—short. Both coxae fused forming coxal plate which borders mouth cavity posteriorly. Legs long with many short segments. Leg I seven-segmented. Leg II with six basal segments and tarsus divided into five small segments. Tarsus of leg III four-segmented, and tarsus of leg IV, five-segmented. Apices of all tarsi terminate in two claws. Coxae of legs large and are close to one another except coxae of I and II pair. A medial row of large terga often present on dorsal side of abdomen. Along sides of abdomen are two rows of small marginal terga, separated from median row by longitudinal furrows of soft skin (Polyocheridae and Ricinoiidae). In this respect Ricinulei reminds us of the fossil arachnids, Anthracomarti and Trigonotarbi, which probably trace their origin from Ricinulei-like ancestors (cf. scheme on p. 588). Sometimes, a common dorsal plate separated by a median line is present (Curculioididae).



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Figs. 1284–1289. Orders Ricinulei and Solifugae.

1284. *Polyochera alticeps* Pocock; dorsal view, × 7. Carboniferous, Western Europe (Pocock, 1911). 1285. *Curculioides ansticii* Buckland; ventral view, × 4. Carboniferous, Western Europe (Pocock, 1911). 1286. *Curculioides sulcatus* (Melander); dorsal view, × 6. Carboniferous, North America (Petrunkevitch, 1913). 1287. *Ricinoides feae* Hansen; ventral view, × 5. Recent (Millot, 1949). 1288. *Protosolpuga carbonaria* Petrunkevitch; dorsal view, × 2. Carboniferous, North America (Petrunkevitch, 1913). 1289. *Gylippus fudaicus* Kraepelin; general view; A—dorsal view, B—ventral view, × 2. Recent (Byalynitskii-Birmly, 1913).

Respiratory organs with a pair of stigmata opening at base of legs III, which bear a bag-like atrium with branching tracheae. These resemble analogous structures of Pseudoscorpionodea and some Araneae. Genital opening located between first and second opisthosomatic sterna. In males the copulatory organs develop at the cost of the distal segments of legs III. Length of body of fossil Ricinulei 15.0–16.5 mm and of the Recent forms from 4.5–10 mm.

Ecology and Biogeography. Recent Ricinulei live in soil and plant litter in tropical Africa, Central and South America. Fossil Ricinulei are known from the Carboniferous of Europe and North America.

Classification, Phylogeny and Systematic Position. The Order Ricinulei till recently was grouped close to the orders Anthracomarti, Opiliones and Uropygi (or all Pedipalpi). However, the presence of a pair of stigmata on the prosoma at the base of legs III and the six-legged larva, strongly suggest affinity of Ricinulei to Solipugae and Acarina. The similarity of Ricinulei with these two orders is not perfect in the sense that the position of the stigmata on the prosoma and the absence of a fourth pair of legs in the larva are due to convergence. The resemblance of Ricinulei to the complex Pedipalpi and particularly Amblypygi has been justified by data from comparative anatomy. Ricinulei probably have their origin from amblypygoid ancestors and attained their peak of development in the Carboniferous giving rise initially to two large orders—Anthracomarti and Trigonotarbi. The relationship of Ricinulei to Opiliones has not been thoroughly clarified. Carboniferous to Recent. Three families: Polyocheridae, Curculioididae, Ricinoididae. The last two are known only from the Recent fauna.

Family POLYOCHERIDAE Scudder, 1884

With four well developed abdominal terga and sterna (Fig. 1284). Coxae of legs, I, III and IV in contact with one another. Coxae of leg II widely separate. One genus from Middle Carboniferous of North America and Western Europe.

Polyochera Scudder, 1884 (= *Poliochera* Petrunkevitch, 1953). Genotype—*P. punctulata* Scudder, 1884, Middle Carboniferous, North America (Mazon Creek). Length of body 12.0–15.5 mm (Fig. 1284). Two species from Middle Carboniferous of North America and one from Middle Carboniferous of England.

Family CURCULIOIDIDAE Cockerell, 1906
(Holotergidae Petrunkevitch, 1913)

Terga of abdomen fused with the common shield which is usually divided along median line into left and right halves. Shield rarely undivided. Sterna of third segment of abdomen divided into three parts. Sometimes ventral side of abdomen without segmentation. Coxae of leg IV in close contact and fused. Carboniferous of North America and England.

Curculioides Buckland, 1837. Genotype—*C. ansticii* Buckland, 1837; Carboniferous, England (Coseley). The diagnostic characters of the family are well developed. Length of body 15.0–16.5 mm (Figs. 1285, 1286). Three species from the Carboniferous of North America and three from the Carboniferous of England.

Class SOLIFUGOMORPHA. Proterosomous Arachnids

(V.B. Dubinin)

445 Body segmented according to the modified trilobate (three tiered) type, into head—proterosoma and the trunk segment—hysterosoma. Proterosoma consists of first three postoral segments forming the primary cephalic, or larvalcomplex, and one postlarval-occipital. The trunk or hysterosomatic segments are represented by separate segments with legs III and IV (Mesosoma) and all abdominal (Opisthosomatic) segments. Body of Solifugomorpha generally comprises 16 segments (Figs. 1288, 1289). Propeltidium large and distinctly separated from the remaining segments. Mouth parts consist of large claw-like chelicerae which assist in mastication of food. A large mouth tube or rostrum is located between bases of the chelicerae. It consists of a fused labrum with feathery setae at the anterior end forming a peculiar net, two lateral lobes also with setae and a ventral dentosternum. Pedipalpi large and leg-like. Legs long and of walking type. Legs I tactile in function and more slender than remaining pairs. Stigmata of tracheae located on abdominal sterna II–IV. Additional pair of stigmata between coxae of legs II and III are neogenic. Abdomen of ten distinct segments. Seventh segment of body (rudimentary first segment of abdomen) present in the form of a small triangular plate between coxae of legs IV. In some species there is small tergum corresponding to the plate lying behind the terga of the two thoracic segments, homologous to the meso- and metapeltidium (Fig. 1289). Genital opening of female located at the trilobed genital cone.

Ecology and Biogeography. Representatives of the only order of the class Solifugomorpha live in dry deserts and steppes, particularly in hilly country of tropical and to some extent of temperate zones. Primarily nocturnal, predaceous animals. Carboniferous to Recent.

Classification and Phylogeny. The presence of paired stigmata of respiratory organs on sterna of IX–XI segments of body (second-fourth segment of abdomen) is an indication of the independent evolution and separate origin of the class Solifugomorpha from primitive Pedipalpides. The class Solifugomorpha with its solitary order Solifugae represents, among other chelicerates, a separate group related to the primitive Pedipalpides, particularly to the order Palpigrades and suborder Schizopeltidia (Uropygi) from which it has originated. The class Solifugomorpha is not related to other terrestrial arachnids which arose much later from amblypygomorphous forms and were included under the class Arachnida, or prosomous arachnids (cf. p. 723 and scheme on p. 588).

Class Solifugomorpha exhibits certain affinities with the mites of class Acaromorpha from which it differs in basic features of structure and biology including the retention of nonsegmented larval tegma of body (proterosoma) which in the mites is divided into gnathosoma and propodosoma. Class Solifugomorpha contains one order—Solifugae.

446 Order SOLIFUGAE

Large chelicerates (length of body 10 to 70 mm) with prominent trilobed division of body. Head fused with one thoracic segment (propeltidium). Thoracic segments distinct, separate and three in number except in the species of the family Hexisopodidae Pocock, where they are fused together. Abdomen ten-segmented (Fig. 1289). Head truncated in front, bears eye tubercle with a pair of eyes or tuft of setae or spines. Chelicerae very large with stout bases, the long digits of chelae with serrated sharp margins. Inner margin of chelicera smooth or with longitudinal folds of sound producing organ. A mouth tube present at base between bases of chelicerae. Large triangular coxae of pedipalpi and smaller coxae of legs I firmly adhere to head segment on ventral side. Pedipalpi adapted for grasping prey and are tactile. Ventral surface of palpal segments with various spines which in the males possess various additional specialized spines and glandular papillae for holding females during copulation.

Thoracic segments smallest in size and covered by soft chitinous terga—usually three on dorsal side. On the ventral side corresponding to these are three pairs of hard plates—the coxae of the walking legs (Fig. 1289). Four pairs of walking legs are attached to thoracic segments. They are usually long, slender and rarely short, the first pair is the most slender and shortest with six segments (trochanter divided into two segments) and play an auxiliary role as sensory organs. Legs II six-segmented and legs III and IV seven-segmented, their trochanters divided into three parts. Tarsi of all posterior pairs of legs with two claws. Claws with a distinct and separate, small structure called the unguiculus. Claws connected to the common pretarsi forming a small lobe (pulvillum) at base. Segments of legs covered with large number of hairs, long setae and shorter spines. Femora and first and second trochanter of legs IV, with two to five peculiar triangular processes (malleoli)—structures of unknown function (Fig. 1289).

Abdomen large, sac-like and ten-segmented. With a prominent triangular plate between coxae of legs IV and first segments of abdomen. This plate is apparently the rudimentary first segment of the abdomen. Each segment with a tergum covered with setae or spines on the dorsal side and with a paired sterna divided by a narrow band of soft cuticle along the ventral median line of the body. The sternum of first abdominal segment is an exception, in this segment the genitalia open and are protected by semilunar valves (Fig. 1289). Under the posterior margins of second and third sterna, near the median line, are a pair of spiracles, that are sometimes covered by pectinate or feathery setae. An unpaired rudimentary spiracle is present under the edge of the fourth segment. Anal opening located on last abdominal segment. Sexual dimorphism weakly developed. Females oviparous. Impregnation by spermatophores. Carboniferous to Recent. Ten families in the Recent fauna, one family (Protosolpugidae) from Carboniferous.

Family PROTOSOLPUGIDAE Petrunkevitch, 1953

Thorax with three free segments; abdomen seven-segmented. Chelicerae with very thick bases and short pointed digits. Pedipalpi leg-like and large. Legs I significantly more slender than remaining pairs of legs. Eyes absent. Length of body with chelicerae 22 mm long and abdomen 12 mm. Middle Carboniferous of North America. One genus—*Protosolpuga* Petrunkevitch, 1913 (Fig. 1288).

Class ACAROMORPHA. Ticks, mites or gnathosomous chelicerates

(V.B. Dubinin)

447 The mouth parts of ticks and mites, unlike other chelicerates, are separated from the rest of body by means of a false head or gnathosoma, also called a capitulum, head, or proboscis. The gnathosoma is formed of three anterior segments: the preoral (acron), the second bearing chelicerae and the third bearings pedipalpi.

Segmentation of the remaining body is partly retained in some very primitive forms (suborder Palaeacariformes, superfamily Pediculoididea, Endeostigmata, etc.). Segmentation is poor or absent in most species. Its presence can be judged from the position of setae forming rather clearly expressed transverse rows on the body; sometimes it is clear from the segmented location of furrows, setae, etc. A tendency towards a partial reduction of the body is noticed in the class Acaromorpha. In some Acariformes there is a shortening of the body at the expense of the disappearing metasoma and one to three segments of the mesosoma. The most primitive—ragoidal—type of body division among Acaromorpha is retained by some Palaeacariform mites in which the head lobe and first two segments (proterosoma) are covered with a shield (Propeltidium, Schizopeltidium) whereas the segments of legs III—IV are separated. Modification of this primary type of division occurs in the trilobate body of some primitive mites (Nanorchestidae; Fig. 1339) wherein a special shield, metapodosoma of legs III–IV is quite distinct. During further fusion of body segments an acaroidal type of segmentation (characteristic of order Acariformes) and arachnoidal type of segmentation (characteristic of the order Parasitiformes) appears. The first type arises due to the fusion of the metapodosoma with the opisthosoma forming a single hysterosoma, and the second—due to the fusion of the metapodosoma with the proterosoma and secondarily convergent prosoma (Parasitiformes) but with the retention of a separate gnathosoma.

The body of ticks and mites consists of 13 primary segments of which three constitute the gnathosoma two (IV–V)—the propodosoma bearing the two anterior pairs of legs, and two (VI–VII)—metapodosoma bearing two posterior pairs of legs. The remaining six segments form the opisthosoma, often called 'abdomen'. The number of opisthosomal segments varies from six (in large mites) to seven–nine (in *Parhypochthonius* and *Pachygnathus*) and further up to ten-eleven (in *Opiliocarina* or *Notostigmata*). The propodosoma in majority of forms is separated from the metapodosoma by a transverse furrow. Consequently, the body of mites is subdivided into two major divisions: anterior—proterosoma consisting of gnathosoma and propodosoma and posterior—hysterosoma consisting of metapodosoma and opisthosoma fused with the former. Only in some forms (for example, in *Speleorchestes*; Fig. 1339) the gnathosoma, propodosoma, metapodosoma, and opisthosoma are completely separated from one another.

448 The following nomenclature of body divisions (tagma) of mites is adopted:

I.	Section of the body comprising mouthparts (Chelicerates and pedipalpi)	Gnathosoma	Proterosoma		Prosoma	
II.	Section of the body to which legs I and II are attached	Propodosoma		Podosoma		Idiosoma
III.	Section of the body to which legs III and IV are attached	Metapodosoma	Hysterosoma			
IV.	Posterior division (abdomen) of body	Opisthosoma				

The prosoma of mites and ticks, as an assemblage of segments, corresponds to the cephalothorax of other arachnids. However, the segments constituting it are not fused and do not form a separate part (Tagma) of the body termed a cephalothorax but are fused with the posterior abdominal segment—the opisthosoma of other chelicerates.

The sclerotized covering of the body is highly variable. In the Notostigmata, it is leathery—a type of thin, granular cuticle. In most forms of the order Acariformes the integument is thin, elastic and transparent forming dense shields at places. In other groups, particularly Oribatei, Holothyroidea are many Mesostigmata, the body is covered with hard protective shields that are occasionally fused with one another. The surface of the cuticle may be smooth or more or less elaborately ornamented. Many cuticular structures are derivatives of hypodermal tissues. Special glands of hypodermal origin open on to the surface of the body. Setae of different shapes and sizes occur on the body and the appendages of mites. They are organs of touch, chemoreception and mechanical defense that determine the intensity of pressure and movement of the media and protect against excessive secretion of water. The shape and distribution of setae (character of chaetotaxy and composition of chetoma) are of great importance in classification. The chemical nature of setae and to some extent that of body cuticle differs in different groups of ticks and mites. Setae, particularly their internal lining in Acariforme mites (Sarcoptiformes and Trombidiformes), exhibit the property of light refraction (white luminescence 'Actinochitin') in polarised light. These are stained with iodide while in the orders Parasitorformes and Opilioacarina the chemical composition of setae is optically inactive and is not stained with iodide. Besides setae, various other structures occur on the body and legs, such as special sense organs in the form of pseudo-stigmatic organs, and sensilla or trichobothriae, the bases of which are situated in complex cup-like depressions (bothrydiae or pseudostigmata). There are also gall forming or rhagidia forming organs on legs of ticks and mites of Ixodidae and Rhagidiidae, etc. Many free living mites are with a single or paired simple eyes situated on the dorsal side of the propodosoma. The chelicerae are usually two-, three or rarely four-segmented and claw-like; in certain groups they become stiletto-shaped, adapted for piercing animal or plant tissues. In males of most Mesostigmata the mobile digit of the chelicera is transformed into an additional Rhagidiid organ. Pedipalpi are located along the sides of the coxae of the chelicerae. In the Devonian *Protacarus crani* Hirst (Fig. 1341) the pedipalpi are seven-segmented; in Recent mites, not more than six segments develop because of the fusion of the basi- and telofemur. The simple pedipalpi resembling legs in some mites are strongly modified and changed to claw-like prehensile organs of predatory Cheyletidae or, in other forms, are greatly reduced to small papillae.

Larvae often have three pairs of walking legs, and nymphs and adults have four pairs. Still mites of the order Eriophyiformes (Fig. 1361), in all stages of development, have only two pairs of legs and in some Podapolipidae, only one pair. In larvae of some parasitic species (as for example, *Demodex bovis* Stiles) there is total suppression of legs. Legs, like pedipalpi, are six to seven-segmented. In a few species the number of segments may be further reduced to a single segment because of the fusion of the primary segments with one another. Rarely there is a secondary subdivision into a large number of segments (up to 18).

Tarsi of legs, in typical cases, have one or two claws. Compared to members of the class Arachnida, all Acaromorpha are characterized by the complete absence of a thorax. In Parasitiformes mites the metamerically segmented thoracic sterna are preserved whereas in Acariformes mites the thoracic sterna are absent and are substituted by the coxae of the walking legs, which are
449 sometimes fused with the integument forming peculiar coxal shields. In the segmented mites of the superfamily Pachygnathidea, family Rhodacaridae, and others the first (pregenital) abdominal segment has a corresponding group of sensory setae.

The external genitalia of females and of some males are composed of three lobed genital cones. In some mites this cone is modified into a longitudinal slit, the genital opening. In females of many mites a transverse slit is present on the surface of the body and is covered by leathery valves and usually by an unpaired valve (epigeni).

The respiratory system in the subclass Acari is of great taxonomic importance. In one group (suborders) it consists of tracheae and their openings (stigmata) and in others by a considerable reduction or absence. Respiration in the latter group is carried out through the thin integument of the body. Location of respiratory openings and their structure is highly varied. In the phalangids of the order Opilioacarina (Notostigmata) four pairs of stigmata are present on the terga of the first four opisthosomal segments. The suborder Holothyroidea (Parasitiformes) has two pairs of stigmata of which the anterior pair is situated along the sides of the body over the coxae of legs III. In other groups of Parasitiformes (suborders Mesostigmata and Ixodides) there is a pair of stigma located on the wide peritrema along the sides of the body at the level of or in front of the coxae of legs III (Mesostigmata), or behind the coxae of legs IV (Ixodides). In Acariform mites of the suborder Trombidiiformes the stigmata open on the dorsal side of the gnathosoma or between the gnathosoma and propodosoma (in the Tarsonemidea one or two pairs of stigmata open on the propodosoma). In males of many species of mites the respiratory system is absent. In beetle mites of the suborder Oribatida (adults) covered with the thick body integument tracheae are developed which open by means of stigmata located near the coxae of the legs and porous areas on many parts of body.

Ticks and mites are dioecious. Sexual dimorphism is variably developed. Fertilization is internal through copulation or insertion of spermatophores. A few mites are parthenogenetic. Females are oviparous or viviparous.

The life cycle is usually characterized by a succession of six consecutive, metamorphic stages. Eggs (in some species one-two embryonic molts known—larvae-protonymphs-deutonymphs—trito or teleonymphs and adult males and females. In many groups, the life cycle may be specialized and some stage of metamorphosis may be omitted. The entire development is characterized by the retention of early juvenile characters exhibiting apomorphic phenomena.

ECOLOGY AND BIOGEOGRAPHY. Ticks and mites are encountered everywhere. Some live above ground, while others are subterranean, may be saprophytes or predators, or some live in fresh water or are marine, and some live as ectoparasites or endoparasites of vertebrates and insects. Between these extreme ecological types are all possible transitions. A large number of species and individual mites are encountered in the moist forest litter and, sometimes, on trees. This most probably explains the occurrence of the large number of species (ninety-five) in the Baltic amber. Because of their small size they are not found as fossils in more ancient deposits. Yet from the Eocene of Punjab a Lyroglyphoid mite *Palaeotyroglyphus fossilis* (Mani, 1945) (—*Gamasus fossilis*), and from the Eocene of Wyoming (Green river)—a parasitic tick *Ixodes* have been described. From the Devonian Red Sandstones of Scotland, Hirst (1923) discovered a complete group of primitive mites belonging to four families (Nunorchestidae, Pachygnathidae, Alicorhagiidae and Tydeidae) which were in the beginning erroneously assigned to the species—*Protocarus crani* Hirst (cf. p. 706). Besides these some species have been described from the brown coals of

Germany (Heyden, 1860, 1862; Thomas, 1877; Trotter, 1899; Kuster, 1911), and some from ten to thirteen thousand-year old buried sphagnum bogs in England (Harrison, 1926). Leaves of over fifteen species of trees and bushes were discovered with felt-like or horn-like galls of the mites of the suborder Eriophyiformes. The remains of galls of Cecidomyiidae and also gall-like mites are known from the Sarmatian stage of Amvrosievka (South Ukrainian SSR) (Pimenova, 1954). Most mites from the Paleogene of Europe (Baltic amber) belong to Recent genera and species. Only a few of these are fossil forms. It is interesting that mites from the Devonian are representatives of recent families (cf. p. 706).

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. Most investigators are inclined to consider the Acarina as one of the orders of the class Arachnida 450 containing up into seven–ten suborders and a large number of families. Petrunkevitch (1949) proposed a new classification of the class Arachnida wherein 13 orders of arachnids are grouped under four subclasses. The order Acari along with the orders Architarbi, Opiliones, Pseudoscorpiones and Scorpiones constitute the subclass Latigastra. Yet, Baker and Wharton (1952) already pointed out that if the classification of Petrunkevitch is recognized then it is more appropriate to reconsider the Acari as an independent subclass. Zakhvatkin (1952) suggested an interesting classification of the entire superclass Chelicerata. Based on the work of Grandjean and further expanding it somewhat on the basis of the presence of anisotropic substance (chitin*) in the setae of mites, he suggested a division of all mites of Acari into three independent orders: First—the order Acariformes of the Recent mites corresponding to the combined suborders Sarcoptiformes, Trombidiiformes, Palaeacariformes. Oribatei and Tetrapodili (Eriophyiformes); second—the order of Gamasoid mites—Parasitiformes corresponding to one suborder in the existing classification, with the inclusion of the suborder Holothyroidea; third—the order of mite-phalangids, Opilioacarina, consisting of the one family Opilioacaridae. These three orders are clearly distinguished by their structural peculiarities (tagmosis and development, structure of respiratory and reproductory system, etc.). However, the phylogenetic relationships of the different orders of mites and ticks with other orders of the class Arachnida established by A.A. Zakhvatkin (1952), almost exclusively on the presence or absence of an anisotropic covering substance in the body setae, and the subclasses of Chelicerata described on this basis lack sufficient justification. In the present work we consider ticks and mites as constituting an independent class Acaromorpha comprising the three orders proposed by Zakhvatkin (1952). The classification suggested by V. Dubinin (1956) includes a maximum number of fossil species and groups of Recent ticks and mites which are represented by the order Acariformes.

A comparison of known fossil and Recent ticks and mites shows that

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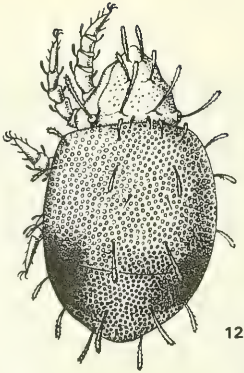
*Editor's note: No chitin present in mites.


1290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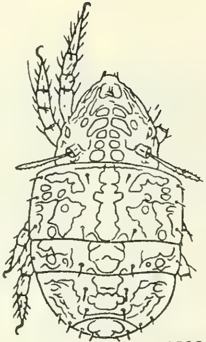
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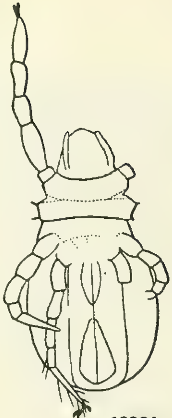
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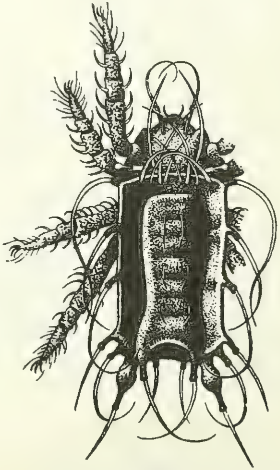
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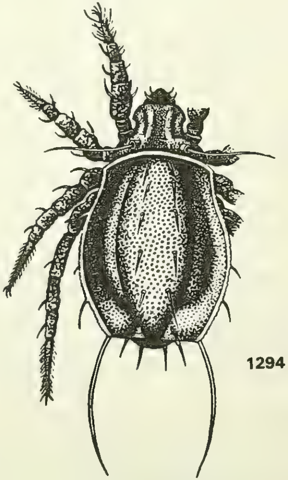
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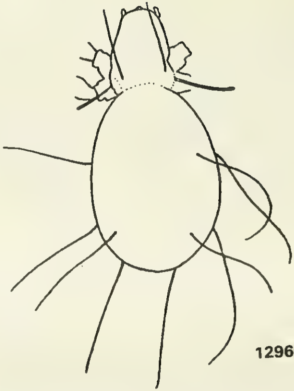

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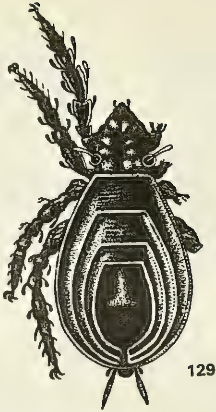


1297

Figs. 1290–1297. Families Acaridae, Hypochthoniidae, Camisiidae and Neoliodidae.

1290. *Palaeotyroglyphus fossils* Mani; ventral view, × 100. Neogene, India (George, 1952). 1291. *Trhypochthonius tectorum* (Berlese); dorsal view, × 100. Recent (Berlese, 1882). 1292. *Brachychthonius brepis* (Michael); dorsal view, × 100. Recent (Hanmer, 1952). 1293. *Camisia spinifer* (Koch); dorsal view, × 110. Recent (Michael, 1887). 1294. *Nothrus palustris* Koch; dorsal view, × 100. Recent (Berlese, 1896). 1295 *Neoliodes theleproctus* (Hermann); dorsal view, × 100. Recent (Michael, 1887). 1296. *Embolacarus pergratus* Sellnick; dorsal view: A – ventral view; B—dorsal view, × 100. Paleogene, Europe (Baltic amber) (Sellnick, 1918). 1297. *Platyliodes doderleinii* (Berlese); dorsal view, × 100. Recent (Berlese, 1896).

terrestrial forms throughout their evolutionary history have retained primitive features of organization and development. More progressive development is shown by species changing over to predation, and particularly to parasitic life on plants and animals.

Distribution in Time. Ticks and mites are known from the Devonian. They were probably distributed in most parts of the world (presently they are not known from Antarctica). Concerning their wide distribution, it has been reported, for example, that specimens closely related to Recent Indian and Javan (one genus) species have been found in Baltic amber. The circumpolar distribution of some Oribatei supports the same.

Order ACARIFORMES. True mites (Trombidii-Sarcoptiformes; Actinochitinosi)

Three types of body division are observed in the Acariformes: Acaroidal, Trilobate and Ragoidal. Acaroidal type: body consists of proterosoma bearing mouthparts and two anterior pairs of legs and hysterosoma. Trunk with two posterior pairs of legs (for majority of the groups see Figs. 1290—1388). In the Trilobate type, opisthosoma more or less sharply differentiated, last two prosomatic segments, i.e., V and VI forming metapodasoma as seen in a few Pachygnathidea, as for example, Nanorchestidae (Fig. 1339) and others. In the Ragoidal type, segments of legs II (occipital) are partly separated from rest of the cephalic ones; segments of legs III and IV more or less distinctly differentiated from each other and from those of opisthosoma: example—Palaecariformes. A secondary, complete fusion of all the divisions, except the gnathosoma, is observed in some forms. In this, the body becomes monolithic and completely loses all traces of segmentation (example, advanced Trombidiformes; Figs. 1346 and 1350–1356).

The most primitive representatives of Acariformes possess a thin, membranous integument with a vague microstructural pattern of ribs and granules which usually become fully developed only during the last molt wherein typical adult features appear. Maximum development of a complex and hard test is found only in Oribatei, though it is mostly embryonic even in the later nymphal stages of these mites. In all other groups of Acariformes a thick chitinous integument is not developed in adult forms. Adult mites of this suborder morphologically correspond to the teleonymphal stage of Oribatei. It is obvious, that only in higher mites with test is there a complete development up to the imaginal stage.

451 Body setae characterized by exceptional regularity of arrangement and uniformity of structure, particularly on dorsal side of proterosoma and metapodosoma. During metamorphosis there is a progressive (phase-wise) increase in new segmental groups of setae (chetomeraes) at tip of opisthosoma, reflecting an anamorphic nature of individual development. All body setae and appendages and their modifications (trichobothria, claws, teeth of chelicerae,

suckers, etc.), with actinochitinous core characterized by optical anistropy.

Legs usually homonomous and of moderate length and thickness, primitively seven-segmented; segments may coalesce with one another forming a four-six segmented leg. In all Oribatei and Sarcoptiformes (s. latu) and most of Trombidiidae, coxae firmly fused with exoskeleton of abdominal region of body, forming a continuous coxosternal skeleton. True sterna absent. Tarsi with a small claw at the tip (Oribatei, Saccoptiformes) which in Trombidiiformes is in the form of an empodium, often pinnate or complexly segmented. Sometimes, the paired setae at apex of tarsus modified into paired claws (Fig. 1297).

In the less advanced Acariformes tracheal system is absent. Only in Oribatei does it appear simultaneously with the development of the thick chitinous integument, that is, only during metamorphosis into the adult "armoured" phase. In Trombidiiformes the tracheal system is characterized by the presence of two pairs of major tracheae opening at the base of the gnathosomal chelicerae.

Post-embryonic development proceeds along the tritonymphal type of metamorphosis. However, in many Sarcoptiformes (*S. latu*), the deutonymph either stops its growth, transforming into settled or quiescent hypopial stage or completely disappears from the developmental cycle. During development, the phenomenon of anomorphism is observed.

ECOLOGY AND BIOGRAPHY. There is an extreme diversity in the ecology and biology in the species of Acariformes. The most primitive forms live in surface layers of soil and litter of decayed vegetal remains. More specialized and modified forms inhabit fresh and marine waters or are parasitic on plants and animals. Largest number of remains of Acariformes are known from Baltic amber. A considerable number of forms discovered from there is related to the Recent genera and species. The most ancient Acariformes are known from the Devonian of Scotland and belong to the families represented by Recent fauna but possess a series of very primitive structural features such as body segmentation, retention of many-segmented chelicerae, etc. (cf. p. 706 – 708).

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. The order Acariformes comprises the most primitive groups of mites showing affinities with the classes Solifugomorpha and Scorpionomorpha (orders Uropygi, Palpigradi and Pseudoscorpionodea).

Devonian to Recent. Five suborders: Palaecariformes, Acaridiae, Oribatei, Trombidiiformes and Tetrapodili (V. Dubinin, 1954), the last four suborders have fossil representatives.

Suborder Acaridiae. Sarcoptid mites

(Sarcoptiformes)

Body division acaroidal type; integument delicate, smooth or thinly striated with granular ornamentation. Sclerites, if present, confined only to dorsal side of body: one is propodosomatic and most constant, one opisthomatic with two marginal pairs; very rarely integument wholly sclerotized (genus *Gohieria* Oudemans, of family Glycyphagidae). Trichobothria absent. Gnathosoma small, connected with anterior end of body and easily visible from dorsal side; camerostome, if present, covers often only base of gnathosoma. Chelicerae smooth, claw-shaped and two-segmented. Pedipalpi simple and two-five segmented. Legs of walking type with five free segments. Coxae fused with the exoskeleton of ventral side of body. They are represented only by narrow sclerites—epimers and epimerites forming in the anterior part of ventral side of body a typical coxo-sternal skeleton. Valves of genital and anal openings soft, slender and without setae. Well developed respiratory organs absent. Respiration carried out through thin integument of body.

Numerous species; live in soil and in heaps of plant litter. Also, live as ecto- and endoparasites on animals. Paleogene to Recent. Seven superfamilies: Pediculoiodidea, Anoetidea, Canestrinidea, Sacroptidea, Analgesidea, Listrophoridea and Acaridea. Only the last one known in fossil state.

452 SUPERFAMILY ACARIDEA. Stored-grain mites

(Tyroglyphoidea Auctorum)

Integument thin, soft, smooth and granular or weakly spinose, very rarely with fine more or less parallel striae. Gnathosoma compact, small and open, joined to anterior end of body. Legs homonomous, similar in both sexes.

Free-living and saprobiotic forms, usually live in heaps of sufficiently damp and decayed plant litter. Some species live on leaves of plants and in soil. Stationary, hypopial stages commonly use epizootic mode of dispersal with the help of insects or vertebrates. Only one family known in fossil state.

Family ACARIDAE Latreille, 1802

(Tyroglyphidae Donnadieu, 1868; Parasitidae Mani, 1945, 1946)

Setae of idiosoma always smooth, hairlike or needlelike. Males with well developed anal and usually two pairs of tarsal copulatory suckers. Females without epigyne. Genital appendage digitate (Fig. 1290). Neogene to Recent. Recent fauna with a large number of genera. Following genera are known in fossil form: *Acarus* Linnaeus, 1758 (*Tyroglyphus* Latreille, 1796) from the Paleogene of Europe (Baltic amber), *Tyroglyphites* Pampaloni, 1902 from the Miocene of Sicily and *Palaeotyroglyphus* W. Dubinin, nom. nov. (= *Gamasus* Mani, 1945, 1946). Genotype—*Gamasus fossilis* Mani, 1945; Larva (and not protonymph as written by Mani, 1945 and George, 1952) (Fig. 1290). Length of the body 0.24 mm. Neogene (?) of Punjab.

Suborder Oribatei. Beetle mites

Body division acaroidal type but gnathosoma hidden under the extensive projection of anterior margin of propodosoma. It is connected at a peculiar depression on ventral side of propodosoma—Camerostoma.

Integument in adults usually strongly sclerotized, thick, dark colored forming an armour (Figs. 1298–1338). In the less evolved oribatids (Fig. 1292) armour-test not so strong and the integument membranous. In the early stages of development integument is weakly sclerotized. Propodosoma in all stages of development with trichobothria the bases of which are lodged in complex cups —bothrydia (Fig. 1297). The size and shape of trichobothria variable. Pedipalpi simple, four-five segmented. In many species dorsal surface of propodosoma with longitudinal keels (Figs. 1303, 1307), ribs (Fig. 1316) or large plate. Sides of propodosoma with various platy projections—Tectopedia (Damaeidae; Fig. 1301); and leaf-like, immovable (Fig. 1331) or movable (Fig. 1335) plates—pteromorphs are developed on sides of notogastral shield, in species of superfamily Notaspididae (Fig. 1324–1336). All these formations protect legs, particularly in preventing joints from becoming dirty and damaged. A few species retain, throughout their life, patches of integument of the preceding state of development on the dorsal surface of hysterosoma (Fig. 1295). In this process, special adaptions to fix these skins are developed.

Legs of walking type. Coxae fused with skeleton of ventral surface of body. Epimers of coxae represented here by coarse transversely disposed cylinders laying parallel to one another. Coxae often fused with chitinous ring around kamerostoma. Tip of tarsi in all immature adult stages of development with one large claw and in fully adult mites with one to three 'claws' (Figs. 1293, 1297).

Sexual dimorphism absent. With three pairs of genital suckers. Valves of genital and anal openings rectangular, strongly chitinized and surrounded by a chitinous frame (Fig. 1305). Females with very long and telescopic ovipositor with three digitate projections at apex.

Respiratory system consists of tracheae and stigmata opening at bases of legs. On the thick test of many species there are porous patches—named porous 454 areas—where tracheae terminate. The tracheal system is a secondary development in Oribatei. In all immature adult stages and in the primitive tests of mites devoid of thick chitinous exoskeleton, tracheae and stigmata are absent.

Post embryonic development of tritonymphal metamorphic type. Larvae and nymphs sharply distinct from adult mites.

Oribatei occur in large numbers (up to 10–20 thousand in an area of 1 m^2) in the upper layers of soil covered by vegetation. They are particularly numerous in forests and meadows, especially on surface soils with abundant moist litter. The mites crawl up trees to a height of 20 meters, inhabit burrows of rodents, and other shelters. The abundance of oribatids in forests explains their frequent occurrence mostly in amber. Paleogene to Recent. Two infraorders: Aptyctima and Ptyctima.

Infraorder Aptyctima

Propodosoma immovably joined with hysterosoma, with a prominent transverse furrow at junction of two (Figs. 1291–1297). Only in certain species (genus *Amerus* Berlese) may the transverse furrow disappear because of fusion of the propodosomal shield with the notogastral shield. Paleogene to Recent. Ten superfamilies: Hypochthoniidea, Camisiidea, Hermanniidea, Damaeidea, Carabodidea, Hermanniellidea, Notaspididea; the remaining three superfamilies—Epilohmanniidea, Eulohomanniidea, Nanhermanniidea—are represented only in Recent fauna.

SUPERFAMILY HYPOCHTHONIIDEA

(Circummarginatae)

Dorsal surface of hysterosoma weakly convex or flat. Integument relatively thin, and soft. Armour clad test so characteristic of all oribatids is absent or there may be only numerous small shields (Fig. 1292). Valves of genital and anal openings very large, in contact with one another, occupy entire length of the abdominal section of the hysterosoma, surrounded by a generally narrow chitinous border. Paleogene to Recent. Four families: Malaconothridae, Lohmanniidae, Trhypochthoniidae, Hypochthoniidae. The last one is known in fossil state.

Family HYPOCHTHONIIDAE Berlese, 1910

Thicker parts of dorsal surface of hysterosoma with dots (Fig. 1292). Dorsal surface of hysterosoma divided by one to four transverse sutures (furrows) giving rise to two-five separate shields (Fig. 1291). Genital shields usually larger than anal. Paleogene to Recent. Eighteen genera in Recent fauna of which the following two are from the Paleogene of Europe (Baltic amber): *Trhypochthonius* Berlese, 1904 (Fig. 1291) (two species) and *Brachychthonius* Berlese, 1910 (Fig. 1292) (one species).

SUPERFAMILY CAMISIIDEA

Dorsal suface of hysterosoma flat with concave median part and raised borders. Integument soft but strongly chitinous. Posterior end of body broadly rounded, truncated or with groove, or with large setae of different sizes and shapes borne on processes or prominences of the shield. Paleogene to Recent. One family—Camisiidae.

Family CAMISIIDAE Sellnick, 1928

(Oribatidae Karsch, 1884)

Genital and anal openings in contact with each other and close to them lie small shields (Figs. 1293, 1294). Paleogene to Recent. Six Recent genera of which the following two are from the Paleogene of Europe (Baltic amber); *Camisia* Heyden, 1826 (Fig. 1293) and *Nothrus* Koch, 1836 (Fig. 1294).

SUPERFAMILY HERMANNIIDEA
(Immarginatae)

Integument strongly chitinized. A dense notogastral shield (test) is seen on dorsal 456 side of hysterosoma. Posterior and lateral, abdominal margins of the shield bent. Genital and anal openings in close contact but not surrounded by a common chitinous cover. Paleogene to Recent. Two families: Neoliodidae and Hermanniidae of which the second is found only in Recent fauna.

Family NEOLIODIDAE Willmann, 1913

Margin of dorsal shield bent ventrally forming narrow projection (tail) at posterior end of body. Valves of genital opening subdivided by transverse furrow. The larval integument of all preceding stages of development retained on dorsal side of hysterosoma (Fig. 1297). Paleogene to Recent. Four genera in Recent fauna. Genus *Embolacarus* Sellnick, 1919 from Paleogene of Europe (Baltic amber). The Recent genera *Neoliodes* Berlese, 1888 (Fig. 1295) and *Platyliodes* Berlese, 1916 (Fig. 1297) are also from Baltic amber.

SUPERFAMILY DAMAEIDEA

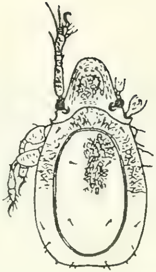
Margins of dorsal shield coincide with body margins or bent towards ventral side of body. Surface of notogastral shield smooth or with dark colored areas (Figs. 1298–1302). Sides of bases of propodosoma of legs I and II with broad triangular, horny projections. Paleogene to Recent. Three families: Cymbaeremaeidae, Damaeidae, Oribatidae.

Family CYMBAEREMAEIDAE Willmann, 1931

Margins of dorsal shield bent particularly along ventral sides of body. Surface of dorsal and propodosomatic shields with a dense reticulate configuration (Figs. 1298–1300). Paleogene to Recent. One extinct genus *Tectocymba* Sellnick, 1919 from the Paleogene of Europe (Baltic amber). Three genera in the Recent fauna of which *Cymbaeremaeus* Berlese, 1896 and *Micreremus* Berlese, 1908 are also found in Baltic amber.

Family DAMAEIDAE Berlese, 1896
(Belbidae Willmann, 1931)

Dorsal surface of propodosoma smooth, not thickened in anterior half. Dorsal margin of shield not bent on ventral side of body. Surface of dorsal shield smooth or with fine pointed ornamentation. Legs usually long, often longer than body; segments long, rod-like, beaded or bottle-shaped. Paleogene to Recent.



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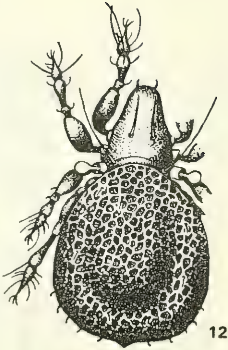

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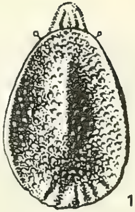

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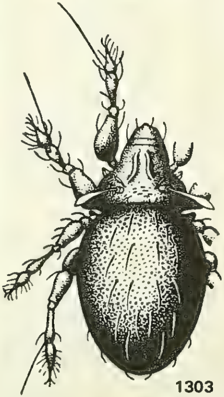

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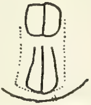
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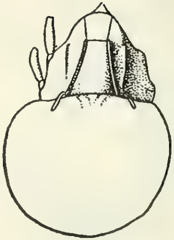
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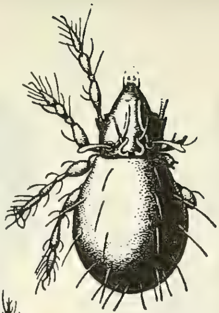
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Figs. 1298–1310. Families Cymbaeremaeidae, Damaeidae, Oribatidae.

1298. *Cymbaeremaeus* (*Scapheremaeus*) *marginalis* (Banks); dorsal view, × 60. Recent (Baker and Wharton, 1952). 1299. *Micreremus brevipes* (Michael); dorsal view, × 100. Paleogene, Recent (Berlese, 1910). 1300. *Tectocymba rara* Sellnick; dorsal view, × 100. Paleogene, Europe (Baltic amber) (Sellnick, 1918). 1301. *Damaeus auritus* (Koch); dorsal view, × 35. Recent (Berlese, 1887). 1302. *Gymnodamaeus retusus* (Berlese); dorsal view, × 40. Recent (Berlese, 1883). 1303. *Eremaeus oblongus* (Koch); dorsal view, × 100. Recent (Berlese, 1910). 1304. *Caleremaeus monilipes* (Michael); dorsal view, × 100. Recent (Berlese, 1887). 1305. *Gradidorsum asper* Sellnick; A—dorsal view; B—valves of genital and anal openings, × 110. Paleogene, Europe (Baltic amber) (Sellnick, 1918). 1306. *Licneremaeus caesareus* Berlese; dorsal view, × 100. Recent (Berlese, 1910). 1307. *Lucoppia lucorum* (Koch); dorsal view, × 100. Recent (Berlese, 1910). 1308. *Oppia longilamellata* (Michael); dorsal view, × 100. Recent (Michael, 1887). 1309. *Ceratoppia bipilis* (Hermann); dorsal view, × 100. Recent (Berlese, 1887). 1310. *Strieremaeus illibatus* Sellnick; dorsal view, × 85. Paleogene, Europe (Baltic amber) (Sellnick, 1918).


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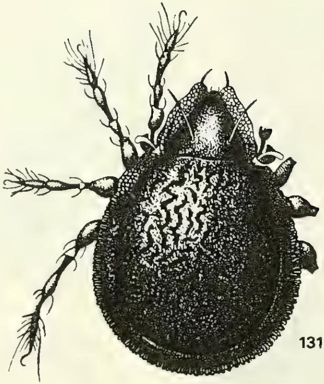
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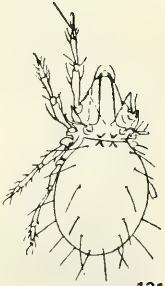
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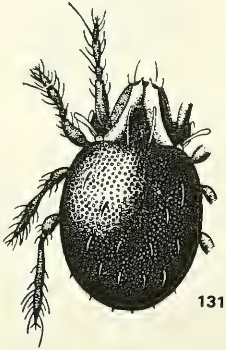
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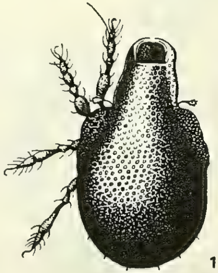
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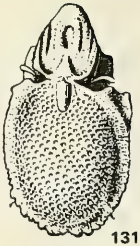

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Figs. 1311–1320. Families: Carabodidae, Liacaridae and Hermanniellidae.

1311. *Carabodes femoratus* Berlese; dorsal view, × 100. Recent (Berlese, 1913). 1312. *Otocepheus damaeoides* Berlese; dorsal view, × 100. Recent (Berlese, 1913). 1313. *Cepheus latus* (Koch); dorsal view, × 90. Recent (Michael, 1887). 1314. *Plategeocranus suicatus* (Karsch); dorsal view, × 85. Paleogene of Europe (Baltic amber) (Sellnick, 1918). 1315. *Scutoribates perornatus* Sellnick; dorsal view, × 90. Paleogene of Europe (Baltic amber) (Sellnick, 1918). 1316. *Xenillus tegeocranus* (Hermann); Recent, × 100. (Michael, 1882). 1317. *Tectocepheus velatus* (Michael); dorsal view, × 80. Recent (Berlese, 1887). 1318. *Ommatocepheus elongatus* (Michael); dorsal view, × 80. Recent (Michael, 1879). 1319. *Cultroribula juncta* (Michael); dorsal view, × 100. Recent (Berlese, 1882). 1320. *Hermanniella granulata* (Nicoli); dorsal view, × 100. Recent (Michael, 1882).

Eight genera in Recent fauna of which the genera *Damaeus* C.L. Koch, 1836 and *Gymnodamaeus* Kulczynski, 1902 (Figs. 1301, 1302) are from the Paleogene (Baltic amber) of Europe. Genus *Belbites* Pampaloni, 1902 has been described from the Miocene of Southern Europe.

Family ORIBATIDAE Kramer, 1877

(Eremaeidae Willmann, 1931)

With dark colored ridges at anterolateral part of dorsal surface of propodosoma and in front of bothridia (trichobothridia). Legs comparatively short, bead-like with stout segments; femurs of legs I and II not slender (Figs. 1303–1310). Paleogene to Recent. About 40 genera in Recent fauna. Three fossil genera: *Gradidorsum* Sellnick, 1919 (Fig. 1305); *Strieremaeus* Sellnick, 1919 (Fig. 1310);*Oppites* Pampaloni, 1902. First two are from Paleogene of Europe (Baltic amber) and the third, from Miocene of Sicily. Besides, from the Paleogene of Europe (Baltic amber) the following Recent genera have been described—*Caleremaeus* Berlese, 1910 (Fig. 1304); *Licneremaeus* Paoli, 1908 (Fig. 1306);*Lucoppia* Berlese, 1908 (Fig. 1307); *Oppia* C.L. Koch, 1836 (Fig. 1308); *Ceratoppia* Berlese, 1908 (Fig. 1309); *Suctobelba* Paoli, 1908; *Eremaeus* C.L. Koch, 1836.

SUPERFAMILY CARABODIDEA W. DUBININ, 1954

Body short, oval, and moderately convex. Dorsal surface of propodosoma with lamellar enlargements in form of keels, ribs, and combs (Fig. 1313). In some species (in the Recent Ameronothidae) they are indistinct or absent; transverse furrow between propodosoma and hysterosoma covered by folds of body and head shields. Margins of propodosoma uniformly rounded. Integument of dorsal surface of body strongly sclerotized with coarse ornamentation; color dark. Legs short. Paleogene to Recent. Five families: Plateremacidae, Zetorchestidae, Ameronothridae, Carabodidae, Liacaridae; only the last two are known in fossil state.

Family CARABODIDAE Willmann, 1931

Legs III and IV attached to sides of body. Femurs of legs I and II stalked and
bottle-shaped. Surface of hysterosoma with coarse ornamental patterns (Figs.
457 1311–1318). Highly xerophilous species. Paleogene to Recent. Twenty-one
genera. Seven genera from the Paleogene of Europe (Baltic amber): extinct
Plategeocranus Sellnick, 1918 (Fig. 1314) and *Scutoribates* Sellnick, 1919 (Fig.
458 1315) and extant *Carabodes* Koch, 1836 (Fig. 1311); *Otocepheus* Berlese, 1910
(Fig. 1312); *Cepheus* Koch, 1836 (Fig. 1313); *Xenillus* Robineau-Desvoidy, 1839
(Fig. 1316); *Tectocepheus* Berlese, 1913 (Fig. 1317); *Ommatocepheus* Berlese,
1913 (Fig. 1318). Moreover, genus *Carabodites* Pampaloni, 1902 described from
the Miocene.

Family LIACARIDAE Willmann, 1931

Legs III and IV attached to ventral surface a considerable distance from the sides of body. Dorsal surface of hysterosoma convex with dotted ornamentation. All segments of legs more or less cylindrical. Paleogene to Recent. Four genera in
459 Recent fauna of which *Cultroribula* Berlese, 1908 (Fig. 1319) is from the Paleogene of Europe (Baltic amber).

SUPERFAMILY HERMANNIELLIDEA

Short cylindrical tubes or warty excretory ducts of fat glands project sharply from margin of hysterosoma (Fig. 1320). With lamellar keels and ribs on dorsal side of propodosoma; surface of both shields exhibits coarse tubercular ornamentation or prominently stripped. Paleogene to Recent. One family.

Family HERMANNIELLIDAE Grandjean, 1934

This family is characterized by the diagonistic features of the superfamily. Paleogene to Recent. Three genera in the Recent fauna. Genus *Hermanniella* Berlese, 1908 (Fig. 1320) is from the Paleogene of Europe (Baltic amber).

SUPERFAMILY NOTASPIDIDEA

(Pterogasterina)

With lamellar shoulder outgrowths or large leaflike movable pteromorphs (Figs. 1321–1326). Some species attain astounding dimensions (Figs. 1335, 1336).
460 Paleogene to Recent. Extensively distributed. Oribatid group represented in Recent fauna by the following eleven families: Microzetidae, Epactozetidae, Tenuialidae, Oripodidae, Oribatulidae, Ceratozetidae, Oribatellidae, Notaspididae, Haplozetidae, Pelopsidae, Galumnidae. The first three have fossil representatives.

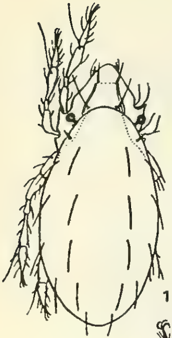
Family ORIPODIDAE Jact, 1925

Lenticular outgrowths of chitin (immovable petromorphs) extend along sides of hysterosoma, somewhat broad at anterior end, extend forward up to half the length of propodosoma where they join to form a thin, broad plate. This plate hangs over propodosoma and protects bases of trichobothria and interlamellar setae and sometimes only the setae. In some forms this lamella fuses with integument of propodosoma. Genital setae two-three pairs (Fig. 1321). Paleogene to Recent. Four genera in the Recent fauna. Genus *Oripoda* Banks, 1904 from the Paleogene of Europe (Baltic amber).

Family ORIBATULIDAE Jacot, 1929

(Scheloribatidae Grandjean, 1933)

With very small, backwardly directed humeral chitinous projections on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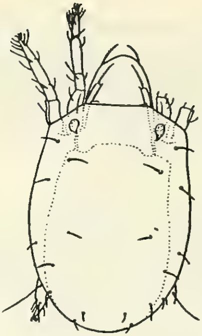
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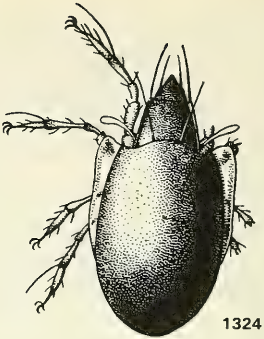
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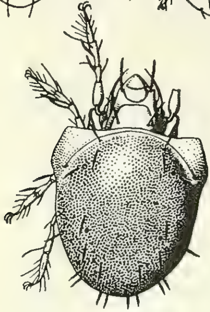
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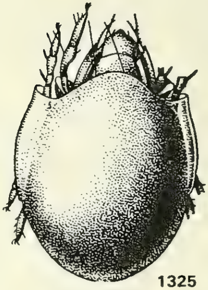
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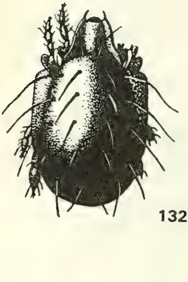
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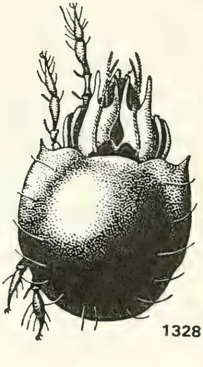
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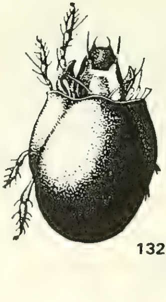
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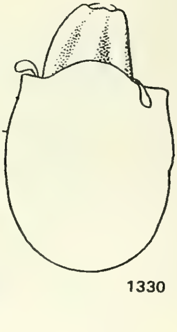
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anterolateral sides of hysterosoma distinctly visible from dorsal side. With weakly developed keels or ribs on propodosoma. Setae on hysterosoma in four longitudinal rows. Each valve of genital opening with four setae (Figs. 1322–1324). Paleogene to Recent. Thirteen genera in Recent fauna of which *Eporibatula* Sellnick, 1928 (Fig. 1322); *Liebstadia* Ondemans, 1906 (Fig. 1323); *Scheloribates* Berlese, 1908 (Fig. 1324), are from the Paleogene of Europe (Baltic amber).

Family CERATOZETIDAE Jacot, 1925

Distinct, broad, immovable, platelike outgrowths (pteromorphs) present on sides of hysterosoma. Pteromorphs connected to one another by narrow chitinous bridge along anterior margin of hysterosoma (Fig. 1327). This cross bridge does not significantly increase dorsal area of propodosoma. Anterior margin of bridge does not reach the level of bothrydia (Trichobothria). Six setae on each valve of genital opening (Figs. 1325–1327). Paleogene to Recent. Twenty-nine genera in Recent fauna of which *Chamobates* Hull, 1916 (Fig. 1325); *Melanozestes* Hull, 1916 (Fig. 1326); *Sphaerozestes* Berlese, 1885(= *Euzetes* Berlese, 1908) (Fig. 1327) are from the Paleogene of Europe (Baltic amber).

Family ORIBATELLIDAE Jacot, 1925

Pteromorphs immovable, large, sharply tapered at anterolateral angles. With very large plates on dorsal side of propodsoma; almost covering entire dorsal surface of propodosoma. Their anterior ends drawn out into pointed processes (Fig. 1328). Trichobothria project forward beyond edge of narrow chitinous cross bar connecting pteromorphs (Figs. 1328–1330). Paleogene to Recent. Four genera in Recent fauna of which *Oribatella* Banks, 1885 (Fig. 1328) and *Tectoribates* Berlese, 1910 (Figs. 1329–1330) are from the Paleogene of Europe (Baltic amber).

Family NOTASPIDIDAE Oudemans, 1900

With very large plates on dorsal surface of propodosoma. Slender pointed tip of

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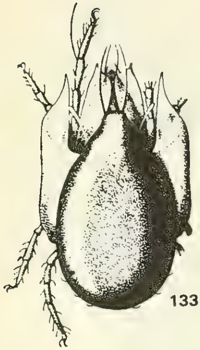
8 Figs. 1321– 1330.Suborder Oribatei. Families Oripodidae, Oribatulidae, Ceratozetidae and Oribatellidae.

1321. *Oripoda elongata* Banks; dorsal view, × 110. Recent (Baker and Wharton, 1952). 1322. *Eporibatula rauschenensis* (Sellnick); dorsal view, × 100. Recent (Sellnick, 1908). 1323. *Liebstadia similis* (Michael); dorsal view, × 100. Recent (Berlese, 1895). 1324. *Scheloribates latipes* (Koch); dorsal view, × 100. Recent (Michael, 1888). 1325. *Chamobates pusillus* (Berlese); dorsal view, × 100. Recent (Berlese, 1895). 1326. *Melanozetes mollicomus* (Koch); dorsal view, × 60. Recent (Michael, 1888). 1327. *Sphaerozetes prudens* Berlese; dorsal view, × 80. Recent (Michael, 1895). 1328. *Oribatella calcarata* (Koch); dorsal view, × 100. Recent (Berlese, 1895). 1329. *Tectoribates piriformis* (Nicolet); dorsal view, × 60. Recent (Berlese, 1895). 1330. *Tectoribates parvus* Sellnick; dorsal view, × 90. Paleogene, Europe (Baltic amber) (Sellnick, 1918).



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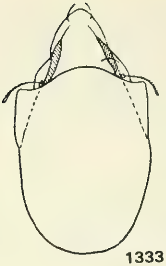

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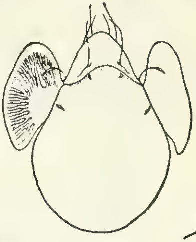

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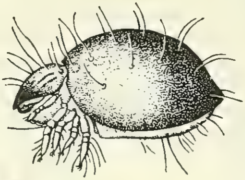

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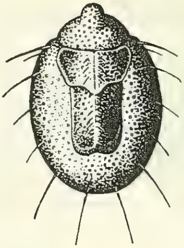

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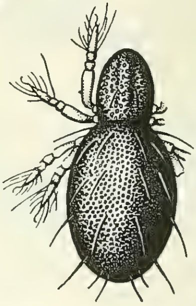


1337A

459 Figs. 1331–1338. Suborder Oribatei. Families Notaspididae, Haplozetidae, Phenopelopodidae, Galuminidae and Phthiracaridae.

1331. *Notaspis nicoletii* (Berlese); dorsal view, × 100. Recent (Berlese, 1882). 1332. *Punctoribates punctum* (Koch); dorsal view, × 90. Recent (Berlese, 1882). 1333. *Protoribates capucinus* Berlese; dorsal view, × 80. Neogene, Europe (Baltic amber) (Berlese, 1908). 1334. *Phaenopelops variolosus* (Nicolet); dorsal view, × 90. Recent (Nicolet, 1855). 1335. *Galumna mucronata* (Canestrini G. and R.); dorsal view, × 60. Recent (Berlese, 1882). 1336. *Neoribates roubali* Berlese; dorsal view, × 80. Recent (Willmann, 1932). 1337. *Hoploderma magnum* (Nicolet); A—with legs spread out, × 60, B—with legs withdrawn, × 60. Recent (Berlese, 1882). 1338. *Oribotritia ardua* (Koch); lateral view, × 80. (Berlese, 1882).

pteromorphs reach level of rostrum of gnathosoma. The anterior margins of propodosomatic plates are truncated and do not form acute projections. Plates of propodosoma fuse together at middle (Figs. 1331, 1332). Paleogene to Recent. Four genera in Recent fauna of which *Notaspis* Hermann, 1804 (Fig. 1331) and *Punctoribates* Berlese, 1908 (Fig. 1332) occur in the Paleogene of Europe (Baltic amber).

Family HAPLOZETIDAE Grandjean, 1936

Pteromorphs small and triangular. Tectopeds of legs IV large and foliaceous. More than five setae on each valve of genital opening (Fig. 1333). Paleogene to Recent. Six genera in Recent fauna of which genus *Protoribates* Berlese, 1908 occurs in the Paleogene of Europe (Baltic amber).

Family PHENOPELOPIDAE Petrunkevitch, 1955

(Pelopsidae Ewing, 1917)

Pteromorphs movably attached to hysterosoma. Chitinous bridge connecting them narrow, broad at middle, looking like a broad lobe hanging on posterior part of propodosoma. Anterior margin of middle lobe occasionally reaches almost up to center of propodosoma (Fig. 1334). Chelicerae with broad bases and sharp tapering ends. Their apices usually long and slender with small claws. With six setae on each valve of genital opening. Paleogene to Recent. Ten genera 461 in Recent fauna of which genus *Phaenopelops* Petrunkevitch, 1955 (= *Pelops* Koch, 1836) (Fig. 1334) occurs in the Paleogene of Europe (Baltic amber).

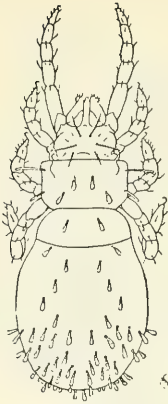
Family GALUMNIDAE Grandjean, 1936

(Parakalummidae Grandjean, 1936; Zakhvatkin, 1953)

Pteromorphs winglike and movable. Chitinous bridge connecting them absent. Chelicerae normal, their anterior ends not extended. Transverse furrows between propodosoma and hysterosoma not always distinct, at times absent. Five or six setae on each valve of genital opening (Fig. 1335). Paleogene to Recent. Twelve genera in Recent fauna of which *Galumna* Heyden, 1826 and *Neoribates* Berlese, 1914 (Fig. 1336) occur in the Paleogene of Europe (Baltic amber).

Infraorder Ptyctima

Propodosoma movably attached to hysterosoma and can bend towards ventral side of body covering legs and gnathosoma (Fig. 1337B). Paleogene to Recent. One superfamily: Phthiracaridea.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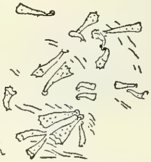
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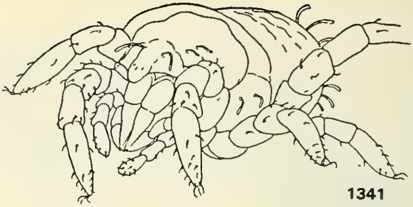
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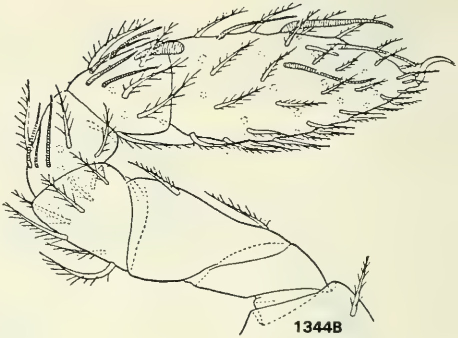
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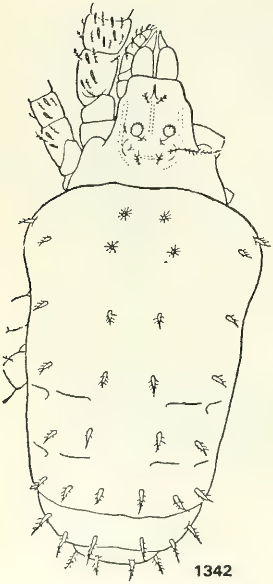
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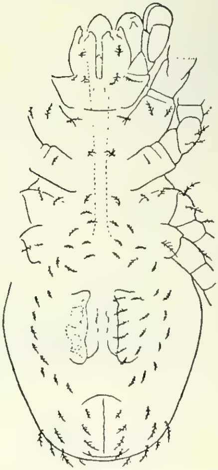
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SUPERFAMILY PHTHIRACARIDEA

(Ptyctima Andre, 1949)

This superfamily is characterized by the diagnostic features of the infraorder (Figs. 1337, 1338). Paleogene to Recent. Three families in Recent fauna: Protoplophoridae, Mesoplophoridae and Phthiriacaridae. Last family known from the Paleogene of Europe (Baltic amber).

Family PHTHIRACARIDAE Perty, 1841

Hysterosoma not divided into 'segments' by furrows; dorsal surface covered by a continuous shield. Valves of genital and anal openings narrow, elongated in some species and closed or even fused with one another, forming extremely long anogenital plates. Integument of ventral side of body soft. Ventral shield not connected with dorsal shield (Figs. 1337–1338). Paleogene to Recent. Thirteen genera in Recent fauna of which genera *Hoploderma* Michael, 1898 and *Oribotritia* Jacot, 1924 are represented in the Paleogene of Europe (Baltic amber).

Suborder Trombidiiformes. Red spider mites

Body division acaroidal type or trilobate type (Fig. 1339). Integument thin and membranous. Shields poorly developed or absent. Surface of chitin usually with fine punctures or slender striations which form a characteristic ornamental figure consisting of parallel lines. Usually with additional setae (Neotrichiae, Fig. 1357), on body. These mask the position of primary setae (Fig. 1344). Additional setae absent only in certain groups, as for example in Tarsonemidea, some Tydeidae (Figs. 1346–1350), Bdellidae (Fig. 1352), Tetranychidae (Fig. 1358) etc. Along with smooth setae, plumose, pinnate and other kinds of setae occur extensively (Figs. 1340, 1342). Trichobothria present or absent on propodosoma. Gnathosoma usually small and attached to anterior margin of body (Cheyletidae, Fig. 1353; Cunaxidae, Bdellidae, Fig. 1352 and others). Fused bases of chelicerae and hyposoma form a large conical tube on sides of which large prehensile pedipalpi are located; pedipalpi often in form of thick spines (Cheyletidae and others: Figs. 1351, 1353, 1356). Chelicerae of various species differ; in some they are claw-shaped and in others (Tetranychidea,

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463 Figs. 1339–1344. Families Nanorchestidae, Pachygnathidae, Alicorhagiidae.

1339. *Speleorchestes poduroides* Hirst; dorsal view, × 130. Recent (Hirst, 1917). 1340. *Protospeleorchestes pseudoprotacarus* W. Dubinin. gen. nov., sp. nov., setae of opisthosoma, × 12. Devonian, Western Europe (Hirst, 1923). 1341. *Protacarus crani* Hirst; general view, × 400. Devonian. Western Europe (Hirst, 1923). 1342. *Petralycus unifornis* Grandjean; dorsal view, × 600. Recent (Grandjean, 1943). 1343. *Pseudoprotacarus scoticus* W. Dubinin; gen. nov., sp. nov.; lateral view, × 450. Devonian, Western Europe (Hirst, 1923). 1344. *Alicorhagia fragilis* Berlese; A – female, ventral view, × 450. B – first leg, × 1500. Recent (Grandjean, 1939).

Myobiidae, Cheyletidae, Trichadenidea), columnar or thick, digitate with small movable digits in form of a spine or needle (Tydeidea, Fig. 1350; Speleognathidae). Legs normally of walking type, in parasitic species they may be modified for clinging to hairs of host animals (legs I in Myobiidae); or, greatly reduced (Demodicidae, Psorergatidae). In aquatic mites (Hydrachmellae) a few pairs of legs modified for swimming and with long hairs on segments. Coxae of legs fused to integument. In certain groups parasitic on ants (Tarsonemidea) or living in plant galls (Trichodenidea), individual legs are reduced. Tarsi of legs with two large claws and plumose empodium between them. In some forms empodium and claws much reduced. Eyes developed or absent. Tracheal system developed in almost all species. A pair of stigmata open on or adjacent to dorsal side of gnathosoma. Stigmata joined with complex perithemes. Male mites without stigmata. Sexual dimorphism indistinct. Genital and anal openings separate, normally situated on abdominal side. In Eupodidae Koch, anal opening shifted to dorsal side, and in representatives of superfamily Cheyletidea 462 and Demodicidea male genital opening shifted to dorsal side. Anal ducts absent. Genital ducts developed in a few species.

Post-embryonic development of tri- or binymphal metamorphic type.

Biology of Trombidiiformes most varied. Together with free living saprophytes this group includes the most primitive forms (Pachygnathidea), specialized predators (Cheyletidea, Rhaphignatidea and others), parasites of plants and insects (Tarsonemidea, Tetranychidea, Trichadenidea and others) and of vertebrates (Demodicidae, Pterygosomatidae, Myobiidae, Trombiculidae and others). A large group of aquatic mites provisionally grouped under Hydrachnellae and the superfamily Halacaridea inhabit fresh or marine waters.

The suborder Trombidiiformes is split up into a series of provisional groups: Tarsonemini, Prostigmata and Hydrachnellae (Hydracarina), which tends to emphasize natural systematic groups (Baker and Wharton, 1952). After a series of investigations, acarologists have divided the suborder Trombidiiformes into 26 superfamilies comprising 86 families. Devonian to Recent. Nine superfamilies are known in fossil form: Pachygnathidea, Rhaphignathidea, Tydeidea, Anystiidea, Bdellidea, Cheyletidea, Smaridiidea, Trombidiidea and Tetranychidea.

REMARKS. Five species belonging to two superfamilies (Pachygnathidea and Tydeidea) which are known from the Devonian of Scotland. These forms until now were erroneously included in one species *Protacarus crani* Hirst, 1923. A few workers even now classify a few species belonging to various families of the primitive Trombidiiformes under *'Protacarus crani'* (Zakhvatkin, 1952, p. 24).

SUPERFAMILY PACHYGNATHIDEA

(Endeostigmata)

Small, soil dwelling mites with well defined hysterosoma. Setae arranged in transverse rows on dorsal side of hysterosoma; with trichobothria on the propodosoma. Gnathosoma relatively large. Pedipalpi five-segmented. Chelicerae large, four-segmented and claw-shaped. Tracheae open on gnathosoma at the dorsal base of the chelicerae. Body integument thin, with slender striations or fine tubercles, shields absent. Legs of walking type, femur divided into basi- and telofemur. Claws and plumose empodia present on tarsi. Valves of genital and anal openings with setae. Genital ducts two or three pairs. Devonian to Recent. Six families in Recent fauna: Terpnacaridae, Lordalychidae, Sphaerolichidae, Pachygnathidae, Alicorhagiidae, Nanorchestidae. The last three are known in fossil form.

Family NANORCHESTIDAE Grandjean, 1937

Body distinctly differentiated by constrictions into gnathosoma, propodosoma, metapodosoma and opisthosoma (trilobate type). Integument soft with narrow furrows; with 64 characteristically club-shaped to funnel-shaped setae with spines on dorsal surface (Fig. 1340). Gnathosoma massive. Pedipalpi with four-five simple movable segments. Legs shifted to anterior half of body from the saclike hysterosoma. Legs IV of jumping type. Tarsi of legs with a single empodial claw. Genital ducts three pairs. Very small forms (0.165–0.350 mm in length), colorless or reddish, living in moss and soil. Devonian to Recent. Five genera of which four known only in Recent fauna. Small forms.

Protospeleorchestes W. Dubinin, gen. nov. Genotype—*P. pseudoprotacarus* W. Dubinin, n.n. (*Protacarus crani* Hirst, 1923; partial remains No. 6. A few pieces of integument with peculiar 'setae'. Hirst, 1923, p. 459, Fig. 1C); Devonian, Scotland (Aberdeenshiri, Red Sandstone). Only setae with opisthosoma preserved. Setae conical, truncated at tip, with small triangular spines on surface, arranged more or less in pairs. Along with large setae, two smaller hairs of similar form and structure on body of mite. Integument thin with slender parallel striation (Fig. 1340). One species.

464 Family PACHYGNATHIDAE Kramer, 1877

Body elongate oval, divisible into gnathosoma, propodosoma and hysterosoma (acaroidal type). Hysterosoma divided by furrows in some species (Figs. 1341, 1342). Integument soft with grooved, reticulate and other patterns. Anterior margin of propodosoma form projections (tectum, rostrum) hanging partly over base of gnathosoma. With two pairs of sensory setae on dorsal side of propodosoma. Gnathosoma comparatively large. Pedipalpi five-segmented in Recent species. In the fossil *Protacarus crani* Hirst, pedipalpi six-segmented. Tarsi with two claws and plumose empodium. Legs I–III of Recent species five-segmented. Legs IV of femur divided into basi- and telofemur. With 3 pairs of genital ducts. Wooly mite (length of body 0.3–0.4 mm), live in soil and moist forest litters. Devonian to Recent. Four genera of which three are from Recent fauna.

Protacarus Hirst, 1923. Genotype—*P. crani* Hirst, 1923 (partly specimen

No. 3; Plate XI; Fig. 6); Devonian Scotland (Aberdeenshire, red sandstone). With transverse furrows on hysterosoma. Eyes absent. Legs six-segmented. Setae on body and trichobothria on propodosoma slightly club-shaped and bent. Pedipalpi with jointed femurs. Size small (Fig. 1341). One species.

Family ALICORHAGIIDAE Grandjean, 1939

Propodosoma demarcated from hysterosoma only by a faint suture (Figs. 1343, 1344). Integument soft with tubercular furrows. Propodosoma with one pair of trichobothria. Digitate projection of anterior margin of propodosoma hangs over gnathosoma; gnathasoma with two setae. Eyes absent. Pedipalpi fivesegmented and simple. Legs with five mobile segments; femurs divided into basi- and telofemur.Trochanters of legs I and II divided (Fig. 1344B). Genital ducts two pairs. Size small (length of body 0.22 to 0.30 mm). Live in damp forest litter (Fig. 1344). Devonian to Recent. One genus in Recent fauna and one in fossil form.

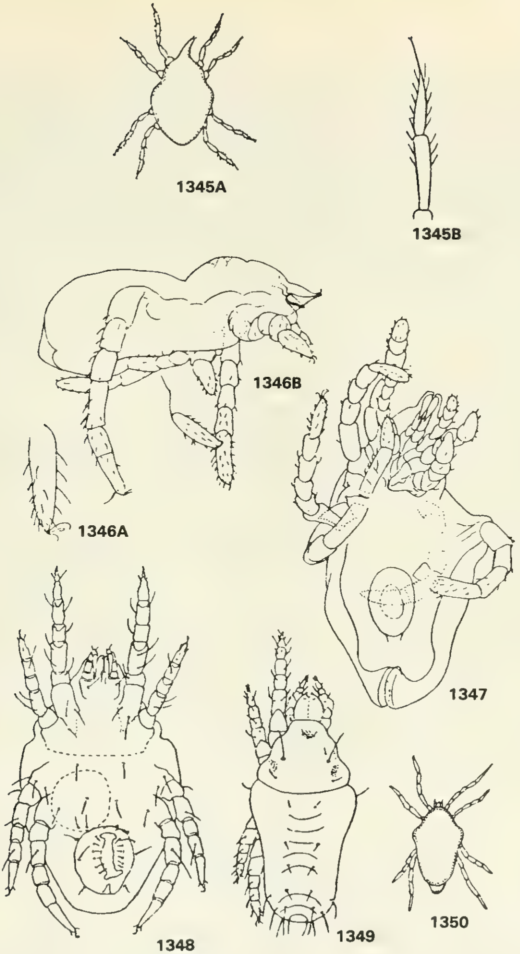
Genus *Pseudoprotacarus* W. Dubinin, gen. nov. Genotype—*P. scoticus* W. Dubinin, nom. nov. (*Protacarus crani* Hirst, 1923; partly specimen No. 1. Mite, lateral view—Pl. XI, Fig. a). Devonian, Scotland. Body elongate with saclike hysterosoma. Gnathosoma comparatively large. Hypsotoma with process on dorsal side of anterior end. Chelicerae large and claw-shaped. Legs large with stout tarsi, five-six segmented with numerous, short, weakly curved setae. Four rows of short, curved setae with three or four setae in each row on dorsal side of posterior end of body apparently along sides of anal slit. Setae on body and legs probably very fine; they escaped the attention of Hirst (1923) in his descriptions and his figures. Length of body 0.29 mm (Fig. 1343). One species. Devonian of Scotland.

SUPERFAMILY RHAPHIGNATHIDEA GRANDJEAN, 1944

Body divisions fused. Transverse furrow between propodosoma and hysterosoma absent. Setae on dorsal surface of body either present or absent. Gnathosoma narrow, conical and elongated. Pedipalpi distinctly longer than oral cone. In some species Gnathosoma free while in others (Cryptognathidae) enclosed in a tubular outgrowth of anterior margin of propodosoma (Fig. 1345A). Chelicerae with columnar digits. Usually with a collection of setae on dorsal side of body. Integument of body thin and striated, or with reticulate ornamentation. Legs five-segmented and of walking type with claws and empodium. In some species femur divided into two parts. Genital ducts absent. Paleogene to Recent. Four families in Recent fauna: Rhaphignathidae, Cunaxidae, Pomearantziidae, Cryptognathidae; the last one is known in fossil form.

Family CRYPTOGNATHIDAE Oudemans, 1902

Body oval. Propodosoma and hysterosoma not divided by transverse furrows.



Figs. 1345–1350. Families Cryptognathidae, Tydeidae and Pentnalodidae.

1345. *Cryptognathus rhombeus* (Koch and Berendt); A—dorsal view, × 100. B—claws on tarsus of first leg, × 600. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1346. *Palaeotydeus devonicus* W. Dubinin, gen. nov., sp. nov.; A—tarsus of walking leg, × 600. B—lateral view of female, × 300. Devonian, Western Europe (Hirst, 1923). 1347. *Paraprotacarus hirsti* W. Dubinin gen. nov., sp. nov.; ventral view of female, × 300. Devonian, Western Europe (Hirst, 1923). 1348. *Lorryia cuperba* Oudemans; ventral view of female, × 300. Recent (Thor, 1933). 1349. *Tydeus (Triophtydeus) pinicolus* (Oudemans); dorsal view, × 200. Recent (Thor, 1933). 1350. *Penthalodes tristiculus* (Koch and Berendt); dorsal view, × 100. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).

Integument weakly chitinized with stippled ornamentation and reticulate design on dorsal side. Anterior margin of propodosoma protrude forward as a tube which is open at the bottom. Gnathosoma hidden in this tube and can be extended or retracted. Chelicerae claw-shaped with small digits devoid of serrations; digits pointed at tip and modified for piercing. Pedipalpi slender and straight and their tips projecting in the form of 'little horns' beyond apex of propodosomal tube (Fig. 1345). Legs long and slender. Tarsi with two claws. Small mites (length of body 0.30–0.40 mm). Live in moss, under stones, bark and in nests of birds and in the white of eggs. Probably predators. Paleogene to Recent. One genus *Cryptognathus* Kramer, 1878 from the Paleogene of Europe (Baltic amber).

SUPERFAMILY TYDEIDEA

(Eupodidea, pars)

Small mites, integument thin with striations and dotted lines. Idiosoma not segmented. Only the transverse furrow between propodosoma and hysterosoma present (Fig. 1346). Gnathosoma small and conical. Pedipalpi five-segmented in free living species and three-segmented in Speleognathidae, Womersley which are parasitic in nasal cavities of vertebrates. Chelicerae with thick bases which sometimes are fused with each other and with the digitate apex. Movable digit of chelicerae very small, resembling pointed spine or needle. Digits of chelicerae not opposable to each other. Fore and hind pairs of legs spaced apart. Legs fivesegmented, tarsi with two claws and plumose empodium. Dorsal side of body with seven to twelve pairs of setae-like spines.

Free living mites, some are parasitic on terrestrial molluscs, reptiles and birds. Devonian to Recent. Seven families in Recent fauna: Speleognathidae, Ereynatidae, Paratydeidae, Eupodidae, Penthaleidae, Tydeidae and Penthalodidae. The last two are fossil families.

Family TYDEIDAE Kramer, 1877

Body oval, integument soft with indistinct striations of fine punctated furrows. Transverse furrow on body either present or absent. Shields weakly developed. Gnathosoma small and short. Pedipalpi five-six segmented. Chelicerae short; movable digit dagger-shaped, modified for piercing, considerably shorter and more slender than the thick immovable digit and not opposable (Figs. 1346, 1347). Legs of walking type. Tarsi with two claws and plumose empodium which may be claw-shaped. Very large genital and slit-like anal openings situated in caudal region on ventral surface of body. Devonian to Recent. Six genera in Recent fauna; two in fossil fauna.

466 *Palaeotydeus* W. Dubinin, gen. nov. Genotype—*P. devonicus* W. Dubinin, nom. nov. (*Protacarus crani* Hirst, 1923, for most part: specimen No. 3. Mite —lateral view, legs II and IV longer. Hirst, 1923, p. 459, text, Fig. 1); Devonian, Scotland (Aberdeenshire, red sandstone). Body oval. Proterosoma occupies a

third of total length and separated from hysterosoma by a deep furrow. Gnathosoma small. Apex of spine-like mobile digit of chelicera not reaching apex of stouter immobile digit. Pedipalpi five-segmented. Legs six-segmented and of normal structure. Legs II and IV considerably longer than remaining pairs. Tarsi with two long curved claws and an equal sized empodium between them (Fig. 1346). Genital openings situated at level of bases of legs IV. Anal openings terminal. Length of body 0.31 mm. One species. Devonian of Scotland.

Paraprotacarus W. Dubinin, gen. nov. Genotype—*P. hirsti* W. Dubinin, nom. nov. (*Protacarus crani* (?) Hirst, 1923, partly specimen No. 4. Ventral view. Hirst, 1923, pp. 458–459, text Fig. 2, 1a); Devonian, Scotland (Aberdeenshire, Red sandstone). Body oval. Proterosoma less than a third of body length. Gnathosoma elongate and triangular. Chelicerae four-segmented (?). Pedipalpi long and six-segmented. Legs six-segmented, of normal structure and approximately of uniform length. Genital opening large, oval-shaped and located behind the level of base of legs IV and located nearer to anal slit lying subventrally. Length of body 0.31 mm (Fig. 1347). One species. Devonian of Scotland.

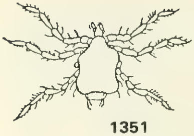
Family PENTHALODIDAE Thor, 1933

Body pear-shaped and narrows towards posterior half. Transverse furrow between propodosoma and hysterosoma absent. Integument relatively strongly sclerotized with reticulate or punctate ornamentation. Living mites with red spots on black background. Single eye on each side of propodosoma. Setae on body and legs short and not numerous. Legs long and slender with six movable segments. Tarsi with two claws and empodium. Gnathosoma small and triangular. Pedipalpi slender, four-segmented. Chelicerae small, a little curved and scissors-like. Genital ducts two pairs. Length of body from 0.33 to 1.50 mm. Free living forms, inhabit moss and decayed plant litter (Fig. 1350). Paleogene to Recent. Three genera in Recent fauna of which *Penthalodes* Murray, 1877 is from the Paleogene of Europe (Baltic amber).

SUPERFAMILY ANYSTIIDEA

(Anystoidea)

Little red mites with round body. Propodosoma and hysterosoma fused or divided by a barely visible suture. Integument thin and densely striated. With shields on propodosoma; in a few forms on opisthosoma. Body with large number of setae on dorsal side. Trichobothria absent. Gnathosoma comparatively large. Movable digit of chelicera columnar and modified for piercing. Pedipalpi long with leglike or hooklike tibia and small tarsus attached to ventral side. Legs long and lateral. Tarsi of legs I and II with sensory organ. Anal opening terminal and subdorsal. Genital ducts absent.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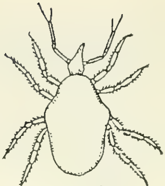
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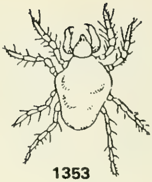
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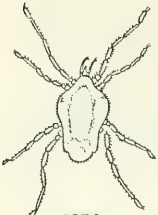
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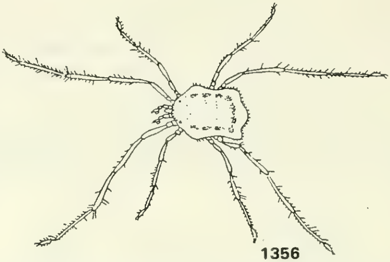
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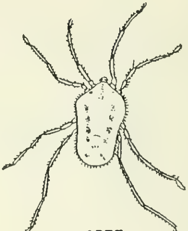
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467 Figs. 1351–1356. Families Anystidae, Bdellidae, Cheyletidae, Erythraeidae.

1351. *Anystis venustula* (Koch and Berendt); dorsal view, × 17. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1352. *Bdellodes lata* (Koch and Berendt); dorsal view, × 50. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1353. *Cheuletus portentosus* Koch and Berendt, × 40. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1354. *Leptus incertus* (Koch and Berendt); × 40. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1355. *Balaustium illustris* (Koch and Berendt), × 40. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1356. *Erythraeus foveolatus* (Koch and Berendt), × 40. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854)

Free living predacious mites living in soil, moss and on plants. Length of body 0.55 to 1.50 mm. Paleogene to Recent. One family.

Family ANYSTIDAE Oudemans, 1902

Coxae of legs very close to anterior third of body. Legs very long, radially divergent (Fig. 1351). Propodosomatic shield not always present, if present, there is no unsclerotized integument but with development of a densely grooved ornamentation. Peritremes present at bases of chelicerae. Gnathosoma short-conical. Movable digit of chelicera hook-like. Pedipalpi large and leg-shaped, with one to three claws on tibia. Tarsi long, 'hairy' and subventrally attached to tibia. Length of body 0.55–1.30 mm.

Free living predators, particularly numerous on leaves of plants. Paleogene to Recent. Seventeen genera in Recent fauna of which one—*Anystis* Heyden, 1826 is from the Paleogene of Europe (Baltic amber).

SUPERFAMILY BDELLIDEA. Big nosed mites

Body oval, soft, and divided by a deep furrow into propodosoma and hysterosoma. Chelicerae and hypstomae produced into long beak from base of 467 which arise slender five-segmented pedipalpi. Apex of tarsus of pedipalpi with two forwardly directed setae (Fig. 1352). Chelicerae elongate with one or more dorsal setae and very small claws. Integument thin and furrowed, shields absent. Two pairs of trichobothria and two pairs of divided eyes situated on dorsal side along margins of propodosoma. A few genera with unpaired median eyes at anterior end of propodosoma. Legs with six movable segments. Three pairs of genital ducts present. Length of body 0.45–1.50 mm. Paleogene to Recent.

Free-living predators; live everywhere in moist substrates along with other mites or in colonies of small insects. Bdellidae are particularly numerous in moss and plant litter, sometimes found on plant leaves. One family.

Family BDELLIDAE Duges, 1834

Family characterized by diagnostic features of the superfamily. Paleogene to Recent. Fourteen genera in Recent fauna of which *Bdellodes* Oudemans, 1937 and *Bdella* Latreille, 1795 are from the Paleogene of Europe (Baltic amber).

SUPERFAMILY CHEYLETIDEA. Predatory mites

Medium and small sized mites with oval or elongate body. Gnathosoma triangular with large median cheliceral cone—'beak' in which the columnar chelicerae are lodged. Pedipalpi three-segmented. Apices of tibiae of palpi are extended into a claw to the base of which is attached a small tarsus. Sometimes pedipalpi modified into powerful prehensile organs (Fig. 1353). Walking legs variedly developed. In free living species these are long and of normal size and structure, and in parasitic forms shortened or modified for clinging to hairs of host animals. Peritremes large, prominent and located on dorsal side of gnathosoma. Predacious forms; free living or parasitic. Length of body 0.2–0.8 mm. Paleogene to Recent. Four families in Recent fauna: Myobiidae, Syringophilidae, Haripirhynchidae and Cheyletidae; the last is known from the Paleogene of Europe (Baltic amber).

468 Family CHEYLETIDAE Leach, 1814

Body oval, somewhat raised, and rarely elongate. Propodosoma and hysterosoma sharply differentiated by the configuration of body margins and by presence of two or more dorsal shields. Gnathosoma with large median 'beak', sides of gnathosoma with very large palpi modified into strong claspers with stout femora and claw-shaped tibiae. With simple smooth and pectinate setae on apices of small tarsi. Free living predators. A few species are regularly encountered on bodies of birds and mammals where they feed on insects. Length of body 0.20 – 0.80 mm (Fig. 1353). Paleogene to Recent. Thirty-seven genera in the Recent fauna of which *Cheyletus* Latreille, 1796 is from the Paleogene of Europe (Baltic amber). A revision is needed for the identification of these forms.

SUPERFAMILY SMARIDIIDEA

(Apobolostigmata)

Body oval and somewhat elongate, convex and covered in adult mites by numerous, densely packed setae. Integument of body thin and striated. Middle of propodosoma with propodosomatic shield in form of a narrow rod-like keel with broadened ends. One or two pairs of lenticular eyes present. Coxae of legs arranged in two groups. Legs long and of running type with six mobile segments. Tarsus of anterior legs usually slightly raised, with two claws and plumose empodium. Gnathosoma in form of extended cone. Chelicerae style-like, long and can be retracted into the body. Pedipalpi large, five-segmented, with claw at apex of tibia. Tarsi of pedipalpi attached subventrally, causing them to appear furcate. Genital ducts absent.

Larvae are parasitic on insects. Length of body 0.5–2.0 mm (Figs. 1354–1356). Paleogene to Recent. Two families in the Recent fauna: Smaridiidae and Erythraeidae. The latter is from the Paleogene of Europe (Baltic amber).

Family ERYTHRAEIDAE Oudemans, 1902

(Balaustiidae Grandjean, 1947)

Gnathosoma not extended into long proboscis. Setae of body and legs smooth or finely plumose. Paleogene to Recent. Eighteen genera in the Recent fauna of which *Leptus* Latreille, 1795 (Fig. 1354), *Erythraeus* Latreille, 1806 (Fig. 1356) and *Balaustium* Heyden, 1826 (Fig. 1355) are from Baltic amber. Besides these, an extinct genus *Arythaena* Menge, 1954 is also from the Paleogene of Europe (Baltic amber).

SUPERFAMILY TROMBIDIIDEA

(Trombeae)

Body oval or constricted in middle (Fig. 1357), with a very dense cover of setae, imparting to the mites a velvety look. Setae on body of larvae in smaller numbers. Body exhibits relatively distinct division into gnathosoma, propodosoma and hysterosoma. Integument of body grooved but smooth near setae. Propodosomatic shield rectangular in larvae, but keel-shaped in adult forms. One pair of trichobothria present on surface of the shield. Trichobothria often stout and club-shaped. A few pairs of setae prominent. Gnathosoma small and triangular. Pedipalpi well developed, five-segmented. Small tarsus of pedipalp attached to ventral side of tibia. Legs with six mobile segments. Tarsi with two claws. Genital opening located on ventral side of body at level of coxae of legs IV. Genital ducts three pairs. Stigmata open at base of chelicerae. Free living predators. Larvae parasitic on arthropods (Trombidiidae) and vertebrates (Trombiculidae). Length of body 0.5–2.0 mm. Paleogene to Recent. Two families in the Recent fauna. Trombidiidae and Trombiculidae. Former is known in the fossil state.

Family TROMBIDIIDAE Leach, 1815

Body of adult not constricted in middle. Larvae usually with more than one dorsal shield. Tectum with (gnathosoma dorsally) numerous setae. Paleogene to Recent. Over sixty genera in the Recent fauna of which *Trombidium* Fabricius, 1775 and *Alotrombium* Berlese, 1903 (Fig. 1357) are from the Paleogene of Europe (Baltic amber).

SUPERFAMILY TETRANYCHIDEA

(Spiderweb mites or Tetranychid mites)

Medium sized herbivorous mites. (Average length of body 0.8 mm). Body oval and at times pear-shaped with more or less prominent humeral convexity. Propodosoma and hysterosoma either fused or divided by weak suture. Integument soft. Shields not developed. Gnathosomatic projection comparatively large, gnathosoma with median cheliceral cone (Fig. 1358). Chelicerae stylet-like. Pedipalpi short with claw-shaped tibia and small tarsus on ventral side. Legs long. Ambulacra and empodium of tarsi may be greatly reduced. Genital ducts absent. Live on green parts of plants, feed on sap and inflict great damage. Paleogene to Recent. Two families in the Recent fauna: Bryobiidae and Tetranychidae. The latter is from the Paleogene of Europe (Baltic amber).

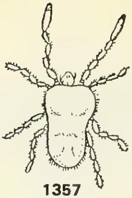
Family TETRANYCHIDAE Donnadieu, 1875

Dorsal side of body with 12–13 pairs of setae. Empodium devoid of glandular hairs and sometimes completely reduced. Peritremes attached to walls of cheliceral cone. With two setae on valves of anal opening. Live in colonies on leaves and exude profuse web. Paleogene to Recent. More than twenty genera in the Recent fauna of which two: *Metatranychus* Oudemans, 1931 (Fig. 1358) and*Schizotetranychus* Tragardt, 1915 are from the Paleogene of Europe (Baltic amber).

SUPERFAMILY LIMNOCHARIDEA

(Limnocharae)

Body soft, sac-like, oval, and of red color. Integument soft and membranous. Lateral eyes placed in highly developed sockets located on sides of median rod-like shield. Gnathosoma cylindrical and broad with horny disc surrounding



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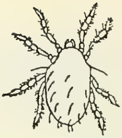

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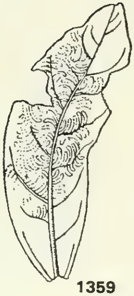

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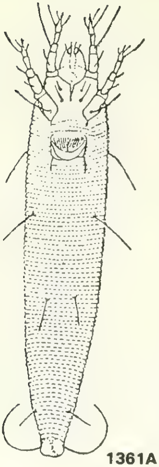

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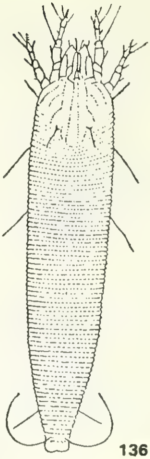

1361B

the margin. Chelicerae large and fused with one another. Legs slender and long, six-segmented. Coxae (epimers) arranged in four groups. The swimming hairs on segments of legs IV absent. Genital ducts absent. Live in bodies of freshwater. 471 Length of body up to 4–5 mm. Three families in the Recent fauna: Limnocharidae, Eylaidae, Protziidae. A reference relating to the occurrence of the genus *Limnochares* Latreille, 1796 in the Tertiary deposits of Germany (Heyden, 1862; Oudemans, 1937) is erroneous.

Suborder Tetrapodili. Four-legged, gall-forming mites

(Eriophyiformes)

Very small, vermiform and herbivorous mites (length of body 0.10–0.25 mm) with a somewhat broad anterior end and long, annulate body narrowing posteriorly. Only two pairs of legs with five short segments in all stages of development. Tarsi with spine-like and hair-like setae, and long, curved, rod-like claws with plumose empodium; remaining segment of legs with solitary spine-like setae (Figs. 1360, 1361, A, B). Dorsal surface of the widened anterior end of body with a shield having a pair of setae on posterior margin; occasionally with setae at anterior margin as well. Rest of body in species living in galls (Fig. 1359), with thin integument and uniformly narrow annular striation. In species living on leaf surfaces, integument somewhat more sclerotized with broad rings on dorsal side. Suckers present at posterior end of body (Fig. 1361 A, B). Gnathosoma greatly modified; its middle part occupied by a beak-like cheliceral cone along whose sides are stout, short pedipalpi with tubular tarsus. Chelicerae slender and stylet-shaped. Respiratory system absent. Genital opening located on abdominal side of body posterior to coxae of legs II. Anal opening located at posterior end of body.

The four-legged mites of the suborder Tetrapodili are related to other herbivorous mites, particularly those of the superfamily Trichadenidea. They are parasitic on plants and drink their sap. Some species (Eriophyidae) induce gall formation (Fig. 1359) while others live only on the surface of leaves (Phyllocoptidae). Paleogene to Recent. Two families: Eriophyidae and Phyllocoptidae.

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469 Figs. 1357–1361. Families Trombidiidae, Tetranychidae, Eriophyidae.

1357. *Allothrombium clavipes* (Koch and Berendt); dorsal view, × 40. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1358. *Metatranychus gibbus* (Koch and Berendt); dorsal view, × 35. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1359. *Phytoptus antiquus*(Heyden); felt-like galls on leaves of *Passiflora*; × 1. Paleogene, Western Europe (Heyden, 1862). 1360. *Aceria ceanothi* Keifer; lateral view of female, × 600. Recent (Keifer, 1839). 1361. *Aceria diversicoloris* Roivainen; A—ventral view of female, B—dorsal view of female, × 700. Recent (Liro and Roivainen, 1951).

Family ERIOPHYIDAE Nalepa, 1898. Four-legged gall-forming mites

Dorsal shield always without any outgrowths hanging over rostrum. Similar fine annulation present on hysterosoma in all stages of development. Width of individual rings on ventral and dorsal sides same (Fig. 1361). Paleogene to Recent. Twelve genera in the Recent fauna of which two are fossil genera: *Phytopus* Dujardin, 1851 and *Eriophyes* Siebold, 1850.

Family PHYLLOCOPTIDAE Nalepa, 1898

Spinal shield usually with anterior growth hanging over rostrum. Chitinous ring on dorsal side of body considerably broader and thicker than on ventral side. Paleogene to Recent. Thirty genera in the Recent fauna. One form (little studied) from the Paleogene has been reported by Heer (Thomas, 1877) from galls on poplar trees.

Order PARASITIFORMES. Gamasoid mites

Body usually oval and covered on dorsal and ventral regions by separate plates. Idiosoma usually absent. Only in the primitive mites of the family Rhodacaridae is a division into cephalothorax or prosoma bearing all appendages and opisthosoma or abdomen typical of cheliarate arachnids noticeable. In Parasitiformes, the gnathosoma characteristic of all mites is very sharply separated in the form of a distinct body division (Figs. 1362, 1363 A). In the vast majority of other gamazoid mites, the cephalothorax and abdomen are completely fused and the border between them can only be distinguished by the structural elements of the exoskeleton and the distribution of setae. Data from comparative anatomy and embryology reveal the fact that the opisthosoma of parasitiformes is made up of nine segments and an anal lobe. The anterior margin of the base of the gnathosoma is extended into an opisthosoma, along the sides of which, in Mesostigmata, lie the gnathobases of gnathocoxae, which are usually in contact along the median line. The narrow slit-like mouth opening is covered dorsally by the upper lip and ventrally by an inner process of the gnathosoma, i.e., hypstoma. Chelicerae large, mobile, and located dorsal to oral slit. In most species, the Chelicerae are three-segmented, and usually claw-shaped. In predacious gamasids (Rhodacaridae, Parasitidae) the chelicerae are
472 prehensile with long fingers or digits with coarse serration. In the blood sucking Laelaptidae, Haemogamagidae, Dermanyssidae and others, on the other hand, the chelicerae are produced into flexible stylets that to pierce the integument and tissues of host animals. Finally, the chelicerae in Ixodides are anchor-shaped and help in firmly adhering to body of host. A forked tritosternum is present behind the base of gnathobase on ventral side in Mesostigmata.

The exoskeleton of the idosoma is present in all stages of development and is characterized by extreme complexity. Usually all representatives of Parasitiformes are characterized by a cephalothoracic shield or sternum (Fig.

1363 A), an anal shield, and in females, a genital shield or epigen (Fig. 1313 A). Many species develop a notogastral or pygidial shield at the posterior end of the body. Sometimes this shield is fused with the cephalothorax and forms a single dorsal shield occupying almost the entire dorsal surface of the body (Fig. 1363 A). The ventral side of the body, in addition to its characteristic sternal shield, may also have anterothoracic (jugular) shields along the sides from the tritosternum in gamasids as well as lateral, epigynal, metapodial, ventral and anal shields behind the gonopore. The structure of the abdominal region of the body is of systematic importance.

All body setae and appendages are devoid of an actino-chitin core and are optically isotropic. During the early stages of development, setae are not numerous and are regularly arranged. Later a large number of additional setae develop (Figs. 1363 B, 1365).

A characteristic of all Parasitiformes is the presence of free cylindrical coxae and division of the telepodite of the legs into six segments: trochanter, undifferentiated femur, patella, tibia and tarsus. At the apices of the tarsi are a membranous pretarsus and two claws. Empodium is claw-shaped and usually consists of a small sclerite and a broad three-lobed pad (pulvillus) (Fig. 1363 B). Very often the legs of the first pair do not take part in locomotion and mainly serve as sensory organs. In Ixodides the coxae of the legs are secondarily fused with the body integument and sometimes form extensive coxal shields (Fig. 1364 B).

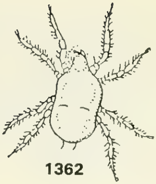
Genital opening located between coxae of legs. Respiratory system consists of tracheae and pair of stigmas opening on the sides of body anteriorly (as in Mesostigmata) or caudal to bases of legs IV (as in Ixodides).

Post embryonic development in gamasoid mites (Mesostigmata) is of binymphal type of metamorphosis and Ixodides pass through only one nymphal stage. Metamorphosis into the adult usually is not brought about without radical changes in morphology as observed in Acariformes. Fertilization in all species is through spermatophores. Life cycles, particularly in the parasitic species, may be highly complex.

Parasitiformes include free-living saprofages, predators and a large number of parasites. All parasitic blood-sucking species are grouped under Ixodides. Paleogene to Recent. Three suborders in the Recent fauna: Mesostigmata, Ixodides, Holothyroidea. The first two are known in fossil form.

Suborder Mesostigmata. Gamasoid mites

Gnathosoma with cylindrical gnathobase inside which are lodged large chelicerae. Pedipalpi long and stout. Ventral side of body, at level of legs I, with forked tritosternum; along median line of body lie one or more sternal plates. Coxae of legs cylindrical and movably articulated with body. Legs long and of running type (Figs. 1362, 1363 A). Stigmata placed along sides of body at level of bases of legs III. Peritremes surrounding them anteriorly form a very long and



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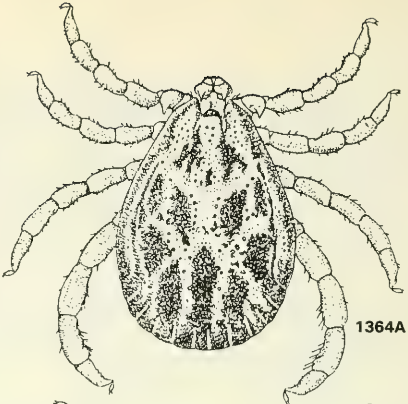

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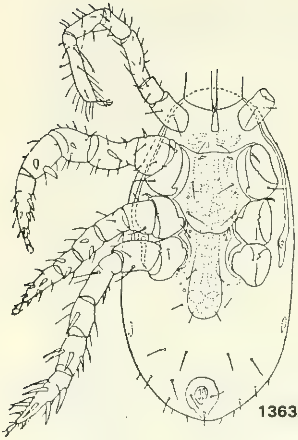

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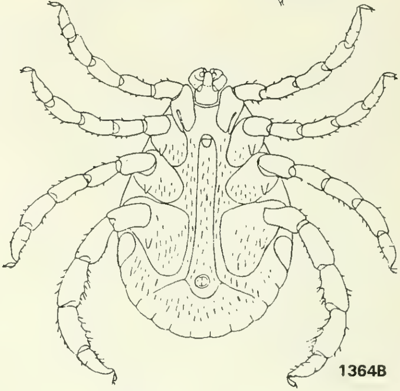

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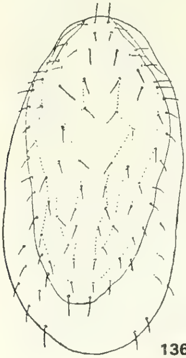

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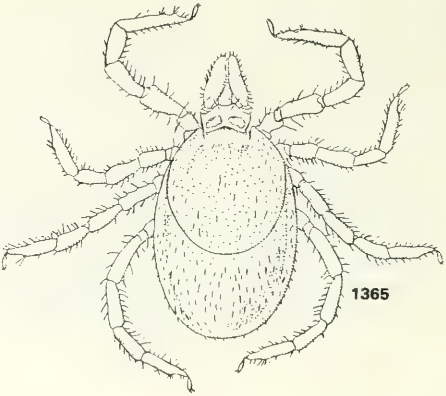

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lenticular appendage extending along sides of body upto the bases of legs II or I (Fig. 1363 A). Dorsal side of body with thick cephalothoracic shield or two shields, sometimes united with one another and then covering almost the entire dorsal side of body. The free-living and parasitic species have very different structure and biology. Paleogene to Recent. Eleven families in the Recent fauna: Megisthanidea, Liroaspidea, Microgyniida, Gamasidea, Thinozerconidea, Diarthrophalidea, Zerconidea, Trachytidea, Uropodidea, Celaenopseidea, Fedrizziidea. Gamasidea is known in fossil state.

SUPERFAMILY GAMASIDEA

(Gamasides)

Epigenal shield well developed in males and females ventrally. Lateral shields absent. Genital opening of males located anterior to sternal shield. Free-living or 473 ectoparasitic. A few species (Rhinonyssidae, Halarachnidae, Entonyssidae) are endoparasitic and live in the air passages of mammals and birds. Paleogene to Recent. More than twenty families in the Recent fauna of which Phytoseiidae and Laelaptidae have fossil representatives.

Family PHYTOSEIIDAE Berlese, 1916

Epigenal shield truncated or concave posteriorly. Large number of setae present on body. Tectum serrated along margins. Tritosternum well developed in the females. Encountered on plants where they hunt other mites and small insects. Active predators. Paleogene to Recent. More than twenty genera in the Recent fauna of which *Sejus* C.L. Koch, 1836 (Fig. 1362) is from the Paleogene of Europe (Baltic amber).

Family LAELAPTIDAE Berlese, 1892

Epigenal shield tear-drop shaped or with a notch at posterior border. Ventral shields in males usually fused into one common shield, only the anal shield normally remains free. Dorsal setae comparatively fewer in numbers: usually about 40 pairs. Projections absent on legs II of males; anterior margin of coxae of legs II with a spine-shaped projection. Mostly parasitic. Paleogene to Recent. More than fifty genera in the Recent fauna of which *Hypoaspis* G. Canestrini, 1885 (Fig. 1363) is from the Paleogene of Europe (Baltic amber).

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470 Figs. 1362–1365. Order Parasitiformes.

1362. *Sejus viduus* Koch; dorsal view, × 25. Paleogene, Europe, Baltic amber (Koch and Berendt, 1854). 1363. *Hypoaspis aculeifer* (Canestrini); A—ventral view of female; B—dorsal view of same female, × 65. Recent (Lange, 1955). 1364. *Dermacentor pictus* Hermann; A—dorsal view of male, B—ventral view of same male, × 15. Recent (Pomerantsev, 1950). 1365. *Ixodes ricinus* (Linnaeus); dorsal view of female, × 20. Recent (Pomerantsev, 1950).

Suborder Ixodes

(Ticks)

This suborder is represented by largest forms of class Acaromorpha. Male of some species of genus *Hyalomma* reach 2 cms in length when fully gorged with blood.

Body oval, a little flat in unfed forms and sac-like in blood filled forms. Only the cephalothoracic shield (Ixodidae) present on dorsal side of body or a shield may be absent (Argasidae). Integument membranous. Gnathosoma has a characteristic structure. Its base consists of a trapezoidal chitinous capsule with extended tongue-like epistoma. Pedipalpi stout, shorter and five-segmented. Chelicerae slender and spinous in Argasidae and anchor-shaped in Ixodidae. Tritosternum absent. Coxae of legs immovably joined to body and appear as thick shields. Spiracles open into short, broad and oval peritremes which do not form a long, narrow process anteriorly. Spiracles situated at the level of, or behind bases of legs IV. Legs long and of walking type. Anal opening adjacent to posterior margin of body. Anal valves with setae (Fig. 1364 B). Paleogene to Recent. Two families in the Recent fauna: Argasidae and Ixodidae. Only ixodid mites have been found in fossils.

Family IXODIDAE Murray, 1877

Gnathosoma projects prominently anteriorly in form of a small head; proboscis or 'capitulum' not hidden by overhanging propodosoma. Cephalothoracic shield in males extends as far as posterior end of body (Fig. 1364 A). In females the shield is restricted by the hind margin of the propodosoma (Fig. 1365). The life cycle of Ixodidae is highly complex and involves a change of hosts and periodic sucking of a large amount of blood, etc. Metamorphosis greatly simplified with only one nymphal instar. Paleogene to Recent. Sixteen genera in the Recent fauna, of which *Ixodes* Latreille, 1795 and *Dermacentor* C.L. Koch, 1844 are from the Oligocene of North America.

Order OPILIOACARINA. Harvest mites

(Notostigmata; Onychopalpida, Pars)

Medium sized mites with length upto 1 mm. Body oval with traces of segmentation. Integument of body soft and striated by furrows and large number of pores. Tritosternum present. With two eyes on dorsolateral sides of podosoma. Chelicerae claw-shaped. Legs very long and slender with long cylindrical segments. Coxae movable; trochanter of legs III and IV divided; two claws on tarsi. Four pairs of stigmata open on dorsal surface at anterior end of hysterosoma. Genital opening located between coxae of legs III. Females with projecting ovipositor.

The harvest mites are the most primitive forms. They live hidden in soil and under stones. Probably predators. One family Opilioacaridae with three genera. No fossil representatives.

Class ARACHNIDA

V.B. Dubinin

474 This class includes terrestrial chelicerates. The body is divided into a prosoma and opisthosoma. The characteristics of the members of this class are those exhibited by many mites of the order Acariformes (Oribatei, Sarcoptiformes) and by decapod crustaceans. The longitudinal axis is characteristically bent; segments IX and X of the opisthosoma are shifted to the ventral side. For example, in the harvest mites of the suborder Cyphophthalmi, the tenth tergum is brought in front of ninth during flexion (correspondingly shifted towards cephalic end and anal opening). Sterna of VI–IX segments of opisthosoma arcuately bent; terga shifted towards ventral side. The shortening of the body by flexion of the posterior end ventrally results in a significant reduction of the ventral side of the flexed segments in Arachnida and a high degree of compactness of the body of chelicerates. The normal number of segments of the body in Arachnida varies from 16 (Opiliones) to 18 (Araneae). In higher Araneae there is a partial reduction of six posterior segments due to the flexion of the posterior end of body ventrally. In this process, the metasoma may completely disappear. Indications of such reduction are manifest by the presence of a two-segmented postabdomen with an anal lobe (Holm, 1940) in the embryos of some spiders (genus *Pholcus* Walcken). The presence of a morphologically well defined postabdomen in the embryo confirms the validity of the suggested phylogenetic relationship between Arachnida to Amblypygi and other primitive Scorpionomorphs.

The dorsal surface of the prosoma is covered by an undemarcated general cephalothoracic shield, but in some forms of Opiliones and in some species of Trigonotarbi and Anthracomarti, transverse sutures are present in the shield demarcating the border between the head shield (propeltidium), meso- and metapeltidium (Figs. 1393, 1401).

The prosmatic shield is sometimes fused with a few terga of the opisthosoma, and the borders of the fused segments are distinctly indicated by sutures. The terga of the mesosoma are separate or greatly reduced in all spiders except in the suborder Liphistimorphae.

The presence of usually large sternal plates on the ventral surface of the prosoma is characteristic; this results in pushing the coxae of the legs (for example, in spiders) to the sides (Figs. 1413, 1422, 1434).

The sternum of the pedipalpal segment functions in Araneae as lower lip. It is considerably reduced in other groups. The ventral surface of the opisthosoma is segmented (the segments coalesce in the majority of spiders). Sterna commonly present, except in Araneae.

Dissimilarity in the development of the appendages in chelicerata reaches a maximum expression in the Arachnida. The chelicerae are three–five* segmented, chelate in one group (Opiliomorphae), in others (Araneae, Anthracomarti) they are hook-like (Figs. 1383, 1447, 1451). The latter are probably adaptations for external digestion and for sucking of liquified food. In spiders and Anthracomarti, the endites of the coxae of the pedipalpi are covered with hairs forming an apparatus through which liquid food is filtered (Fig. 1383B). Pedipalpi in all forms of this class are simple and leg-like, with a cylindrical tarsus. Normally, they are short though they can attain large size (Figs. 1378, 1426), but never function as prehensile organs.** The walking legs are long with six† basic segments (coxa, trochanter, femur, patella, tibia, and tarsus). In many orders the tarsi are further divided into two to five‡ segments; the trochanter, and rarely the femur, are sometimes divided into two segments. Tarsi with two claws. The appendages of the mesosoma are greatly reduced. A genital operculum is present only in a few Opiliones and Haptopoda, on the eighth segment. The posterior margin of the eighth segment in Araneae has a pair of openings of pulmonary sacs. These openings are probably modified genital opercula, since the sterna of IX and X have their paired pulmonary sacs. On the tenth segment of Araneae are appendages in the form of the first pair of spinnerets. The presence of pulmonary sacs in those segments, as in scorpionoid chelicerates, suggests affinities between these two groups. It is interesting that in place of the pectines of the ninth segment, only in Amblypygi and Uropygi, on the one hand and in Araneae on the other, there is either a second pair of pulmonary sacs or a pair of tracheae. In spiders the second pair of spinnerets is located on the eleventh segment. The remaining segments of mesosoma and metasoma, in Arachnida, are devoid of abdominal appendages. The external genitalia of Arachnida are in the form of a transverse genital slit, hidden in front by an unpaired fold formed by the sternum of eighth segment. The three-lobed genital cone is characteristic of all Solifugomorpha and the most primitive Scorpionomorpha (Palpigradi).

CLASSIFICATION, PHYLOGENY AND SYSTEMATIC POSITION. The class Arachnida traces its origin to the Amblypygi type or arthropods which in the Carboniferous gave rise to a group of arachnid chelicerates of which two groups

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* Editor's note: Not known for *any* arachnid, living or fossil.

** Editor's note: This statement is incorrect.

† Editor's note: Seven including metatarsus.

‡ Editor's note: or more.

(Opiliones and Araneae) have survived up to the present. Branching and further evolution of various groups (subclasses) did not take place simultaneously. The subclass Opilimorphae, considered as the most primitive Arachnida, has retained complete segmentation of the body, paired genital opercula on the eighth segment, and median eyes on a tubercle at the center of the cephalothoracic shield. Probably the branching of Opiliomorphae from the ancestral forms of Amblypygi occurred before the separation of the order Ricinulei. The evolution of the latter was characterized by a thickening of the integument. To retain the mobility of the opisthosoma, and the possibility of its extension during the intake of food and development of eggs, these shields were sclerotized in individual areas, forming one median and two marginal zones of terga and sterna. Thereby, Ricinulei have retained the more primitive features of the organization of the early Scorpionomorpha. Subclass Soluta originating from the ancestors of Scorpionomorpha, and in view of a transition to life in arid terrestrial conditions have acquired more dense shields. But a major change involved, as in other Arachnida, the bending of the posterior segments of the body towards the ventral side. Order Araneae probably appeared almost simultaneously along with other orders of subclass Soluta. Ricinulei evolved not from the typical Amblypygi but from the earlier forms. The phylogeny of the order Anthracomarti and the origin of the Trigonotarbi originating from it with spiders of the order Araneae is confirmed by the similarity of structure of the mouthparts, the development of claw-shaped chelicerae, and a filter net on the endites of the coxae of the pedipalpi (Fig. 1383B), the large sternum, etc. Spiders of order Araneae trace their origin from the more primitive Amblypygi. This is evident from the retention of rudiments of the postabdomen in some spiders during embryogenesis, and of the two pairs of pulmonary sacs and abdominal appendages, the 18 segmented of body, etc., in members of primitive groups. It is also evident from the absence of longitudinal furrows on the opisthosoma and the divided terga and sterna of the three body divisions. Class Arachnida exhibits a graded diversity in the degree of heterogeneity of its organization and this is reflected in the division of this class into three subclasses. In spite of this, the totality of characters of the various orders of class Arachnida point to their single direction of evolution, as revealed by the bending of the longitudinal axis of the body and the related high degree of integration of the segmented part of the body.

The class Arachnida reached the peak of its development in the Carboniferous, and the orders Opiliones and Araneae have survived up to the present day. The class Arachnida is represented by three subclasses: Opiliomorphae, Soluta and Araneae.

476 Subclass OPILIOMORPHAE. Phalangids

Body large or oval. Propodosoma broadly fused with abdomen. Furrows—

traces of past division into propeltidium, meta- and mesopeltidium—present. Eyes present or absent, in one group two or six eyes located directly on surface of shield; in others, borne on triangular eye tubercle. Abdomen 9–12 segmented, last segment located at posterior part of ventral side of body. Terga X and XI form anal plate. Sternum present or not. Space between tips of coxae of legs strongly chitinized in some species. Sterna prominent. Sternum I of opisthosomatic segment in one group triangular, located between and behind coxae of legs IV, while in others, anterior sterna considerably shifted forward, included between coxae of legs (higher Opiliones) Chelicerae three-segmented and claw-shaped. Pedipalpi leg-like. Legs seven-segmented. Genital opening located on sternum of segment VIII of body; many species without paired genital opercula. Respiratory organs in higher Opiliomorphae (Orders Haptopoda and Phalangistarbi) located on sterna IX and X; in majority of Opiliones only one pair of tracheae on sternum segment IX. Carboniferous to Recent.

Ecology and Geographical Distribution. These are terrestrial chelicerates living in the soil, in mosses, under the roots of plants, and in various cavities and depressions of the soil, etc. Most are predators, and some are saprophagous. In the Recent epoch they are distributed everywhere except the cold regions. In the Carboniferous they lived in land masses represented by present-day Europe and North America.

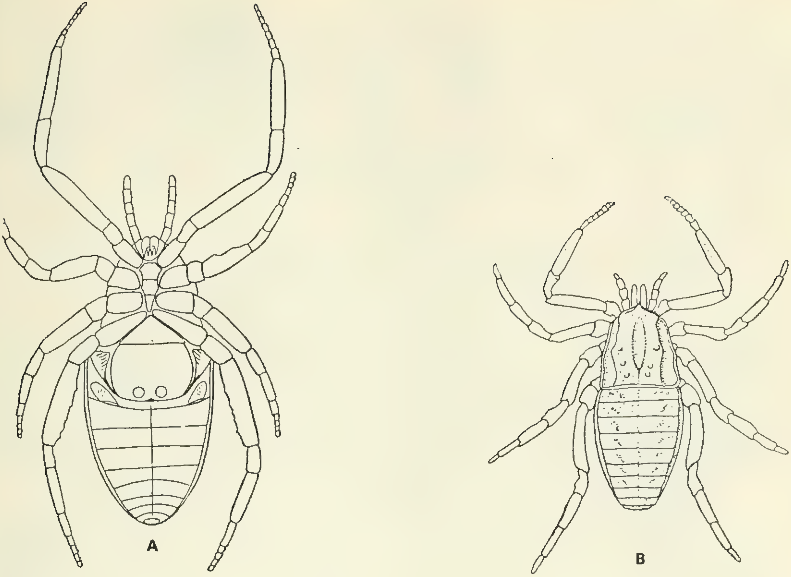
Classification, Phylogeny and Systematic Position. Opiliomorphae are related to the primitive classes of Scorpionomorpha, particularly the Amblypygi, from which they originated (see scheme on page 384). The most primitive Haptopoda probably are the ancestors of higher Opiliomorphae, for example Cyphophthalmi, a suborder of Opiliomorphae which shows many characters common to Haptopoda. All Opiliomorphae evolved parallel with the two other subclasses of Arachnida. All these groups are linked in origin to the general amblypygoid ancestors and the general trends of morphogenesis are related to the curving of the longitudinal axis of the body.

Subclass Opiliomorphae is divided into three orders: Haptopoda, Phalangiotarbi, and Opiliones. Only the last order has living representatives.

Order HAPTOPODA

(Haptopodida)

Small terrestrial chelicerates with large prosoma, segmented opisthosoma. Cephalothorax broadly joined with abdomen. Prosoma comparatively large, occupies one-third of body length. Integument thick, with coarse spinous ornamentation. Longitudinal axis of shield with four furrows, middle furrows forming distinct border of narrow rachydial zone of propeltidium, lateral ones bordering pleural parts. Pair of large eyes placed close to anterior end of shield. Abdomen eleven-segmented (Petrunkevitch, 1949). Terga and sterna with fine dots. Pleurae soft, without sclerites. Terminal segments of opisthosoma bent to

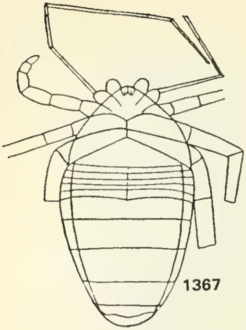


477 Fig. 1366. Order Haptopoda.

1366. *Plesiosiro madeleyi* Pocock; A—ventral view, × 6, B—dorsal view, × 4.5. Carboniferous. Western Europe (Pocock, 1910).

ventral side (Fig. 1366). This process just noticeable in Haptopoda. Three-segmented sternum present on ventral side of prosoma. Chelicerae three-segmented, short, claw-shaped. Pedipalpi simple, short, leg-like, six-segmented. Coxae of chelicerae fused with those of pedipalpi into one plate. Endites of coxae of pedipalpi elongate, forming maxillary processes. Legs long, slender, of walking type, movable, cylindrical, seven-segmented. Tarsi slender, five-segmented. Patellae shorter or equal in length to tibiae. First sternum of opisthosoma triangular, situated between and behind coxae of legs IV. Sternum of segment VIII very wide. Genital opening in form of transverse slit located
477 near posterior margin of sternum VIII. Sides of genital opening with paired valves, rudiments of abdominal appendages of genital segment VIII (Fig. 1366 A). Folded pulmonary sacs located along margins of segments IX, X. Sterna of segments X–XVIII with longitudinal furrow along median line of body.

Haptopoda were terrestrial and respired with the help of pulmonary sacs. They were probably predatory chelicerates.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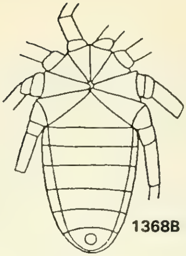
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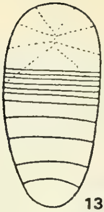
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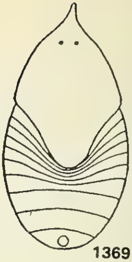
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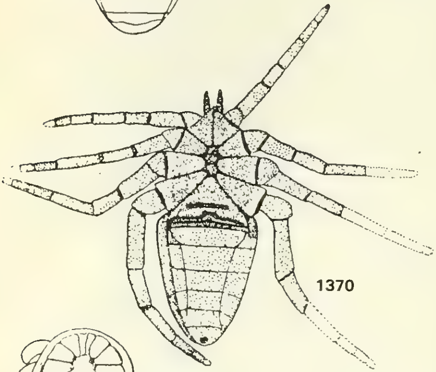
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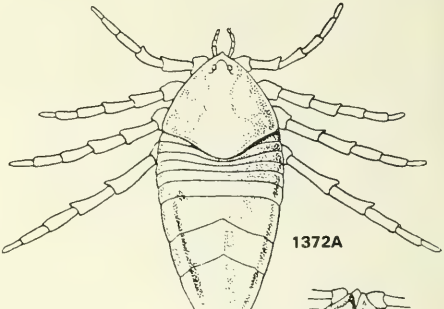
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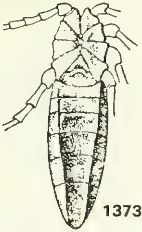
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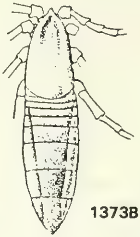
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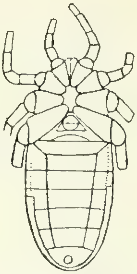
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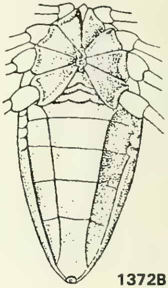
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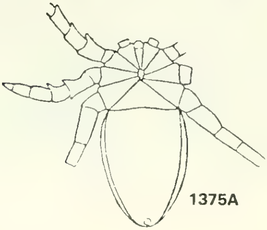
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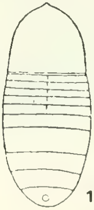
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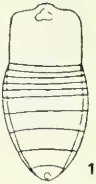
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Carboniferous. The most primitive forms of subclass Opiliomorphae originated from amblypygoid organisms and gave rise to other pseudospiders of the orders phalangiotarbi and Opiliones. The single family Pleisiosironidae, with a single genus and species (*Plesiosiro* Pocock, 1911); known from the Carboniferous of England (Fig. 1366).

Order PHALANGIOTARBI

(Architarbida)

This order contains extinct terrestrial Chelicerates with widely oval or elongate body (Figs. 1372, 1373). Prosoma joined with abdomen along entire width of body. Prosomatic shield large, elongate (Fig. 1373), triangular (Fig. 1372) or quadrangular (Fig. 1375B). Posterior margin rectangular (Fig. 1374B), weakly convex (Fig. 1373) or with middle part strongly extended posteriorly (Fig. 1369). Anterior margin of shield wide rounded or with narrow finger-like projection (Figs. 1368, 1369). Surface of shield with large dotted ornamentation, without longitudinal furrows. Anterior third of shield with two large eyes* Opisthosoma oval or egg shaped, ten- to twelve-segmented; last segment located on ventral side of body. Terga of segment XII of abdomen represented in many species by valve of anal opening. Terga of first opisthosomatic segments considerably shortened. Sharply narrowing terga usually bend posterior margin of cephalothoracic shield (Figs. 1368, 1372A). Sterna considerably fewer than terga, usually seven; their Number rarely equals that of terga. Sterna with two longitudinal furrows along margin of body (Fig. 1372B). Sternum of first abdominal segment triangular, lying between and behind coxae of legs IV. Genital opening in form of transverse slit on sternum VIII (Fig. 1370). Paired genital opercula present. Respiratory system consists of pulmonary sacs located 479 along sides of sterna of segments IX–XI of opisthosoma. Chelicerae three-segmented, claw-shaped. Pedipalpi short, slender, leg-like, six-segmented. Coxae of pedipalpi with gnathobases. Coxae of legs triangular, closely pressed

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478 Figs. 1367–1375. Order Phalangiotarbi.

1367. *Heterotarbus ovatus* Petrunkevitch; ventral view, × 4. Carboniferous, North America (Petrunkevitch, 1913). 1368. *Opiliotarbus elongatus* (Scudder); A—ventral view, B—dorsal view × 4. Carboniferous. North America (Petrunkevitch, 1913). 1369. *Architarbus minor* Petrunkevitch; dorsal view, × 4. Carboniferous, North America (Petrunkevitch, 1913). 1370. *Architarbus rotundotus* Scudder; ventral view, × 2.5. Carboniferous, North America (Petrunkevitch, 1913). 1371. *Phalangiotarbus subovalis* (Woodward); ventral view, × 3. Carboniferous, North America (Pocock, 1911). 1372. *Goniotarbus angulatus* (Pocock); A—dorsal view, B—ventral view, × 4. Carboniferous, Western Europe (Pocock, 1911). 1373. *Leptotarbus torpedo* (Pocock); A—ventral view, B—dorsal view, × 4. Carboniferous, Western Europe (Pocock, 1911). 1374. *Orthotarbus minutus* (Petrunkevitch); A—ventral view, B—dorsal view, × 5. Carboniferous, North America (Petrunkevitch, 1913). 1375. *Geratarbus lacoei* Scudder; A—ventral view, B—dorsal view, × 4. Carboniferous, North America (Petrunkevitch, 1913).

* Editor's note: Actually *six* eyes in most species.

against one another, immovably fused with thorax. In some species coxae of legs IV probably movable. Legs long, seven-segmented, of walking type. Carboniferous. Terrestrial saprophages or predators living possibly in forest litter.

This order is very close to the order Haptopoda, from which probably it originated, and is also close to the ancestral forms of the order Opiliones, the ancestors of which also appeared in the Carboniferous but is extant. There are three families: Heterotarbidae, Opiliotarbidae and Architarbidae.

Family HETEROTARBIDAE Petrunkevitch, 1913

Legs of first pair very slender, long, with tubular elongate segments. Legs II short, legs III and IV longer with stout segments. Coxae of legs I placed at acute angle to longitudinal axis of body, at considerable distance from one another. Coxae of legs II small, lying along sides of prosoma. Coxae of legs III and IV narrow, rectangular, stretching transverse to body, in close contact with each other along median line (Fig. 1367). Opisthosoma with ten terga, first five very narrow. Length 14 mm. Carboniferous of North America. One genus—*Heterotarbus* Petrunkevitch, 1913.

Family OPILIOTARBIDAE Petrunkevitch, 1945

Legs of all pairs equal, elongate, moderately stout. Coxae of all legs triangular, radially placed, closely set, with apices almost in contact at center of thorax. Trochanters of legs III and IV two-segmented. Opisthosoma eleven-segmented, first six terga very narrow (Fig. 1368). Length of body 14–15 mm. Middle Carboniferous of North America. Single genus—*Opiliotarbus* Pocock, 1900.

Family ARCHITARBIDAE Karsch, 1882

Legs of all pairs similar, slender, medium size, for walking. Coxae of legs triangular, closely pressed against each other, but apices do not reach center of thorax. Coxae of pedipalpi fused with coxae of legs I or remain free; in that case lying between leg I coxae. Abdomen with ten terga, first five–six distinctly shortened. Sterna nine (Figs. 1369, 1375). Carboniferous—12 genera.

Architarbus Scudder, 1868 (*Geraphrynus* Scudder, 1884). Genotype— *A. rotundatus* Scudder, 1868. Middle Carboniferous. North America. Prosoma without eye tubercle. Eyes placed directly at anterior end of the shield. Shield rhombic, with digitate process at anterior end, with extended middle part of posterior margin. Length of body 15–22 mm (Figs. 1369, 1370). Middle Carboniferous. Two species from North America and West Europe, besides the genotype.

Phalangiotarbus Haase, 1890. Genotype—*Architarbus subovalis* Woodward, 1872; Middle Carboniferous, England. Eyes and eye tubercle absent. Prosoma broader than longer, broadly rounded in front, semicircular, posterior margin straight. Abdomen oval, somewhat broader anteriorly. First four terga narrowed. Length of carapace 5.8 mm (Fig. 1371). Single species. Middle Carboniferous of West Europe.

Goniotarbus Petrunkevitch, 1945. Genotype—*Geraphrynus tuberculatus* Pocock, 1911. Middle Carboniferous, England. Body oval. Eye tubercle with six eyes along sides around anterior margin of prosoma. Prosoma broadly rhombic-triangular anteriorly with extended middle part of posterior margin (Fig. 1372 A, B). First five terga of opisthosoma compressed. They are partly bent by the posterior margin of the shield. Length of body 16–18 mm. Two species. Middle carboniferous of West Europe.

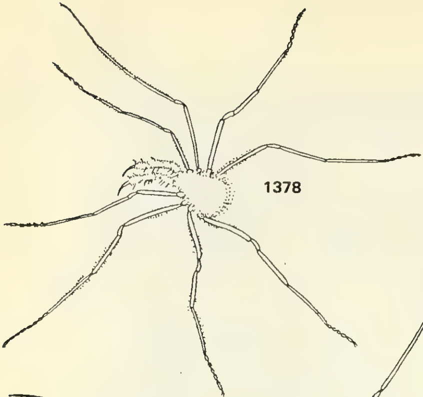
Mesotarbus Petrunkevitch, 1949. Genotype—*M. intermedius* Petrunkevitch, 1949; Middle Carboniferous, England. Very similar to preceding genus, but eye tubercle triangular with three pairs of eyes along sides. Anterior margin of prosoma with pointed median projection; posterior margin broadly rounded. 480 Five anterior terga narrow in middle, with two rows of tubercles. Length of body 10–18 mm. Three species. Middle Carboniferous, West Europe.

Leptotarbus Petrunkevitch, 1945. Genotype—*Geraphrynus torpedo* Pocock, 1911; Middle Carboniferous, England. Body narrow, cigar-shaped. Prosoma considerably longer than broad, pointed in front, broadly rounded at posterior end. Eye tubercle triangular, with six eyes. Four anterior terga narrow, length of fifth tergum equal to half length of sixth. Length of abdomen 2.5 times width. Length of body 13.5 mm, width 2.86 mm (Fig. 1373). One species. Middle Carboniferous, West Europe.

Orthotarbus Petrunkevitch, 1945. Genotype—*Geratarbus minutus* Petrunkevitch, 1913; Middle Carboniferous, North America. Eyes absent. Prosoma with straight posterior margin, cupola-shaped front margin, with small pointed median projection. Abdomen oval, 1.5 times longer than carapace. Anterior five tergites narrowing; with median furrow on surface. Coxae of legs IV distinctly longer than others. Bases of all coxae rounded, area of integument between them fairly wide. First sternum of abdomen small, triangular (Fig. 1374). Legs I and II more slender than legs of hind pairs. Length of body 9.0–11.5 mm. Middle Carboniferous. Two species from North America, one from Czechoslovakia.

Geratarbus Scudder, 1890. Genotype—*G. lacoei* Scudder, 1890. Carboniferous, North America. Prosoma rectangular with straight parallel sides, rounded antero-lateral corners, median frontal projection (Fig. 1375). Posterior margin of prosoma straight. Triangular eye tubercle on anterior margin at base of frontal projection. Abdomen oval. First five terga narrow; first sternum very large, triangular. Blunt spine-like growths (Fig. 1375 A, B) on ventral side of segments of legs, pedipalpi. Length of body 10–12 mm. Middle Carboniferous. Two species from North America and Czechoslovakia.

Besides this from the Middle Carboniferous of North America contains genera *Hadrachne* Melander, 1903; *Metatarbus* Petrunkevitch, 1913;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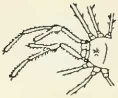
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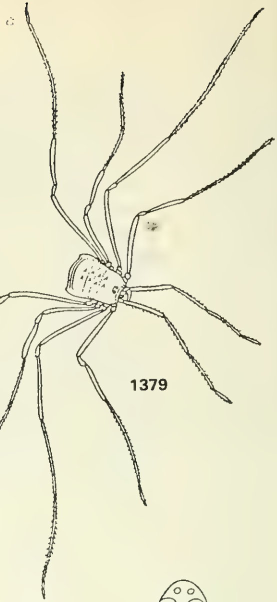
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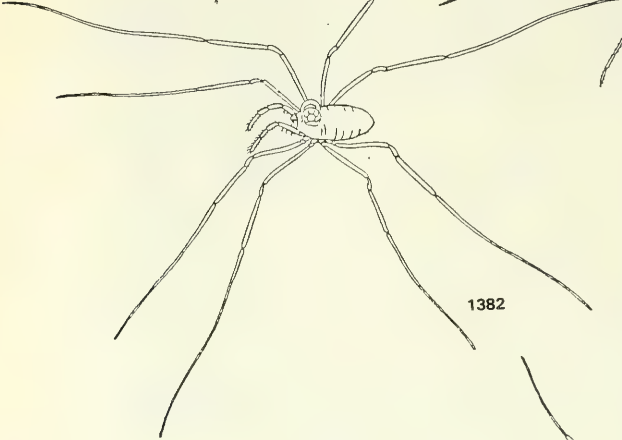
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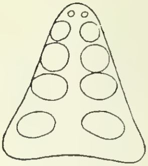
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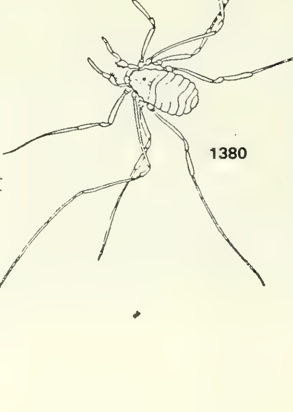
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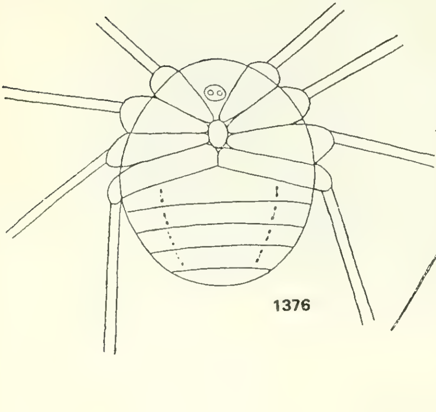
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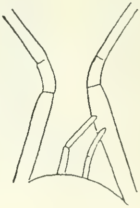
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Paratarbus Petrunkevitch, 1945; *Discotarbus* Petrunkevitch, 1913; *Ootarbus* Petrunkevitch, 1945.

Order OPILIONES. Pseudospiders

(Phalangioidea)

Body short, oval, or rounded with segmented opisthosoma joined along width with prosoma. In most forms legs very long (Figs. 1382, 1379). Prosoma formed by fusion of six segments covered with shield; surface of shield in various species (Gonyleptidae, Gagrellinae) with furrows indicating probable limits of segments. Eye tubercle with two (at times very large) or more eyes (Fig. 1382) at anterior end of prosoma. Opisthosoma short, ten-segmented, nine segments prominent, tergum of tenth represented by operculum. In some species long spines grow on prosoma (Triaenonychidae, some Gonyleptidae). Usually opisthosomatic sterna II and III fused forming an extensive common plate with two tracheal openings along sides. Terga of segments IX and X of opisthosoma shifted towards ventral side of posterior end of body. Chelicerae three-segmented, claw-shaped, sometimes very large (Ischyropsalidae). Pedipalpi vary, either simple, thin, leg-like (Figs. 1377, B, 1382), or very long (Fig. 1379). Large, finger-like projections appear at tips of tibia or patella of pedipalpi, 482 attaining huge lengths, with hook-like tarsus, with rest of segments modified. Coxae of legs large, immovably fused with body, in very close contact. Coxae located along sides of sterna, extended anteriorly. Endites of coxae of pedipalpi and legs I (sometimes coxae of legs II and III) with gnathobases. Appendages of mesosomatic segments represented in some Opiliones by paired genital opercula, pair of tracheal spiracles homologous with the first pair of pulmonary sacs of other chelicerates. Genital opening shifted far to front; in female, long ovipositor projects between palps. Legs comparatively short in forms of suborder Cyphophthalmi, in other Opiliones legs usually long with tubular segments (Fig. 1380). Legs slender, seven-segmented. Tarsi with two claws. Length of the body 1–22 mm.

Ecology and Geographical Distribution. Most species are surface dwellers, living in mosses, under stones and amidst decayed plant debris. Only

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481 Figs. 1376–1382. Order Opiliones.

1376. *Nemastomoides elaveris* Thavenin; ventral view, × 5. Carboniferous, Western Europe (Petrunkevitch, 1953). 1377. *Eotrogulus fayoli* Thevenin; A—prosoma, ventral view with coxa of legs, B—base of forelegs and pedipalpi, × 10. Carboniferous, Western Europe (Petrunkevitch, 1953). 1378. *Gonyleptes nemastomoides* Koch and Berendt; dorsal view, × 1.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1379. *Nemastoma tuberculatum* Koch and Berendt; dorsal view, × 2. Paleogene. Europe (Baltic amber) (Koch and Berendt, 1854). 1380. *Opilio ovalis* Koch and Berendt; dorsal view, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1381. *Opilio ramiger* Koch and Berendt; appendages and anterior end of body, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1382. *Platybunus dentipalpus* Koch and Berendt; dorsal view, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).

a few advanced Opiliones (as for example, Phalangiidae) have left the damp substrata and come on to rock cliffs, trunks of trees, walls of houses etc. Predators. Present day Opiliones are distributed throughout the world, except Antarctica. Fossil forms are known from the Carboniferous and Jurassic of North America and Western Europe. A large number of species are recorded from Baltic amber.

Classification, Phylogeny and Systematic Position. The systematic position of Opiliones has not yet been established. Kastner (1935) on the one hand brings them close fossil Phalangiotarbi and Haptopoda, and on the other hand to some Scorpionomorpha and the mites. Detailed examination of general structural features of Opiliones and other Chelicerata lead Kastner to conclude the affinity of Opiliones to the orders of subclass Pedipalpides and then even with scorpions and mites. In our opinion order Opiliones is related to order Phalangiotarbi and Haptopoda all of which constitute a single group (subclass) Opiliomorphae (ref. p. 588). Opiliones undoubtedly trace their origin from the primitive Scorpionomorpha, probably from amblypygoid chelicerates. The branching off of Opiliones took place somewhat earlier than the origin of Ricinulei, Soluta and Araneae (ref. p. 587 and scheme on p. 588).

Order Opiliones is divided into three suborders. Cyphophthalmi, Laniatores and Palpatores.

Suborder Cyphophthalmi

(Cyphophthalmina)

Body oval, poorly demarcated. On dorsal side prosomatic terga, eight segments of opisthosoma well demarcated. Terga IX, X located subventrally. Genital opening shifted anteriorly but not covered by sterna of segments VII, IX. Pedipalpi short, slender, leg-like. Length 2–3 mm.

Petrunkevitch's (1949, 1953) inclusion of the genera *Nemastomoides* Thevenin and *Eotrogulus* Thevenin under the suborder Palpatores is not correct because in all forms of this suborder the genital opening is shifted far to the front and covered by the sterna of the anterior abdominal segments. Carboniferous to Recent. Single family in the Recent fauna (Sironidae) and one in the Carboniferous (Nemastomoididae).

Family NEMASTOMOIDIDAE Petrunkevitch, 1955

(Eotrogulidae Petrunkevitch, 1955)

Body rounded or oval. Prosoma occupies ⅓–½ of body. Two eyes. Coxae of pedipalpi separate. Coxae of legs large, increasing in size from front to back. Proximal ends of coxae of legs IV broadest, rectangular, almost close to median line of body (Fig. 1376). Legs long, slender. Proximal ends of coxae enclose small oval area of thorax. Pedipalpi simple, slender, leg-like (Fig. 1377 B). Length 2.7–12.0 mm. Middle and Upper Carboniferous of North America and Europe. This family includes two genera which Petrunkevitch (1955) placed in two separate families.

Nemastomoides Thevenin, 1901 (*Protopilio* Petrunkevitch, 1913). Genotype—*N. elaveris* Thevenin, 1901; Upper Carboniferous, Western Europe. Coxae of all legs devoid of gnathobases. Size of coxae increases from first leg to last. Coxae of leg IV rectangular, touching median line of body. Legs very long, slender; trochanter not divided. With two small eyes near anterior margin of prosoma (Fig. 1376). Middle and Upper Carboniferous. Two species from Western Europe and North America.

Eotrogulus Thevenin, 1901. Genotype—*E. fuyoli* Thevenin, 1901; Upper Carboniferous, Western Europe. Prosoma triangular, considerably longer than wide, with two small eyes at anterior end. Coxae of legs arranged in two parallel 483 rows, rounded. Pedipalpi small, simple, leg-like (Fig. 1377A). Trochanters of legs tubular. Length 12 mm, carapace 5.5 mm long. One species. Upper Carboniferous of Western Europe.

Suborder Laniotores

Body more shortened, rounded, clearly subdivided into prosoma and opisthosoma, former with indistinct traces of segmentation. Genital opening covered by anteriorly shifted abdominal sterna. Pedipalpi large, claw-shaped tarsi; other segments variously modified, provided with spines, needles etc. (Fig. 1378). Tarsi of legs III and IV with two claws, or three-clawed due to modification of pretarsus (arolium) or claw-like development of dorsal margin of tip of tarsus itself (Pseuderychium). Larger species. Length up to 10 mm. Paleogene to Recent. Six families in the Recent fauna: Oncopodidae, Phalangodidae, Assamiidae, Cosmetidae, Triaenonychidae and Gonyleptidae, the last family with fossil representatives.

Family GONYLEPTIDAE Simon, 1879

Pedipalpi stout, long, terminal segment claw-shaped, capable of pressing against tibia, with spines on last, also on bent segment; sometimes on others as well (Fig. 1378). Tarsi of legs III and IV with two claws; tarsi with claw-like tips on other legs (Pseudonychium). Terga of segments VI and VIII of opisthosoma free. Walking legs slender, long. Length of body ranges from 5 mm (in a majority of species) up to 18 mm. Paleogene to Recent. More than 300 genera in the Recent fauna of which *Gonyleptes* Kirby, 1819 (Fig. 1378), is known from the Paleogene of Europe (Baltic amber).

Suborder Palpatores

Body rounded or short-oval. Prosoma sometimes with transverse furrows only in posterior half. Eyes in some species attain enormous dimensions (Fig. 1382).

Pedipalpi simple, usually of small size; tarsi rounded at tip. In some species, dorsal surface of tibia or of bent segments with finger-like projections (Fig. 1381). Legs very long, slender. Tarsi of legs III and IV with only one claw. Carboniferous to Recent. Two superfamilies in the Recent fauna: Trogulidea and Phalangiidea.

SUPERFAMILY TROGULIDEA
(Dyspnoi)

Tarsus of pedipalpi shorter than tibia. Finger-like projections on coxa of leg II absent or very small. Legs without stigmata. Four families in Recent fauna: Trogulidae, Acrosopilionidae, Ischyropsalidae, Nemastomatidae. The last two are known from the Paleogene of Europe (Baltic amber).

Family ISCHYROPSALIDAE Simon, 1879

Prosoma without projection. Chelicerae very large, larger than body. Metapeltidium separate. Pedipalpi slender, shorter than legs and chelicerae. Paleogene to Recent. Four genera in the Recent fauna of which *Sabacon* Simon, 1879 is known from the Paleogene of Europe (Baltic amber).

Family NEMASTOMATIDAE Simon, 1872

Anterior margins of cephalothoracic shield rounded, without median projection. Meso- and metapeltidium fused (Fig. 1379). Pedipalpi long, leg-like. Paleogene to Recent. Two genera in the Recent fauna of which *Nemastoma* C.L. Koch, 1836 is known from the Paleogene of Europe.

SUPERFAMILY PHALANGIIDEA
(Eupnoi)

Tarsus of pedipalpi longer than tibia, with distinct projection of coxae of leg II. Leg with accessory stigmata on femora. One family—Phalangiidae in the Recent fauna, also known from the Paleogene of Europe (Baltic amber).

Family PHALANGIIDAE Simon, 1879

Body soft. Eyes located on tubercle of prosoma. Tarsi of legs multisegmented. Paleogene to Recent. Over 120 genera in Recent fauna of which *Opilio* Herbst, 1798 (Figs. 1380, 1381); *Platybunus* C.L. Koch, 1854 (Fig. 1382); *Caddo* Bansk, 1892; *Cheiromachus* Menge, 1854; *Dicranopalpus* Doleschall, 1852; *Liobunum* C.L. Koch, 1854 are known from the Paleogene of Europe (Baltic amber). Also known from the Paleogene of North America is the genus *Phalangium* Linnaeus, 1758.

Subclass SOLUTA. Armored spiders

485 Body oval, often with broad opisthosoma movably connected with prosoma, contact surface equal to width of body. Integument of entire body with very dense tubercles (Figs. 1393, 1401), reticulate (Fig. 1399B), dotted (Fig. 1386), or with other distinct ornamentation (Figs. 1407, 1413A). Prosomatic shield uniformly convex (most Anthracomarti) or with distinctly separate median and marginal zones (Figs. 1387, 1393). In some species transverse furrows indicate borders between fused pro-, meso- and metapeltidia at posterior part of the shield. Usually with two large eyes (Fig. 1385). Opisthosoma eleven-segmented, some fused, indistinct. Two segments bent ventrally. Sterna of these segments reduced; one tergum of eleventh segment modified into anal valve (Figs. 1383A, 1409). Terga divided by two longitudinal furrows into median and two lateral rows. In Anthracomarti lateral plates of terga greatly expanded, forming more or less wide marginal areas (Figs. 1408A, 1413A). (Armored spiders inherited similar structure of terga from the ancestors of Ricinulei, from whom they originated.) Ventral surface of prosoma covered with wide coxae of pedipalpi (few of which apparently movable), walking legs [in certain species leg coxae in contact with one another along median line of body (Fig. 1402B)]. Coxae enclose wide oval area in which sternum is located (Fig. 1383A). Coxae of pedipalpi and also of leg I without long hairs (sometimes serrated) forming a filtering apparatus as in order Araneae (Fig. 1383A). Sterna of opisthosoma well developed. Posterior sterna arcuately bent, surrounding anal opening and stergites of terminal segments of body (Figs. 1392A, 1408B). Chelicerae short, three-segmented, hook-like as in spiders* (Fig. 1383). Probably in armored spiders digestion was external. Pedipalpi short, simple (Fig. 1413A). Walking legs comparatively short, stout, partly segmented. Tarsi with two [actually 3] claws. Genital opening located on sternum of eighth segment. Genital valves paired, sometimes in form of two papillae (Fig. 1402B). Pulmonary sacs located along margins II, III and IV sterna of Opisthosoma. Devonian to Permian**.

Ecology and Geographical Distribution. Land chelicerates; probably predators. The presence in Anthracomarti of wide marginal areas is perhaps suggestive of life in sinking substrata. Widely distributed in Eurasia and America during Devonian, Carboniferous and Permian**.

Classification, Phylogeny and Systematic Position. The Armored spiders of the subclass Soluta originated from primitive Scorpionomorpha—probably the ancestors of the Amblypygi. The indications of similar phylogenetic affinity are the presence of a sternum, a movable articulation between the cephalothorax and abdomen, pulmonary sacs in the first abdominal segments, paired opercula of the genital opening and also the retention, in some

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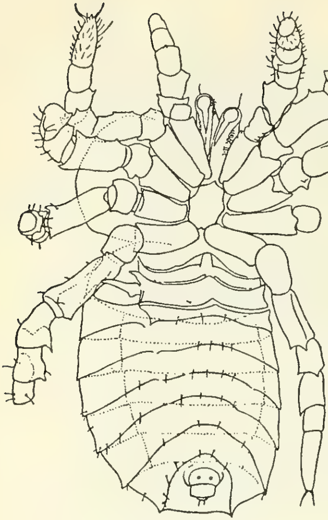
*Editor's note: Spider chelicerae not 3-segmented.

**Editor's note: No Permian records provided here or known.



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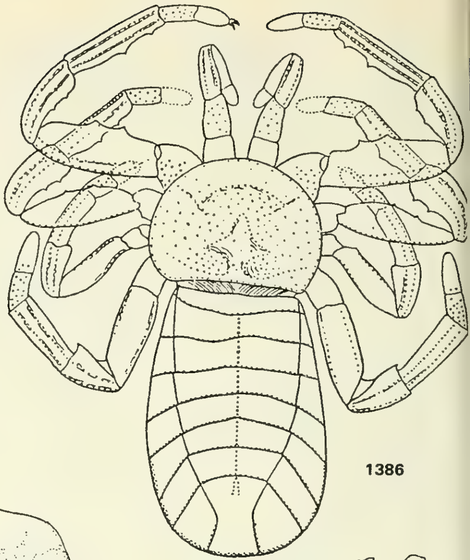

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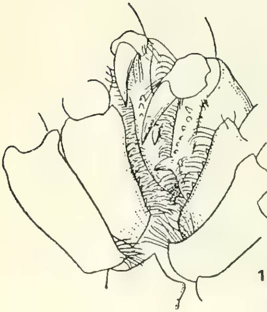

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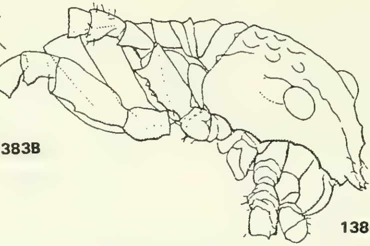

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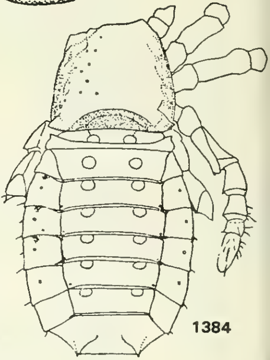

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Figs. 1383–1386. Families Palaeocharinidae, Anthracosironidae.

1383. *Palaeocharinoides hornei* Hirst; A—ventral view, × 40, B—chelicerae and coxae of pedipalpi and anterior legs, × 120, C—carapace, lateral view, × 40. Devonian, Western Europe (Hirst, 1923). 1384. *Palaeocharinus* sp.; dorsal view, × 30. Devonian, Western Europe (Hirst, 1923). 1385. *Palaecharinus rhyniensis* Hirst; lateral view, × 40. Devonian, Western Europe (Hirst, 1923). 1386. *Anthracosiro woodwardi* Pocock; general view from top, × 5. Carboniferous, England (Petrunkevitch, 1949).

Devonian Trigonotarbi (*Palaeocharinoides hornei* Hirst), of rudiments of segments XII and XIII of the opisthosoma in the form of a small cylindrical 'tail' behind the anal opening (Fig. 1383A). In other Trigonotarbi and in all Anthracomarti these rudiments are absent, but in present-day spiders they appear during embryonal development. The assumption by some workers about the affinity and even the origin of the ixodid mites from the Anthracomarti, based on a comparison of the structure of dorsal shields, is erroneous. All Soluta, including Anthracomarti, possess a true prosoma while all Acarina and hence Ixodides possess a membranous prosoma without incorporating the acron and the first two oral segments, resulting in a separate gnathosoma in mites. Similarly, the head shields of the Anthracomarti and the ixodids are not homologous. The subclass Soluta is related to the spiders of the subclass Araneae with which it shares a common origin. The order Trigonotarbi is more primitive than the Anthracomarti, with its more specialized marginal extensions of the terga. Two orders: Trigonotarbi and Anthracomarti.

486 Order TRIGONOTARBI

Body divided into prosoma (cephalothorax) and opisthosoma (abdomen), movably joined. Prosoma always smaller than abdomen, shape highly variable, from hemispherical (Fig. 1386) to triangular or conical (Fig. 1395). Integument of prosoma thick, forming a continuous armor (Fig. 1383B). Median part of prosoma normally sharply isolated from lateral parts, in few species boundaries of fused primary pro-, meta- and mesopeltidia marked by furrows (Fig. 1387). Two eyes usually present, sometimes large (Figs. 1385, 1401). Opisthosoma eleven-segmented. In some Palaeocharinidae rudiments of two opisthosomatic segments (XII and XIII) present in form of 'tail-like' appendage behind anal opening (Fig. 1383A). Only eight segments discernible from dorsal side. Terga divided into median and marginal rows by two longitudinal furrows. Postero-lateral angles of terga occasionally form spine-like projections either along borders or at posterior end (Figs. 1390, 1403). Chelicerae three-segmented and hook-like. The presence of a filtering apparatus on coxae of pedipalpi and legs I (Fig. 1383B) suggests, on the basis of analogy with spiders, external digestion in Trigonotarbi (Fig. 1383B). Sternum occupies middle part of thorax; movable coxae of walking legs located on sides of sternum (Figs. 1383A, 1392B). Legs moderately long, seven-segmented; ventral surface of some segments with teeth (Figs. 1383A, 1386). Tarsi of legs with two claws. Genital opening located on eighth sternum (second abdominal): in form of a transverse slit with two opercula. (Figs. 1392B, 1402B). Respiratory system three pairs of pulmonary sacs located along sides of sterna of second, third and fourth opisthosomatic segments. Devonian of Europe and Carboniferous of North America.

Classification, Phylogeny and Systematic Position. The order Trigonotarbi was included under Anthracomarti prior to the investigations of Petrunkevitch (1949). On the one hand it was found to be related to pseudospiders of the order Opiliones and on the other, to real spiders of the order Araneae. Such an intermediate position correctly reflects the actual phylogenetic affinity of the Trigonotarbi. They originated from amblipygoid chelicerate spiders and pseudospiders which is reflected in the possession of characteristic features of both groups, and also of some peculiarities of primitive Scorpionomorpha (Amblypygi, Ricinulei) as: retention of metasoma, division of terga into three parts by longitudinal furrows, etc. Five families: Palaeocharinidae, Anthracosironidae, Eophrynidae, Trigonotarbidae, Trigonomartidae.

Family PALAEOCHARINIDAE Hirst, 1923

Opisthosoma of thirteen segments, nine with well developed terga, sterna. Terga X and XI of opisthosoma bent at abdominal region. Tergum of twelfth segment forms anal valve, behind it lie two rudimentary tubular segments homologous with metasoma of Amblypygi and other Scorpionomorpha (Fig. 1383). Devonian. Two genera.

Palaeocharinoides Hirst, 1923. Genotype—*P. hornei* Hirst,1923; Devonian, Western Europe, Scotland. Sternum 'star-shaped' with eight pointed corners. Posterior margin convex. Surface of cephalothorax smooth and dotted (Fig. 1383A, B). Length 2.2 mm. Single species. Devonian of Western Europe.

Palaeocharinus Hirst, 1923. Genotype—*P. rhyniensis* Hirst, 1923; Devonian, Western Europe, Scotland. Sternum oval with rounded projecting corners. Hind margins of shield straight. With two large eyes (Figs. 1384, 1385). Length of prosoma 1.5–2.0 mm and of opisthosoma, 2 mm. Four species. Devonian of Western Europe.

Family ANTHRACOSIRONIDAE Pocock, 1903

Abdomen of ten visible segments (first tergum reduced). Prosoma hemispherical, broadly rounded in front, at sides. Opisthosoma extended oval in shape. Integument with sharp, dotted ornamentation. Legs long. Femur, patella, tibia of first two pairs of legs with tubercles on sides (Fig. 1386). Carboniferous of Western Europe. One genus *Anthracosiro* Pocock, 1903.

Family EOPHRYNIDAE Karsch, 1882

Abdomen nine-segmented dorsally. Tergum IX located between plates of eighth
488 tergum. Distal segments reduced, shifted to ventral side, forming anal valve (Fig. 1392). Prosomatic shield triangular, usually with narrow rustrum, concave posterior margin. Eyes present or absent. Four pairs of pulmonary sacs located on opisthomatic sternites II–V. Carboniferous of North America and Europe. 14 genera.

Stenotrogulus Fritsch, 1904. Genotype—*Eophrynus salmii Stur,* 1887; Carboniferous, Czechoslovakia. Posterior end of body with four small, pointed projections. Terga VIII and X of opisthosomatic segments fused. Terga of middle zone with two longitudinal depressions, four rows of tubercles (Fig. 1388); middle region of prosomatic shield with group of two large posterior, three smaller anterior oval tubercles. Prosoma triangular, with elongate rostral part. Eyes absent. Length of prosoma 10 mm. Single species. Carboniferous of Europe.

Cyclotrogulus Fritsch, 1904. Genotype—*Eophrynus sturii* Haase, 1890; Carboniferous, Czechoslovakia. Body pear-shaped, with small triangular prosoma pointed in front; almost disc-like opisthosoma broadly rounded at posterior end. Middorsal zone of terga formed by two longitudinal depressions. With six rows of tubercles along depressions, furrows on terga. Tergum of opisthosomatic segment IX devoid of tubercles (Fig. 1389). Length of carapace 6.5 mm, of abdomen, 14 mm. One species. Carboniferous of Europe.

Petrovicia Fritsch, 1904. Genotype—*P. proditoria* Fritsch, 1904. Carboniferous, Czechoslovakia. Body egg-shaped, with four large spines arranged in one row at posterior end. Terga with four longitudinal rows of tubercles. Prosoma triangular with long pointed rostrum. Eyes absent (Fig. 1390). Single species. Carboniferous of Europe.

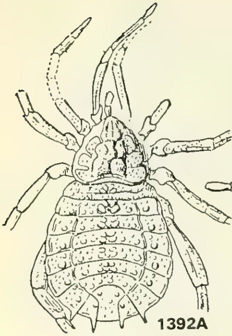
Hemiphrynus Fritsch, 1899. Genotype—*H. longipes* Fritsch, 1899. Carboniferous, Czechoslovakia. Body egg-shaped, broad at anterior half and with four small projections at posterior margin. Terga devoid of longitudinal depressions, tubercles. Prosoma triangular, with long narrow rostrum. Eyes absent. Legs long, slender (Fig. 1391). Length of body 28 mm. Carboniferous of Europe.

Vratislavia Fritsch, 1904. Genotype—*Architarbus silesiacus* Roemer, 1878; Middle Carboniferous, Poland. Terga not divided by longitudinal depressions, without tubercles. With four triangular projections at posterior end of body. Terga of opisthomatic segments VIII and IX divided by furrow. Legs comparatively stout, short. Structures of prosoma not known. Single species. Carboniferous of Europe.

The following are recorded from the Carboniferous of Europe: *Eophrynus* Woodward, 1871 (Fig. 1392); *Acrokreischeria* Petrunkevitch, 1953 (Fig. 1393); *Pseudokreischeria* Petrunkevitch, 1953; *Anzinia* Petrunkevitch, 1953; *Hemikreischeria* Fritsch, 1904 (Fig. 1394). The following are from the Carboniferous of North America: *Pleophrynus* Petrunkevitch, 1945 (Fig. 1395); *Pocononia* Petrunkevitch, 1953 (Fig. 1396); *Areomartus* Petrunkevitch, 1913 (Fig. 1397).

Family TRIGONOTARBIDAE Petrunkevitch, 1949

Opisthosoma eight-segmented dorsally. Marginal row of terga only on seven segments. Eighth tergum surrounded by plates of seventh tergum. Seven sterna, two terga displaced to ventral side of body. Four posterior sterna arranged semicircularly in front of anal opening. Cephalothoracic shield triangular, with



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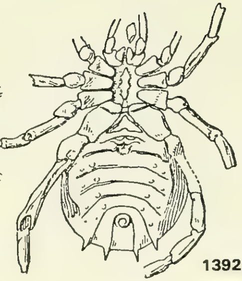

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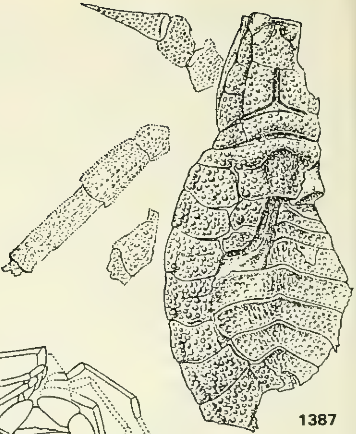

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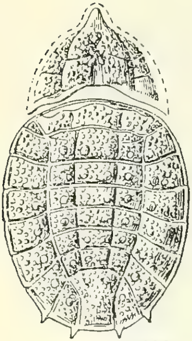

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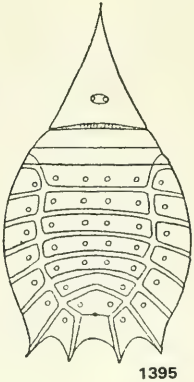

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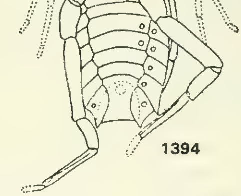

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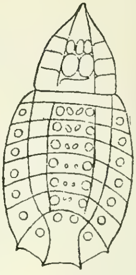

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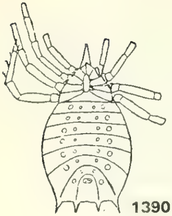

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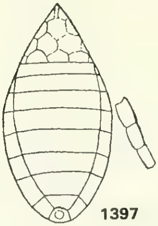

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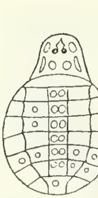

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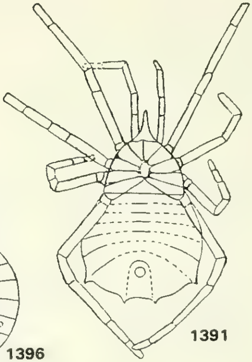

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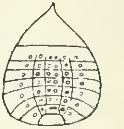

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two eyes. Pulmonary sacs located on second, third sterna (morphologically third, fourth). Length 4.7 mm (Fig. 1398A, B). Carboniferous. Single genus—*Trigonotarbus* Pocock, 1911 from Western Europe.

Family TRIGONOMARTIDAE Petrunkevitch, 1949

Opisthosoma eight-segmented dorsally. Eighth tergum with triangular marginal plates. Intersegmental borders of terga straight, parallel to one another. Longitudinal furrows on dorsal side of abdomen converge towards posterior end of body. Surface of prosoma, terga with reticulate (Fig. 1399B) or tubercular (Fig. 1401) ornamentation. Eyes present. Carboniferous. Six genera.

Trigonomartus Petrunkevitch, 1913. Genotype—*Anthracomartus* 489 *pustulatus* Scudder, 1884; Middle Carboniferous. North America and Western Europe. Prosoma narrow, triangular, rounded at tip. Dorsal surface of body with reticulate ornamentation. Prosoma divided into two parts by transverse furrow. Eyes absent. Coxae of legs IV considerably larger than others (Fig. 1399 A, B). Length 16–18 mm. Four species. Middle Carboniferous of Western Europe and North America.

Planomartus Petrunkevitch, 1953. Genotype—*Anthracomartus krejcii* Kusta, 1883; Carboniferous. Czechoslovakia. Prosoma large, triangular. Opisthosoma wide, egg-shaped, rounded posteriorly. Tergum VIII of opisthosoma square. Marginal row of terga inclined posteriorly (Fig. 1400). Length of abdomen 11.5 mm. Single species. Carboniferous of Europe.

The following are recorded from the Carboniferous of Western Europe: *Aphantomartus* Pocock, 1911 (Fig. 1401); *Elaverimartus* Petrunkevitch, 1953 (Fig. 1402); *Phrynomartus* Petrunkevitch, 1945 (Fig. 1403); also from the Carboniferous of North America—*Lissomartus* Petrunkevitch, 1949 (Fig. 1404).

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487 Figs. 1387–1397. Family Eophrynidae.

1387. *Kreischeria wiedei* Geinitz; general view, × 3. Carboniferous, Western Europe (Petrunkevitch, 1953). 1388. *Stenotrogulus salmii* (Stur); dorsal view, × 2. Carboniferous, Western Europe, (Petrunkevitch, 1953). 1389. *Cyclotrogulus sturmii* (Haase); dorsal view, × 2. Carboniferous, Western Europe (Petrunkevitch, 1953), 1390. *Petrovicia proditoria* Fritsch; ventral view, × 2.5. Carboniferous, Western Europe (Petrunkevitch, 1953). 1391. *Hemiphrynus longipes* Fritsch; ventral view, × 2.5. Carboniferous, Europe (Petrunkevitch, 1953). 1392. *Eophrynus prestvici* (Buchland); A—dorsal view, B—ventral view, × 2. Carboniferous, Western Europe (Pocock, 1911). 1393. *Acrokreischeria verrucosa* Pocock; dorsal view, × 2.5. Carboniferous, Western Europe (Pocock, 1911). 1394. *Hemikreischeria geinitzi* Thevenin; ventral view from bottom, × 2.5. Carboniferous, Europe (Petrunkevitch, 1953). 1395. *Pleophrynus ensifer* Petrunkevitsch; dorsal view, × 3. Carboniferous, North America (Petrunkevitch, 1949). 1396. *Pocononia whitei* (Ewing); dorsal view, × 2. Carboniferous. 1397. *Areomartus ovatus* Petrunkevitch; dorsal view, × 2.5. Carboniferous, North America (Petrunkevitch, 1943).


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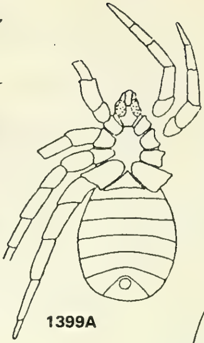
1398B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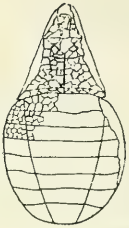
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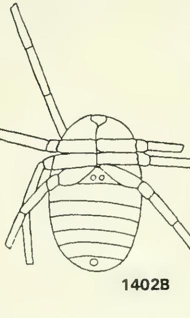
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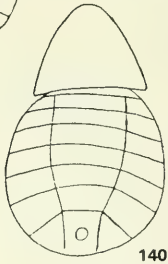
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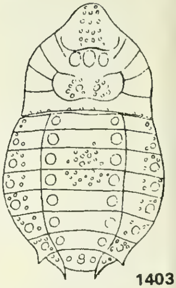
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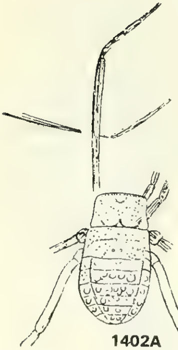
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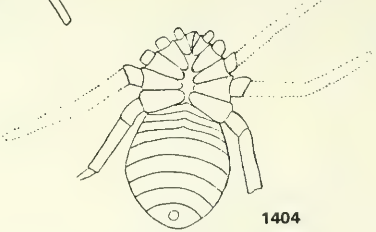
1404

Figs. 1398–1404. Families Trigonotarbidae, Trigonomartidae.

1398. *Trigonotarbus johnsoni* Pocock; A—dorsal view, B—ventral view, × 7. Carboniferous, Western Europe (Pocock, 1910). 1399. *Trigonomartus pustulatus* (Scudder); A—ventral view, B—dorsal view, × 3. Carboniferous, North America (Petrunkevitch, 1913). 1400. *Planomartus krejcii* Kušta; dorsal view, × 3. Carboniferous, Europe (Petrunkevitch, 1913). 1401. *Aphantomartus aerolatus* Pocock; dorsal view, × 6. Carboniferous. Western Europe (Pocock, 1911). 1402. *Elaverimartus pococki* (Petrunkevitch); A—dorsal view, B—ventral view, × 6. Carboniferous, Western Europe (Pocock, 1911). 1403. *Phrynomartus waechteri* Guthorl; dorsal view, × 3. Carboniferous. Western Europe (Petrunkevitch, 1953). 1404. *Lissomartus carbonarius* (Petrunkevitch); ventral view, × 3. Carboniferous. North America (Petrunkevitch, 1949).

Order ANTHRACOMARTI

Prosoma in most species rounded or triangular (Figs. 1405A, 1410). Dorsal surface of prosoma without sharply demarcated median zone, flat or weakly convex with dotted ornamentation (Fig. 1413A). Eyes absent. In some genera (*Maiocercus* Pocock) ornamentation of prosoma similar to ornamentation in Trigonotarbi (Fig. 1408A). Opisthosoma movably articulated with prosoma; margin of contact wide. Abdomen ten-segmented; two posterior segments bent towards ventral side, their terga form horse-shoe shaped anal segment and anal valve (Fig. 1409 B). Dorsal surface of abdominal terga divided into median and two marginal rows by longitudinal lines as in Trigonomarti. Marginal terga extend outward, form wide marginal zone considerably enlarging area of body (Figs. 1408, 1413). Sternum of first opisthosomatic segment small, triangular, placed between, behind coxae of legs IV. Ventral surface of opisthosoma more convex than dorsal (Fig. 1413B). Surface of terga with pointed dots, very rarely with tubercles (Fig. 1407), complex ornamentation (Fig. 1413A).

Chelicerae three-segmented, claw-shaped, bent towards ventral region. Pedipalpi short, six-segmented, simple (Fig. 1413B). Coxae of all legs movable, narrow, triangular-cylindrical, placed along margin of ventral side of prosoma (Fig. 1413B). Sternum usually elongate, rarely circular. Walking legs seven-segmented with divided trochanters. Tarsi simple, cone-shaped, with two claws. Three pairs of pulmonary sacs located along margins of second, third and fourth sterna of opisthosoma. Genital opening in form of transverse slit covered by unpaired plate and located on eleventh segment (Fig. 1409). Genital atrium of females located in the third opisthosomatic sternum, contains paired seminal vesicles.

Ecology and Biogeography. Terrestrial chelicerates, probably predators with external digestion. They lived in forest litter and on decaying substrata. The widened marginal zones of the terga considerably enlarged the surface area of the body and prevented sinking of animals in the substratum. Their flat bodies facilitated movement in layers of substrata (Fig. 1413C). Anthracomarti were numerous during the Carboniferous to Permian*. They probably are the ecological counterparts of Recent Oribatei and some Nemastomatidae. They lived in land masses represented by modern Europe and North America.

Classification, Phylogeny and Systematic Position. The order Anthracomarti is very close to the order Trigonotarbi with which it was grouped, and both were considered as constituting a single taxon. Anthracomarti trace their origin from primitive Trigonotarbi (see scheme on p. 384) but are more specialized than Soluta.** Members of Anthracomarti were often used for constructing phylogenetic schemes of Chelicerata. One family: Anthracomartidae.

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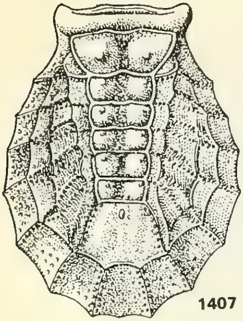
* Editor's note: No known Permian records.

** Editor's note: According to earlier set-up, they are included in Soluta.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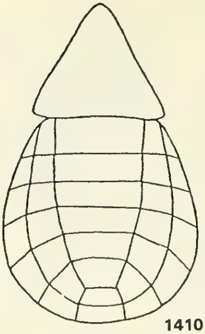
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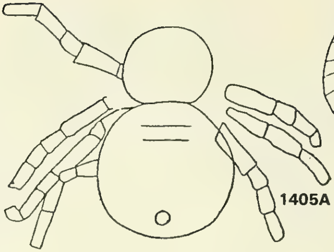
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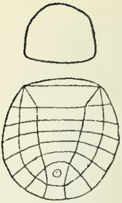
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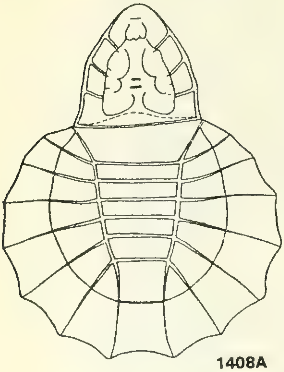
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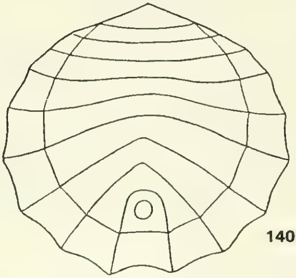
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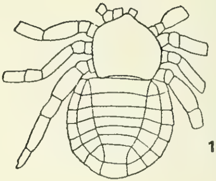
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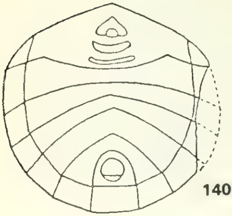
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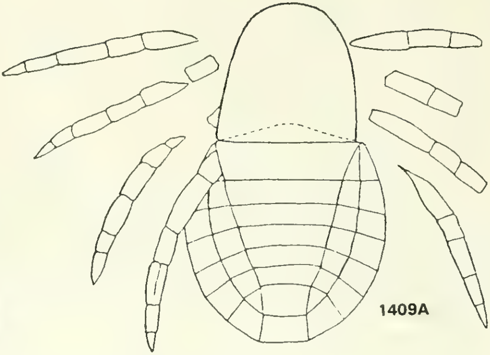
1409A

Family ANTHRACOMARTIDAE Haase, 1890

(Brachypygidae Pocock, 1917; Pleomartidae Petrunkevitch, 1945; Promygalidae Fritsch, 1899; Coryphomartidae Petrunkevitch, 1945)

Family characterized by features of the order. Carboniferous to Permian*. Ten genera. Systematic position of two additional genera not clear.

Brachylycosa Fritsch, 1904. Genotype—*Arthrolycosa carcinoides* Fritsch, 1899; Carboniferous, Czechoslovakia. Prosoma comparatively small, rounded. Opisthosoma disc-like, with smooth borders. Dorsal surface of prosoma smooth, its anterior margin broadly rounded. The width of marginal expansion of tergites equal to width of lateral parts of tergites (Fig. 1405). Length 12.0–20.3 mm. Two species. Carboniferous of Czechoslovakia.

Promygale Fritsch, 1899. Genotype—*Kreischeria bohemica* Fritsch, 1899; Carboniferous, Czechoslovakia. Prosoma longer than broad; anterior margins converge at obtuse angle. Opisthosoma wide, disc-like, with smooth borders. Width of marginal expansion less than width of lateral expansion of terga (Fig. 1406A, B). Length 9.8 × 20.5 mm. Three species. Carboniferous of Czechoslovakia.

Oomartus Petrunkevitch, 1953. Genotype—*O. nyranensis* Petrunkevitch, 1953; Carboniferous, Czechoslovakia. Body egg-shaped; rounded at anterior end of prosoma, at wide posterior end of opisthosoma (Fig. 1411). Prosoma almost hemispherical, longer than broad; with straight posterior margin. Length 17.5 mm. One species.

492 *Anthracomartus* Karsch, 1882. Genotype—*A. voelkelianus* Karsch, 1882; Carboniferous, Poland. Resemble *Pleomartus*, but with more convex median zone on surface of prosoma. Ratio of length of median zone of terga to width: 1 : 0.8. Furrows almost parallel. Anterior margin of prosoma widely rounded, posterior straight. Four poorly described species known, all from the Carboniferous of Czechoslovakia and Poland.

Anthracophrynus Andree, 1913. Genotype—*A. tuberculatus* Andree, 1913. Carboniferous, Western Europe (Dubweiler, Saar). Opisthosoma with broadly rounded lateral, posterior margins, almost squarely truncated anteriorly. Width

491 Figs. 1405–1410. Family Anthracomartidae.

1405. *Brachylycosa carcinoides* (Fritsch); A—dorsal view, B—ventral view, × 2.5. Carboniferous, Europe (Petrunkevitch, 1950). 1406. *Promygale bohemica* (Fritsch); A—dorsal view, B—ventral view, × 2.5. Carboniferous, Europe (Petrunkevitch, 1950). 1407. *Brachypyge carbonis* Woodward; abdomen, dorsal view, × 5. Carboniferous, Western Europe (Pocock, 1911). 1408. *Malocercus carbonis* (Howard and Thomas); A—dorsal view, B—ventral view, × 4. Carboniferous, Western Europe (Petrunkevitch, 1953). 1409. *Cleptomartus plantus* Petrunkevitch; A—dorsal view, B—ventral view, × 8. Carboniferous, Western Europe (Petrunkevitch, 1958). 1410. *Coryphomartus triangularis* (Petrunkevitch); dorsal view, × 4. Carboniferous, Western Europe (Petrunkevitch, 1913).

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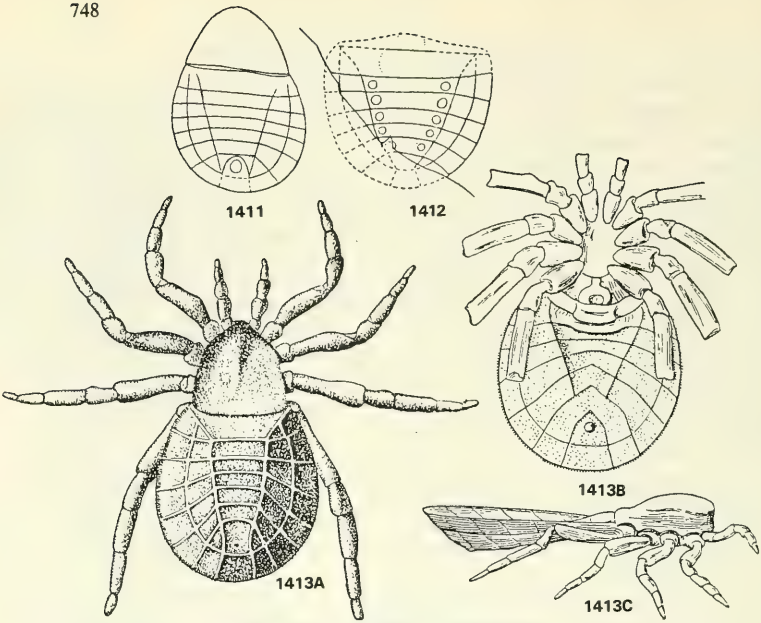
* Editor's note: No known Permian records.



Figs. 1411–1413. Family Anthracomartidae.

1411. *Oomartus nyranensis* Petrunkevitch; ventral view, × 3. Carboniferous, Europe (Petrunkevitch, 1953). 1412. *Anthracophrynus tuberculatus* Andree; dorsal view of abdomen, × 3. Carboniferous, Europe (Petrunkevitch, 1953). 1413. *Cryptomartus hindi* (Pocock); A—dorsal view, B—ventral view, × 2.5. Carboniferous, Western Europe (Pocock, 1911).

of marginal zone nearly equal to width of lateral row of terga. Lateral row delimited from wide middle row by straight furrows tapering towards rear. Two rows of five rounded tubercles present along borders of median row of terga (Fig. 1412). One species. Carboniferous of Western Europe.

The following are from the Carboniferous of Western Europe: *Brachpyge* Woodward, 1878 (Fig. 1407); *Mariocercus* Pocock, 1911 (Fig. 1408A, B); *Cleptomartus* Petrunkevitch, 1949 (Fig. 1409A, B); *Cryptomartus* Petrunkevitch, 1949 (Fig. 1413A, B). The following are from the Carboniferous of North America: *Coryphomartus* Petrunkevitch, 1945 (Fig. 1410); *Paleomartus* Petrunkevitch, 1945.

Subclass ARANEAE. Spiders

Body divided into comparatively small prosoma or cephalothorax, bearing

appendages, large opisthosoma or abdomen. Abdomen (unlike other chelicerates) connected with prosoma by narrow, short, tube-like stalk (Fig. 1427). Prosoma comprised of acron and six segments of body, with appendages.
493 Stalk formed by seventh body segment. Abdomen (Opisthosoma) in order Liphistiomorphae and some Arachnomorphae (ref. p. 751 and 753) twelve-segmented (Fig. 1419 A). In advanced spiders included under orders Mygalomorphae and Araneomorphae, abdomen consists of five fused mesosomatic segments (segments VII to XI and terminal anal segment XVIII). Remaining abdominal segments develop only in the embryos, reduced during course of development; in adults segments XII and XIII represented by nuromers of subpharyngeal ganglion.

Cephalothoracic shield completely covers prosoma dorsally, borders extend forming the forehead, sides. With small depression in middle of shield—(central pit from which furrows diverge radially; see Fig. 1419 B). Anterior margin of shield (forehead) with eight eyes, arranged usually in two–three transverse rows (Fig. 1426 B, 1433 B). Abdominal terga present only in segmented spiders of order Liphistiomorphae. In all other spiders, abdomen unsegmented, covered with soft chitinous integument. Small chitinized areas present only at places of attachment of dorsoventral muscles, lung covers. Abdominal region of prosoma with large sternum surrounded by large coxae of pedipalpi and walking legs (Figs. 1428, 1434 B, 1438 A). Sternite of pedipalpi (second prosomatic) segment placed in front of sternum. Sternum formed by fusion of sternites of walking legs (III–VI). In many species, borders of fusion indicated by depressions and projections along sides of sternum (Fig. 1456 A). Posterior part of sternum of many spiders has median process which probably corresponds to sternite of terminal segment of prosoma. Chelicerae large, two-segmented, with massive base, claw-shaped tarsus (Figs. 1451, 1490 B, 1497 B) at ends of which, in nearly all species, open ducts of poison glands. Oral cavity bounded on anterior side by bases of chelicerae, on sides by gnathobases of coxae of pedipalpi, posteriorly by anterior margin of pedipalpal sterna (lower lip; Fig. 1490 B). In arthropods, primitively gnathobases of pedipalps appear as modifications for mastication, with dense network of hairs which criss-cross and form peculiar net, serving to filter food already taken in liquid form. Pedipalpi simple, short, usually third or quarter of size of walking legs. In males, terminal segments of pedipalpi enlarged, modified, functioning as organs for transfer of sperms into female genital opening (Figs. 1439B, 1493, 1516). Pedipalpi in females developed normally, six-segmented. Walking legs similar in structure, differing in length; usually legs III shorter. Legs seven-segmented; tarsi divided into metatarsus and tarsus proper. Tip of tarsi with two comb-shaped claws, tuft of setae, large toothed or serrated spines. In female spiders of many families peculiar formation called calamistrum present at tip of tarsi of legs IV, consisting of long row of curved hairs arranged with great regularity along the pretarsus.

Transverse genital opening on ventral side of abdomen immediately behind attachment of stalk (pedicil), the location of which identifying eighth body

segment (second opisthosomatic). In females morphology of genital opening made complex by formation of epigynes, consisting of long, unpaired chitinous appendage and paired thick basal plate. First pair of pulmonary sacs located at level of genital opening (in family Caponiidae replaced by tracheae). Second pair of pulmonary sacs present on ninth segment in less advanced spiders (orders Liphistiomorphae, Arachnomorphae, Mygalomorphae). In higher forms of spiders of order Araneomorphae unpaired stigma of trachea in front of spinnerets, leading to atrium into which two pairs of tracheae open. Three pairs of spinnerets located at posterior end of body (at side of disappearing tenth and eleventh body segments) (Figs. 1435 E, 1473 B, 1513 C, 1516). Anterior and posterior pairs of spinnerets two-three segmented; in some forms very long (Figs. 1428 B, 1436). Spinnerets modified abdominal legs of tenth and eleventh segment, inner pair of small furrows during development separates from rudiments of hind pairs, consequently not independent extremities. Cleft between bases of posterior pair of spinnerets occupied by small conical appendage, colulus. In some female spiders with calamistrum, in front of
494 posterior spinnerets (besides colulus) transverse, often double plate, sieve-like, pierced by pores (cribellum). Presence of this double plate is of great taxonomic importance. Spinnerets contain special glands through which secretions come out, harden in air, form web (Fig. 1473 B). Anal opening is located behind the web area, at posterior end of abdomen. Sometimes anal opening lies on a small conical elevation. Carboniferous* to Recent.

Ecology and Biogeography. These spiders, with stray exceptions (genus *Argyroneta*), are terrestrial and are encountered literally everywhere. They are predators feeding on arthropods, mainly insects, dissolving the body of the crushed insect in their gastric juice and sucking it through chelicerae. The majority of spiders build a trap-net out of cobweb, or live in burrows.

Classification, Phylogeny and Systematic Position. Workers justly consider the Araneae as closely related to the Amblypygi, and Liphistiomorphae as the most primitive group. The affinity of spiders with other subclasses of Arachnida has been mentioned earlier. Neither broad division of Araneae into suborders (= orders!) such as Tetrapneumones (four-lunged) and Dipneumones (two-lunged) nor the classification into 'suborders' Orthognatha and Labidognatha as envisaged by Berland (1932) is satisfactory, since such a natural group as the segmented spiders of the family Liphistiidae has been artificially combined with the four-lunged spiders, and the family Hypochilidae (with four lungs), nevertheless showing many similarities, has been combined with the two-lunged spiders. Kastner (1938) corrected this irregularity and divided all spiders into three suborders—Mesothelae, Orthognatha, and Labidognatha which, as their names suggest, indicate the location of chelicerae relative to the longitudinal axis of the body. Still earlier, Pocock (1892) and Millot (1933) had suggested for these 3 suborders more natural names as Liphistiomorphae,

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* Editor's note: More likely Devonian.

Mygalomorphae and Araneomorphae. Petrunkevitch (1933) has described three new suborders—Hypochilomorphae, Apneumonomorphae and Arachnomorphae. Only forms of the last suborder are found in the fossil state (families Archaeometidae and Pyritaraneidae). Distinction of other two orders is doubtful and some authors relate those included under the suborders of the family to the suborders Mygalomorphae and Araneomorphae (Millot, 1949).

Similarly, the classification suggested by Petrunkevitch (1933) of different suborders and smaller taxonomic units was not based on a sound basis, but was primarily based on the number of ostia of the heart. The classification of Kastner (1938) and Millot (1949), which is better founded, has been adopted in this book and the suborders suggested by these authors are treated as independent orders. Devonian to Recent. Four orders: Liphistiomorphae, Arachnomorphae, Mygalomorphae and Araneomorphae.

Order LIPHISTIOMORPHAE. Spiders with segmented abdomen

Abdomen clearly segmented, with eleven terga. Seven or eight spinnerets present, far in front of anal tube. Sterna of posterior segments located between posterior spinnerets. Gnathobases of pedipalpi not developed. Chelicerae paraxial. Tarsi with three claws. Eyes eight, borne on common tubercle. Epigyne absent. Carboniferous to Recent. Three families, of which two are from the Palaeozoic (Arthromygalidae and Arthrolycosidae), and one Recent (Liphistiidae).

Family ARTHROMYGALIDAE Petrunkevitch, 1923

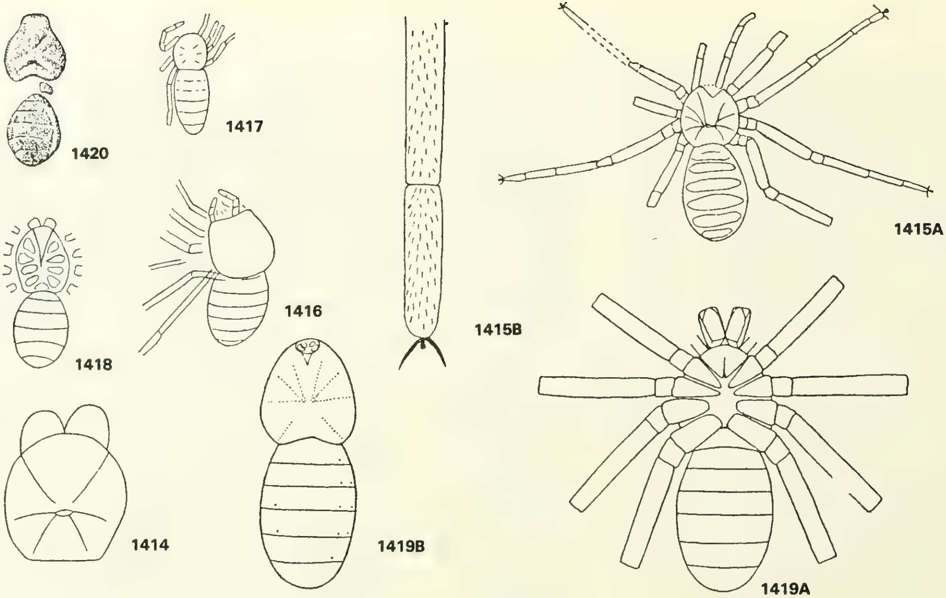
Without eye tubercle on cephalothoracic shield. Eyes apparently absent. Carboniferous. Eight genera.

Protolycosa Roemer, 1866. Genotype—*P. anthracophila* Roemer, 1866; Carboniferous, Poland. Without transverse rows of tubercles on dorsal side of eleventh segment. Single species. Carboniferous of Europe.

Arthromygale Petrunkevitch, 1923. Genotype—*Arthrolycosa fortis* Fritsch, 1904; Carboniferous, Czechoslovakia. Cephalothoracic shield almost disc-like, with wide, rounded anterior, lateral margins, with six prominent furrows radially diverging from median pit. Abdomen segmented, posterior end rounded. Legs comparatively stout. Cephalothorax ⅔ length of abdomen. Length of body 15 mm, of carapace, 6.57 mm (Fig. 1414). Single species. Carboniferous of Europe. 495

Palaranea Fritsch, 1873. Genotype—*P. borassifoliae* Fritsch, 1873; Carboniferous, Czechoslovakia. Cephalothoracic shield rounded in front, width exceeds length. Tarsi of legs without pulvilla. Legs long, legs IV longer than body. Length 23 mm. One species. Carboniferous of Europe.

Geralycosa Kusta, 1888. Genotype—*G. fritschi* Kušta, 1888; Carboniferous,



Figs. 1414–1420. Families Arthromygalidae, Arthrolycosidae.

1414. *Arthromygale fortis* (Fritsch); dorsal view of prosoma, × 5. Carboniferous, Europe (Petrunkevitch, 1953). 1415. *Geralycosa fritschi* Kušta; A—dorsal view, × 5. B—tibia and tarsus of leg III, × 15. Carboniferous, Europe (Petrunkevitch, 1953). 1416. *Kustaria carbonaria* (Kušta); general view, × 3. Carboniferous, Europe (Petrunkevitch, 1953). 1417. *Racovnicia antiqua* Kusta; dorsal view, × 2. Carboniferous, Europe (Petrunkevitch, 1933). 1418. *Protocteniza britannica* Petrunkevitch; general view, × 2.5. Carboniferous, Western Europe (Petrunkevitch, 1953). 1419. *Arthrolycosa danieisi* Petrunkevitch; A—ventral view, B—dorsal view, × 2.5. Carboniferous, North America (Petrunkevitch, 1913). 1420. *Eocteniza silvicola* Pocock; dorsal view, × 3. Carboniferous, Western Europe (Pocock, 1911).

Czechoslovakia. Length of cephalothorax exceeds width. Cephalothorax rounded at anterior end, concave at posterior, smooth, without eyes, with five pairs of radially diverging furrows. Legs long, slender (Fig. 1415). Tarsi of legs with two claws and pulvilla (Fig. 1415 B). Length 14.5 mm. Single species. Carboniferous of Europe.

Kustaria Petrunkevitch, 1953. Genotype—*Scudderia carbonaria* Kušta, 1888; Carboniferous of Czechoslovakia. Cephalothoracic shield rounded, with concave anterior margin, wide rounded lateral, posterior margins. Eyes absent. Pedipalpi short, slender. Legs long (Fig. 1416). Length 5.7 mm. Single species. Carboniferous of Europe.

Rakovnicia Kusta, 1884. Genotype—*R. antiqua* Kušta, 1884; Carboniferous, Czechoslovakia. Cephalothoracic shield short, oval, slightly longer than broad, smooth, with three pairs of radially diverging furrows. Abdomen extended oval, almost twice as long as wide (Fig. 1417). Legs short, slender. Length 6.6 mm. One species. Carboniferous of Europe.

Another genus from the Carboniferous of Western Europe is *Protocteniza* Petrunkevitch, 1949 (Fig. 1418).

496 **Family ARTHROLYCOSIDAE Petrunkevitch, 1923**

Spiders with segmented abdomens; with eye tubercle of cephalothorax (Figs. 1420, 1419 A). Carboniferous of Europe and North America. Two genera: *Arthrolycosa* Harger, 1874 (North America) and *Eocteniza* Pocock, 1911 (Western Europe).

Arthrolycosidae Incertae sedis

Eolycosa Kušta, 1885. Genotype—*E. lorenzi* Kušta, 1885. Carboniferous, Czechoslovakia. The poorly preserved remains of a spider resemble the genus *Arthrolycosa* Harger. Single species.

Palaeocteniza Hirst, 1923. Genotype—*P. crassipes* Hirst, 1923; Devonian, Scotland. From the old Red Sandstone of Scotland, amidst numerous remains of Trigonotarbi and mites. Resembles spiders in certain features and Trigonotarbi in others. Needs further study.

Pleurolycosa Fritsch, 1904. Genotype—*Arthrolycosa prolifera* Fritsch, 1904; Carboniferous, Czechoslovakia. Systematic position not clear.

497 Order ARACHNOMORPHAE*

Abdomen completely segmented, or only at posterior end. Terga four to seven. Gnathobases of pedipalpi with hairs forming filter apparatus (Fig. 1450). Chelicerae, legs, spinnerets developed as in Recent Araneomorphae. Eyes closely set, placed at anterior margin of cephalothorax. Copulatory organs of

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* Editor's note : There is no evidence supporting this description.

females complex. Respiratory organs as in present-day Aranomorphae.

A small group of Carboniferous spiders distinguished by a combination of characters of those spiders with segmented abdomens of the order Liphistiomorphae, as well as those of the present-day spiders of the order Araneomorphae. Petrunkevitch (1933, 1949, 1953) draws attention to the segmentation of abdomen in these spiders along with the possession of characters of present-day Araneomorphae. He does not, however, elucidate the precise systematic position of Archaeometidae and Pyritaraneidae, but refers to them as Paleozoic Arachnomorphous spiders close to the Recent forms. Carboniferous. Two families: Archaeometidae and Pyritaraneidae.

Family ARCHAEOMETIDAE Petrunkevitch, 1949

Spiders with segmented abdomen, anteriorly placed legs (Figs. 1422, 1423). Carboniferous. Three genera.

Eopholcus Fritsch, 1904. Genotype—*E. pedatus* Fritsch, 1904; Carboniferous, Czechoslovakia. Cephalothoracic shield oval, rounded anteriorly. Abdomen disc-like, with traces of segmentation. Two eyes on small tubercle. Legs long, slender. Trochanter longer than femur (Fig. 1421). Length 27.16 mm. Carboniferous of Europe.

Other genera from the Carboniferous of Western Europe are: *Archaeometa* Pocock, 1911 (Fig. 1422 A, B) and *Arachnometa* Petrunkevitch, 1949 (Fig. 1423).

Family PYRITARANEIDAE Petrunkevitch, 1953

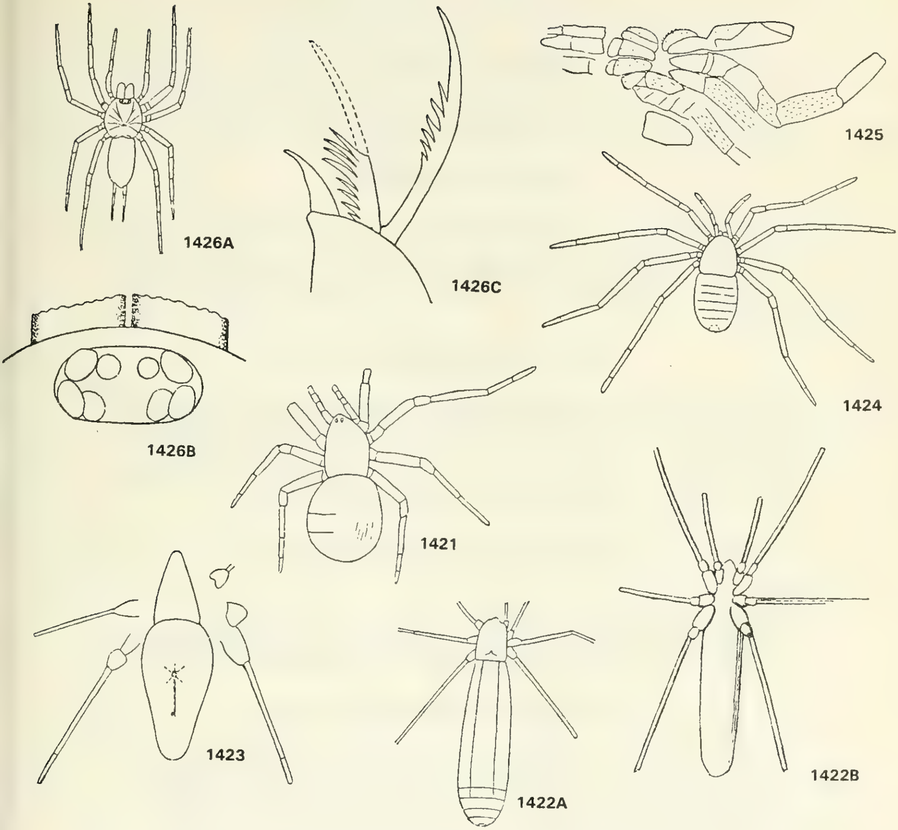
Abdomen fully segmented. Legs laterally placed, thin, long. Carboniferous. Two genera. *Pyritaranea* Fritsch, 1899. Genotype—*P. tubifera* Fritsch, 1899. Carboniferous, Czechoslovakia. Cephalothoracic shield oval, longer than broad; rounded anteriorly, straight truncated posteriorly. Eyes absent. Legs long, slender. Length of pedipalpi greater than width of body (Fig. 1424). Length 11 mm. Single species. Carboniferous of Europe.

Dinopilio Fritsch, 1904. Genotype—*D. gigas* Fritsch, 1904; Carboniferous, Czechoslovakia. Legs very long, comparatively stout, placed along sides. Coxae of legs (Fig. 1425) lie almost parallel to one another. Coxae of pedipalpi with narrow gnathobases, short hairs (Fig. 1425). Carapace 7.5–8 mm long. Distance between coxae of legs 11.4 mm. Two species. Carboniferous of Europe.

Order MYGALOMORPHAE

(Tetrapneumones, Orthognatha)

Abdomen not segmented externally. Spinnerets two to six, at posterior end of abdomen. Chelicerae paraxial. Coxae of pedipalpi with or without weakly developed gnathobases. Pulmonary sacs two pairs. Eyes closely set, located at



Figs. 1421–1426. Families Archaeometidae, Pyritaraneidae, Dipluridae.

1421. *Eopholcus pedatus* Fritsch; dorsal view, × 4. Carboniferous, Europe (Petrunkevitch, 1946). 1422. *Archaeometa nephilina* Pococo: A—dorsal view, B—ventral view, × 5. Carboniferous, Europe. 1423. *Arachnometa tuberculata* Petrunkevitch; dorsal view, × 7. Carboniferous, Western Europe (Petrunkevitch, 1953). 1424. *Pyritaranea tubijera* Fritsch; dorsal view, × 3. Carboniferous, Western Europe (Petrunkevitch, 1946). 1425. *Dinopilio gigas* Fritsch; dorsal view, × 2. Carboniferous, Europe (Petrunkevitch, 1949). 1426. *Clostes priscus* Menge: A—dorsal view, × 5.5, B—claws of tarsus of leg IV, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946).

anterior border of cephalothorax. Copulatory organs of females simple. Paleogene to Recent.

Three suborders in the Recent fauna: Nelipoda, Hypodemata and Pycnothelidea. They live primarily in tropical countries, and are mostly wandering and arboreal species living in burrows or in webbed galleries and shelters. The first two suborders are known as fossil forms.

Suborder Nelipoda

Tarsi of all legs with three claws. Without tufts of setae at tips of tarsi (Fig. 1426 B). Paleogene to Recent.

Recent fauna with four families—Ctenizidae, Migidae, Atypidae and Dipluridae. The last family is known from the Paleogene of Europe (Baltic amber)*.

Family DIPLURIDAE Pocock, 1894

Spinnerets two or three pairs, posterior pair long. Chelicerae without 'rake'. 498 Weave nets around bases of trunks of trees or bushes, between stones. Most forms small.

About thirty genera in Recent fauna, single species of genus *Clostes* Menge, 1869 (Fig. 1426) is from the Paleogene of Europe (Baltic amber).

Suborder Hypodemata

(Theraphosina)

Tarsi of all legs with two claws, tuft of setae. Paleogene to Recent.

Two families in the Recent fauna: Barychelidae and Theraphosidae, the latter known also from the Paleogene of Europe (Baltic amber).

Family THERAPHOSIDAE Thorell, 1869

With two pairs of spinnerets, posterior pair long, three-segmented. Last segment of posterior spinnerets of same length as preceding one. Paleogene to Recent.

Ten genera in the Recent fauna. The extinct genus *Eodiplurina* Petrunkevitch, 1922, is from the Paleogene of Europe.

Order ARANEOMORPHAE. True spiders

(Labidognatha, Dipneumonomorphae)

Abdomen unsegmented externally. Spinnerets located at posterior end of body. Chelicerae usually diaxial. Pedipalpi with well developed gnathobases. Anterior pair of respiratory organs in form of lungs, posterior, in form of tracheae. Species of families Hypochilidae an exception, having four lungs. In family

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* Editor's note: Several fossil atypics known also, but Dubinin missed them.

Telemidae, lungs are replaced by tracheae; in species of some families pulmonary sacs absent. Very widely distributed; weave net. Paleogene to Recent. Two suborders: Ecribellatae and Cribellatae.

Suborder Ecribellatae

Cribellum absent. In females, row of hairs forming calamistrum on tarsi of legs IV absent. Paleogene to Recent. Two infraorders: Haplogynae and Entelogynae.

Infraorder Haplogynae

Eyes usually six. Spermathecae of females open directly into genital pore. Copulatory organ of male simple, without blood vessels and skeleton. Paleogene to Recent. Two superfamilies: Dysderidea and Caponiidea, the latter only in the Recent fauna.

SUPERFAMILY DYSDERIDEA

(Dysderiformia)

Plates (lamellae) absent at margin of groove on basal segment of chelicera. Five families in the Recent fauna: Oonopidae, Dysderidae, Segestriidae, Leptonetidae, Telemidae; last two not known in fossil form.

Family OONOPIDAE Simon, 1892

Tracheal openings located behind lung openings. Gnathobases meet in front of lower lip. Tips of tarsi with two or three claws. Spinnerets arise from common base.

Recent species live under stones and in plant debris of all continents. Paleogene to Recent. More than ten genera in the Recent fauna.*Orchestina* Simon, 1892 (Fig. 1427) is from the Paleogene of Europe (Baltic amber).

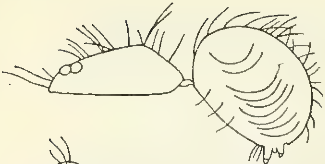
Family DYSDERIDAE C.L. Koch, 1837

Tracheal openings located behind those of lungs. Gnathobases long, almost parallel. Lower lip elongate. Eyes six or absent.

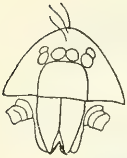
Recent species lead a semiwandering life and are often encountered under stones and under the bark of trees. Paleogene to Recent. Nineteen genera in the Recent fauna, of which the following are known from the Paleogene of Europe (Baltic amber): *Harpactes* Templeton, 1834 (Fig. 1428 A–D); *Thereola* Petrunkevitch, 1955 (= *Thera* Koch and Berendt, 1854) (Fig. 1429); *Dysdera* Latreille, 1804 (Fig. 1430).

Family SEGESTRIIDAE Petrunkevitch, 1933

This family is very closely related to the preceding family. Eyes six. Sternum

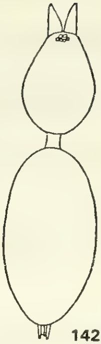


1427A



1427B

1427C



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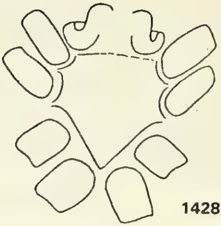

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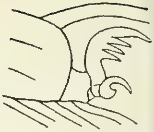

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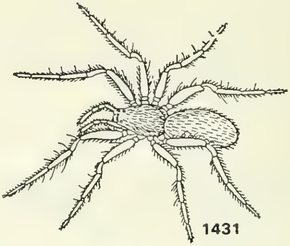

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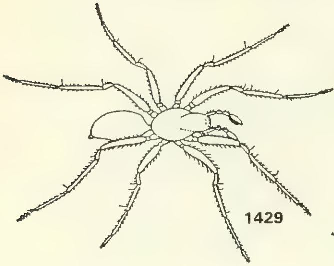

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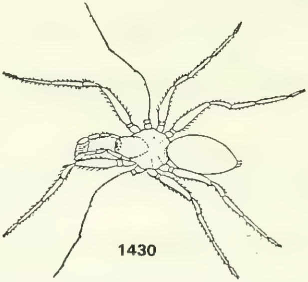

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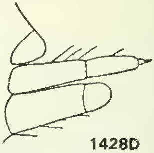


1428D

499 Figs. 1427-1431. Families Oonopidae, Dysderidae, Segestriidae.

1427. *Orchestina baltica* Petrunkevitch; A—lateral view, × 6, B—front end of head, × 10, C—leg IV, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1428. *Harpactes extinctus* Petrunkevitch; A—dorsal view, × 7, B—coxosternal area, × 20, C—claws of tarsus of leg III, D—spinnerets, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1429. *Thereola petiolata* (Koch and Berendt); dorsal view, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1430. *Dysderatersa* Koch and Berendt; dorsal view, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1431. *Segestria tomentoza* Koch and Berendt; dorsal view, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).

oval, with a projection at posterior margin, usually prominent because of thin peripheral integument. Tarsi with three claws (Fig. 1431). Paleogene to Recent. Two genera in the Recent fauna, of which *Segestria* Latreille, 1804, is known from the Paleogene of Europe (Baltic amber).

499 Infraorder Entelogynae

Majority of species with eight eyes in two rows. Spermathecae of females open outside the peculiar genital openings (Species of superfamily Pholcoidea and family Tetragnathidae are an exception). Epigyne well developed. Copulatory organs of males complex, terminal segment of pedipalpi modified into boat-like structure. Paleogene to Recent. Eleven superfamilies, of which the following nine are from the Paleogene of Europe (Baltic amber): Pholcidea, Zodariidea, Hersiliidea, Argiopidea, Lycosidea, Drassodidea, Clubionidea, Thomisidea, Salticidea. Two Recent superfamilies are: Ammoxenidea and Homalonychidea.

SUPERFAMILY PHOLCIDEA

(Pholciformia)

Trichobothria of tarsi absent. Chelicerae connected at base by common membrane, their basal segment with large sharp tooth, which together with movable, claw-like terminal segment forms claw-like clamp. Gnathobases closely set (Fig. 1432). One family: Pholcidae.

500 Family PHOLCIDAE Walckenaer, 1837

Eyes usually eight, rarely six, closely set. Lower lip fused with sternal plate. With large plate in front of genital opening in many species. Tracheae absent.

Recent species weave nets in open cavities, openings in rocks and other hollows. There are thirty-three genera and over 220 species in the Recent fauna. One species of the genus *Micropholcus* Petrunkevitch is known from the Paleogene of Europe (Baltic amber) (Fig. 1432).

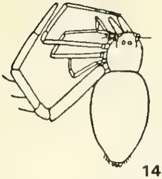
SUPERFAMILY ZODARIIDEA

(Zodariiformia)

Posterior pair of spinnerets much smaller than anterior. Spinnerets often greatly
501 reduced or absent. Two families—Palpimanidae and Zodariidae. The latter occurs in the Baltic amber, from whence the extinct family Spatiatoridae also has been described.

Family ZODARIIDAE Simon, 1892

Tarsi with three, rarely two claws. Margin of groove at base of chelicera without serrations, or rarely with single tooth. Colulus absent. Recent species—spider-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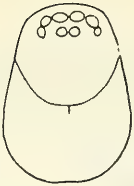
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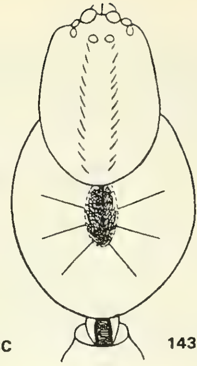
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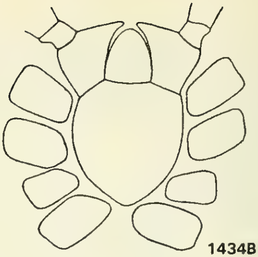
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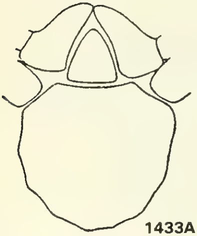
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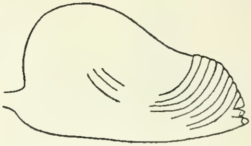
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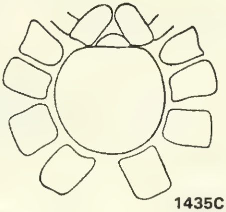
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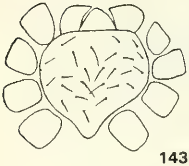
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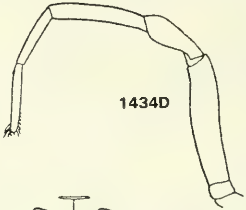
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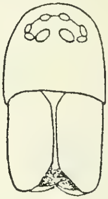
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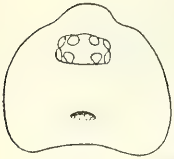
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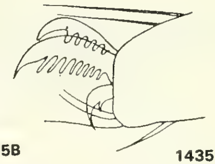
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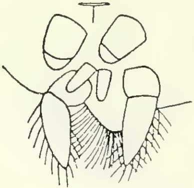
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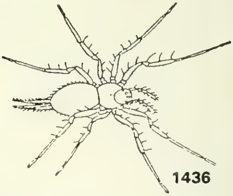

1436

Figs. 1432–1436. Families Pholcidae, Zodariidae, Spatiatoridae, Urocteidae, Hersiliidae.

1432. *Micropholcus heteropus* Petrunkevitch; general view, × 4.5. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1433. *Anniculus balticus* Petrunkevitch; A—sternal plate and coxae of pedipalpi, × 25, B—carapace, × 1500, C—feather-like hairs on leg segments, × 50. Paleogene, Europe (Petrunkevitch, 1942). 1434. *Spatiator praeceps* Petrunkevitch; A—carapace, × 35, B—coxosternal area, × 20, C—abdomen (lateral view), × 30, D—leg II, × 12, E—head, front view, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1435. *Paruroctea blauvelti* Petrunkevitch; A—coxosternal area of male, × 15, B—carapace, × 15, C—coxosternal area of female, × 15, D—claw of tarsus of leg III, × 20, E—spinnerets, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1436. *Hersilia miranda* Koch and Berendt; dorsal view, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).

hunters weave sac-like nests or do not build nests. Some species live in small holes indoors. Paleogene to Recent. Seven genera in the Recent fauna, of which the extinct genus *Anniculus* Petrunkevitch, 1942 is known from the Paleogene of Europe (Baltic amber) (Fig. 1433 A–B).

Family SPATIATORIDAE Petrunkevitch, 1942

Middle part of forehead of cephalothoracic shield slightly projecting. Shield extended oval, sides almost parallel. Eyes arranged in three groups (Fig. 1434 E). Bases of chelicerae parallel to one another with narrow marginal widening, not raised up. Scopula present. Gnathobases of coxae of pedipalpi wide, pentagonal, forming sides of lower lip (Fig. 1434). Legs with long patella. Tarsi with three claws. Trichobothria present. Colulus present or absent. Paleogene. Two genera from the Paleogene of Europe (Baltic amber): *Spatiator* Petrunkevitch, 1942 (Fig. 1434 A–E) and *Adorator* Petrunkevitch, 1942.

SUPERFAMILY HERSILIIDEA

(Hersiliaeformia)

Posterior spinnerets extraordinarily long, movable. Gnathobases converge. Two families in the Recent fauna are Urocteidae and Hersiliidae, also known from the Paleogene of Europe (Baltic amber).

Family UROCTEIDAE Simon, 1875

Chelicerae weak, connected to one another at base by membrane. Anal operculum large, divided into two divisions by rim of long chalybeate hairs. Paleogene to Recent. Single genus in the Recent fauna. The extinct genus *Paruroctea* Petrunkevitch, 1942 is from the Paleogene of Europe (Baltic amber) (Fig. 1435 A–E).

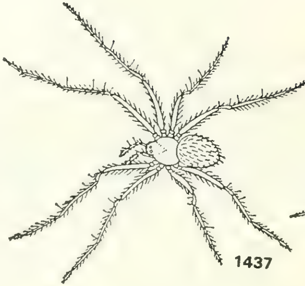
Family HERSILIIDAE Thorell, 1869

Anterior part of cephalothorax somewhat raised, high (Fig. 1436). Posterior spinnerets long, with two irregular rows of spinning tubes on ventral side. Colulus well developed. Fast runners on tree bark catching insects and rolling them with threads of web. Paleogene to Recent. Four genera in the Recent fauna. One Recent genus *Hersilia* Audouin, 1827 (Fig. 1436) and one extinct genus—*Gerdia* Menge, 1869 are known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY ARANEIDEA

(Argiopiformia)

Tarsal trichobothria absent. Spinnerets usually short, closely set, together with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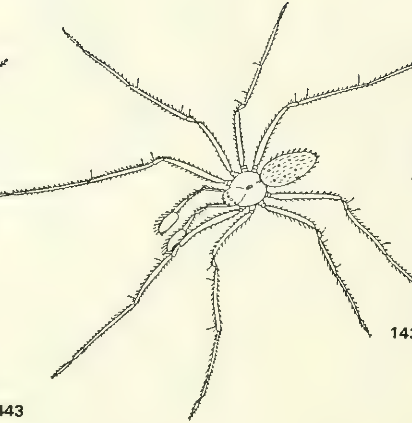
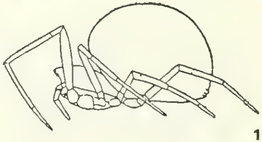

1439A


1439B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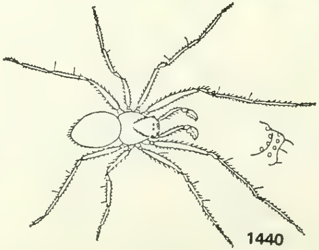
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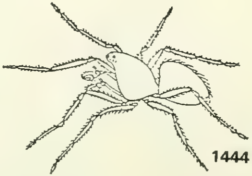
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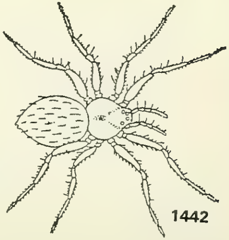
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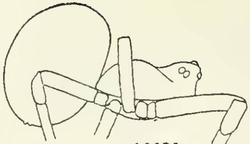
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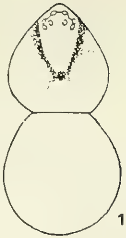
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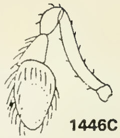
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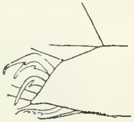
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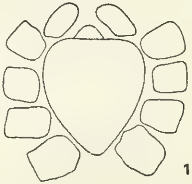
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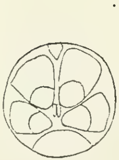
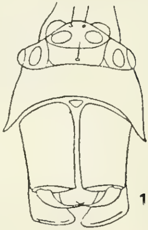

1438B


1446D

Figs. 1437–1446. Family Theridiidae.

1437. *Theridion hirtum* Koch and Berendt; dorsal view of female, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1438. *Steatoda suciini* Petrunkevitch; A—coxosternal area, × 20, B—spinnerets, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1439. *Elegia longimana* Koch and Berendt; A—dorsal view of male, × 3, B—same, cephalothorax and pedipalp, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1440. *Clya lugubris* Koch and Berendt; male (drawing of anterior margin of carapace with eyes is depicted by the side), × 25. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1441. *Mizalia pilosula* Koch and Berendt; dorsal view, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1442. *Clythia alma* Koch and Berendt; dorsal view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1443. *Eodipoena baltica* Petrunkevitch; female (lateral view), × 4.5. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946). 1444. *Nactodipoena infulata* (Koch and Berendt); lateral view of male, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt 1854). 1445. *Municeps pulcher* Petrunkevitch; claws of tarsus of leg III, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1955). 1446. *Eomysemena moritura* Petrunkevitch; A—lateral view of male, × 5, B—same from dorsal side, × 5, C—pedipalpi of male, × 15, D—head from front, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946).

colulus, anal tubercles form rosette. Present-day cobweb spiders. Paleogene to Recent.

The following ten families are known in the Recent fauna: Nesticidae, Symphytognathidae, Theridiidae, Archaeidae, Mimetidae, Micryphantidae, Linyphiidae, Araneidae, Tetragnathidae, Ephalmatoridae*. The first two are not known in fossil form. The following two extinct families are known from the Paleogene of Europe (Baltic amber)—Muthridae and Adjutoridae.

Family THERIDIIDAE Sundevall, 1833

Tibia, metatarsus devoid of spines. Six to ten curved setae present at distal side of tarsi of posterior legs, used while enveloping prey with sticky thread. Pedipalpi of males without apophyses on tibia and patella (Fig. 1439 B).

Over 30 genera are found in the Recent fauna. The following two genera are known from the Paleogene of Europe (Baltic amber)—*Theridion* Walckenaer, 1805 (Fig. 1437) and *Steatoda* Sundevall, 1833 (Fig. 1438 A, B). The following eight extinct genera are also from the same fauna. *Flegia* Koch and Berendt, 1854 (Fig. 1439A, B), *Clya* Koch and Berendt, 1854 (Fig. 1440), *Mizalia* Koch and Berendt, 1854 (Fig. 1441), *Clythia* Koch and Berendt, 1854 (Fig. 1442), *Eodipoena* Petrunkevitch, 1942 (Fig. 1443), *Nactodipoena* Petrunkevitch, 1942 (Fig. 1444), *Municeps* Petrunkevitch, 1942 (Fig. 1445), *Eomysmena* Petrunkevitch, 1942 (Fig. 1446 A–D).

Family ARCHAEIDAE Koch, 1837

Margin of groove of chelicerae with long spines (Fig. 1447 A, B). Anterior part
503 of cephalothorax strongly raised in front as a result of which bases of chelicerae,
coxae of pedipalpi considerably separated (Fig. 1447). Basal segment of
chelicera very long. Paleogene to Recent.

Two genera in the Recent fauna of the southern hemisphere of which the

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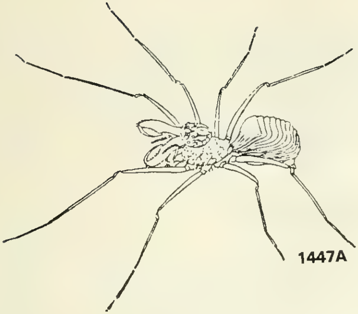
504 Figs. 1447–1454. Families Archaeidae, Mimetidae, Micryphantidae, Adjutoridae.

1447. *Archaea paradoxa* Koch and Berendt; A—lateral view of female, × 2, B—head from front, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1448. *Ero setulosa* Koch; dorsal view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1449. *Micryphantes regularis* Koch and Berendt; dorsal view, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1450. *Erigone stigmatosa* Koch and Berendt; dorsal view, of male, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1451. *Eogonatium robustum* Petrunkevitch; head from front, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946). 1452. *Adjutor mirabilis* Petrunkevitch; A—abdomen of female, × 7, B—cephalothorax of female, × 7. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1453. *Admissor aculeatus* Petrunkevitch; lateral view of female, × 9. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1454. *Adjuctor similis* Petrunkevitch: A—dorsal view of female, × 8, B—leg II of female, × 5. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).

* Editor's note: This family is extinct (One species known from Baltic amber).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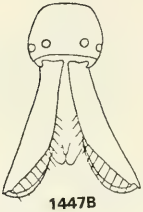
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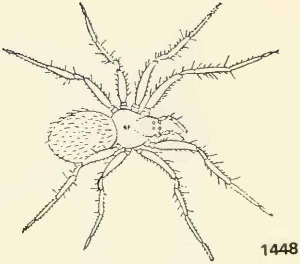
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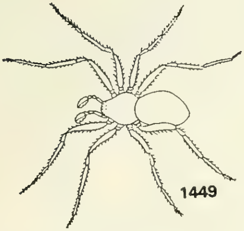
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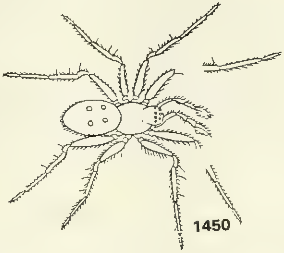
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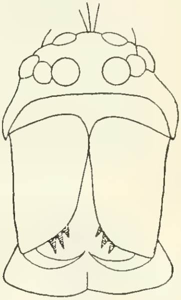
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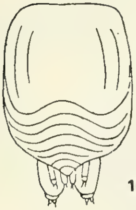
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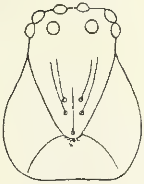
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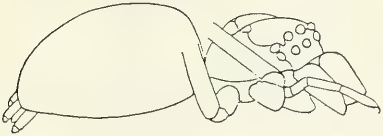
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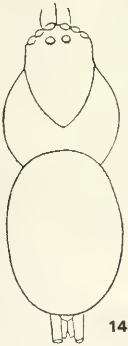
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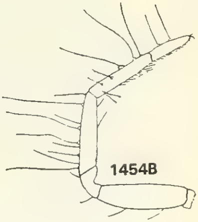

1454B

genus *Archaea* Koch and Berendt, 1854 is known from the Paleogene of Europe (Baltic amber) (Fig. 1447 A, B).

Family MIMETIDAE Simon, 1895

Chelicerae resemble those of preceding family. Metatarsal segments, often tibia of first two pairs of legs with rows of long, slightly bent spines with smaller spines between curved at ends. Trap-nets not woven. Four genera in the Recent fauna, of which the genus *Ero* C.L. Koch, 1837 is known from the Paleogene of Europe (Baltic amber) (Fig. 1448).

Family MICRYPHANTIDAE Bertkau, 1885
(Erigonidae Simon, 1926)

Abdomen soft, small. Legs without spines. Lateral eyes adjacent. Forehead somewhat raised up, inflated. Cephalothorax slightly widened at posterior half. Trichobothria present on first, four metatarsal segments. Upper claw of tarsus simple, thin, with five slender teeth.

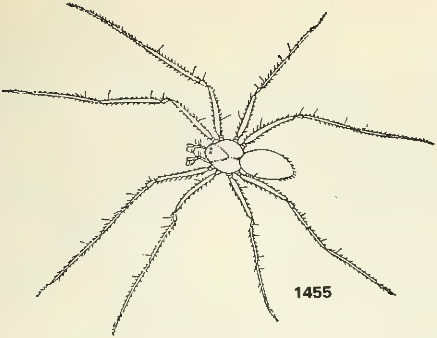
More than ten genera in the Recent fauna, of which the following three genera are known from the Paleogene of Europe (Baltic amber): *Micryphantes* Koch, 1875 (Fig. 1449), *Erigone* Savigny (Fig. 1450), *Eogonatium* Petrunkevitch, 1942 (Fig. 1451).

Family ADJUTORIDAE Petrunkevitch, 1942

Long, hair-like trichobothria present on tibial metatarsal segments of all legs (Fig. 1454). Colulus well developed. Anal projection conical (Fig. 1452). Cephalothoracic shield widened at posterior part, with semicircular furrow in

507 Figs. 1455–1464. Families Linyphiidae, Mithraeidae.

1455. *Linyphia oblonga* Koch and Berendt; dorsal view of male, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854), 1456. *Eopopino longipes* Petrunkevitch; A—coxosternal area, × 15, B—pedipalpi of male, × 10, C—claw of tarsus of leg II, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1457. *Malleator niger* Petrunkevitch; A—cephalothorax of male, × 6, B—pedipalpi of male, × 12. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1458. *Custodela cheiracantha* (Koch and Berendt); general view, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1459. *Meditrina circumvallata* Petrunkevitch; A—lateral view of female, × 5.5, B—dorsal view of cephalothorax, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1460. *Obnisus tenuipes* Petrunkevitch; A—lateral view of body of male, × 2.5, B—spinnerets, × 10, C—terminal part of left pedipalp of male, × 26. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1461. *Liticen setosus* Petrunkevitch; A—lateral view of male, × 5, B—dorsal view of cephalothorax, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1462. *Mystagogus glaber* Petrunkevitch; A—dorsal view of male, × 3.5, B—pedipalp, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1463. *Impulsor neglectus* Petrunkevitch; male, A—coxosternal area, × 25, B—dorsal side of pedipalpi, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1464. *Androgeus militaris* Koch and Berendt; dorsal view of male, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).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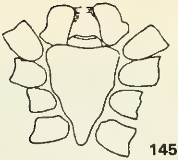
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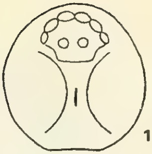
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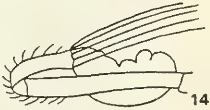
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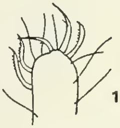
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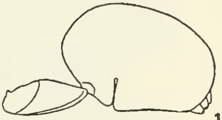
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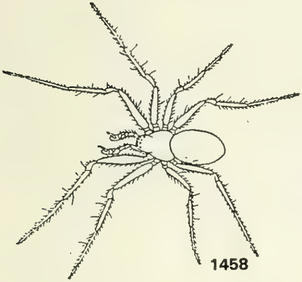
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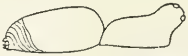
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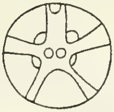
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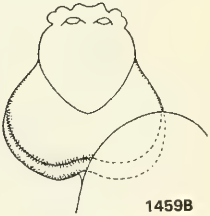
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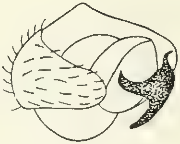
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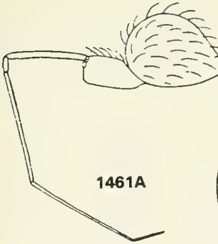
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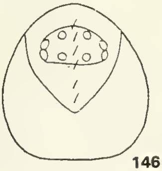
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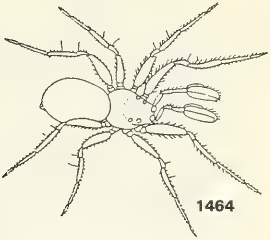
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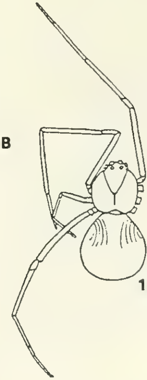
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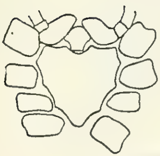
1463A


1463B

middle demarcating elevated anterior part. Eyes arranged in two rows (Figs. 1452, 1454). Chelicerae with thin margin, but without projections. Pedipalpi thin, comparatively long (Fig. 1454). Legs with spines, without scopulae but with three claws, greatly reduced at times. Length 1–1.8 mm. Paleogene. The following three genera are known from the Paleogene of Europe (Baltic amber), *Adjutor* Petrunkevitch, 1942 (Fig. 1452), *Admissor* Petrunkevitch, 1942 (Fig. 1453), *Adjunctor* Petrunkevitch, 1942 (Fig. 1454).

Family LINYPHIIDAE Latreille, 1804

Trichobothria absent on tarsi, and femora. Eyes shifted from anterior margin of cephalothoracic shield (Fig. 1455). Anterior margin of lower lip swollen. Margin of groove at base of chelicerae with numerous teeth. Pedipalpi of males with well developed paracymbium (Fig. 1456). Paleogene to Recent.

Over forty genera are found in the Recent fauna, of which the genus *Linyphia* Latreille, 1804 is known also from the Paleogene of North America (Fig. 1455). The following eight extinct genera have been recorded: *Eopipino* Petrunkevitch, 1942 (Fig. 1456); *Malleator* Petrunkevitch, 1942 (Fig. 1457 A, B); *Custodela* Petrunkevitch, 1942 (Fig. 1458); *Meditrina* Petrunkevitch, 1942 (Fig. 1459 A, B); *Obnisvs* Petrunkevitch, 1942 (Fig. 1460 A, B); *Liticen* Petrunkevitch, 1942 (Fig. 1461 A, B); *Mystagogus* Petrunkevitch, 1942 (Fig. 1462 A, B); *Impulsor* Petrunkevitch, 1942 (Fig. 1463 A, B).

Family MITHRAEIDAE Koch and Berendt, 1854

Cephalothorax pear-shaped, with weakly projecting frontal margin. Two large eyes, remaining eyes shifted posteriorly, to the dorsal side of anterior part of carapace. Solitary trichobothria present on tibiae and patellas. Pedipalpi of males with very large terminal segments (Fig. 1464). One genus *Androgenus* Koch and Berendt, 1854 recorded from the Paleogene of Europe (Baltic amber).

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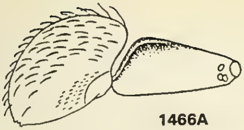
508 Figs. 1465–1473. Families Araneidae, Ephalmatoridae.

1465. *Zilla porrecta* Koch and Berendt; female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1466. *Eustaloides succini* Petrunkevitch; female; A—body (lateral view), × 7, B—dorsal view, × 9, C—claws of tarsi of leg III, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1467. *Gea epeiroidea* Koch and Berendt; male, × 3 (eyes on anterior margin of carapace shown in adjoining diagram); Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1468. *Acrometa cristata* Petrunkevitch, cephalothorax of male, dorsal view, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1469. *Theridiometa edwardsi* Petrunkevitch; young female, × 6. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1470. *Memoratrix rydei* Petrunkevitch; A—lateral view of female, × 5. B—head from front, × 12. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1471. *Elucus injelix* Petrunkevitch; lateral view, × 10. Paleogene, Europe (Baltic amber) (Petrunkvitch, 1942). 1472. *Elucus inermis* Petrunkevitch; cephalothorax of male, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1473. *Ephalmator fossilis* Petrunkevitch; male: A—lateral view, × 10, B—spinnerets exuding threads, × 7, C—coxosternal area, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950).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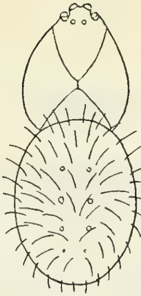
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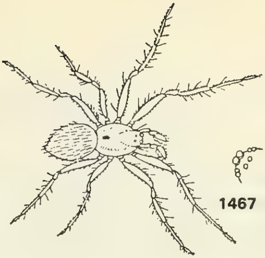
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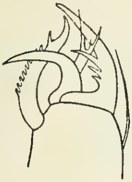
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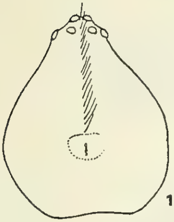
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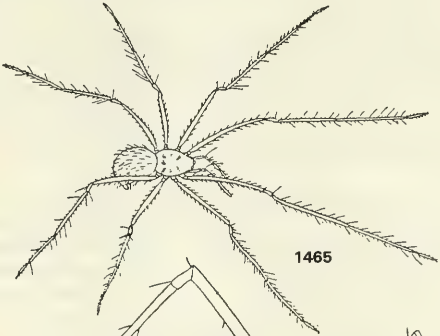
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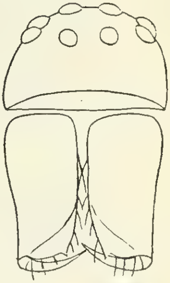
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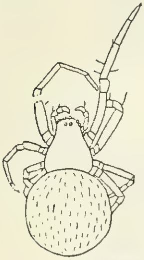
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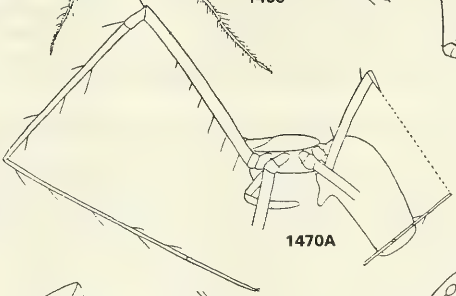
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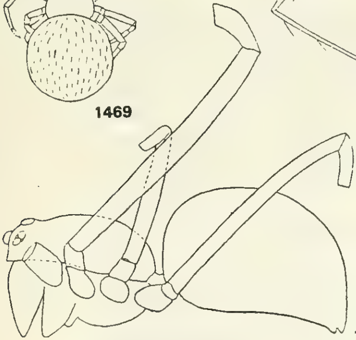
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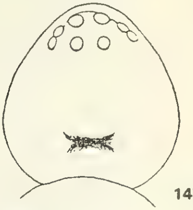
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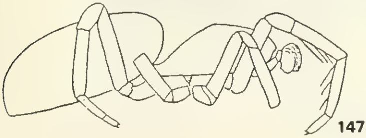
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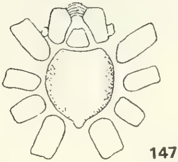
1473B


1473C

Family ARANEIDAE Leach, 1819

(Argiopodae Simon, 1893; Epeiridae Sundevall, 1833)

Coarse thread spinning spiders closely related to preceding families. Margin of groove at bases of chelicerae with teeth (Fig. 1470). Tarsi with three claws. Besides serrated setae, thick spine (Fig. 1466 C) under claws of tarsi of last pair of legs. Paleogene to Recent.

More than thirty genera in the Recent fauna, of which genus *Zilla* C.L. Koch is also known from the Paleogene of Europe (Baltic amber) (Fig. 1465) and the genera *Nephila* Leach, 1815 and *Epeira* Walckenaer, 1805 are known from the Paleogene of North America.

The extinct genus *Tethneus* Scudder, 1890 is from the Paleogene of North America. The following extinct genera are from Western Europe (Baltic amber): *Eustaloides* Petrunkevitch, 1942 (Fig. 1466 A–C); *Gea** Koch and Berendt, 1854 (Fig. 1467); *Acrometa* Petrunkevitch, 1942 (Fig. 1468); *Theridiometa* Petrunkevitch, 1942 (Fig. 1469); *Memoratrix* Petrunkevitch, 1942 (Fig. 1470 A, B); *Elucus* Petrunkevitch, 1942 (Figs. 1471, 1472).

Family TETRAGNATHIDAE Simon, 1892

Femur of legs with two rows of simple trichobothria. Chelicerae long. Body elongate. Paleogene to Recent. Five genera in the Recent fauna, of which genus *Tetragnatha* Latreille, 1904 is known from the Paleogene of North America. Also from the same fauna are two extinct genera—*Palaeometa* Petrunkevitch, 1922 and *Palaeopachygnatha* Petrunkevitch, 1922.

Family EPHALMATORIDAE Petrunkevitch, 1950

Large spine-like setae on ventral surface of tibiae, metatarsi of first, second pair of legs (Fig. 1473 A). Trichobothri solitary; three claws on tarsi of legs. Colulus absent (Fig. 1473 B). Chelicerae with projections. Lower lip free, smooth (Fig. 1473 C). Gnathobases of coxae of pedipalpi lie parallel to one another. Legs placed forward. Spinnerets six (Fig. 1473 B). Paracymbium, projections on tibia absent from palpi of males (Fig. 1473 A). Paleogene. Genus *Ephalmator* Petrunkevitch, 1950 with single species from the Paleogene of Europe (Baltic amber) (Fig. 1473 A–C).

SUPERFAMILY LYCOSIDEA

(Lycosiformia)

One or two rows of trichobothria present on legs (Fig. 1480). Spinnerets stout, conical (Fig. 1476 B). Paleogene to Recent.

The following seven families are recorded in the Recent fauna: Hahniidae, Oxyopidae, Senoculidae, Agelenidae, Argyronetidae, Lycosidae, Pisauridae.

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* Editor's note: Not extinct.

The first three are not known in fossil form. Additional extinct family—Insecutoridae.

Family AGELENIDAE Walckenaer, 1805

Margins of groove at base of chelicerae with numerous teeth. Tarsi without scopulae. Tibia of pedipalpi of males with apophyses. Hairs on body for most part plumose. If anterior spinnerets wide apart, colulus absent. If close, colulus present. Paleogene to Recent.

More than fifteen genera in the Recent fauna of which *Agelena* Walckenaer, 1805 (Fig. 1474) and *Myro* O.P. Cambridge, 1876 (Fig. 1475) are also known from the Paleogene of Europe (Baltic amber). The following extinct genera are from the same fauna—*Eocryphoeca* Petrunkevitch, 1946 (= *Tegenaria* Koch and Berendt, 1854) (Fig. 1476 A, B); *Thyelia* Koch and Berendt, 1854 (Fig. 1477); *Textrix** Sundevall, 1833 (Fig. 1478).

Family ARGYRONETIDAE Menge, 1869

Family close to Agelenidae, but unpaired spiracle of trachea situated far in front of spinnerets. With few regular rows of short hairs on cephalothoracic shield (Fig. 1479). Basal segment of large chelicerae with four teeth. Single genus *Argyroneta* Latreille, 1804 in the Recent fauna, as well as from the Miocene of Europe.

Family PISAURIDAE Simon, 1897

Closely related to families Agelenidae and Lycosidae. With numerous trichobothria on dorsal surface of tarsi often arranged in two rows (Fig. 1480). Hairs usually plumose. Distal margin of trochanters with semilunar incision. Eyes in three-four rows (Fig. 1481). Paleogene to Recent. Twelve genera in the Recent fauna. One extinct genus *Esuritor* Petrunkevitch from the Paleogene of Europe (Baltic amber).

Family INSECUTORIDAE Petrunkevitch, 1942

Chelicerae biaxial (Fig. 1483). Two pulmonary sacs present. Cribellum, calamistrum, colulus absent. Spinnerets six, anterior pair stouter, longer than posterior. Anal tubercle two-segmented with setae. Scopulae absent on tarsi. Tarsi with three small claws. Legs long, with spine-like setae (Fig. 1482 A). Trichobothria solitary—in two rows on tibia; single row on tarsus, metatarsus. Chelicerae with parallel bases, long hairs (Fig. 1483 C). Cephalothoracic shield with separate anterior part (Fig. 1483). Eyes eight, arranged in two rows. Single genus—*Insecutor* Petrunkevitch, 1942 (Figs. 1482 A, B; 1483 A, B), known from the Paleogene of Europe (Baltic amber).

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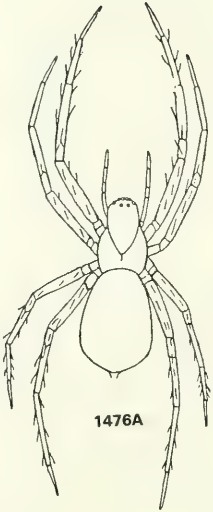
* Editor's note: Not extinct.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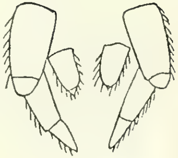
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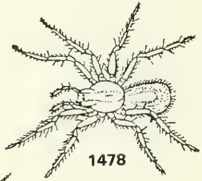
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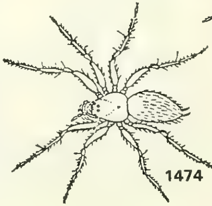
1475A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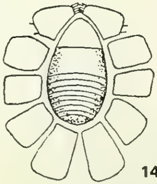
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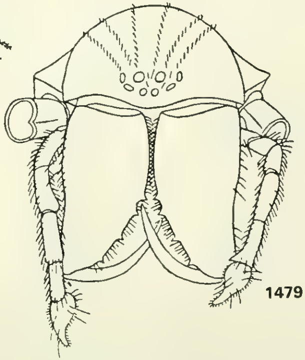
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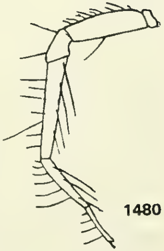
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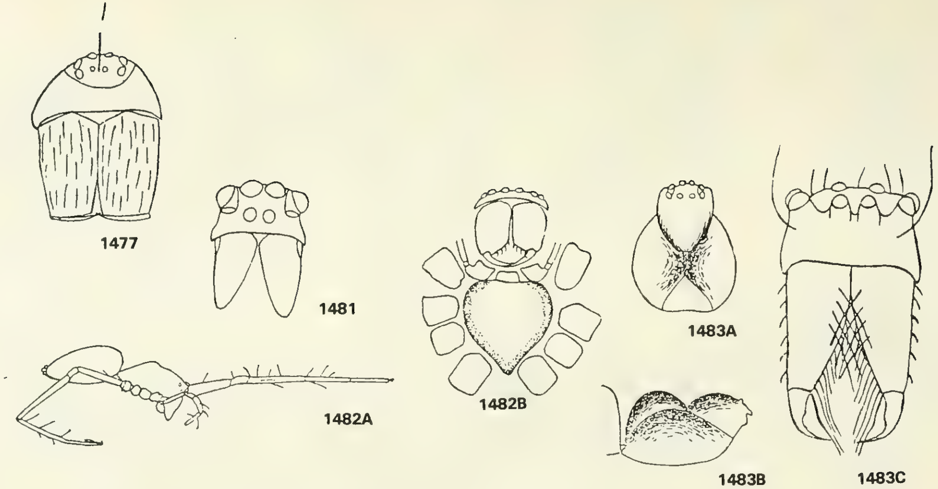

Figs. 1474–1483. Families Agelenidae, Argyronetidae, Pisauridae, Insecutoridae.

1474. *Agelena tabida* Koch and Berendt; general view of female, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1475. *Myro hirsutus* Petrunkevitch; A— head, front view, × 15, B—coxosternal area, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1476. *Eocryphoeca distincta* Petrunkevitch; female: A—dorsal view, × 6, B—spinnerets, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1477. *Thyelia anomala* Koch and Berendt; head of male front view of male, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1478. *Textrix funesta* Koch and Berendt; general view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1479. *Argyroneta aquatica* Clerk: head, front view, × 15. Recent (Crane, 1955). 1480. *Esuritor spinipes* Petrunkevitch; leg IV of young female, × 6. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1481. *Esuritor spinipes* Petrunkevitch; head of female, front view, × 7. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1482. *Insecutor rufus* Petrunkevitch; female: A—lateral view, × 4.5, B—coxosternal area, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1483. *Insecutor mandibulatus* Petrunkevitch; female: A—cephalothorax, dorsal view, × 6, B—same (lateral view), × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).

SUPERFAMILY DRASSODIDEA

(Drassiformia)

Anterior spinnerets large, far apart. Colulus present. Chelicerae free, their bases not part of integument. Eyes eight, arranged in two transverse rows. Tarsi with two claws, between which lie tufts of scapula-like hairs. Three families in the Recent fauna—Prodidomidae, Platoridae and Drassodidae. The last family is also known from the Paleogene of Europe (Baltic amber).

Family DRASSODIDAE Petrunkevitch, 1942

(Drassidae, Gnaphosidae)

Anterior spinnerets considerably larger than posterior. Colulus absent. Two serrated claws on tarsi of legs. Lower lip long. Palpal organ on pedipalpi of males simple. Paleogene to Recent.

Over sixteen genera in the Recent fauna. Two extinct genera—*Captrix* Petrunkevitch, 1942 (Fig. 1484) and *Pytonyssa* C.L. Koch, 1837 (Fig. 1485) are known from the Paleogene of Europe (Baltic amber), and the extinct genus *Palaeodrassus* Petrunkevitch, 1942, is from the Oligocene of North America.

SUPERFAMILY CLUBIONIDEA

(Clubioniformia)

Anterior spinnerets close together. Colulus absent. Tarsi of legs with tufts of scapula-like hairs between claws, with two rows of trichobothria, scopulae. Large anterior eyes similar to other eyes in size. Paleogene to Recent.

Four families in the Recent fauna: Ctenidae, Selenopidae, Clubionidae and Sparassidae. The last two are known from the Paleogene of Europe (Baltic amber). Two extinct families—Inceptroridae and Parattidae.

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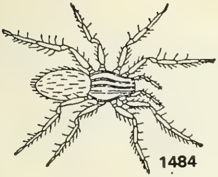
511 Figs. 1484-1493. Families Drassodidae and Clubionidae.

1484. *Captrix lineata* (Koch and Berendt); general view of female, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1485. *Pytonyssa affinis* Koch and Berendt; general view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1486. *Clubiona sericea* Koch and Berendt; general view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1487. *Anyphaera fuscata* Koch and Berendt; general view of male, × 3.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1488. *Micaria procera* Koch and Berendt; general view of male, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1489. *Melanophora mundulata* Koch and Berendt; general view of male, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1490. *Massula klebsi* Petrunkevitch; male: A—dorsal view with translucent borders of coxae and sternum, × 12, B—chelicerae, gnathobases of coxae of pedipalpi and lower lip viewed from ventral side, × 30. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1491. *Ablator trigattatus* (Koch and Berendt); general view of male, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1492. *Abliguritor niger* Petrunkevitch; male: A—cephalothorax, dorsal view, × 15, B—pedipalpi, × 25, C—claws and setae on tarsus of leg III, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1493. *Desultor depressus* Petrunkevitch; male: A—pedipalpi, dorsal view, B—same, ventral view, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).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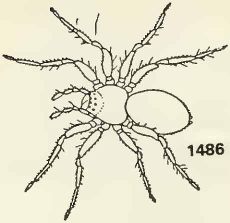
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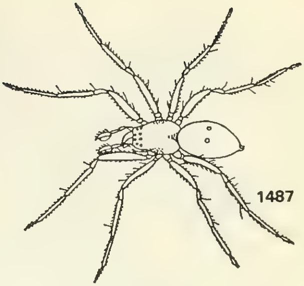
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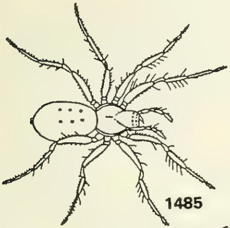
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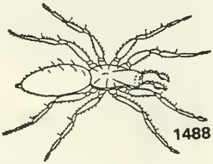
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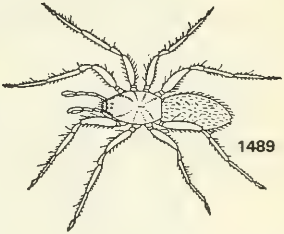
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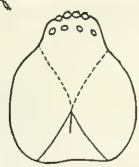
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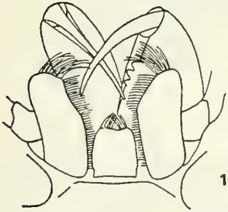
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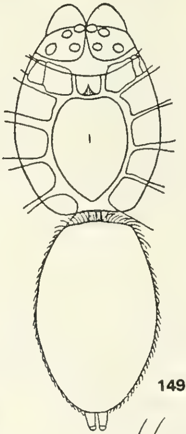
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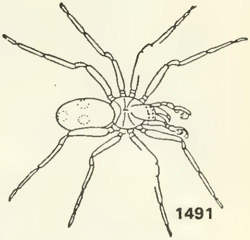
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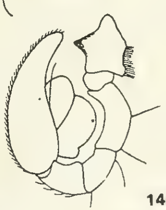
1490C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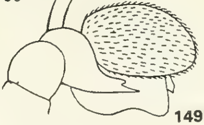
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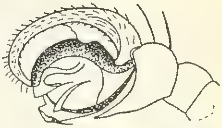

1493B

Family CLUBIONIDAE Simon, 1895
(Anyphaenidae Bertkau, 1878)

Margin of cheliceral groove serrated (Fig. 1490 B). Anterior spinnerets longer than posterior (Fig. 1488). Gnathobases of coxae of pedipalpi extended, placed parallel to one another. Length of lower lip greater than width (Fig. 1490 B). Over thirty-five genera in the Recent fauna. *Clubiona* Latreille, 1804 (Fig. 1486) is from the Paleogene of North America. *Anyphaena* Sundevall, 1833 (Fig. 1487) and *Micaria* L. Koch, 1875 (Fig. 1488).*Melaenophora* C.L. Koch, 1875 (Fig. 1489); *Massula* Petrunkevitch, 1942; (Fig. 1490 A, C); *Ablator* Petrunkevitch, 1942 (Fig. 1491); *Abliguritor* Petrunkevitch, 1942 (Fig. 1492 A, B); *Desultor* Petrunkevitch, 1942 (Fig. 1493) are known from the Paleogene of Europe (Baltic amber). Also, from the Paleogene of North America—*Eoversatrix* Petrunkevitch, 1922; *Eobumbatrix* Petrunkevitch, 1922; *Eostentatrix* Petrunkevitch, 1922.

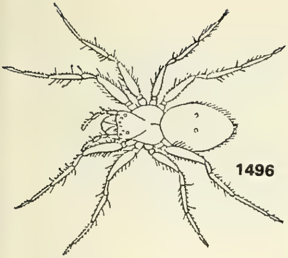
Family EUSPARASSIDAE Petrunkevitch, 1940
(Sparasidae)

Close to Clubionidae. Eyes in two rows. Two or more teeth at hind margin of cheliceral groove. Legs in many species shifted far to sides as in crab spiders (Figs. 1494–1496). Paleogene to Recent.

Over thirty genera in the Recent fauna, of which the following are also known from the Paleogene of Europe (Baltic amber): *Olios* Walckenaer, 1805 (Fig. 1494); *Heteropoda* Latreille, 1804; *Zachria* C.L. Koch, 1875 (Fig. 1495 A, B) and the extinct genera—*Sosybius* Koch and Berenstein, 1854 (Fig. 1496); *Collacteus* Petrunkevitch, 1942 (Fig. 1497 A-C); *Caduceator* Petrunkevitch, 1942 (Fig. 1498); *Adulatrix* Petrunkevitch, 1942 (Fig. 1499); *Eostaianus*
509 Petrunkevitch, 1942 (Fig. 1500 A, B); *Eostasina* Petrunkevitch, 1942 (Fig. 1501 A, B).

512 Figs. 1494–1501. Family Eusparassidae.

1494. *Olios crassipes* (Koch and Berendt); general view of female, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1495. *Zachria peculiata* Petrunkevitch; A—dorsal view of female, × 7, B—Tarsus of leg IV, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946). 1496. *Sosybius minor* Koch and Berendt; dorsal view of female, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1497. *Collacteus aeptivus* Petrunkevitch; A—head, front view, × 15, B—claw of chelicera, × 35, C—anterior part of sternum, lower lip and gnathobases of coxae of pedipalpi, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1498. *Caduceator quadrimaculatus* Petrunkevitch; dorsal view of female, × 6. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1499. *Adulatrix fusca* Petrunkevitch; head of female from front, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch; 1942). 1500. *Eostainus succini* Petrunkevitch; A—dorsal view of female, × 6.5, B—leg IV, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1501. *Eostasina aculeata* Petrunkevitch; A—ventral view of female, × 6.5, B—claws of tarsus of leg IV, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).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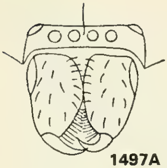
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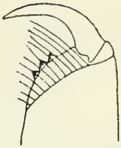
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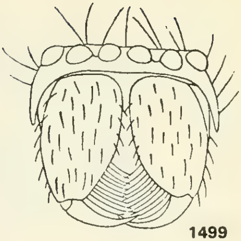
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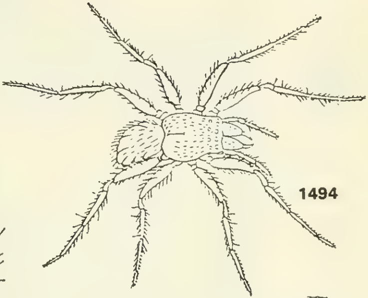
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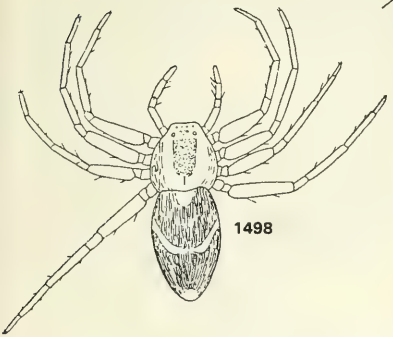
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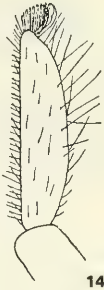
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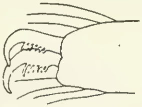
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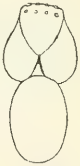
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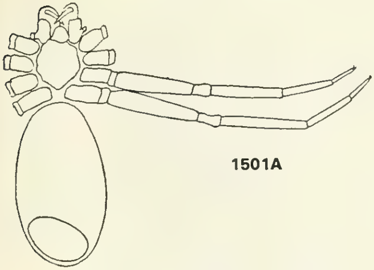
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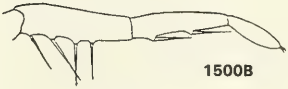
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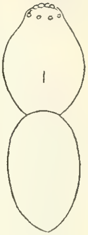
1500A

Family INCEPTORIDAE Petrunkevitch, 1942

Cephalothoracic shield egg-shaped, broadly rounded at both ends and sides (Fig. 1503 C). Eight eyes in two rows along forehead (Fig. 1502). Chelicerae with broad rectangular bases (Fig. 1503). Gnathobase of coxa of pedipalpi rectangular, narrow. Lower lip small, free (Fig. 1503). Sternum oval. Legs slender, long; tarsi with two simple claws. Scopulae, widened setae absent. Pedipalpi of females with claw. Spinnerets six, anterior pair longer than posterior (Fig. 1503 D). Colulus absent. Genus *Inceptor* Petrunkevitch, 1942 from the Paleogene of Europe (Baltic amber) (Figs. 1502, 1503 A–D).

Family PARATTIDAE Petrunkevitch, 1922

Eyes of posterior row considerably smaller than those of anterior row, posterior row sharply arcuate, shorter than anterior. Eyes of anterior row approximately at equal distance. Two median eyes of posterior row close. Paleogene. Oligocene of North America. Single genus—*Parattus* Scudder, 1890.

SUPERFAMILY THOMISIDEA
(Thomisiformia)

Anterior spinnerets close together. Colulus always present. Tarsi with one trichobotothrium, or one row of trichobothria. Eyes more or less of same size (Fig. 1506). Legs normally directed laterally, spiders run sideways (Fig. 1506). Paleogene to Recent. Two families in the Recent fauna—Aphantochilidae and Thomisidae. The latter is also known from the Paleogene of Europe (Baltic amber).

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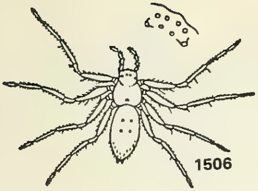
513 Figs. 1502–1511. Families Inceptoridae and Thomisidae.

1502. *Inceptor dubius* Petrunkevitch; dorsal view, × 9. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1946). 1503. *Inceptor aculeatus* Petrunkevitch; A—head, front view, × 10, B—coxosternal area, × 10, C—cephalothorax, dorsal view, × 10, D—anal cone and spinnerets, lateral view, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1504. *Misumena samalandensis* Petrunkevitch; dorsal view of female, × 6. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1505. *Philodromus dubius* Koch and Berendt; dorsal view of male × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1506. *Syphax gracilis* Koch and Berendt; dorsal view of female, × 2.5. Eyes shown separately in front, × 15. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1507. *Fiducia tenuipes* Petrunkevitch; coxosternal area of female, × 18. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1508. *Eothanatus diritatis* Petrunkevitch; A—cephalothorax of male, front view, × 15, B—tarsus with claws and hairs of leg II of male, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1509. *Facundia clara* Petrunkevitch; female, front view, × 6. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1510. *Filiola argentata* Petrunkevitch; A—dorsal view, × 5, B—cephalothorax, front view, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1511. *Medela baltica* Petrunkevitch; head of female (front view), × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).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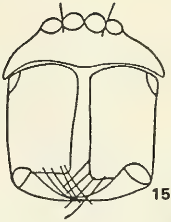
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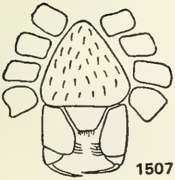
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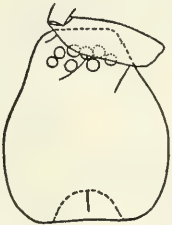
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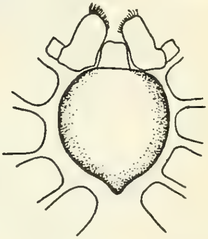
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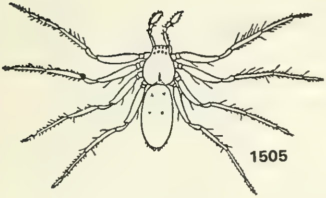
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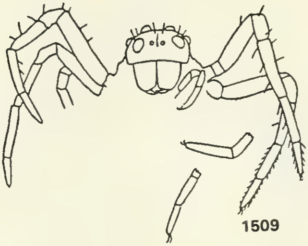
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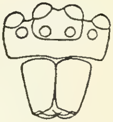
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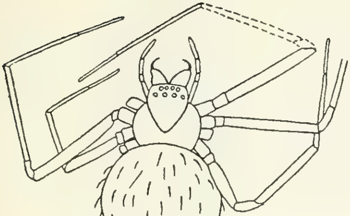
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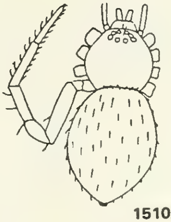
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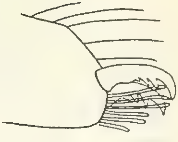
1508B

Family THOMISIDAE Sundevall, 1833

Short spinnerets, along with colulus, anal tubercle close together. Margin of groove at base of chelicerae smooth or with one to three teeth. Both posterior pairs of legs usually weaker, smaller than anterior. Paleogene to Recent.

Over thirty genera from the Recent fauna include *Misumena* Latreille, 1804 (Fig. 1504). *Philodromus* Walckenaer, 1805 (Fig. 1505) from the Paleogene of Europe (Baltic amber). *Thomisus* Walckenaer, 1805 from the Paleogene of North America and Neogene of Europe. The following extinct genera are from the Paleogene of Europe (Baltic amber): *Siphax* Koch and Berendt, 1854 (Fig. 1506); *Fiducia* Petrunkevitch, 1942 (Fig. 1507); *Eothanatus* Petrunkevitch, 1950 (Fig. 1508 A, B); *Facundia* Petrunkevitch, 1942 (Fig. 1509); *Filiola* Petrunkevitch, 1955 (Fig. 1510 A, B); *Medela* Petrunkevitch, 1942 (Fig. 1511).

SUPERFAMILY SALTICIDEA
(Salticiformia)

Anterior spinnerets arranged in row. Colulus absent. Tarsi with one or two rows of trichobothria. Anterior median eyes uncommonly large (Figs. 1512, 1513). Paleogene to Recent. Two families in the Recent fauna: Lyssomanidae, Salticidae. The latter is also known from the Paleogene of Europe (Baltic amber).

Family SALTICIDAE Cambridge, 1900. Jumping spiders
(Attidae Sundevall, 1833)

Four eyes in front row, two each in second and third rows. (Fig. 1516 B). Margin of cheliceral groove with a projection (Figs. 1512 A, 1513 B). More than 50 genera in the Recent fauna.

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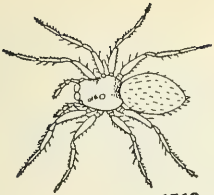
514 Figs. 1512–1520. Family Salticidae.

1512. *Parevophrys succini* Petrunkevitch; male: A—cephalothorax (front view), × 15, B—coxosternal area, C—pedipalpi, × 20, D—anterior part of cephalothorax with eyes, × 7, E—tarsus of leg III, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1513. *Gorgopsina frenata* (Koch and Berendt); A—dorsal view of female, × 4 (Koch and Berendt, 1854), B—head of male (front view), × 15, C—anal cone and spinnerets (lateral view), × 15, D—armor around tarsus of leg III, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1514. *Eolinus succineus* Petrunkevitch; female: A—anterior margin of cephalothorax, × 10, B—tarsus of leg IV, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1515. *Eolinus theryi* Petrunkevitch; pedipalp of male, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1516. *Paralinus crosbyi* Petrunkevitch; male: A—dorsal view, × 9, B—palp, lateral view, × 30, C—palp, dorsal view, × 30, D—head, front view, × 8. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1517. *Cenottus exophthalmicus* Petrunkevitch; dorsal view of female, × 7. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1518. *Phidippus paululus* Koch and Berendt; dorsal view of female, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1519. *Steneattus promissus* (Koch and Berendt); dorsal view of female, × 2.5. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1520. *Eophrys gibberulus* Koch and Berendt; general view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854).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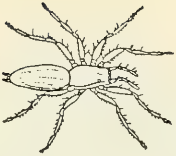
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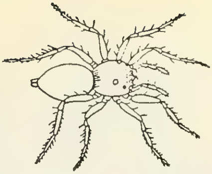
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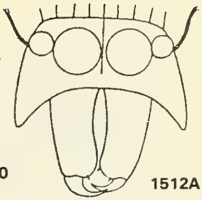
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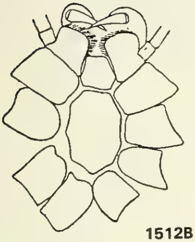
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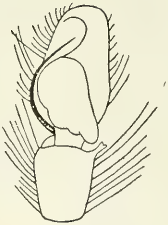
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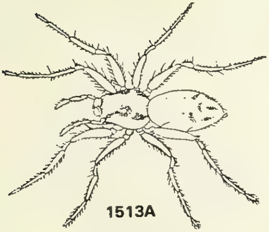
1513C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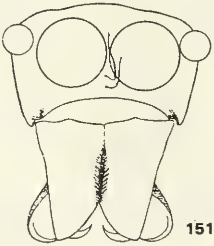
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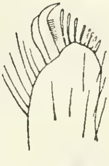
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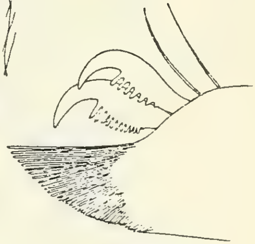
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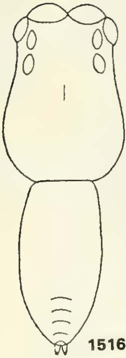
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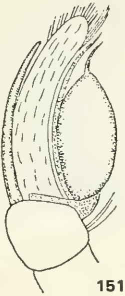
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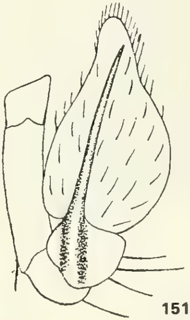
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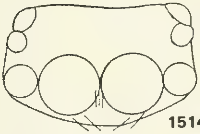
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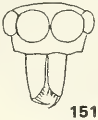
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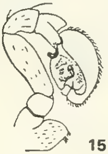
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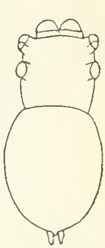
1517

The following extinct genera are known from the Paleogene of Europe (Baltic amber): *Parevophrys* Petrunkevitch, 1942 (Figs. 1512 A–E); *Gorgopsina* Petrunkevitch, 1955 (= *Gorgopsis* Menge, 1854) (Fig. 1513 A–D); *Eolinus* Petrunkevitch, 1942 (Fig. 1514, 1515); *Paralinus* Petrunkevitch, 1942 (Fig. 1516 A–D); *Cenattus* Petrunkevitch, 1942 (Fig. 1517); *Pseudopropetes* W. Dubinin nom. nov. (pro Propetes Menge, 1854), non Walker, 1851, Insecta); *Phidippus** Koch and Berendt, 1854 (Fig. 1518); *Steneattus* Bronn, 1856 (= *Leda* Koch and Berendt, 1854, non. Schumacher, 1817) (Fig. 1519); *Eophrys** Menge, 1854 (Fig. 1520). The following are from the Oligocene of France—*Eoattopsis* Petrunkevitch, 1955 (= *Attopsis* Gonrret, 1886, non Weer, 1849); *Attoides* Brongniart, 1902.

Suborder Cribellatae

A sieve plate—cribellum present between posterior pair of spinnerets. Hairs on tarsi of legs VI form calamistrum; may be reduced in males of some species. Two infraorders: Palaeocribellatae and Neocribellatae.

Infraorder Palaeocribellatae

Two pairs of fan-shaped pulmonary sacs open between adjacent (VIII, IX) segments of abdomen. One family in the Recent fauna: Hypochilidae.

Infraorder Neocribellatae

One pair of pulmonary sacs. Second pair of spiracles fused into unpaired slit

Figs. 1521–1530. Families Zoropseidae, Eresidae, Dictynidae, Amaurobiidae, Anthrodictynidae, Psechridae.

1521. *Adamator succienus* Petrunkevitch; coxosternal area of female, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1522. *Eresus monachus* Koch and Berendt; dorsal view of female, × 3. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1523. *Eolathys succini* Petrunkevitch; lateral view of female, × 9. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1524. *Eolathys debilis* Petrunkevitch; A—coxosternal area, × 10, B—cephalothorax, dorsal view, × 10, C—cephalothorax, front view, × 12. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1525. *Amaurobius rimosus* Koch and Berendt; general view of female, × 4. Paleogene, Europe (Baltic amber) (Koch and Berendt, 1854). 1526. *Amaurobius succini* Petrunkevitch; A—anterior end of chelicera, × 20, B—claw of tarsus of leg IV, × 20. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1527. *Auximus succini* Petrunkevitch; spinnerets and cribellum, × 25. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1528. *Auximus fossilis* Petrunkevitch; dorsal view of female, × 15. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1950). 1529. *Arthrodictyna segmentata* Petrunkevitch; A—lateral view, × 8, B—ventral view of abdomen, × 8, C—claws of tarsus of leg III, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942). 1530. *Eomatachia latifrons* Petrunkevitch; male: A—pedipalp, × 15, B—spinnerets, × 20, C—location of eyes on forehead, × 10, D—lower lip and gnathobases of coxae of pedipalpi, × 10. Paleogene, Europe (Baltic amber) (Petrunkevitch, 1942).

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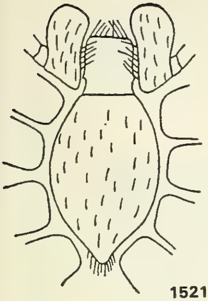
* Editor's note: Not extinct.



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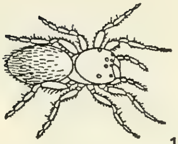

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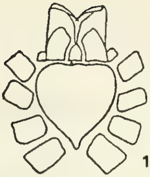

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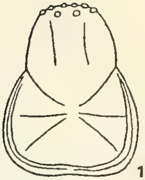

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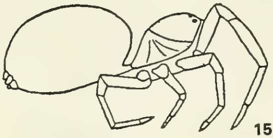

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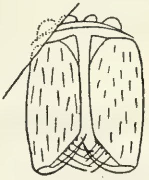

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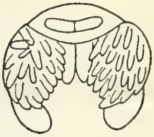

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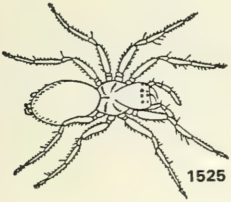

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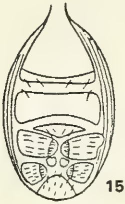
1526A

1526B



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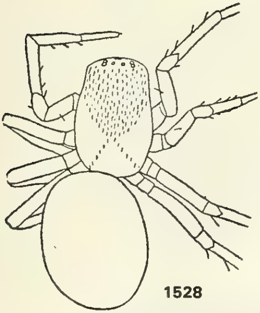

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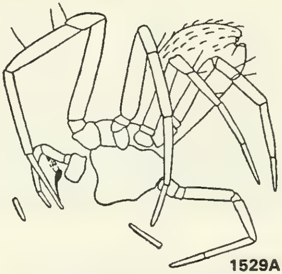

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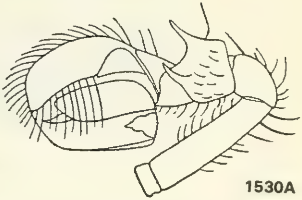

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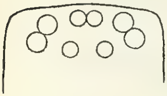
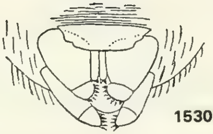


1530C



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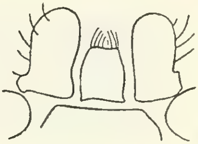

1530D

deep into which open tracheae. Morphology as in typical Araneomorphae. Paleogene to Recent. Six superfamilies in the Recent fauna: Filistatidea, Oecobiidea, Zoropseidea, Eresidea, Dictynidea, Amaurobiidea. The first two occur in the fossil state also.

SUPERFAMILY ZOROPSEIDEA

(Zoropsidiformia)

Tarsi of all legs with two claws, tufts of hairs, scopulae. Paleogene to Recent. Two families in the Recent fauna: Zoropseidae and Acanthoctenidae, of which the first occurs in the Paleogene of Europe (Baltic amber).

Family ZOROPSEIDAE Simon, 1892

Anterior legs with spines and scopulae on tarsal, sometimes on metatarsal segments. Trichobothria present. Eyes arranged in two or three rows, anterior row always with four eyes. Cribellum small, divided into two halves. Calamistrum short. Large forms; weave wide webs in large irregular holes under stones. Paleogene to Recent. Three genera in the Recent fauna. The extinct genus *Adamator* Petrunkevitch, 1942 (Fig. 1521) is known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY ERESIDEA

(Eresiformia)

Posterior spinnerets short. Paired claws of tarsi irregularly serrated. Single family.

Family ERESIDAE C.L. Koch, 1868

Eyes arranged in three rows (Fig. 1522). Chelicerae stout. Tarsi with three claws and trichobothriae. Posterior spinnerets shorter, more slender than anterior ones. Intromittant organ of male simple. Paleogene to Recent.

Five genera in Recent fauna, of which the genus *Eresus* Walckenaer, 1805 (Fig. 1522) is also known from the Paleogene of Europe (Baltic amber).

SUPERFAMILY DICTYNIDEA

(Dictynaeformia)

Tarsi of all legs three-clawed, without trichobothria. Bases of chelicerae dentate (Fig. 1524 C). Small spiders; externally resemble spiders of family Theridiidae. Paleogene to Recent.

Three families in Recent fauna: Dictynidae, Dinopidae, Uloboridae. Dictynidae is also known from the Paleogene of Europe (Baltic amber).

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Family DICTYNIDAE Simon, 1874

Margin of cheliceral groove simple. Eight eyes arranged in two rows (Fig. 1524

B). Chelicerae peculiarly modified in males of some species. Weave web. Paleogene to Recent. Fifteen genera in the Recent fauna. The extinct genus *Eolathys* Petrunkevitch, 1950, is known from the Paleogene of Europe (Baltic amber) (Figs. 1523, 1524 A–C).

SUPERFAMILY AMAUROBIIDEA
(Amaurobiiformia)

Tarsi with one or two rows of trichobothria. External appearance, some peculiarities of structure similar to members of family Agelenidae. Paleogene to Recent. The following three families are present in the Recent fauna: Amaurobiidae, Psechridae, Tengellidae. The last one is without fossil forms. One extinct family—Arthrodictynidae.

Family AMAUROBIIDAE C.L. Koch, 1868

Eyes arranged in two rows. Margin of groove at base of chelicerae serrated (Fig. 1526). Gnathobases more or less parallel. Cribellum divided into two parts. Tarsi with one row of trichobothria, without scopulae (Fig. 1528). Paleogene to Recent. There are five genera in the Recent fauna, of which *Amaurobius* C.L. Koch, 1837 (Figs. 1525, 1526 A–B) and *Auximus* Simon, 1892 (Figs. 1527, 1528) are also known from the Paleogene of Europe (Baltic amber).

Family ARTHRODICTYNIDAE Petrunkevitch, 1942

Abdomen with traces of segmentation, with two sterna at anterior part of ventral surface. Posterior to them, broad cribellum, six spinnerets. First pair of spinnerets very large. Anal cone wide (Fig. 1529 B). Chelicerae not stout. Gnathobases of coxae of pedipalpi inclined in front of lower lip. Sternum shieldlike (Fig. 1529 A). Tarsi of pedipalpi with claws. Tarsi of legs three-clawed (Fig. 1529 B). Calamistrum on metatarsus consists of curved setae. Integument of body with sparse rigid hairs (Fig. 1529 A). Trichobothria on tibiae, metatarsi, tarsi long. Small spiders. Length of abdomen 0.8 mm. Paleogene. Single genus—*Arthrodictyna* Petrunkevitch, 1942 from Europe (Baltic amber) (Fig. 1529 A–C).

Family PSECHRIDAE Simon, 1892

Large spiders with long anterior legs. Body with long hairs. Resemble representatives of family Agelenidae. Eight eyes arranged in two rows (Fig. 1530 C). Chelicerae stout with teeth on margin of groove, with large hook at base. Small scopulae lie on metatarsus, tarsus. Gnathobases of coxae of pedipalpi rounded anteriorly, parallel to one another (Fig. 1530 D). Paleogene to Recent. Six genera in the Recent fauna. *Emoatachia* Petrunkevitch, 1942 is from the Paleogene of Europe (Baltic amber) (Fig. 1530 A–D).

REFERENCES

Agassiz, L. 1844. Recherches sur les poissons fossils. Neuchatel, vol. 2.

Ammom, L. von. 1901. Ueber Anthracomartus aus dem pfälzischen Carbon. Geog. nostische Jahreshefte. 13-ter Jahrgang. 1900, pp. 1–6.

Andre, M. 1949. Ordre des Acariens (Acari Nitzsch. 1818). *Traité de Zoologie,* vol. 6, pp. 794–892.

Andree, K. 1913. Ueber *Anthracophyrynus tuberculatus* nov. gen., nov. spec. aus dem produktiven Karbon von Dudweiler im Saar-Rivier, hebst einer Liste der bisher im Karbon Deutschlands gefunden Arachnoiden-Reste. *Jahresberichte u. Mitt. des Oberrtheinischen geol. Verein.* n. F., vol. 3. pp. 89–93.

Andree, K. 1925. Ostpreussens Bernstein und seine Bedeutung Ostdeutscher Naturwart. Breslau, pp. 15–19.

Andree, K. 1929. Bernstein Forschungen. Berlin u. Leipzig.

Andreeva, O.N. 1957. Novye nakhodki Chlenistonogikh v vostochnoi Sibiri (New finds of Arthropods in Eastern Siberia). *Ezhogodn. Vses. Paleontol. Ob-va*, vol. 16, pp. 80–86.

Bachofen-Echt, A. 1928. Leben und Sterben im Bernsteinwald. *Palaeobiologica*, vol. 1, pp. 1–50.

Bachofen-Echt, A. 1934. Beobachtung uber in Bernstein vorkommende Spinnengewebe. *Biol. Generalis.* Wien, vol. 10.

Baker, E. and G. Wharton. 1952. An introduction to acarology. New York, pp. 1–465.

Baldwin, W. and W.N. Sutelifie. 1904. *Eoscorpius sparthensis* nov. sp. from the Middle Coal Measures of Lanchashire. *Geol. Soc. London Quart. Journ.* , vol. 60, pp. 396–398.

Bather, F.A. 1911. The holotypes of the fossil scorpions *Palaeomachus anglicus* and *Palaeophonus caledonicus. Ann. Mag. Nat. Hist., London,* ser. 8, vol. 3, pp. 673–677.

Beecher, C.E. 1889. Note on the spider *Arthrolycosa antiqua* Harger. *Amer. Journ. Sci.*, vol. 38, pp. 219–223.

Beecher, C.E. 1901. Discovery of Eurypterid Remains in the Cambrian of Missouri. *Amer. Journ. Sci.*, vol. 4, No. 12.

Beecher, C.E. 1902. Note on a new Xiphosuran from the Upper Devonian of Pennsylvania. *Amer. Geol.*, vol. 29, pp. 143–146.

Beier, M. 1932. Ordnung der Arachnida. Pseudoscorpionidea. *Handbuch d. Zoologie*. Kukenthal-Krumbach, vol. 3, Halite 2, pp. 117–192.

Beier, M. 1932. Pseudoscorpionidea, 1–11. *Das Tierreich Lief.* 57, pp. 1–258.

Beier, M. 1933. Revision der Chernetidae. *Zool. Jahrb., Abt. Syst.*, vol. 64, pp. 509–548.

Beier, M. 1937. Pseudoscoplone aus dem baltischen Bernstein Festschr. Prof. E. Strandt, vol. 2, 302 p.

Bekker, E. and G. Uarton. 1955. Vvedenie v akarologiyu (Introduction to

Acarology). Izd. Inostr. Lit-ry-Moscow, 475 p.

Beklemishev, V.N. 1952. Osnovy srvnitelnoi anatomii bespozvonochnykh (Principles of Comparative Anatomy of Invertebrates). Izd. Sovetskaya Nauka, Moscow, 698 p.

Bertkau, P. 1878. Einige spinnen und ein Myriapode aus der Braunkohle von Rott. Verhandl. Nat. Hist. Ver. Preuss Rheinl. u. Westf. (4), vol. 5.

Berendt, C.C. 1830. Die Insekten im Bernstein. Danzig, pp. 1–38.

Berland, L. 1933. Les Arachnides. Encyclopedie entomologique, vol. 16, pp. 1–385. Description de quelques Araignees fossiles. Revnue francaise d'entomologie, vol. 6, pp. 1–9.

Berland, L. 1949. Ordre des Opilions (Opiliones Sundevall. 1833; Phalangidae auct.). *Traite de zoologie*, vol. 6, pp. 761–793.

Birulya, A.A. 1926. Zur ausseren Morphologie der fossilen und recenten Skorpione. *Zool. Anz.*, vol. 67, pp. 61–71.

Birulya, A.A. 1938. Falangi (Solifuga). Fauna SSSR. Paukoobrasnye (Solifugae: Fauna USSR—Arachnida), vol. 1, No. 3, pp. 1–177.

Bode, A. 1951. Ein liassischer Scorpionide. *Palaeontol. Ztschr.*, vol. 24, pp. 58–65.

Borner, C. 1904. Beitrage zur Morphologie der Arthropoden. I. Ein Beitrag zur Kenntnis der Pedipalpen. *Zoologica*, vol. 42, pp. 1–174.

Borre, A.P., de. 1886a. Note sur les Myriapodes et Arachnides fossiles. *Compt. Rend. Soc. Entom.*, Belgique (3).

Borre, A.P., de. 1886b. Analyse de deux travaux recents de M. Scudder et Brongniart sur les Arachnides fossiles. *Compt. Rend. Entom.* Belgique (3), No. 68, CXXXI.

Bristowe, W.S. 1932. The Liphistid Spiders. *Proc. Zool. Soc. London*, pp. 1015–1057.

Bristowe, W.S. 1938. The classification of Spiders. *Proc. Zool. Soc. London*, pp. 285–321.

Brodie, P.B. 1882. On fossil Arachnida, including Spiders and Scorpions. *Proc. Warwickshire Naturalists and Archaeol. Club.*, pp. 9–19.

Brongniart, Ch. 1877. Note sur une Araneide fossile des terrains tertiaires d'Aix (Provence). *Ann. Soc. Entomol., France* (5), vol. 7.

Bronn, H.C. 1849. Handbuch der Geschichte Natur. Stuttgart, vol. 3, Abt. 2, Teil 3 (Index d. Palaeontologie), p. 587.

Bronn, H.G. 1849. Handbuch der Geschichte der Natur. Stuttgart, vol. 3, Abt. 2, Teil 3 (Index Paleontol), p. 587.

Brooks, H.K. 1955. Healed wounds and galls on fossil leaves from the Wilcox Deposits (Eocene) of Western Tennessee. *Psyche.*, vol. 68, No. 1, pp. 1–9.

Brues, C.T., A.H. Melander and F.M. Carpenter. 1954. Classification of Insects. *Bull. Mus. Comparat. Zool.* Harvard College, Cambridge, vol. 108, pp. 1–917.

Buckland, W. 1837. Bridgewater Treatise Geol. Miner. 2 ed., vol. 2.

Burmeister, H. 1845. Geschichte der Schopfung. Eine Darstellung des

Entwickelungsganges der Erde und ihter Bewohner. Auil. 2, Leipzig.

Byalnitskii-Birulya, A.A. 1917. Skorpiony fauna Rossii. Paukoobrasnye (Arachnida) (Scorpions: Fauna of Russia—Arachnida), vol. 1, Petrograd, p. 227.

Caster, K.E. and H.K. Brooks. 1956. New fossils from the Canadian-Chazyan (Ordovician) hiatus in Tennessee. *Bull. Amer. Paleontol.*, vol. 36, No. 157, pp. 157–185.

Caster, K.E. and W.B. Macke. 1952. An agiaspid merostome from the Upper Ordovician of Ohio. *Journ. Paleontol.*, vol. 26, pp. 753–757.

Caster, K.E. and E.N. Kjellesvig-Waering. 1953. *Melbournopterus*, a new Silurian Eurypterid from Australia. *Journ. Paleontol.*, vol. 27, pp. 153–156.

Caster, K.E. and E.N. Kjellesvig-Waering. 1955. *Marsupipterus*, an unusual Eurypterid from the Downtonian of England. *Journ. Paleontol.*, vol. 29, No. 6, pp. 1040–1041.

Chamberlin, J.C. 1929. Synoptic Classification of False Scorpions, pt. I. *Ann. Mag. Nat. Hist.*, ser. 10, 4, pp. 50–80.

Chamberlin, J.C. 1930. Synoptic classification of False Scorpions, pt. II. *Ann. Mag. Nat. Hist.*, ser. 10, 5, pp. 1–48.

Chamberlin, J.C. 1931. The Arachnid Order Chelonethida. *Stanford Univ. Publ. Biol. Sci.*, vol. 7, No. 1, pp. 1–284.

Chernyskev, B.I. 1945. Ob obrutschewia i drugikh Arthropoda s p. Angary v Sibiri (On obrutschewia and other Arthropods from river Angara in Siberia). *Ezhegodn. Vses. Paleontol. Ob-va*, vol. 12, p. 68.

Chernyshev, B.I. 1948. Novyi predstavitel Merostomata iz nizhnego karbona (New representative of Merostomata from the Lower Carboniferous).*Kievsk. Gos. Un-t. im. Shevchenko. Geol. Sb.*, No. 2, pp. 121–130.

Chernyshev, B.I. 1953. Novye chlenistonogie s p. Angary. (New Arthropodes from river Angara). *Ezhegodn. Vses. Paleontol. Obova*, vol. 14, pp. 106–122.

Chernyshev, B.I. 1953. Arthropoda s Urala i drugikh mest SSSR (Arthropods from the Urals and other areas of USSR). *Mater. TsNIGRI, Paleontologiya i Stratigraphiya*. cb. No. 1, pp. 16–24.

Clarke, J.M. 1901. Notes on Paleozoic Crustaceans. Report of N.Y. State Paleontologist, pp. 83–112.

Clarke, J.M. and R. Ruedemann. 1912. The Eurypterida of New York. *New York State Mus. Mem.*, 14, p. 439.

Claypole, E.W. 1890. *Carcinosoma newlini*. *Amer. Geologist*, vol. 6, pp. 255–260.

Cockerell, T. 1916. Note (Curculioididae nom. nov. for Holotergidae Petrunkevitch). *Journ. Washington Acad. Sci.*, vol. 6, p. 236.

Comstock, J.H. 1912. The Spider Book. Doubleday Page and Co. Garden City, New York, pp. 1–740.

Conde, B. 1948. Sur le male de *Koenenia mirabilis* Grassi (Arachnides, Palpigrades). *Bull. Mus. Hist. Nat.*, ser. 2, vol. 20, No. 3, pp. 252–253.

Cope, E.D. 1886. An interesting connecting genus of Chordäta (Myeterops). *Amer. Nat.*, vol. 20, p. 1027.

Corda, A.J.C. 1835. Ueber den in der Steinkohlenformation ber Chomle gefundenen fossilen Scorpion. *Verh. Ges. Vaterl. Mus. Bohmen.* April, p. 36.

Corda, A.J.C. 1839. Ueber eine fossile Gattung der Afterscorpione. *Verh. Ges. Vaterl. Mus. Bohmen.*, April, pp. 14–18.

Currie, L.D. 1927. On *Cyamocephalus*, a new Synziphosuran from the Upper Sihirian of Lesmahagow, Lancashire. *Geol. Mag.*, vol. 64, pp. 153–157.

Dahl, F. 1926. Salticidae. In: Tierwelt Deutschlands. vol. 3, Lief. 1, pp. 1–55.

Dahl, M. 1931. Familie Agelenidae. Die Tierwelt Deutschlands. 23. Teil. Spinnentiere, VI: Agelenidae—Araneidae, pp. 1–46.

Dawydoff, C. 1949. Classe des Arachnides (Arachnida). II. Development embryonnaire des Arachnides. *Traite de Zoologie*, vol. 6, pp. 320–385.

De Kay, J.E. 1825a. On a fossil Crustaceous Animal. *Ann. N.Y. Lyceum Nat. Hist.*, vol. 1, pp. 1–101.

De Kay, J.E. 1825b. Observations on a fossil crustaceous animal of the order Branchiopoda. *Ann. N.Y. Lye. Nat. Hist.*, vol. 1, pp. 375–377.

Demanet, F. and V. Straelen. 1938. Classe des Arachnides. In: Renier A. Stockmans F., Demanet F. and van Straelen, V. *Flore et faune houillieres de la Belgique*. Bruxelles, vol. 3, pp. 206–209.

Diener, C. 1924. Euryptenda Fossilium catalogus, 1: Animalia. pt. 25.

Dix, E. and J. Pringle. 1930. Some Coal measure Arthropods from the South. Wales Coalfield. *Ann. and Mag. Nat. Hist.*, ser. 10. vol. 6, pp. 136–144.

Dorlodot, J.H. 1914. Decouverte de *Gravophonus anglicus* dans le Couchant de Mons. *Ann. Soc. geol. Belgique,* vol. 51, p. 252.

Dunbar, C.O. 1923. Kansas Permian insects. Pt. 2. *Paleolimulus*, a new genus of Paleozoic Xiphosura, with notes on other genera. *Amer. Journ. Sci.*, vol. 5, art. 37, pp. 443–454.

Dubinin, W.B. 1951. Perevye Kleshchi (Analgesoidea Ch. 1. Fauna SSSR (Analgesoidea. Pt. 1, Fauna USST), vol. 6, No. 5.

Dubinin, W.B. 1954. Novaya klassifikatsiya perevykh kleshchei nadsemeistva. Analgesoidea i polozhenie ego v sisteme otryada Acariformes A. Zachv. (A new classification of the superfamily Analgesoidea and its position in the order Acariformes A. Zachv.).

Dubinin, W.B. 1956. Otryady kleschchei polozhenie ikh v sisteme chelicerata [Order Ticks (Acaromorpha) and their systematic position in Chelicerata]. Tr. 11 Nauchnoi Konferentsii parasitologov USSR. *Izd. zool. In-ta AN USSR*, Kiev, pp. 6–51.

Dubinin, W.B. 1957. Ob orientatsii golovnogo kontsa i devonskikh piknognov roda Palaeoisopus i polozhemi ukh v sisteme Arthropoda (On the orientation of head end in the Devonian pycnogonides of the genus *Palaeoisopus* and their position in Arthropoda). *Dokl. AN SSSR*, vol. 117, No. 5, pp. 881–884.

Dubinin, W.B. 1959b. O filogeneze Khelitserovykh zhinotnykh podtipa chelicerophora W. Dub. i rodstne chelicerata s Pycnogonides (On the phylogeny of chelicerates—subphylum Chelicerophora W. Dub. and the affinities of Chelicerata with Pycnogonides). *Tr. In-ta. Morfologii Zhivotnykh AN SSSR*, No. 27, pp. 134–150.

Dubinin, W.B. 1959a. Khelitseronosnye zhivotnye (podtip Chelicerophora W. Dubinin, nom. nov.) i polozhenie ikh v sisteme. [Chelicerates (subphylum chelicerophora W. Dubinin, nom. nov.) and their systematic position]. *Zool. Zhurn.* vol. 38, No. 8, pp. 1163–1189.

Eichwald, E. 1860. *Lethaea Rossica*. I. Stuttgart.

Elias, M.K. 1936. Character and significance of the late Paleozoic flora of Garnett. *Journ. Paleontol.*, vol. 44, pp. 9–28.

Elias, M.K. 1937. A new Scorpion from the Pennsylvanian Walchia beds near Garnett, Kansas. *Journ. Paleontol.*, vol. 11, pp. 335–336.

Eller, E.R. 1938. A review of the Xiphosuran genus *Belinurus* with the description of a new species *B. alleganyensis*. *Ann Carnegie Mus.*, vol. 27, Pittsburg.

Ewing, N.E. 1930. A fossil Arachnid from the Lower Carboniferous shales (Pocono formation) of Virginia. *Ann. Entomol. Soc. Amer.*, vol. 23, pp. 641–643.

Fedotov, D.M. 1924. On the relations between the Crustacea, Trilobita, Merostomata and Arachnida. *Bull. Acad. Sci. Russie*, 1924, pp. 383–408.

Fritsch, A. 1873. Fauna der Steinkohlenformation Bohmens. Archiv fur Landesdurchforschung, vol. 2, No. 2, p. 9.

Fritsch, A. 1899. Fauna der Gaskohle und der Kalksteine der Permformation Bohmens, vol. 4, No. 2, pp. 56–63.

Fritsch, A. 1899. Preliminary note on *Prolimulus woodwardi* Fritsch, from the Permian Gaskohle at Nyran, Bohemia. *Geol. Mag.*, ser. 4, vol. 6, p. 57.

Fritsch, A. 1901. Fauna der Gaskohle, vol. 4, Permische Arachniden, p. 56.

Fritsch, A. 1902. Notizen uber die Arachniden der Steinkohlenformation. *Zool. Anz.*, vol. 25, pp. 483–484.

Fritsch, A. 1904. Palaeozoische Arachnides. Prague, pp. 1–86.

Geinitz, H.B. 1882. *Kreischeria wiedei*, ein fossiler Pseudoscorpion aus der Steinkholenformation von Zwickau. Ztschr. *Deutsch. geol. Ges.*, vol. 34, pp. 238–242.

George, V.P. 1952. On some Arthropod Microfossils from India. *Agra Univers. Journ. Res.*, vol. 1, pp. 83–108: vol. 6, p. 57.

Gerhardt, U. 1932. Merostomata. In: Kukenthal *Handbuch der Zoologie*, vol. 3, Halfte 2, Lief II.

Gerhardt, U. and A. Kastner. 1937. Araneae-Echts Spinnen-Webspinnen. In: Kukenthal. *Handbuch der Zoologie,* vol. 3, Halfte 2, Lief II, pp. 394—496.

Gerhardt, U. and A. Kastner. 1938. Araneae-Echte Spinnen-Webspinnen. In:

Kukenthal. *Handbuch der Zoologie*, vol. 3, Halfte 10, Lief 12, pp. 497–636.

Giebel, C.C. 1856. Die Insecten und Spinnen der Vorwelt. Fauna der Vorwelt, vol. 2, p. 18.

Gill, E.H. 1909. An Arachnid from the Coal Measures of the Tyne Valley. *Newcastle Trans. Nat. Hist. Soc.*, vol. 3, pp. 510–523.

Gill, E.H. 1911. A Carboniferous Arachnid from Lancashire. *Geol. Mag.*, sec. 5, vol. 8, pp. 395–398.

Gill, E.H. 1924. Fossil Arthropods from the Tyne Coalfield. *Geol. Mag.*, vol. 61, pp. 445–471.

Goldenberg, F. 1873. Fauna saraepontana fossils. Die fossilen Thiere aus der Steinkohlenformation von Saarbrucken. Saarbrucken, vol. 1, p. 12.

Gourett, P. 1886. Recherches sur les Arachnides tertiares d'Aix en Provence. *Rec. Zool. Snisse.*, vol. 4, pp. 431–496.

Grandjean, F. 1939–1943. Quelques generes d'Acariens appartenant an group des Endeostigmata. *Ann. Sci. Nat. Zool. et Biolog. Animal.* Paris. ser. 11, vol. 2, No. 1, pp. 1–122; vol. 4, No. 1, pp. 85–135; vol. 5, No. 1, pp. 1–59.

Guthorl, P. 1934. Die Arthropoden aus dem Karbon und Perm des Saar-Nahe-Pialz-Gebietes Abh. Preuss. Landesanst., N.F., vol. 164, pp. 1–219.

Guthorl, P. 1938. *Eophrynus waechteri* n. sp. (Arachn. Anthracom) aus der Tiefbohrung Stangenmuhle Saar-Karbon Senckenbergiana, vol. 20, No. 6, pp. 465–470.

Guthorl, P. 1940. Zur Arthropoden Fauna des Karbons und Perms. 10 *Trigonomartus pustulatus* (Scudder) (Arach., Antracom) aus der Grube Nordstern. Aachener Karbon. *Paleontol. Ztschr.*, vol. 22, pp. 63–74.

Haase, E. 1890. Beitrage zur Kenntnis der fossilen Arachniden. *Ztschr. Dtsch. Geol. Ges.*, vol. 42, pp. 629–657.

Hadzi, J. 1931. Scorpionenreste aus dem tertiaren Sprudelsinter von Bottigen (Schwabische Aib). *Palaeontol. Ztschr.*, vol. 13, pp. 134–138.

Hahn, C.W. 1820–1836. Monographia Aranearum. Nurnberg.

Hahne, C. 1939. Ein seltenes Spinnentier (*Trigonomartus dorlodoti* Pruvost) aus dem Aachener Steinkohlengebirge. *Palaeontol. Ztschr.*, vol. 21, pp. 218–223.

Hall, J. 1859. Paleontology of New York: *N. 4. Geol. Sur.*, vol. 3, pp. 382–424.

Hall, C.E. 1862. Natural History of New York, pt. 6. Paleontology.

Hansen, H.J. 1926. Biospeologica 53. Palpigradi (ser. 2). *Archives zool. exper. gen.*, vol. 65, pp. 167–180.

Hansen, H.J. 1930. Studien on Arthropoda III. Class Arachnida. London, pp. 290–340.

Hansen, H.J. and W. Sorensen, 1904. On two Orders of Arachnida (Opiliones and Ricinulei). Cambridge Univ. Press, Opiliones, pp. 1–182.

Hardt, H. 1954. Der Berenstein: seine Entstehung und Verwendung. *Die Neue Brehm-Bucherei*, vol. 128, pp. 1–44.

Harger, O. 1874. Notice of a new spider from the Coal Measures of Illinois. *Amer. Journn. Sci.*, vol. 7, pp. 219–223.

Harrison, H.J.W. 1926. Zoocecidia from a Reatber near Birtley. Co. Durham, with some reference to other insect remains. *The Entomol.*, 61, No. 758, pp. 177–179.

Harvey, F.L. 1866. On *Anthracomartus trilobitus* Scudder. *Proc. Acad. Philadelphia*, pp. 231–232.

Haughton, S. 1877. Description of a fossil spider *Architarbus subovalis* from the Middle Coal Measures. Burnley, Lancashire. *Journ. Geol. Soc. Ireland*, N.S., vol. 4, p. 222.

Heer, O. 1876. The Primaeval World of Switzerland. English transl. ed. by James Heywood. London.

Heyden, C. 1860. Achter Beobachtungen der Oberschales. *Ges. f. Nat. u. Heimkunde*, p. 63.

Heyden, C. 1862. Cliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Rohn. *Paleontographica*, vol. 10,No.2, pp. 62–82.

Hibbert, S. 1836. On the freshwater limestone of Burdiehouse in the neighborhood of Edinburgh belonging to the Carboniferous group of rocks etc. *Trans. Roy. Soc. Edinburgh*, vol. 13, pp. 169–282.

Hirst, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed. Aberdeenshire). *Ann. Mag. Nat. Hist.*, ser. 9, vol. 12, pp. 455–474.

Holdhaus, K. 1954. Die Spuren der Eiszeit in der Tierwelt Europas. *Abh. Zool. Bot. Ges. in Wien.*, vol. 18, pp. 1–493.

Holm, A. 1940. Studien uber die Entwicklung und Entwicklungsbiologie der Spinnen. *Zoologiska Bidrag tran Uppsala*, vol. 19, pp. 1–214.

Howard, F.T. and T.H. Thomas. 1896. Note on *Eophrynus. Report and Transactions. Cardiff Naturalist's Soc.*, vol. 28, pp. 52–53.

Hunter, J.R.S. 1886. Notes on the Discovery of a fossil Scorpion (*Palaeophones caledonicus*) in the Silurian Strata of Logan Water, *Trans. Geol. Soc.*, Glasgow, vol. 8, pp. 169–170.

Hunter, J.R.S. 1888. Notes on a new fossil Scorpion (*Palaeophonus caledonicus*) from the Upper Silurian Shales, Logan Water. Lesmahagow. *Trans. Edinburg. Geol. Soc.*, vol. 5, pp. 185–191.

Karsch, F. 1882. Ueber ein neues Spinnenthier aus der schlesischen Steinkohle und die Arachnoiden der Steinkohlenformation uberhaupt. *Stschr. Disch. Geol. Ges.*, vol.·34, pp. 556–561.

Karsch, F. 1884. Neue Milben im Bernstein Berliner Entomolog. *Ztschr.*, vol. 28, No.1, pp. 175–176.

Kästner, A. 1923. Die vergleichend anatomische Bedeutang der Interpulmonarialte der Araneen. *Zool. Anz.*, vol. 58, pp. 97–102.

Kästner, A. 1925. Vergleichend-morphologische Untersuchungen der Grathocoxen der Araneae. *Ztschr Morphol. u. Okol. Tiere.*, vol. 4, pp. 711–738.

Kästner, A. 1928. Afterscorpione (Pseudoscorpionida). In: Tierwelt Mittelearopas, vol. 3, Lief. 1, pp. 1–4.

Kästner, A. 1928. Scorpione (Scorpionida). *Tierwelt Mitteleuropas*, vol. 3, No. 1.

Kästner, A. 1929. Bau und Funktion der Fachertracheen einiger Spinnen. *Ztschr. Morphol. u. Okol. Tiere.*, vol. 13, pp. 463–558.

Kästner, A. 1931a. Arachnida. *Handworterbuch der Naturwissenschaften*, 2, Auil, vol. 1, pp. 356–387.

Kästner, A. 1931b. Die Hufte und ihre Unformung zu Mundwekzeugen bei den Arachniden. *Ztschr. Morphol. u. Okol. Tiere*, vol. 22, pp. 721–758.

Kästner, A. 1932a. Ueber die Cliederung der Solifugae. *Ztschr. Morphol. u. Okol. Tiere.*, vol. 24, pp. 342–358.

Kästner, A 1932b. 2. Ordnung der Arachnida: Pedipalpi Lalreille Geissel-Scorpione. *Handb. Zool.,* Kükenthal-Krumbach, vol. 3, Hälfte 2, pp. 1–76.

Kästner, A. 1932c. 3. Ordnung der Arachnida. Palpigradi Thorell. *Handb. Zool.* Kükenthal-Krumbach, pp. 77–98.

Kästner, A. 1932d. 4. Ordnung der Arachnida. Ricinulei Thorell. *Handb. Zool.* Kükenthal-Krumbach, vol. 3, Hälfte 2, Lief. 5, pp. 99–116.

Kästner, A. 1933. 6. Ordnung der Arachnida Solifugae Sundevall-Walzenspinnen. *Handb. Zool.,* Kükenthal-Krumbach, vol. 3, Hälfte 2, pp. 193-299.

Kästner, A. 1935. Ordnung der Arachnida: Opiliones Sundevall-Weberknechte. *Handb. Zool.* Kükenthal-Krumbach, vol. 3, Hälfte 2, pp. 300–393.

Kästner, A. 1937. Ueber die Gliederung der Spinnen. *Zool. Anz.*, vol. 119, pp. 49–57.

Kästner, A. 1953. Die Mundwerkzeuge der Spinnen, ihr Bau, ihre Function und ihre Bedeutung für das System, 2 Teil. Herleitung und biologische Bedeutung der Labidognathie. *Zool. Jahr. Abt. Anat.,* vol. 73, No. I, pp. 1–47.

Keferstein, C. 1834. Die Naturgeschichte der Erdkörpers. Berlin, vol. 2, pp. 375–376.

Kharitonov, D.E. 1932. Kataloggrusskikh paukov (Catalogue of Russian spiders). *Ezhegodmik. Zool. Muzeve. AN USSR*, vol. 32, Prilozhenie, pp. 1–206.

Kiellesvig-Waering, E.N. 1951. Downtonian (Silurian) Eurypterida from Perton near Stoke Edith, Herefordshire. *Geol. Mag.*, vol. 88, No. 1, pp. 1–23.

Kiellesvig-Waering, E.N. 1954. Note on a New Silurian (Downtonian), scorpion from Shropshire, England. *Journ. Paleontol.*, vol. 28, No. 4, pp. 485–486.

Kiellesvig-Waering, E.N. 1955. *Dorfopterus*, a new genus of Eurypterida from the Devonian of Wyoming. *Journ. Paleontol.*, vol. 29, No. 4, pp. 696–697.

Kiellesvig-Waering, E.N. 1955a. *Doriopterus*, a new genus of Eurypterida from the Devonian of Wyoming. *Journ. Paleontol.*, vol. 29, No. 4, pp. 696–697.

Kiellesvig-Waering, E.N. 1958. The genera, species and subspecies of the family Eurypteridae Burmeister, 1845. *Journ. Paleontol.*, vol. 32, No. 6, pp. 1107–1148.

Kiellesvig-Waering, E.N. 1959. A taxonomic review of some late Paleozoic Eurypterida. *Journ. Paleontol.*, vol. 33, No. 2, pp. 251–256.

Kittary, M. 1848. Anatomicheskve issledovanie obyknovennoi (*Galeodes araneoides*) i kolyuchei (*G. dorsalis*) solpugi [Anatomy of the ordinary (*Galeodes aranesides*) and spiny (*G. dorsalis*) Solifugae]. *Ucp. Zap. Kazansk.*, Un-ta, No. 2.

Kjellesvig-Waering, E.N. and L. Størmer. 1952. The *Dolichopterus–Strobilopterus* group in the Eurypterida. *Journ. Paleontol.*, vol. 26, No. 4, pp. 660–661.

Klebs, R. 1889. Aufstellung und Katalog des Bersteinmuseums von Stantien und Becker. Konigsberg.

Kliver, F. 1886. Ueber einige neue Arthropodenreste aus der Saarbrucker und der Wettin-Lobejuner Steinkohlenformation Paleontogr., vol. 32, pp. 99–115.

Kobayashi, T. 1933. On the occurrence of Xiphosuran Remains in Chosen (Korea), Japan. *Journ. Geol. Geogr.*, vol. 10, No. 3–4, pp. 175–182.

Koch, C.H. and G.C. Berendt. 1854. Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. *Organische Reste im Bernstein*, Br. I, Abt. 2, pp. 1–124.

Koenig, C. 1820. Icones Fossilium Sectites.

Kraepelin, K. 1893. Revision der Scorpione. *Jahrb. Hamburg. Wiss. Anst.*, vol. 8, pp. 1–144.

Kraepelin, K. 1894. Revision der Scorpione II. *Jahrb. Hamburg. Wiss. Anst.*, vol. 11, pp. 1–248.

Kraepelin, K. 1895. Revision der Scorpione III. *Jahrb. Hamburg. Wiss. Anst.*, vol. 12, pp. 1–24.

Kraepelin, K. 1895. Revision der Tarantuliden. *Abh. naturh Ver Hamburg.*, vol. 13, pp. 1–53.

Kraepelin, K. 1897. Revision der Uropygi. *Abh. naturh. Ver. Hamburg.*, vol. 15, pp. 1–60.

Kraepelin, K. 1899a. Scorpiones und Pedipalpi. *Das Tierreich*. Lief 8, pp. 1–265.

Kraepelin, K. 1899b. Zur Systematik der Sohfugen. *Mitteil. naturh. Mus. Hamburg.*, vol. 16, pp. 197–258.

Kraepelin, K. 1901. Palpigradi und Solifugae. *Das Tierreich*. Lief. 12, pp. 1–59.

Kraepelin, K. 1905. Die geographische Verbreitung der Skorpione. *Zool. Jahrb. Abt. Syst.*, vol. 22, pp. 321–364.

Krendovskii, M.E. 1885. Presnovodnye akaridy yuzhnoi Rossii (Freshwater Acarines of Southern Russia). *Kharkov Izd. un-ta*, pp. 1–150.

Krishtofovich, A.N. 1941. Paleobotanika (Paleobotany). 3rd Edn. Gosgelizdat, pp. 1–495.

Kutorga, S. 1838. Beitrag zur kenntniss der organischen Ueberreste des Kupfersandsteins am westlichen Abhange des Urals. St. Petersburg, pp. 1–38.

Kukuk, P. 1928. Stratigraphie und Tektonik der Rechtsrheinisch-Westtahschen Steinkohlenablagerung. *Compt. Rend. geol. Mijn. Genootsch Nederland en Kolonien*. Liege, pp. 407–448.

Kusta, J. 1882. Notiz uber den Fung eines Arachniden-restes bei Petrovie. *Sitzungsber. Kon. bohm. Ges. Wiss.*, p. 258.

Kusta, J. 1883. *Anthracomartus* Krejcii, eine neue Arachnide aus dem bohmischen Karbon. *Sitzungsber. Kon. bohm. Ges. Wiss.*, p. 340.

Kusta, J. 1884a. *Thelyphonus bohemicus* n. sp., ein fossiler Geisselkorpion aus der Steinkohlenformation von Rakonitz. *Sitzungsber. Kon. bohm. Ges. Wiss.*, pp. 186–191.

Kusta, J. 1884b. Ein neuer Funddort von *Cycloplithalmus* senior Corda. *Sitzungsber. Kon. bohm. Ges. Wiss.*, pp. 48–401.

Kusta, J. 1884c. Neue Arachniden aus der Steinkohlenformation von Rakonitz. *Sitzungsber. Kon. bohm. Ges. Wiss.*, pp. 398–403.

Kusta, J. 1855. Neue fossile Arthropoden aus dem Neogerathienschiefer von Rakonitz. *Sitzungsber. Kon. bohm. Ges. Wiss.*, p. 7.

Kusta, J. 1888. Neue Arachniden aus der Steinkohlenformation bei Rakonitz. *Sitzungsber. Kon. bohm. Ges. Wiss.*, pp. 194–208.

Kuster, E. 1911. Allgemeiner Teil. Die Zoocecidien, Stuttgart. vol. 1. *Zoologica*, vol. 24. Lief I, pp. 105–165.

Lamont, A. 1955. Scottish Silurian Chelicerata. *Trans. Edinburgh Geol. Soc.*, vol. 16, No. 2, pp. 200–216.

Lameere, A. 1950. Precis de Zoologie, vol. 3, Les Mollusques—Caracteres fondamentaux des Arthropodes, les Arachnomerphes et les Crustaces. Publ. de l'Inst. Zool. Torley-Rousseau Univ. libre de Bruxelles, pp. 1–547.

Lange, W. 1923. Uber neue Fossillunde aus der Trias von Gottingen. *Ztscher. Dtsch. Geol. Ges.*, vol. 74, p. 162.

Lankester, E.A. 1911. Articles on Arachnida and Arthropoda. *Encyclopaedia Britanica*.

Lankester, E.A. 1926. Arachnida. *Encyclopaedia Britanica*. 13th ed., vol. 2, pp. 287–311.

Laurie, M. 1892. On same eurypterid remains from the Upper Silurian rocks of the Pentland Hill. *Trans. Roy. Soc.* Edinburgh, vol. 37.

Laurie, M. 1899a. On a Silurian scorpions and some additional Eurypterid remains from the Pentland Hills. *Trans. Roy. Soc.* Edinburgh, vol. 39. (1900), pp. 575–590.

Laurie, M. 1899b. The eurypterid-bearing rocks of the Pentland Hills. Rept. Brit. Assoc., 68th meeting, pp. 557–558.

Leach, W.E. 1819. Dictionnaire des sciences naturelies, vol. 14, p. 538.

Lehmann, W.M. 1944. *Palaeoscorpius devonicus* n.g. n. sp., ein Scorpion aus dem rheinischen Unterdevon. *Neues Jahrb. Miner.*, pp. 177–185.

Lehmann, W.M. 1956. Beobachtungen an Weinbergina opitzi (Merost., Devon). *Senckenbergiana Lethaea.*, vol. 37, pp. 67–77.

Mani, M.S. 1945. Arthropod fossil from India. *Indian Journ. Entomol.*, vol. 6, pp. 61–64.

Mani, M.S. 1946. On some Arthropod fossils from India. *Proc. Nat. Acad. Sci., India*. Udaipur Symposium, vol. 16(2–4), pp. 43–56.

Martynov, A.V. 1934. Klass Arachnida (Class Arachnida) in: Tsittelya '*Osnovy Paleontologii*', Pt. 1, *Besposvonochnye*. ONTI, pp. 976–983.

Matthew, G.F. 1889. On some remarkable organisms of the Silurian and Devonian rocks in Southern New Brunswic. *Trans. Roy. Soc. Canada*, vol. 6, ser. 4, pp. 49–62 (1888).

McCook, H. 1888. A new fossil Spider, *Eoatypus woodwardii. Proc. Acad. Philadelphia*, pp. 200–202.

Meek, F.B. and A.H. Wortheu. 1868a. Preliminary notice of a scorpion, a *Eurypterus* and other fossils from the Coal Measures of Illinois and Iowa. *Amer. Sci. Arts.*, ser. 2, vol. 45, p. 25.

Meek, F.B. and A.H. Wortheu. 1868b. Articulated fossil of the Coal Measures. Arachnida. *Geol. Surv. of Illinois*, vol. 3, pp. 560–563.

Melander, A.L. 1903. Some addition to the Carboniferous terrestrial Arthropod fauna of Illinois. *Journ. Geol.*, vol. 2, pp. 178–198.

Menge, A. 1854. *Trombidium saccatum* ist ohne Zweifel ein *Rhyncholophus*. Progr. Petrischule. Danzig.

Menge, A. 1855. Uber die Scheerenspinnen Neueste Schriften der Naturforschendea Gesellschaft in Danzig, vol. 5.

Menge, A. 1856. Lebenszeichen vorweltlicher im Bernstem eingeschlossener Tiere. Prog. Petrischule. Danzig.

Menge, A. 1869. Uber einen Scorpion und zwei Spinnen im Bernstein. Schrift. Naturl. Ges Danzig. n. ser., vol. 2, Lief 2.

Meschinelli, A. 1892. Fungi fossiles. In: Saccardo Sylloge fungorum, Potavii, vol. 10, pp. 741–808.

Meschinelli, A. 1902. Fungorum fossilium omnium hucus que cognitorum iconographia Vicetiae (1898), pp. 1–144.

Meyer, H. 1861. Beitrage zur Naturgeschichte der Vorwelt Palaeontographica, pp. 1–203.

Miller, S.A. 1874. Genus *Megalograptus*. *Cincinati Quart. Journ. Sci.*, vol. 1, pp. 343–346.

Miller, S.A. 1877. The American Paleozoic fossils. A catalogue of the genera and species etc., pp. 1–253. Cincinnati. Ohio.

Millot, J. 1942. Sur l'anatomie et l'histophysiologie de *Koenenia mirabilis* Grass (Arachnida. Palpigradi) *Rev. frane. Entomol.*, vol. 9, pp. 37–51.

Millot, J. 1945a. La constitution de l'abdomen des Ricinulei. *Bull. Soc. Entomol. France*, pp. 72–74.

Millot, J. 1945b. Les Ricinulei ne sont pas des Arachnides primitiis. *Bull. Soc. Zool. France*, vol. 70, pp. 106–108.

Millot, J. 1945c. L'anatomie interne des Ricinulei. *Ann. Sci. Nat. Zoologie*, II, ser, vol. 7, pp. 1–29.

Millot, J. 1949a. Classe des Arachnides (Arachnida) I. Morphologie generale of anatomie interne. *Traite de Zoologie*, vol. 6, pp. 263–319.

Millot, J. 1949b. Ordre des Palpigrades. *Traite de Zoologie*, vol. 6, pp. 520–532.

Millot, J. 1949c. Ordre des Uropyges. *Traite de Zoologie*, vol. 6, pp. 533–562.

Millot, J. 1949d. Ordre des Amblypyges. *Traite de Zoologie*, vol. 6, pp. 563–588.

Millot, J. 1949e. Ordre des Araneides. *Traite de Zoologie*, vol. 6, pp. 589–743.

Millot, J. 1949f. Ordre des Ricinuleides. *Traite de Zoologie*, vol. 6, pp. 744–769.

Millot, J. and M. Vachon. 1949a. Ordres des Scorpiones. *Traite de Zoologie*, vol. 6, pp. 386–436.

Millot, J. and M. Vachon. 1949b. Ordre des Solifuges. *Traite de Zoologie*, vol. 6, pp. 482–519.

Moore, J.J. 1923. A review of the present knowledge of fossil scorpions with the description of a new species from the Pottsville Formation of Clay County, Indiana. *Proc. Indiana Acad. Sci.*, vol. 38, pp. 125–134.

Moysey, L. 1911. On some arthropod remains from the Nottinghamshire and Derbyshire Coalfields. *Geol. Mag.*, dec. 5, vol. 8, pp. 497–507.

Nelepa, A. 1888. Die Anatomie der Phytopten. *Sitzungsber. d. Math. Naturwiss. Classe Kais. Akad. Wissensch.*, vol. 96, Abt. I. No. 3, pp. 115–165.

Neiszkowski, J. 1859. Der Eurypterus remipes aus den obesilurischen. Schichten der Insel Osel. *Arch. Naturk. Liv., Esth. u. Kurlands* (I), vol. 2 (1861), pp. 297–344.

Novojilov, N. 1958. Merostomates du Devonien inferiur et moyen de Siberie. *Ann. Soc. Geol. Nord.*, vol. 78, pp. 243–258.

Novozhilov, N. 1958. *Polystomurum stormeri*—Novyi rod i vid evripterid izdevona Voronezhskoi oblasti (*Polystomurum stormeri*—a new genus and species of Eurypterid from the Devonian of Voronezhsk region). *Materialy k 'Osnovam Paleontologii'*, No. 2, pp. 47–50.

Novojilov, N.I. 1958. Merostomates du Devonian inferieur et moyen de Siberie.*Ann. Soc. Geol. Nord.*, vol. 78, pp. 243–258 (1959).

O'Connor, 1896. On several fossils, including a Spider (*Eophrynus*) from the 9. Coal Seam at Tynybedw, Rhonda Valley. *Cardiff Nat. Soc., Rep. and Tr.*, vol. 28, pt. 1, pp. 50.

Oppenheim, P. 1887. Die Insektenfauna des lithographischen Schiefers in Baiern. *Paleontographica*, vol. 34, pp. 215–247.

Oudemans, A.C. 1936. Kritisch historisch Overzicht der Acarologie. *Derde Gedeelte*, 1805–1850. Leiden, vol. A, pp. 1–430.

Oudemans, A.C. 1937. Kritisch historisch Overzicht der Acarologie. *Derde Gedeelte*, 1805–1850, vol. C, D, E. Leiden, pp. 799–2735.

Packard, A.S. 1886. On the Carboniferous Xiphosurous fauna of North America. *Mem. Nat. Acad. Sci. Washington*, vol. 3, pp. 141–157.

Page, D. 1856. Advanced textbook of geology, p. 135.

Palmer, A.R. 1955. Remarkably preserved Miocene Arthropods from the

Mojave Desert. *Sci.*, vol. 121, No. 3148, p. 626.

Palmer, A.R. and A.M. Bassett. 1954. Nonmarine Miocene Arthropods from California. *Sci.*, vol. 120, No. 3110, pp. 228–229.

Pampaloni, L. 1902. Mikroflora e mikrofauna nel disodile di Melilli in Sicilia. *Rend. Acad. Lincei.*, vol. 2, p. 252.

Parker, W.A. 1909. The fossil Arthropods and Pisces of Sparth Rochdale. *Lancashire Naturalist.*, Darwen, new ser., vol. 2, pp. 2–8.

Pavlovskii, E.N. 1916. O znachenii polovogo apparata dlya sistematiki skorpionov (On the importance of the genitalia for the taxonomy of Scorpions). *Russk. Entomol. Obozrenie*, vol. 16, No. 3–4, pp. 134–140.

Pavlovskii, E.N. 1917. Materialy k Sravnitelnoi anatomii i istorii razvitiya skorpionov (Material on comparative anatomy and history of development of Scorpions). Petrograd, pp. 1–318.

Pavlovskii, E.N. 1924. Studies on the organization and development of Scorpions. *Quarterly Journ. Micr. Sci.*, vol. 68.

Peach, B.N. 1883. On some new species of fossil scorpions from the Carboniferous Rocks of Scotland and the English Borders, with a review of the genera *Eoscorpius* and *Mazonia* of Meek and Worthen. *Trans. Roy. Soc. Edinburgh.*, vol. 30, pp. 397–412.

Pernet, G. 1925. Historical notes on scabies with remarks on the paleontology of the *Acarus. Brit. Journ. Dermatol. Syphilis. London*, vol. 37, pp. 312–316.

Petrunkevitch, A. 1911. Catalogue of American Spiders. *Bull. Amer. Mus. Nat. Hist.*, vol. 29, pp. 1–809.

Petrunkevitch, A. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. *Trans. Connect. Acad. Arts a. Sci.*, vol. 18, pp. 1–137.

Petrunkevitch, A. 1916. The shape of the sternum in scorpions as a systematic and a phylogenetic character. *Amer. Naturalist*, vol. 50, pp. 600–608.

Petrunkevitch, A. 1922a. The circulatory system and segmentation in Arachnids. *Journ. Morphol.*, vol. 36, pp. 157–188.

Petrunkevitch, A. 1922b. Tertiary spiders and opilionids of North America. *Trans. Connect. Acad. Arts a. Sci.*, vol. 25, pp. 211–279.

Petrunkevitch, A. 1923. On families of spiders. *Ann. New York Acad. Sci.*, vol. 29, pp. 145–180.

Petrunkevitch, A. 1928. Systema Aranearum. *Trans. Connect. Acad. Arts a. Sci.*, vol. 29, pp. 1–270.

Petrunkevitch, A. 1933. The natural classification of spiders based on a study of their internal anatomy. *Trans. Connect. Acad. Arts a. Sci.*, vol. 81, pp. 299–389.

Petrunkevitch, A. 1942. A study of amber spiders. *Trans. Connect. Acad. Arts a. Sci.*, vol. 34, pp. 119–464.

Petrunkevitch, A. 1945a. *Calcitro fisheri*, a new fossil Arachnid. *Amer. Journ. Sci.*, vol. 243, pp. 320–329.

Petrunkevitch, A. 1945b. Palaeozoic Arachnida of Illinois. An inquiry into their evolutionary trends. *Sci. Papers. Illinois State Mus.*, vol. 3, No. 2, pp. 1–72.

Petrunkevitch, A. 1945c. Ricinulei. *Sci. Papers Illinois State Mus.*, vol. 3, No. 2, pp. 65–67.

Petrunkevitch, A. 1946. Fossil spiders in the collection of the American Museum of Natural History. *Amer. Mus. Novitates*, No. 1328, pp. 1–36.

Petrunkevitch, A. 1948. The case of *Phalangiotarbus subovalis* (Woodward). *Amer. Sci.*, vol. 246, pp. 353–362.

Petrunkevitch, A. 1949a. A study of Palaeozoic Arachnida. *Trans. Connect. Acad. Arts a. Sci.*, vol. 37, pp. 69–315.

Petrunkevitch, A. 1949b. Arachnida. *Encyclopedia Britannica*.

Petrunkevitch, A. 1949c. Studies of the types of fossil Arachnida. *Amer. Phil. Soc. Yearbook* 1949 (publ. 1950), pp. 161–163.

Petrunkevitch, A. 1950. Baltic amber spiders in the Museum of comparative zoology. *Bull. Mus. Compar. Zool., Cambridge*, vol. 103, No. 5, pp. 259–357.

Petrunkevitch, A. 1953. Palaeozic and Mesozoic Arachnida of Europe. *Geol. Soc. Amer., Mem.*, vol. 53, pp. 1–122.

Petrunkevitch, A. 1955a. *Trigonotarbus arnaldi*, a new species of fossil Arachnid from Southern France. *Journ. Paleontol.*, vol. 29, No. 3, pp. 475–477.

Petrunkevitch, A. 1955b. Arachnida. *Treatise on Invertebrate Paleontology*, pt. P. Arthropoda, 2. pp. P44–P175.

Pierce, W.D. 1950a. Fossil Arthropods of British Columbia, VI. Fossil spider silk. *Bull. South Calif. Acad. Sci.*, vol. 49(1), pp. 3–9.

Pierce, W.D. 1950b. Fossil Arthropods from onyx marble. *Bull. South. Calif. Acad. Sci.*, vol. 49, pp. 101–104.

Pierce, W.D. 1951. Fossil Arthropods from onyx marble. *Bull. South. Calif. Acad. Sci.*, vol. 50, pp. 34–49.

Pimenova, N.V. 1954. Sarmatskaya flora Amvrosievki (Sarmat Flora of Amvrosievka). Izd. AN USSR. Kiev, pp. 1–96.

Pocock, R.J. 1901. The Scottish Silurian scorpion. *Quart. Journ. Microsc. Sci.*, vol. 44, pp. 291–311.

Pocock, R.J. 1902a. The taxonomy of recent species of *Limulus Ann. Mag. Nat. Hist.*, ser. 7, vol. 9, pp. 256–266.

Pocock, R.J. 1902b. On some points in the anatomy of the alimentary and nervous systems of the Arachnidan suborder Pedipalpi. *Proc. Zool. Soc. London*, vol. 2, pp. 169–188.

Pocock, R.J. 1902c. *Eophrynus* and allied Carboniferous Arachnida. *Geol. Mag.*, N.S., dec. 4, vol. 9, pt. I, pp. 439–448; pt. 2, pp. 487–493.

Pocock, R.J. 1903a. A new Carboniferous Arachnid. *Geol. Mag.*, N.S., vol. 10, pp. 247–251.

Pocock, R.J. 1903b. Further remarks upon the Carboniferous Arachnid *Anthracosiro* with the description of a second species of the genus. *Geol. Mag.*, N.S., vol. 10, pp. 405–408.

Pocock, R.J. 1910. Notes on the morphology and generic nomenclature of some

Carboniferous Arachnida. *Geol. Mag.*, Dec. 5, vol. 7, pp. 505–512.

Pocock, R.J. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. Palaeontolographical Soc., London, vol. for 1940, pp. 1–84.

Presl, I.S. 1822. Additamenta ad Faunam protogaeum. In: Presl, I.S. and C.B. *Delictae pragenses*, vol.1, pp. 191–210.

Presl, I.S. 1823. Additamenta ad Faunam protogaeum. In: Isis. fasc. 4, pp. 374–375.

Protescu, O. 1937. Elude geologique of paleobiologique l'ambre Roumain. *Bull. Soc. Roumaine Geol.*, vol. 3, pp. 65–110.

Pruvost, P. 1912. Note sur les Araignees du terrrain houiller du Nord de la France. *Ann. Soc. Geol. Nord.*, vol. 41, pp. 85–100.

Pruvost, P. 1919a. La faune continentale du terrain houiller du Nord de la France. *Mem. Carte Geol. detaillee de la France*, Paris.

Pruvost, P. 1919b. Introduction a vetude du terrain houiller du Nord et du Pas-de Calasit la France continentale du terrain houiller du Nord de la France. Theses. Univers de Lille, pp. 1–584.

Pruvost, P. 1922. Les Arachnides fossile du houiller de Belgique. *Ann. Soc. Sci. Bruxelles*, vol. 41, pp. 349–353.

Pruvost, P. 1923. Un Eurypteride nouveau du terrain houiller de Chrleroi. *Ann. Soc. Geol. du Nord.*, vol. 48, pp. 143–151.

Pruvost, P. 1926. Description de deux fossiles du terrain houiller de Noeux (*Antracosiro corsini* nov. sp., et. Fayolia sterzell Weiss). *Ann. Soc. Geo. Nord.*, Lille, vol. 51, pp. 144.

Pruvost, P. 1930. La Faune continentale du terrain houiller de la Belgique. *Mem. Mus. Roy. Hist. Nat. Belg.*, vol. 44, pp. 206–217.

Raasch, G.O. 1939. Cambrian Merostomata. *Geol. Soc. Amer.*, No. 19, pp. 1–146.

Raymond, P.E. 1944. Late Paleozoic Xiphosurans. *Bull. Mus. Comparat. Zool. Harv. College*, vol. 94, No. 10, pp. 474–508.

Reimoser, Ed. 1919. Katalog der echten Spinnen (Araneae) des Palaarktischen Gebietes. *Ab. zool-bot. Ges. Wien*, vol. 10, pp. 1–280.

Reimoser, Ed. 1937. Gnaphosidae, Anyphaenidae, Clubionidae. In: *Tierwelt Deutschlands*, Teil 33, pp. 1–99.

Resser, C.E. 1931. A New Middle Cambrian Merostome Crustacean. *Proc. U.S. Nat. Mus.*, vol. 79, art. 33, pp. 1–4.

Reus, A.E. 1855. Ueber eine neue Krusteer Species aus der bohmischen Steinkohleformation. Denkschr. K.K. Akad. Wiss., Wien, vol. 10, pp. 81–83.

Richter, R.U. and E. Richter. 1929. Weinbergina opitzi n.g.n. sp., ein Schwerttrager (Merost., Synziphos.) aus dem Devon (Rheinland). Senckenberglana, vol. 2, pp. 193–209.

Riek, E.F. 1955. A new Xiphosuran from the Triassic sediments at Brookwale. *New South Wales. Rec. Australian Mus.*, vol. 23, pp. 281–282.

Roemer, F. 1866. *Protolycosa anthracophila*, eine fossile Spinne aus dem Steinkohlengebirge Oberschlesiens. *Neues Jahrb. Miner.*, vol. 136.

Roemer, F. 1878. Auffindung und Verlegung eines neuen Gliedenthieres in dem Steinkohlengelite der Ferdinandsgrube bei Glatz. 56 Jahresber. *Schles. G. vaterl., kultur*, pp. 54–55.

Rower, C.F. 1923. Die Weberknechte der Erde. Jena, pp. 1–1116.

Rower, C.F. 1927. Weitere Weberknechte. *Abh. Nat. Ver. Bremen*, vol. 26, pp. 261–402.

Rower, C.F. 1928a. Araneae. Echte order Weberspinnen. *Die Tierwelt Mitteleuropas*, vol. 3, Lief. 2, pp. 1–4, 1–144.

Rower, C.F. 1928b. Weberknechte (Opiliones). In: *Tierwelt Mitteleuropas*, vol. 3, Lief. 1, pp. 1–5, 1–10.

Rower, C.F. 1934a. Solifuga. In Bronn's *Klassen und Ordnungen des Tierreichs*, vol. 5, Abt. 4, Buch. 4, Lief. 1–5, pp. 1–723.

Rower, C.F. 1934b. Palpigradi. In Bronn's *Klassen und Ordnungen des Tierreichs*, vol. 5, Buch 4, pp. 609–723.

Rower, C.F. 1935. Alte und neue Assamiidae. Veroff. deutsch. Kolonial. und Uebersee Mus. Bremen, vol. 1, pp. 1–68.

Rower, C.F. 1936–1940. Phalangida (Opiliones). In: Bronn's *Klassen und Ordnungen des Tierreichs*, vol. 5, Abt. 4, Buch. 6, Lief. 1–3, pp. 1–348.

Rower, C.F. 1938. Phalangoidae. *Veroff. deutsch. Kolonial. und Uebersee Mus. Bremen*, vol. 2, pp. 81–169.

Rower, C.F. 1939. Opilioniden im Berstein Paleobiologica, vol. 7, pp. 1–5.

Rower, C.F. 1940. Chelonethi oder Pseudoskorpione. In: Bronn's H.G. *Klassen und Ordnungen des Tierreichs*, vol. 6, pp. 1–258.

Rower, C.F. 1942. Katalog der Aranea von 1758 bis 1940. Bremen, vol. 1, pp. 1–1040.

Rower, C.F. 1943. Ueber Gonyleptiden. *Senckenbergiana*, vol. 26, (1–3), pp. 12–68.

Roth, J. 1851. Ueber fossile Spinnen der Lithographischen Schiefers. K. Bayer. *Akad. Wissensch. Munchen Gel. Anzeigen*, vol. 31, p. 164.

Ruedemann, R. 1921. A recurrent Pitsford (Salina) Fauna. *N.Y. State Mus. Bull.*, No. 219, 220, pp. 1–13.

Ruedemann, R. 1934. Eurypterids from the Lower Devonian of Beartooth Butte. *Wyoming. Proc. Amer. Phil. Soc.*, vol. 13, pp. 163–167.

Ruedemann, R. 1935. Appendix the Eurypterids of Beartooth Butte. *Wyoming Proc. Amer. Phil. Soc.*, vol. 15, No. 2, pp. 129–141.

Ruedemann, R. 1939. Type invertebrate fossils of North America (Devonian) Eurypterida. Wagner Free Inst. Sci.

Salter, J.W. 1864. A monograph of British Trilobites. *Ann. Mag. Nat. Hist.*, ser. 2, vol. 20, p. 321.

Sarle, C.J. 1903. A new Eurypterid fauna from the base of the Salina of Western New York. Rept. N.Y. State Paleontologist, 1902, pp. 1080–1180.

Schimkewitch, W. 1884. Etude sur l'anatomie de l'Epeire. *Ann. Soc. Nat. Zool.*, vol. 17, pp. 1–94.

Schmidt, F. 1883. Miscellanea Silurica. III. Die crustaceenfauna der Eurypterusschichten von. Rootzikull. *auf. ocsel. Mem. de L' Acad. Imp. Sci.* St. P. ser., 5, vol. 20, No. 3, pp. 99–105; ser. 7, vol. 31, No. 5, pp. 28–88.

Shchelkanovtsev, Y.P. 1897. K istorii razvitiya lozhnoskorpionov (Chernitidae) [On the history of development of Pseudoscorpions (Chernitidae)]. *Dnevniki zool. otd. k zool. Muzeya*, vol. 2, No. 5, *Iz. imp. ob-va lyubit estestv. antrop i entnorp.*, vol. 86, pp. 5–8.

Shchelkanovtsev, T.P. 1903. Materialy po amatomii lozhnoskorpionov (Pseudoscorpionides) (Material on the Anatomy of Pseudoscorpionides). Moscow, pp. 1–202.

Schlechtendal, D. 1912. Untersuchung uber die Karbonischen Insekten und Spinnen von Wettin unter Berucksichtigung verwandter Faunen. Nova Acta Abh. K. Leop. Carol. Deutsch. Akad. Naturforsch. Halle, vol. 28, pp. 99–162.

Schlechtendal, D. 1913. Uber die karbonischen Insekten und Spinnen von Wettin unter Beruck-scihtigung verwandter Faunen, vol. 1. Leipzig.

Schulze, P. 1923. Acarina Biologie d. Tiere Deutschlands. Lief 3, Berlin, pp. 1–62.

Schulze, P. 1932. Uber die Korpergliederung der Zecken, die Zusammensetzung der Gnathosoma und die Reziehungen der Ixodoidea zu den fossilen Anthracomarti, *Sitzungsber, u. Abh. Naturi. Ges. Rostock. dritte Folge*, vol. 3, pp. 104–126.

Schulze, P. 1939. Bemerkenswerte palaeozoische Arthropoden. die wahrscheinlich in der Spinnentierreihe Gehoren. *Zeitschr. Morphol. Oekol. der Tiere*, vol. 35, pp. 169–182.

Schwarzbach, M. 1935. Spinnentiere (Arachnoiden) aus dem schlesischen Oberkarbon. Jahresber. Geol. Verein. Oberschles, pp. 1–8.

Scudder, S.H. 1878. New and interesting insects from the Carboniferous of Cape Breton. *Canad. Nat. Quart. Journ. Sci.*, vol. 8, pp. 88–90.

Scudder, S.H. 1882. Fossil Spiders. *Harv. Univ. Bull.*, vol. 2.

Scudder, S.H. 1884. A contribution to our knowledge of Palaeozoic Arachnida. *Proc. Amer. Acad. Arts and Sci.*, vol. 20, pp. 15–20.

Scudder, S.H. 1885. Note on *Anthracomartus carbonis. Compt. Rend. Soc. Entomol. Belg.*, vol. 29, pp. 84–85.

Scudder, S.H. 1886. Systematic review of our present knowledge of fossil insects, Myriapods and Arachnids. *Bull. U.S. Geol. Surv.*, No. 31.

Scudder, S.H. 1888. Supplement to descriptions of Articulates. Description of fossil insects fauna on Mazon Creek and near Morris, Grundy Co., Ill. *Geol. Surv. of Illinois*, vol. 3, pp. 566–572.

Scudder, S.H. 1890a. Illustrations of the Carboniferous Arachnida of North America. *Mem. Boston Soc. Nat. Hist.*, vol. 4, pp. 443–456.

Scudder, S.H. 1890b. A classed and annotated bibliograpy of fossil insects. *Bull. U.S. Geol. Surv.*, No. 69, pp. 1–101.

Scudder, S.H. 1891. Index to the known fossil insects of the world, including Myriapodes and Arachnids. *Bull. U.S. Geol. Surv.*, No. 71, pp. 1–744.

Scudder, S.H. 1893. Insect fauna of the Rhode Island Coal field. *Bull. U.S. Geol. Surv.*, No. 101, p. 9.

Sellnick, M. 1918 (1919). Die Oribatiden der Bernsteinsammlung der Universitat Konigsberg. Schrift. *Phys. okon. Ges., Konigsber*, vol. 59, pp. 21–42.

Sellnick, M. 1927. Rezente und fossile Oribatiden (Acarina, Oribatei). Schrift. *Phys. okon. Ges. Jharg.*, 65, pp. 114–116.

Sellnick, M. 1931. Milben im Bernstein Bernsteinforschungen, No. 2, pp. 148–180.

Silvestri, F. 1905. Note Aracnologiche. I–III. Redia, vol. 2, pp. 239–261.

Simon, E. 1878. Essai d'une classification des *Galeodes. Ann. Soc. Entom. France*, pp. 93–154.

Simon, E. 1892. Histoire naturelle des Araignea. Paris, vol. 1.

Simon, E. 1903. Histoire naturelle des Araignea. Paris, vol. 2.

Snodgrass, R.E. 1948. The feeding organs of Arachnida, including mites and ticks. Publ. 3944. *Smithson. Misc. Coll.*, vol. 110, No. 10, pp. 61–80.

Størmer, L. 1934. Merostomata from the Downtonian Sandstone of Ringerike, *Norway. Skr. Vid. Akad. Oslo*, 1. Math. Nat. Kl., 1933, No. 10, pp. 1–125.

Størmer, L. 1935. Uber den neuen von W. Gross beschreibenen Eurypteriden aus dem Unterdevon von Overath im Rheinland. *Jahrb. Preuss. Geol. Landesanst. N.F.*, vol. 35, No. 1, pp. 284–291.

Størmer, L. 1936. Eurypteriden aus dem rheinsichen Unterdevon. *Jahrb. Preuss. Geol. Landesanst.*, Abh. N.F.H., 175, p. 74.

Størmer, L. 1944. On the relationships and phylogeny of fossil and recent Arachnomorpha. Skr. *Norske Vid. Akad. Oslo*, 1944. Mat. Nat. Kl., No. 5, pp. 1–158.

Størmer, L. 1951. A new Eurypterid from the Ordovician of Montgomeryshire, *Wales. Geol. Mag.*, vol. 88, No. 6, pp. 409–422.

Størmer, L. 1952. Phylogeny and taxonomy of fossil horseshore crabs. *Journ. Paleontol.*, vol. 26, No. 4, pp. 630–640.

Størmer, L. 1955. Chelicerrata. Treatise on Invertebrate Paleontology, pt. P, Arthropoda 2, pp. 1–41.

Størmer, L. 1956. A new merostome from the Lower Cambrian of Kinnekulle, Sweden. *Arkiv. Zool* (*Stockholm*), Ser. 2, vol. 9, No. 25, pp. 507–519.

Stur, D. 1877. Die Culmilora II. *Abh. Geol. Reichsanstalt*, vol. 8, p. 5.

Tarnani, I.K. 1904. Anatomiya Telifona (*Thelyphonus caudatus* (H): Anatomy of Thelyphonida [*Thelyphonus caudatus* (H)] Prilozh. k t. XVI *zapisok Novo-Aleksandriiskogo in-ta. skh i kesividstva*, Varsgava, pp. 1–288.

Thevenin, A. 1901. Sur la decouverte d'arachnides dans la terrain houiller de Commentry. *Bull. Soc. Geol. France*, ser. 4, pp. 605–611.

Thevenin, A. 1902. Sur un araignee du terrain houiller de Valenciennes. *Proc.*

Verb. Soc. Hist. Nat. Autum., vol. 15, pp. 115–203.

Thomas, Fr. A.W. 1877. Altere und neue Beobachtungen über Phytoptoceidien. *Ztschr. Ges. Naturwiss.*, vol. 49, pp. 329–388.

Thor, S. 1934. Acarina: Edellidae, Nicoletiellidae, Cryptognathidae. *Das Tierreich*, Lief. 56, pp. 1–65.

Thor, S. 1935. Acarina. Tvededae, Erevnetidae. *Das Tierreich*, Lief. 60, pp. 1–84.

Thor, S. and C. Willmann. 1941. Eupodidae, Penthalodidae, Penthaleidae, Rhagidiidae, Pachygnathidae, Cunaxidae. *Das Tierreich*, Lief. 71, pp. 1–186.

Thor, S. and C. Willmann. 1941. Trombidiidae. *Das Tierreich*, Lief. 71a, pp. 187–541.

Thorell, T. and G. Lindstrom. 1855. On a Silurian Scorpion from Gotland. *Kongl. Svenska Vet. Akad. Handl.*, vol. 21, No. 9. pp. 1–33.

Tornquist, A. 1910. Die in der Kongl. Univ. Bernsteinsammlung ein getuhrte Konwervierungmethode fur Bernstein Einschlusse. *Schrift. Phys. Okon. Ges. Konigsber*, vol. 51

Tragardt, I. 1946. Outlines of a new classification of the Mesostigmata (Acarina) based on comparative morphological data. *Lunds Univ. Arsskif N.F.*, Avd. 2, 42, No. 4, pp. 1–37.

Trotter, A. 1899. Credette Redi davvero che le galle ad produtton di esse generati da un anima vegetativas'' delle piante?. *Bull. della Soc. Veneto Trentina di Sci, Mat. Padova*, vol. 6, pp. 208–212.

Trotter, A. 1903. Studi cecidologici III. Le gale ed i cecidozoi fossili. Rivista italiana di paleontologia. Bologna, 9, pp. 12–21.

Tsittel', K. 1934. Osnovy Paleontologii Pt. 1. Besnozvonochnye (Principles of Paleontology, Part 1. Invertebrates). ONTI, p. 1056.

Unger, F. 1852. Iconographia Platarum fossilium Wien, pp. 1–4.

Vachon, N. 1934. Sur le developpement postembrionnaire des Pseudoscorpionides. *Bull. Soc. Zool., France*, vol. 59, pp. 154–160.

Vachon, N. 1934. Sur le developpement postembrionnaire des Pseudoscorpionides. *Bull. Soc. Zool., France*, vol. 59, pp. 405–416.

Vachon, N. 1938. Recherches anatomiques et biologiques sur la reproduction et le developpement des Pseudoscorpions. Thèse Fac. Sci. Paris, ser. A, No. 1779, pp. 1–208.

Vachon, N. 1949. Ordre des Pseudoscorpions. *Traite de Zoologie*, vol. 6, pp. 437–481.

Verluys, J. 1919. Die Kiemen von Limulus und die Lungen der Arachniden. *Bijdragen tot de Dierkunde*, vol. 21, pp. 1–17.

Verluys, J. and R. Demoll. 1920. Die Verwandschait der Merostome ata mit den Arachnida und den anderer Abteilungen der Arthropoda. *Kon. Akad. Wetensschappen Amsterdam, Proceedings*, vol. 23, No. 5, pp. 739–765.

Verluys, J. and R. Demoll. 1922. Das Limulus Problem. Die Verwandschaftsbeziechungen der Merostomen und Arachnoideen.

Ergebnsse und Fortschritte der Zoologie.

Vitzthum, H. 1929. Acari. Milben. Die Tierwelt Mitteleuropas, vol. 3, Lief. 3, pp. 1–112.

Vitzthum, H. 1931. Acari. *Handbuch d. Zoologie*, Kukenthel, vol. 3, Halfte 2, pp. 1–160.

Vitzthum, H. 1940–1943. Acarina. Bronn's *Klassen und Ordnun gen des Tierreichs*, vol. 5, Abt. 4, Buch 5, No. 1–7, pp. 1–101.

Volger, O. 1860. Plantarum fossilium. Bericht. Oberthessischen Ges. Nat. und Heilkunde, pp. 63–70.

Walcott, Cl.D. 1910. Cambrian geology and paleontology, II. Abrupt appearance of the Cambrian fauna on the North American Continental. *Smiths. Misc. Collections*, vol. 57, No. 1.

Walcott, Cl.D. 1911. Middle Cambrian Merostomata. *Smiths. Misc. Collections*, vol. 57, No. 2, pp. 17–41.

Walcott, Cl.D. 1912. Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. *Smiths. Misc. Collections*, No. 6, pp. 145–228.

Walker, T.L. 1934. Univers. Toronto studies geol. ser., No. 36, *Contrib. to Canadian Mineralogy*, pp. 5–10.

Walker, T.L. 1934. *Proc. Geol. Soc. Amer.*, p. 418.

Warburton, C. 1909. Embolobranchiata. Cambridge natural history. London.

Waterlot, G. 1934. Etude de la fauna continentale du terrain houiller sarrolorrain. Theses de l'Universite de Litlle. Merostomates, Arachnides, pp. 222–275.

Waterlot, G. 1949. Les Arachnides fossiles. *Traite de zoologie*, vol. 6, pp. 893–905.

Waterlot, G. 1953. Classe des Merostomes. *Traite de paleontologie*, vol. 3, pp. 529–554.

Waterlot, G. 1953. Classe des Arachnides (Arachnida Cuvier, 1812). *Traite de paleontologie*, vol. 3, pp. 555–584.

Warner, F. 1935. Scorpiones, Pedipalpi. Bronn's *Klassen und Ordnungen des Tierreichs*, vol. 5(4), pp. 1–490.

Wevenbergh, H. 1869a. Sur les insectes fossiles calcaire lityographique de la Baviere. qui se trouvent au Musee Teyler. *Arch. Mus. Teyler, Haarlem*, vol. 2, pp. 247–294. Des Arachnides, p. 253.

Wevenbergh, H. 1869b. Prodromus en algemeene beschouwing der fossile insecten van Bejeren. *Tijdschr. f. Entomol.*, vol. 4(2). Arachnida, p. 257.

Wevenbergh, H. 1874a. Notes sur quelques insects du calcaire jurassique de la Baviere. Sur le *Hasseltides primigenius* Weyenbergh. *Arch. Mus. Teyler*, vol. 3, pp. 234–236.

Whiteaves, J.F. 1884. Palaeozoic fossils of Canada. *Geol. and Nat. Hist. Surv. of Canada*, vol. 3, pt. 1, 43 p.

Whitefield, R.P. 1882. Descriptions of new species of fossils from Ohio, with remarks on some of the geological formations in which they occur. *Ann. N.J. Acad. Sci.*, vol. 2, pp. 193–244.

Whitefield, R.P. 1885a. An American Silurian Scorpion. *Sci.*, vol. 6, p. 87.

Whitefield, R.P. 1885b. On a fossil Scorpion from the Silurian Rocks of America. *Bull. Amer. Mus. Nat. Hist.*, vol. 5, art 9, p. 181.

Wiehle, H. 1931. Das Tierwelt Deutschlands, Teil 23, Spinnentiere, VI: Aselenidae–Araneidae, pp. 47–136.

Wiehle, H. 1937. Theridildae. Die Tierwelt Deutschlands, Teil 33, pp. 119–222.

Wiehle, H. 1953. Spinnentiere order Arachnoidea (Araneae). 9: Orthognatha–Cribellatae–Haplogynae (Pholcidae, Zodariidae, Ozyopidae, Mimetidae, Nesticidae). Die Tierwelt Deutschlands. Teil 42, Jena, pp. I–VIII + 1–150.

Wills, L.J. 1910. On the fossiliferous Lower Keuper Rocks. *Proc. Geol. Assoc. London*, vol. 24, pp. 249–331.

Wills, L.J. 1925. The morphology of the Carboniferous Scorpion *Eobuthus* Fritsch. *Journ. Linnean Soc. Zool. London*, vol. 36, pp. 87–97.

Wills, L.J. 1934. Notes on a rare Carboniferous Scorpion from the Oranje Nassau Mine. No. III. Jaarverslag Geo. Bureau Nederlands, 1933, pp. 101–103.

Wills, L.J. 1947. A monograph of the British Triassic scorpions. London. Paleontogr. Soc., vol. 100–101, pp. 1–137.

Willmann, G. 1927. Subfossile Oribatiden in Paul u. Ruoff. Pollenstatistischen Mooruntersuchungen im sudlichen Bavern. *Ber. Bayr. Bot. Ges.*, p. 19.

Willmann, G. 1931. Moosmilben oder Oribatiden (Cryptostigmata). Die. Tierwelt Deutschlands, 22. Teil, Spinnentiere, V; Acarina, pp. 79–200.

Withers, R.B. 1933. A new genus of fossil King Crab. *Proc. Roy. Soc. Vict.*, vol. 45, pt. 1, pp. 18–22.

Woodward, H. 1866–1877. Monograph of British fossil Crustacea belonging to the Order Merostomata, pp. 1–5. Palaeontograph Soc. (London), pp. 1–263.

Woodward, H. 1887. On a new species of *Eurypterus* from the Lower Carboniferous shales of Glencartholm, Eckadale. *Scotland. Geol. Mag.* N.S., vol. 4, pp. 481–484.

Woodward, H. 1888. On a New Limuloid crustacean (*Neolimulus falcatus*) from the Upper Silurian of Lesmahagow. *Lanarkshire. Geol. Mag.*, vol. 5, pp. 1–3.

Woodward, H. 1871. On the discovery of a new very perfect arachnid from the Ironstona of the Dudley Coalfield. *Geol. Mag.*, vol. 8, pp. 385–388.

Woodward, H. 1872. On a new fossil arachnid from the Coal Measures of Lancashire. *Geol. Mag.*, vol. 9, pp. 383–387.

Woodward, H. 1876. On the discovery of a fossil scorpion in the British Coal Measures. *Quart. Journ. Geol. Soc. London*, vol. 32, pp. 57–59.

Woodward, H. 1878a. Discovery of the remains of a fossil crab (Decapoda, Brachyura) on the Coal Measures of the environs of Mons, Belgium. *Geol. Mag. N.S.*, Dec. 2, vol. 4, pp. 433–463.

Woodward, H. 1878b. Decouverte d'une espece de Decapode brachyure dans le terrain houiller des environs de Mous. *Bull. Acad. Rev. Belgique*, 2e ser., vol. 45, pp. 410–414.

Woodward, H. 1907. Further notes on the Arthropoda of the British Coal Measures. *Geol. Mag.*, vol. 4, pp. 539–549.

Zakhvatkin, A.A. 1941. Tiroglifoidnie kleshchi (Tyroglyphoidea. Fauna USSR. Arachnida), vol. 6, No. 2, pp. 1–475.

Zakhvatkin, A.A. 1952a. Razdelenie Kleshchei (Acarina) na ptryady i ikh polozhenie v sisteme Chelicerata (Division of Acarina into orders and their systematic position in Chelicerata). *Parazitology, Sborn. Zool. In-ta AN SSSR*, vol. 14, pp. 5–46.

Zakhvatkin, A.A. 1952b. Evolyutsiya i morfologicheskoe obosnovanie sistemy kleshchei (Evolution and morphological basis of the classification of the Acarina). *Chteniya pamyati N.A. Kholodkovskogo* 3a 1951 g. *Izd. AN SSSR*, pp. 53–66.

Zakhvatkin, A.A. 1953. Issledovaniya po morfologii i postembrionalnomy razvitiyu Tiroglifid (Sarcoptiformes, Tyroglyphoidea) [Investigations on the morphology and post-embryonic development of Tyroglyfid (Sarcoptiformes, Tyroglyphoidea)]. *Sb. nauchn. rabot.* A.A. Zakhvatkina. Izd. Mosk. Un-ta, Moscow, pp. 19–120.

Zakhvatkin, A.A. 1941. Tyroglyfoidnie kleshchi (Tyroglyphoidea). Fauna SSSR. Paukobraznye (Tyroglyphoidea. Fauna USSR. Arachnida), vol. 6, No. 2, pp. 1–475.

Zittel, K. 1881–1885. Handbuch der Palaeontologie, Palaeozoologie, vol. 2, pp. 640–645.

Superclass PYCNOGONIDES. Sea spiders

(Pantopoda)

V.B. Dubinin

525 This superclass includes a special group of marine arthropods combining some of the peculiarities of crustacea and Recent chelicerata. The type of early stages of segmentation, the presence of protruding eyes and the peculiar frontal organs are similar to those in crustacea. The absence of the antennules, and the absence of the deutocerebrum in the supraphryngeal ganglion, presence of oral cone, modification of anterior appendages into chelicerae (cheliphores) and pedipalpi and other features of Pycnogonides are reminiscent of modern chelicerates.

MORPHOLOGY. Body divided into proboscis, cephalothorax and abdomen. The proboscis is only an outgrowth of structures surrounding the mouth—the oral cone. Morphologically the proboscis is ventral and ought not to be considered as a distinct tagma of the body though topographically, in adults, it forms the anterior end of body. The shape and size of the proboscis varies greatly. The cephalothorax consists of seven to nine segments. The dorsal side of the anterior segment usually bears a protruding eye. Cephalothoracic segments possess sharply projecting lateral processes to which are attached seven pairs of appendages. The anterior four segments of the cephalothorax are fused and constitute the head with the proboscis projecting anteriorly; the head bears four pairs of appendages. The first pair (Chelicerae) are three–four-segmented, claw like, and sometimes absent. The pedipalpi and ovophores* are comparatively short and leg-like. The latter, in some forms, are present in males and serve as attachment for egg masses. Occasionally these appendages may be absent. The first pair of long walking legs is attached to the distal part of lateral projections of the cephalic margins; these legs are articulated into three parts by the trochanter. The remaining three–four pairs of walking legs (in Dodecalopoda there are six pairs of legs) are attached to individual segments, the sutures of which sometimes are absent. It is interesting that in view of the development of the proboscis not a single appendage bears a gnathobase.

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* Editor's note: Ovophores are currently referred to as ovigers.

Abdomen of Recent pantopods is rudimentary, unsegmented and sac-like. In the Palaeozic Palaeopantopoda, the abdomen is long and five-segmented. The body of ancient Palaeopantopoda consisted of 14 segments of which the Recent Pantopoda have retained only eight to nine. This process of oligomerization is most strongly reflected in the shortening of the abdomen (metasoma) and fusion of the first four segments with the cephalic lobe. The peculiarity in the structure of the digestive system that helps locomotion is the extension of narrow blind caeca of the middle intestine into the leg. Individual outgrowths of the testes of males extend to this area; in females the ovaries are located in the hollows of the femora. Development proceeds with metamorphosis. A three-legged larva emerges from the egg. Post-embryonic development complicated by anamorphosis.

Ecology and Geographical Distribution. The sea spiders inhabit all seas and oceans of the world. They are predators. The Recent Pantopoda feed mainly on polyps of coelenterates. Fossil remains are exceptionally rare.

Classification, Phylogeny and Systematic Position. The inclusion of Pycnogonides in the super class Chelicerata on the basis of the absence, in both
526 the groups, of antennae I and the presence of claw-like, first post-antennular appendages is erroneous. This is contradicted by differences in the tagmosis of the body. In Pycnogonides the prosoma is absent and the last pairs of walking legs (VII–IX) are attached to the mesosoma and hence the differentiation of prosoma and opisthosoma, so characteristic of Chelicerata, is not observed in this case. The fusion of the first four segments into a single cephalic division in Pycnogonides corresponding to the proterosoma of Solifugae is probably the retention of a segmentation pattern of the primitive trilobate ancestors. Similarly, retention of the primitive features of arthropod organization is reflected by the presence of nine pairs of appendages. Pycnogonides differ from trilobate forms in the oligomerisation of body segments, loss of first antennae, considerable simplification in the structure of the primary biramous legs, and specialization of the first three pairs of appendages functioning as chelicerae, pedipalpi and ovophores [ovigers]. The evolution of an archecephalon in both Pycnogonides and Chelicerata ought to receive more attention. The bending of the anterior portion of the body axis upward and backward is characteristic of both groups. This resulted in the reduction of antennae and displacement of the cephalic lobe with the eyes directed towards the dorsal side of the body. All these justify inclusion of both the groups in a special subphylum Chelicerophora.

The traces of a trilobate type of organization leaves no doubt as to the origin of Pycnogonides from primitive Precambrian Trilobitomorpha. Probably the first stages of evolution in pycnogonids and Chelicerates proceeded in parallel, which explains the above noted similarity in modern pantopods and Chelicerates. Further evolution in the two groups, however, proceeded in different directions resulting in the formation of two allied superclasses.

A correct assessment of the phylogenetic affinities of primitive Pycnonogides was considerably delayed because of the erroneous interpretation of the anterior and posterior ends of body of the Devonian *Palaeoisopus problematicus* Broili. The six-segmented narrow, slender process covered with hairs and tapering distally, was considered by Broili (1928–1933) and other authors (Størmer, 1944; Hedgpeth, 1955) as a proboscis whereas in reality it was the abdomen. This was established by the author during a study of photographs of this form (Dubinin, 1957) which was later confirmed by special studies of the remains using X-ray techniques (Lehmann, 1959). The studies showed that the anterior bulging end of the body is in fact the large closed Chelicerae, and not a bulging proboscis. The latter is of very small size and cannot be distinguished dorsally (Fig. 1531). Devonian to Recent. Two classes: Protopantopoda and Pantopoda.

Class PROTOPANTOPODA. Sea spiders

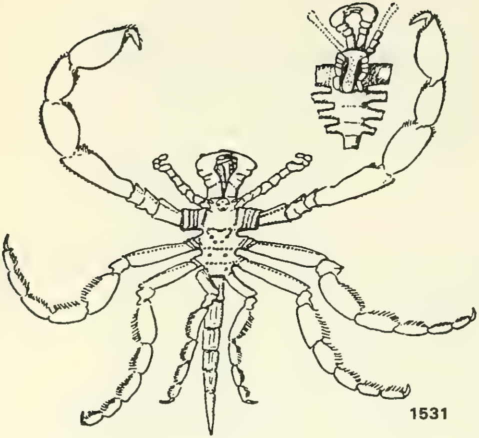
(W.B. Dubinin)

527 Chelicerae large and four-segmented. Proboscis short and slender. Abdomen long and larger than cephalothorax, five-segmented and with pointed telson. Devonian. Single family: Palaeoisopodidae.

Family PALAEOISOPODIDAE W. Dubinin, 1957

Eye tubercle with eyes present. Chelicerae in the form of stout claws curved towards each other and with a small movable fourth segment. Pedipalpi short and slender and lie near the slender proboscis. Ovophores [ovigers] longer than chelicerae and are hook-like at the apex. The fourth body segment attained considerable size and bore the anterior pair of walking legs which are stronger than others and undoubtedly functioned as grasping and pinching organs (Fig. 1532). Devonian. One genus *Palaeoisopus* Broili, 1928.

Palaeoisopus Broili, 1928. Genotype—*P. problematicus* Broili, 1928. Lower Devonian, Germany. Body elongate. All segments of cephalothorax separate. Three anterior ones are closely adjacent the form of folded neck-like strand between the chelicerae and the fourth segment bearing the huge grasping legs. Abdomen long, six-segmented excluding telson and longer than cephalothorax. Legs of fourth segment very large, stout; the remaining three pairs of legs are of walking type. Length of body 14.2 cm. Ecologically, the animals cling to sea lillies by means of grasping legs (Fig. 1531). Single species. Devonian of Germany.



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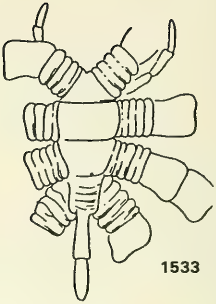

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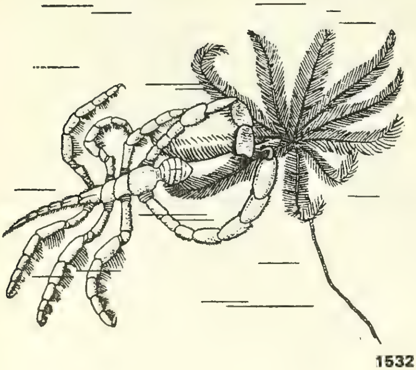


1532

Figs. 1531–1533. Superclass Pycnogonides.

1531. *Palaeoisopus problematicus* Broili (reconstruction); ventral view, × 1; Devonian, Germany (Lehmann, 1959). 1532. *Palaeoisopus problematicus* Broili; holding on to sea lily of genus *Cyathocrinus* (reconstruction) (Dubinin, 1957). 1533. *Palaeopantopus maucheri* Broili; dorsal view, × 0.7. Lower Devonian, Western Europe (Hedgpeth, 1955).

Class PANTOPODA

(W.B. Dubinin)

529 Chelicerae small, three- or two-segmented, and sometimes absent. Proboscis well developed and occasionally longer than cephalothorax. Abdomen reduced to a short process, sometimes segmented at base (Palaeopantopoda). Devonian to Recent. Two orders—Palaeopantopoda and Eupantopoda. Only the former is known to occur in fossil state.

Order PALAEOPANTOPODA

Bases of anterior pair of walking legs close to anterior end. Eye tubercle, proboscis, chelicerae and pedipalpi not observed. Probably these are small or sometimes absent. Abdomen consists of telson, one long segment and the reduced wrinkles of the basal segments. Devonian. Single family—Palaeopantopodidae.

Family PALAEOPANTOPODIDAE Hedgepeth, 1955

Bases of all appendages wrinkled (redimentary segmentation ?). Cephalothorax consists of three distinct segments. Ovigerous legs short, slender and probably four-segmented. Lower Devonian of Western Europe. Single genus—*Palaeopantopus* Broili, 1929 with single species (Fig. 1533).

Order EUPANTOPODA

Bases of anterior pair of walking limbs are widely separated and between them are situated the proboscis and usually chelicerae, pedipalpi and eye tubercle at the top. Recent. Eight families; fossil representatives absent.

530

REFERENCES

Beklemishev, V.N. 1952. Osnovy sravnitelnoi anatomii besnozvonochnykh (Principles of Comparative Anatomy of Invertebrates). Izd. 'Sovetskaya Nauka', Moscow, pp. 1–698.

Borner, C. 1903. Die Beingliederung der Arthropoden Situngsber. *Ges. Nat. Frd. Berlin*, pp. 229–335.

Broili, F. 1828. Crustaceenfunde aus dem rhenischen Unterdevon. *Situngsber. bayr. Akad. Wissensch.* (*Math. Nat.*). pp. 197–201.

Broili, F. 1929. Beobachtugnen an neuen Arthropodenfunden aus den Hunsruckschifern. Ein Pantopoda aus dem rheinischen Underdevon. Ibid., pp. 272–280.

Broili, F. 1930. Ueber ein neues Exemplar von *Palaeopantopus* Ibid., pp. 209–214.

Broili, F. 1932. *Palaeoisopus* ist ein Pantopode. Ibid., pp. 45–60.

Broili, F. 1933. Wietere Beobachtungen an *Palaeoisopus*. Ibid., pp. 33–47.

Calman, W. 1909. The problem of the Pycnogonids. *Sci. Progress in the Twentieth Century, London*, pp. 687–693.

Calman, W. 1929. The Pycnogonida. *Journ. Quekett. Microscop. Club. London*, vol. 2, pp. 95–106.

Calman, W. and J. Gordon. 1933. A Dodecapodous Pycnogonid. *Proc. Roy. Soc., London*, vol. 113, pp. 107–115.

Dogel', V.A. 1913. Embryologische Studien an Pantopoden. *Ztschr. f. wiss Zoollogie*, vol. 107, pp. 575–741.

Dubinin, W.B. 1957. Ob orientatsii golovnogo kontsa u devonskikh piknogonov roda *Palaeoisopus* i polozhenii ikh v sisteme Arthropoda (On the orientation of the cephalic end of the Devonian Pycnogonids of the genus *Palaeoisopus* and their systematic position in Arthropoda). *Dokl. AN SSSR*, vol. 117, No. 5, pp. 881–884.

Fage, L. 1949. Classe des Pycnogonides. *Traite de Zoologie*, vol. VI, pp. 906–941.

Gordon, J. 1932. Pycnogonida. Discovery reports. Cambridge, vol. 6, pp. 1–138.

Hedgpeth, I.W. 1955. Pycnogonida. *Palaeoisopus*. In Treatise on Invertebrate Paleontology, pt. P. Arthropoda 2, pp. 171–173.

Helfer, H. 1932. Pantopoda. In: Kukenthel-Krumbach. *Handbuch d. Zoolog.*, vol. 3, pp. 1–66.

Helfer, H. and E. Schlottke. 1935. Pantopoda. In: *Bronn's Klassen u. Ordn. Tierreichs*. vol. 5, pt. 4, pp. 1—314.

Lehmann, W.M. 1959. Neue Entdeckungen an *Palaeiosopus Paleontol. Ztschr.*, vol. 33, No. 1/2, pp. 96–103.

Losina-Losinsky, L. 1923. Pantopoda Cobrannye e'kspeditsiei nauchnoissledovatelskogo Okeanologicheskogo instituta v 1921 g. (Pantopoda, collected during the expedition of the Scientific-Research Oceanological Institute in 1921). *Tr. In-ta Okeanologii*, vol. 4(3), pp. 63–87.

Schimkewitsch, V. 1929 – 1930. Morskie pauki (Pantopoda) [Marine spiders (Pantopoda)]. In: *'Fauna SSSR i Soprodelnikh Strain'*, vol. 5, No. 1, pp. 1–532.

Wieren, E. 1918. Zur Morphologie und Phylogenie der Pantopoden. *Zool. Bidrag Fran Uppsala*, vol. 6, pp. 41–181.

PHYLUM
MALACOPODA

First Tracheates or the Soft Legged Forms

PHYLUM MALACOPODA

(A.G. Sharov)

533 This phylum includes small vermiform animals (length of body—1.5 to 20 cm) with soft cuticular integument, one pair of antennae, one pair of jaws in the oral cavity, one pair of oral papillae and a varying number of (not less than ten pairs) short annular appendages at the base of which open nephridial ducts. Recent Malacopoda respire through tracheae which open at different places on the surface of the body. They are related to annelid worms and are not direct ancestors of Arthropoda. Cambrian to Recent. One class: Onychophora.

Class ONYCHOPHORA

Body not segmented externally. Appendages with two to six apical claws. Cambrian to Recent. Orders: Protonychophora and Euonychophora. The latter is an extinct order.

Order PROTONYCHOPHORA

Antennae short. A pair of well developed eyes present. Cambrian. Single family: Aysheaiidae.

Family AYSHEAIIDAE Walcott, 1911

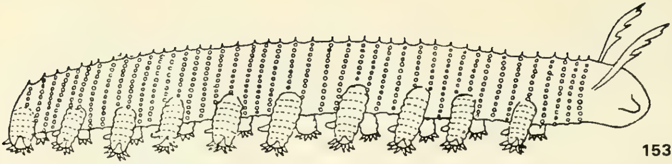
Antennae filiform, extremities with six claws. Single genus. Cambrian.

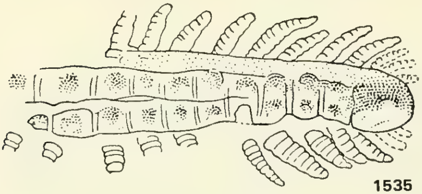
Aysheaia Walcott, 1911. Genotype—*A. pedunculata* Walcott, 1911; Middle Cambrian of North America. Length of body from carapace to the termina tenth segment, 33 mm (Fig. 1534). One species. Middle Cambrian of North America.

534

Malacopoda Incertae sedis

Xenusion Pompecky, 1927. Genotype—*X. auerswaldae* Pompecky, 1927; Precambrian. Western Europe. Body distinctly segmented. Anterior 12 (?)





Figs. 1534–1535. Phylum Malacopoda.

1534. *Aysheaia pedunculata* Walcott (reconstruction), × 2.2. Middle Cambrian, North America (Hutchinson, 1930). 1535. *Xenusion auerswaldae* Pompeckj; dorsal view of impression, × 0.6. Precambrian, Western Europe (original drawing from photograph of holotype; Pompeckj, 1927).

segments bear conical, segmented appendages attached to sides of body. Paired prominences are present on dorsal side of each segment. The preserved portion of the impression is 8.5 cm long (Fig. 1535). Single species. Precambrian of Western Europe.

REFERENCES

Dechaseaux, C. 1953. Onychophora. In: J. Piveteau *Traité de paléontologie,* vol. III, pp. 3–7.

Heymons, R. 1928. Uber Morphologie und verwandtschaftliche Beziehungen des *Xenusion auerwaldae* Pomp. aus dem Algonkium. *Ztschr. Morph. Okol. d. Tiere*, vol. 10, No. 2/3, pp. 307–329.

Hutchinson, G.E. 1930. Restudy of some Burges shale fossils. *Proc. U.S. Nat. Mus.*, vol. 78, pp. 1–24.

Pompecky, J.F. 1927.Ein neues Zeugnis uralten Lebens. *Paleontol., Ztschr.*, vol. 9, pp. 287–318.

Walcott, C.D. 1911. Cambrian geology and paleontology. II. No. 5. Middle Cambrian Annelids. *Smiths.Misc. Coll.*, vol. 57, pp. 307–329.

PLATES I – XXII

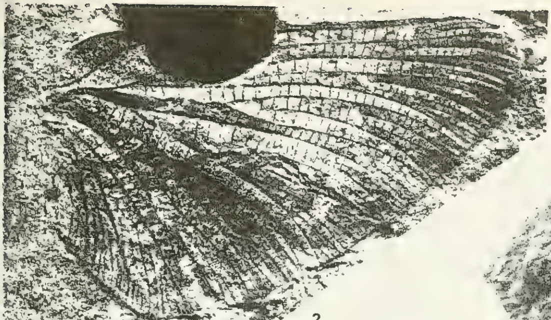
PLATE I

Order Ephemeroptera

Fig. 1. *Ephemeropsis trisetalis* Eichwald: a—general view, photograph of slab, positive print, × 1.8; b—forewing, positive print; Upper Jurassic, Transbaikal (Chernova, 1961).

Fig. 2. *Ephemeropsis trisetalis* Eichwald; hindwing, photograph of counterslab, negative print, × 3. Upper Jurassic, Transbaikal (Chernova, 1961).

Fig. 3. *Ephemeropsis trisetalis* Eichwald; Nymph, photograph of slab, positive print, × 3.6. Upper Jurassic, Transbaikal (original photograph).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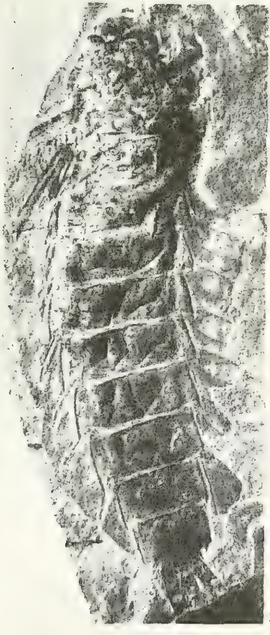
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PLATE II

Family Archimylacridae
(Subfamily Archimylacrinae)

Fig. 1. *Kunguroblattina microdictya* Bekker-Migdisova: a—general view, positive print, × 3; b—general view, negative print, × 1.7; c—ovipositor, positive print, × 4; d—ovipositor, negative print, × 4. Lower Permian, Kungurian Stage, Urals (Original photograph).

1a

1b

1c

1d

PLATE III

Family Archimylacridae
(Subfamily Archimylacrinae)

Fig. 1. *Phyloblatta picturata* Bekker-Migdisova; tegmen, × 3.2; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 2. *Balachonoblatta zheltojarica* Bekker-Migdisova; tegmen, × 3.2; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 3. *Grypoblattites tortuosus* Bekker-Migdisova; tegmen, × 4.9; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 4. *Archaeotiphites petrablattinoides* Bekker-Migdisova; tegmen, × 3.7; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

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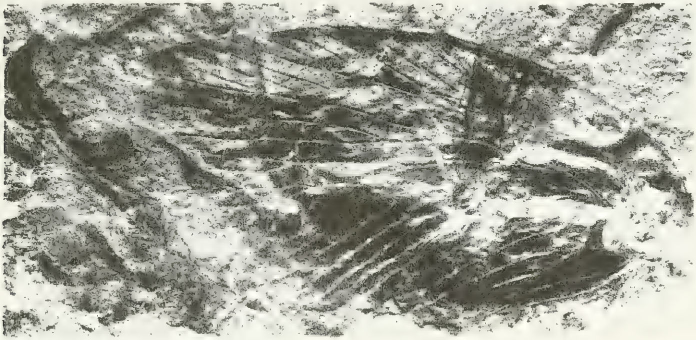

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PLATE IV

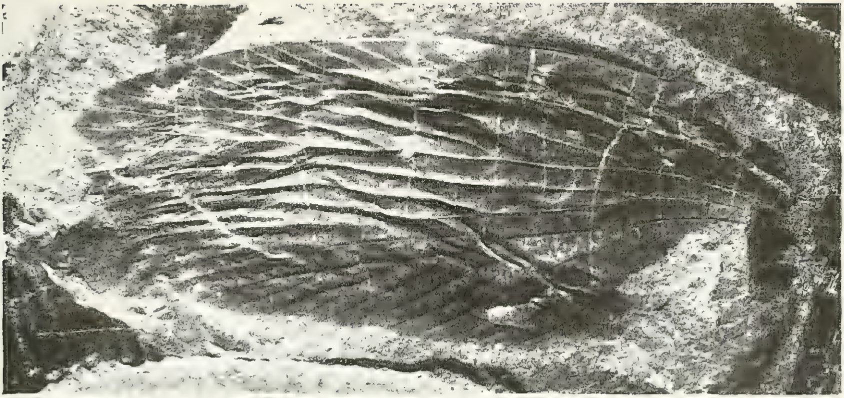
Families Archimylacridae (Subfamilies Archimylacrinae and Spiloblattininae) and Poroblattinidae

Fig. 1. *Phyloblatta poryvajkaensis* Bekker-Migdisova; tegmen, × 3.8; Upper Carboniferous, Upper Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 2. *Phyloblatta kuznetskiensis* Bekker-Migdisova; tegmen, × 3.7; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 3. *Zavjaloblatta rotundata* Bekker-Migdisova; tegmen, × 2.7; Middle Carboniferous. Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 4. *Ishanoblattina fodinensis* (Bekker-Migdisova); tegmen, × 4; Middle Carboniferous. Upper Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1962).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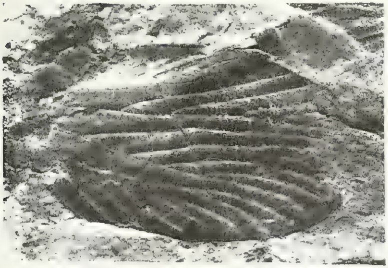
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PLATE V

Families Euryptilonidae and Ideliidae

Fig. 1. *Euryptilon blattoides* Martynov; general view, × 3.9; Lower Permian, Kungurian Stage, Urals (Photograph of holotype).

Fig. 2. *Euryptilodes cascus* Sharov; forewing, × 5; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 3. *Archidelia ovata* Sharov; forewing, × 2.3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 4. *Aenigmidelia incredibilis* Sharov; forewing, × 2.2; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

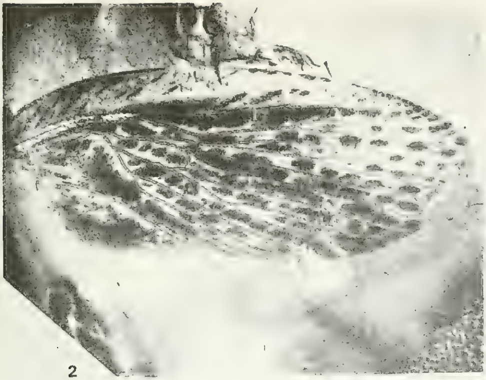

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PLATE VI

Families Ideliidae, Narkemidae and Liomopteridae

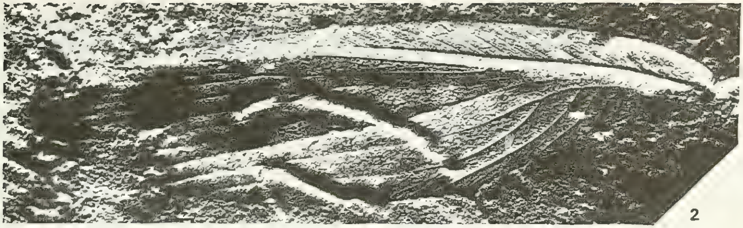
Fig. 1. *Rachimentomon reticulatum* G. Zalessky; general view, × 2.7; Kungurian Stage, Lower Permian, Urals (Yu. Zalessky, 1939).

Fig. 2. *Stenaropodites permiakovae* (M. Zalessky); forewing, × 2.7; Upper Permian, Kazanian Stage. Priurals (M. Zalessky, 1929).

Fig. 3. *Camptoneurites reticularis* Martynov; forewing, × 6.9. Upper Permian, Kazanian Stage, Urals (Martynov, 1928).

Fig. 4. *Narkemina angustiformis* Sharov; forewing, × 2.8; Middle Carboniferous, Kuznetsk Basin (Sharov, 1961).

Figs. 5–6. Liomopteridae incertae sedis; pronotum, × 11; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).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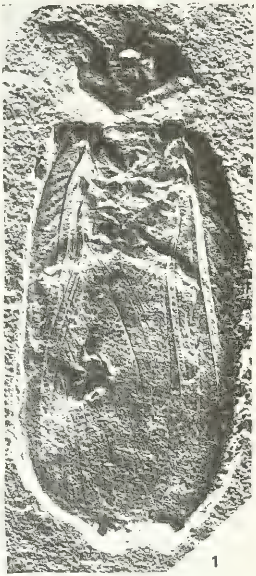
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PLATE VII

Families Liomopteridae, Sylvaphlebidae and Lemmatophoridae

Fig. 1. *Parapermula sibirica* Sharov; forewing, × 2.9; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 2. *Climaconeurites asiaticus* Sharov; forewing, × 4.6; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 3. *Liomopterella vulgaris* Sharov; forewing, × 4.5; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 4. *Kaltanella lata* Sharov; forewing, × 5; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 5. *Kaltanympha thysanuriformis* Sharov; nymph, × 6.5; Lower Permian, Kuznetsk Basin (Sharov, 1961).

Fig. 6. *Sylviodes perloides* Martynov; general view, × 2; Lower Permian, Kungurian Stage, Urals (original photograph of paratype).

Fig. 7. *Lemmatophora typa* Sellards; general view, × 7; Lower Permian, North America (Carpenter, 1935).


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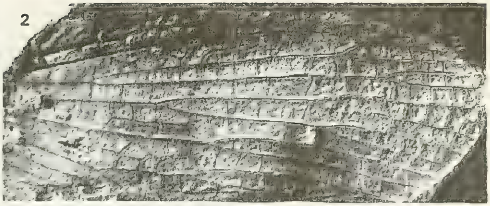
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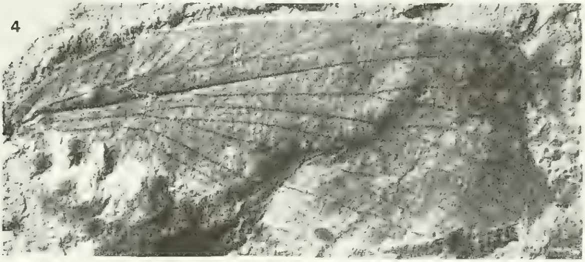
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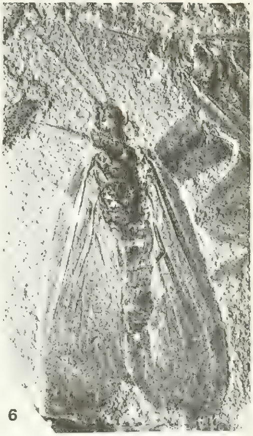
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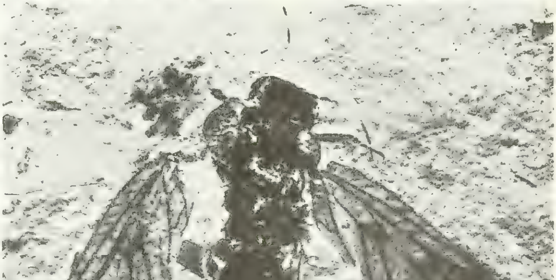
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PLATE VIII

Families Atactophlebiidae, Megakhosaridae, Perlopseidae and Taeniopterygidae.

Fig. 1. *Atactophlebia termitoides* Martynov; forewing, × 2; Upper Permian, Kazanian Stage, Urals (Martynov, 1930).

Fig. 2. *Megakhosara explicata* Sharov; forewing, × 4.3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 3. *Gurianovella blattoides* (Martynov); nymph, × 4.7; Lower Permian, Kungurian Stage (Martynov, 1940).

Fig. 4. *Perlopsis jilicornis* Martynov; general view, × 2.6; Lower Permian, Kungurian Stage, Urals (original photograph of plesio type).

Fig. 5. *Mesonemura turanica* Martynov; forewing, × 0.4; Lower Jurassic, Central Asia (Martynov, 1937).


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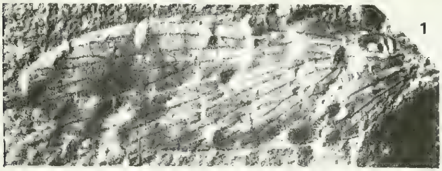
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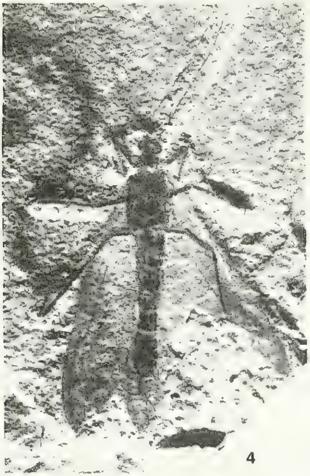
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PLATE IX

Plecoptera incertae sedis and family Sthenaropodidae

Fig. 1. *Mesoleuctra gracilis* Brauer; Redtenbacher, Ganglbauer; nymph, × 5; Lower Jurassic, Irkutsk Province (original photograph of plesio type).

Fig. 2. *Platyperla platypoda* Brauer, Redtenbacher, Ganglbauer; nymph, × 5; Lower Jurassic, Irkut Province (original photograph of plesio type).

Fig. 3. *Adumbratus extentus* Sharov; forewing, × 4.7; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Sharov, 1961).

Fig. 4. *Kamia angustovenosa* Martynov (*Permacridites maximus* Martynov); forewing, × 2.5; Upper Permian, Kazanian Stage, Urals (original photograph of holotype).


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PLATE X

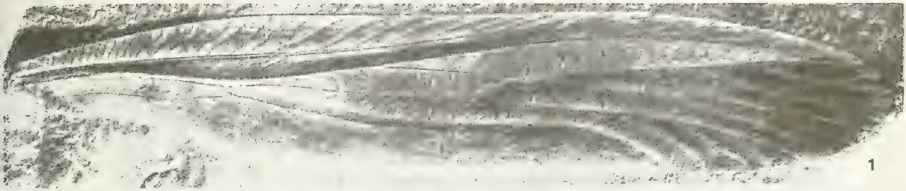
Families Oedischiidae and Tcholmanvissidae

Fig. 1. *Jasvia reticulata* G. Zalessky; forewing, × 4; Lower Permian, Kungurian Stage, Urals (Photograph by Yu. M. Zalessky).

Fig. 2. *Metoedischia magnifica* Martynov; forewing, × 3.2; Upper Permian, Kazanian Stage, Arkhangelsk Province (Martynov, 1928).

Fig. 3. *Pinegia longipes* (Martynov); forewing, × 2.4; Lower Permian, Kungurian Stage, Urals (Yu. Zalessky, 1951).

Fig. 4. *Pinegia longipes* (Martynov); general view, × 3.7; Lower Permian, Kungurian Stage, Urals (Martynov, 1940).



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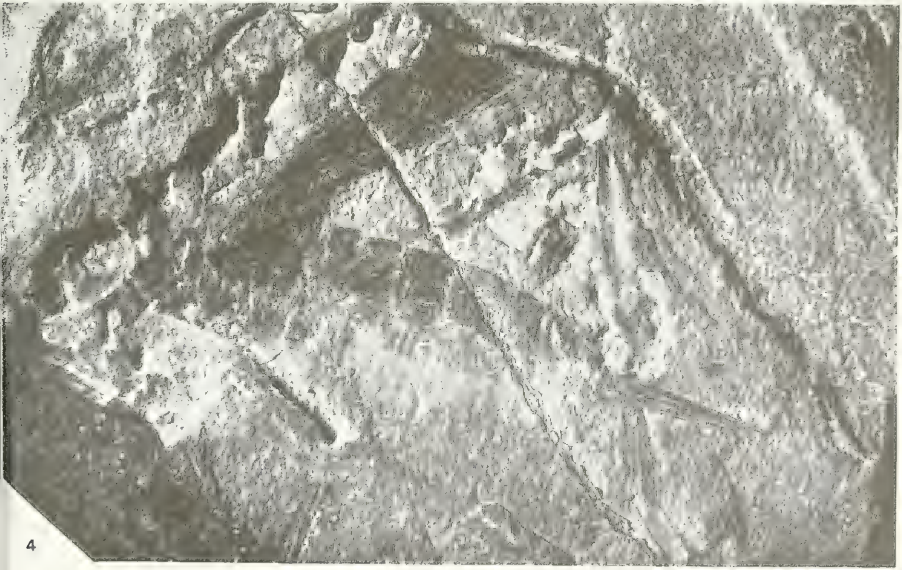

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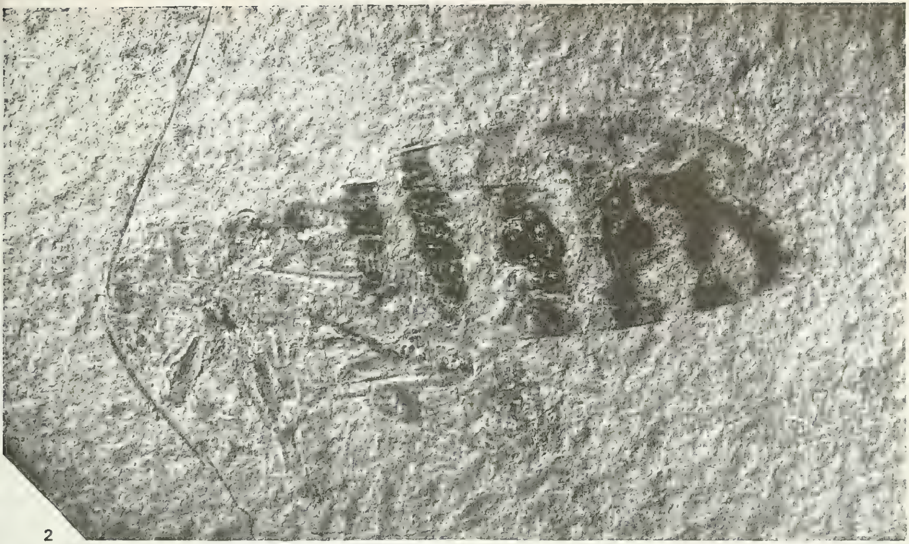
PLATE XI

Fig. 1. *Permelcana sojanensis* Sharov: a—forewing; b—hindwing, × 8.1; Upper Permian, Kazanian Stage, Arkhangelsk Province (Sharov, 1962).

Fig. 2. *Aboilus sp.*, general view, × 1.2; Upper Jurassic, Kazakhstan (Hecker, 1948).

Fig. 3. *Pseudohagla pospelovi* (O. Martynova); forewing, × 3.7; Jurassic, Kuznetsk Basin (photograph of holotype).

Fig. 4. *Archaboilus kisul-kiensis* Martynov; base of forewing, × 2.8; Lower Jurassic, Central Asia (Martynov, 1937).



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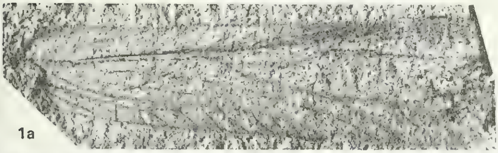

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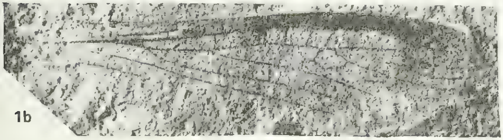

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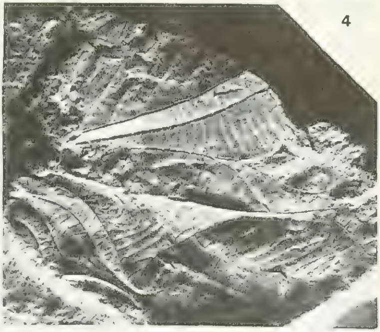

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PLATE XII

Families Blattoprosbolidae and Prosbolidae

Fig. 1. *Blattoprosbole tomiensis* Bekker-Migdisova; tegmen, × 5.5: a—positive print; b—negative print; Middle Carboniferous, Lower Balachonian Series, Kuznetsk Basin (Bekker-Migdisova, 1958).

Fig. 2. *Evansia speciosa* Bekker-Migdisova; tegmen, × 3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 3. *Evansia rectimarginata* Bekker-Migdisova; hindwing, × 3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 4. *Prosbole sojanensis* Martynov; tegmen, × 2.3; Upper Permian, Kazanian Stage, Arkhangelsk Province (Martynov, 1935).

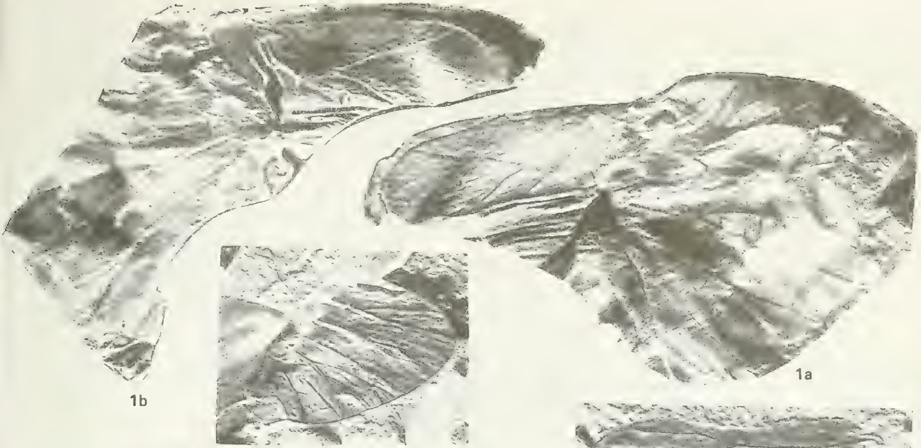
Fig. 5. *Kaltanetta nigra* Bekker-Migdisova: a—tegmen, × 9.1; b—hindwing. × 10.5; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

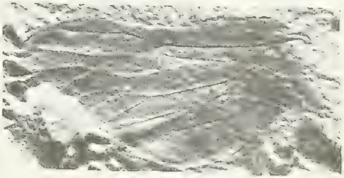
Fig. 6. *Pervestigia veteris* Bekker-Migdisova; hindwing, × 7.9; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 7. *Permocicada umbrata* Bekker-Migdisova; tegmen, × 5.7; Upper Permian, Kazanian Stage, Arkhangelsk Province (Martynov, 1928).

Fig. 8. *Sojanoneura kazanensis* M. Zalessky; tegmen, × 4; Upper Permian, Kazanian Stage, Arkhangelsk Province (Bekker-Migdisova, 1940).

Fig. 9. *Prosboloneura kondomensis* Bekker-Migdisova; tegmen, × 11.2; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

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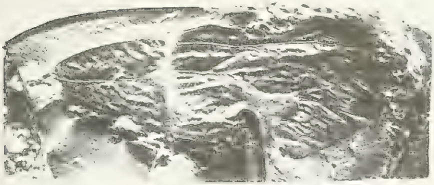
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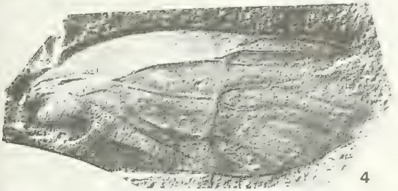
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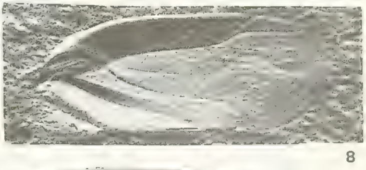
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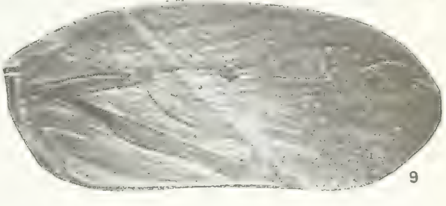
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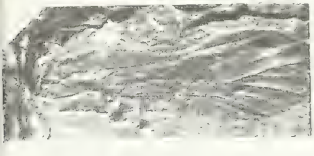
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PLATE XIII

Families Palaeontinidae, Tettigarctidae, Cicadidae and Prosbolidae

Fig. 1. *Orthoscytina pallida* Bekker-Migdisova; tegmen, × 10.5; Upper Permian, Ilinian Series, Kuznetskian Basin (Bekker-Migdisova, 1961).

Fig. 2. *Cicadoprosbole sogutensis* Bekker-Migdisova; tegmen, × 3.2: a—positive print; b—counter slab; ret. Issyk-Kul Province (photograph of holotype).

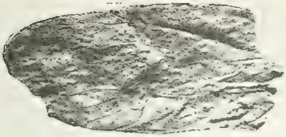
Fig. 3. *Soljuktocossus prosboloides* Bekker-Migdisova; tegmen, × 2.8; Lower Jurassic, Central Asia (Bekker-Migdisova, 1949).

Fig. 4. *Plachutella rotundata* Bekker-Migdisova; hindwing, × 3.7; Lower Jurassic, Central Asia (Bekker-Migdisova, 1949).

Fig. 5. *Pseudocossus zemcuznicovi* Martynov; tegmen, × 1.7; Lower Jurassic, Irkutsk Province (Martynov, 1931).

Fig. 6. *Plachutella derupta* Bekker-Migdisova; hindwing, × 3; Lower Jurassic, Central Asia (Bekker-Migdisova, 1949).

Fig. 7. *Tomiocicada gorbunovi* Bekker-Migdisova; tegmen, × 2.5; Miocene, West Siberia (Bekker-Migdisova, 1954).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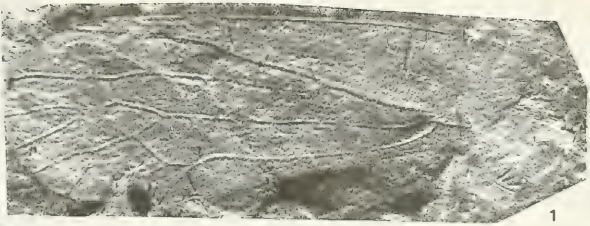
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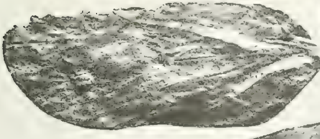
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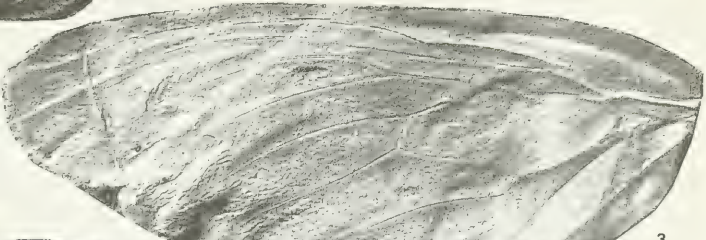
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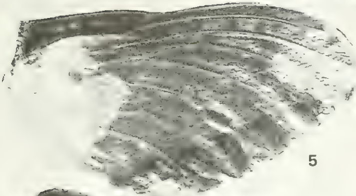
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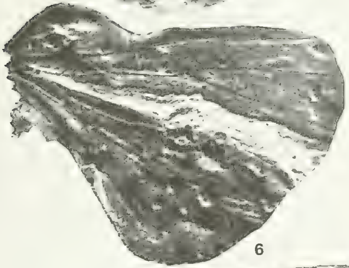
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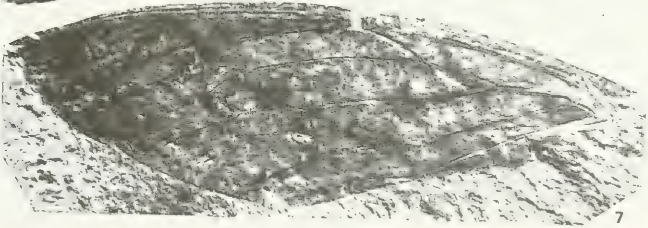
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PLATE XIV

Families Scytinopteridae, Jassidae and Pereborridae

Fig. 1. *Scytinoptera picturata* Bekker-Migdisova; tegmen, × 9.3; Lower Permian, Kuznetsk Series (Bekker-Migdisova, 1961).

Fig. 2. *Scytinoptera sp.*, hindwing, × 8.1; Lower Permian, Kuznetskian Series (Bekker-Migdisova, 1961).

Fig. 3. *Permolamproptera grandis* Bekker-Migdisova; hindwing, × 6.8; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 4. *Kaltanospes kuznetskiensis* Bekker-Migdisova; tegmen, × 13.1; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

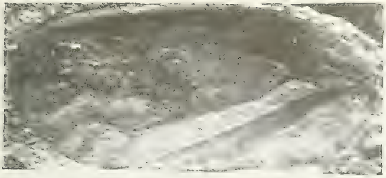
Fig. 5. *Permododa membracoides* Bekker-Migdisova; tegmen, × 10.3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 6. *Durgades miocoenia* Bekker-Migdisova; general view, × 10.6; Miocene, Central Asia (photograph of holotype).

Fig. 7. *Newropibrocha ramisubcostalis* Bekker-Migdisova; tegmen, × 3.4; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 8. *Neuropibrocha paradunstaniodes* Bekker-Migdisova; tegmen, × 3.1; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 9. *Borisrohdendrofia picturata* Bekker-Migdisova; part of hindwing, × 3.2; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1959).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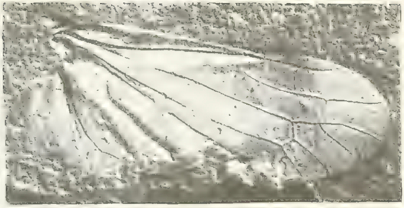
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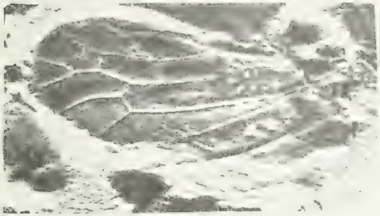
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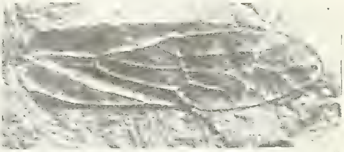
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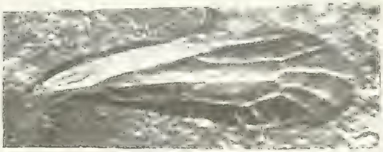
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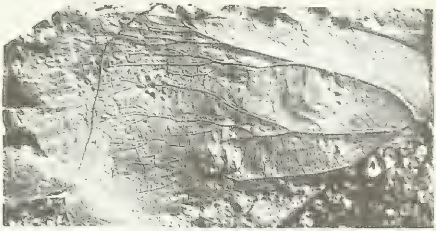
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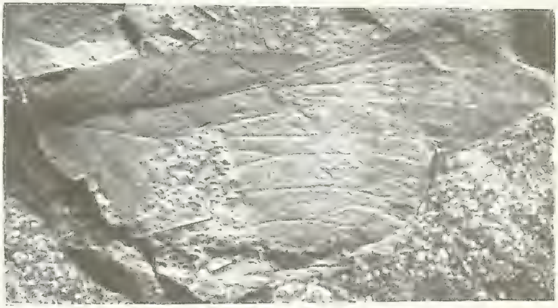
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PLATE XV

Families Mesocixiidae, Ipsviciidae, Archescytinidae, Permaphidopseidae, Coleoscytidae, Cicadopsyllidae, and Permaleurodidae

Fig. 1. *Mesocixiella asiatica* Martynov; tegmen, × 12.5; Lower Jurassic, Central Asia (Martynov, 1937).

Fig. 2. *Reticulocicada brachyptera* Bekker-Migdisova; tegmen, × 8.9; Upper Permian, Ilinian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 3. *Tychtoscarta sokolovensis* Bekker-Migdisova; tegmen and pronotum, × 12.2; Upper Permian. Erunakovian Series, Kuznetsk Basin (photograph of holotype).

Fig. 4. *Permopsylla kuznetskiensis* Bekker-Migdisova; body with wings; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 5. *Kaltanaphis permiensis* Bekker-Migdisova; forewing; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1959).

Fig. 6. *Kaltanoscyta reticulata* Bekker-Migdisova; tegmen; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1959).

Fig. 7. *Sojanopsylla kaltanica* Bekker-Migdisova; forewing; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 8. *Cicadopsis rugosipenna* Bekker-Migdisova; forewing, × 9.3; Lower Permian, Kuznetskian Series, Kuznetsk Basin (Bekker-Migdisova, 1961).

Fig. 9. *Permaleurodes rotundatus* Bekker-Migdisova; pupa, × 8.3; Upper Permian, Ilinian Series, Kuznetsk Basin (Bekker-Migdisova).

Magnifications

Fig. 4 × 21; Fig. 5 × 8.4; Fig. 6 × 9.5; Fig. 7 × 10.

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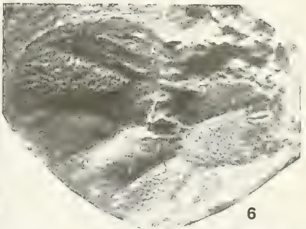

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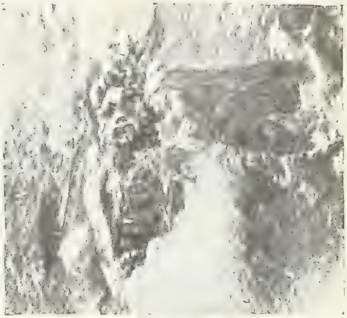

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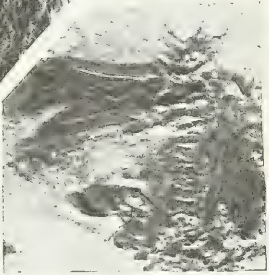

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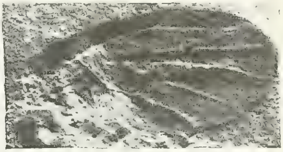

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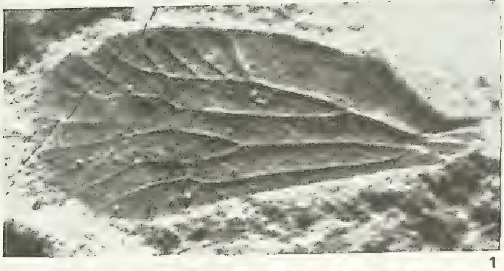

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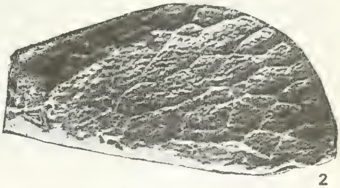

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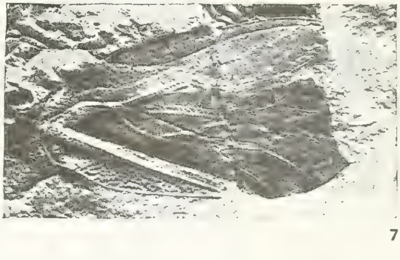

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PLATE XVI

Orders Psocoptera and Perielytrodea

Fig. 1. *Surijokopsocus radtchenkoi* Bekker-Migdisova; forewing, × 11; Upper Permian, Ilinian Series, Kuznetsk Basin (photograph of holotype).

Fig. 2. *Zoropsocus tomiensis* Bekker-Migdisova; forewing, × 18; Upper Permian, Ilinian Series, Kuznetsk Basin (photograph of holotype).

Fig. 3. *Perielytron mirabile* G. Zalessky: a—complete insect; b—forewing; Lower Permian, Kungurian Stage. Chekarda (Yu. Zalessky, 1943).

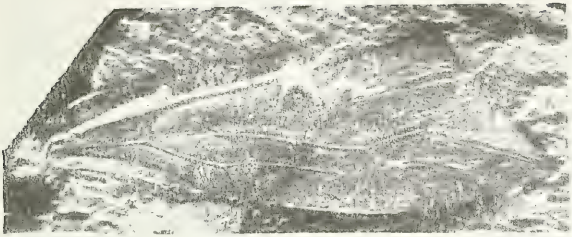

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PLATE XVII

Family Austrolimulidae

Austrolimulus fleetcheri Riek, 1955, × 2; Middle Triassic, New South Wales (Australia) (photograph: Courtesy, Riek).

PLATE XVIII

Superfamilies Eurypteridea and Peterygotidea

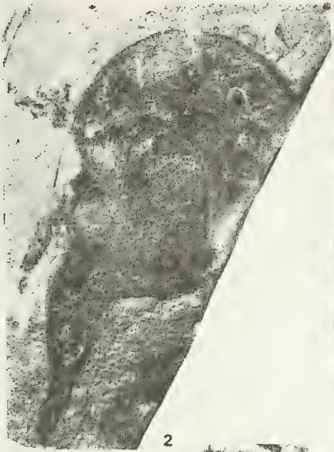
Fig. 1. *Hughmilleria* sp., Scale- or step-like ornamental lines on terga, × 10; Lower Devonian South Siberia (South-West Taimur) (Collection of the Paleontological Institute, No. 1138/4).

Fig. 2. *Hughmilleria* sp., indet. Prosoma with two left appendages, × 1; Middle Devonian (Z. Zhivetian stage), Tuva (Novojilov, 1958).

Figs. 3, 4. *Hughmilleria lata*? Stormer, 1933; 3—body with broken prosoma and without latter segments of opisthosoma; 4—latter segments of opisthosoma of the same specimen, × 2 ?; Lower Devonian, East Siberia (Krasnoyar District) (Novojilov, 1958).

Fig. 5. *Tylopterella menneri* (Novojilov), 1958. Body without telson. Right walking and swimming legs seen, × 3; Lower Devonian, North Siberia (South-West Taimur) (Novojilov, 1958).

Figs. 6, 7. *Pterygotus* (*Pterygotus*) Agassiz, 1839; 6—fragment of immovable finger of chela with stout teeth; 7—fragment of tergum, × 1; Middle Devonian, Scotland (Collection of Hamaley, No. 2084/36 and 2084/37).



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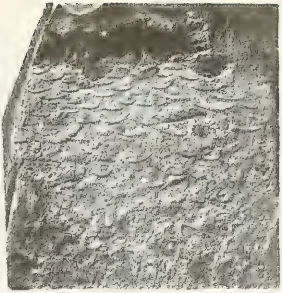

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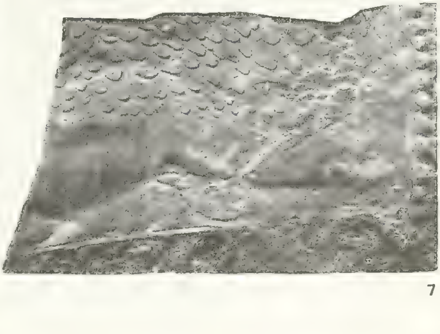

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PLATE XIX

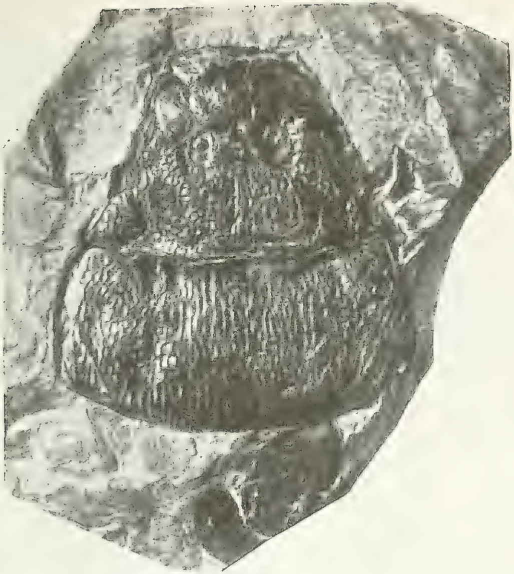
Families: Stylonuridae, Rhenopteridae, Mucteropidae

Figs. 1–4. *Stylonurus ruedemanni*? Størmer, 1933, × 2; 1—prosoma; 2—three-fore terga of opisthosoma; 3—operculum with genital appendage of male; 4—prosoma and five terga of mesosoma, deformed and covered by rock from left side; Lower Devonian, Khakass (Novojilov, 1958).

Fig. 5. Rhenopteridae; fragment with six terga? of opisthosoma, × 2; West Siberia, Kuznetsk Basin; Middle Carboniferous, Collection of the Paleontological Institute No. 1293/8.

Fig. 6. *Glaucodes mathieui* Pruvost, 1923; prosoma with first large segment of opisthosoma, × 0.5; Upper Carboniferous, Belgium (Pruvost, 1923).

Fig. 7. *Borchgrevinkium taimyrense* Novojilov, 1958, × 3; Lower Devonian, North Siberia (South-West Taimur) (Novojilov, 1958).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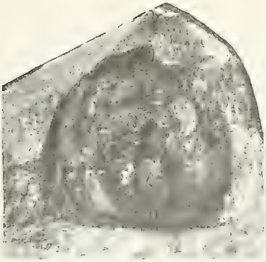
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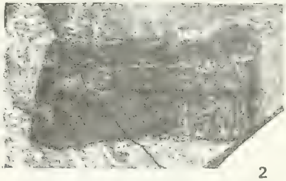
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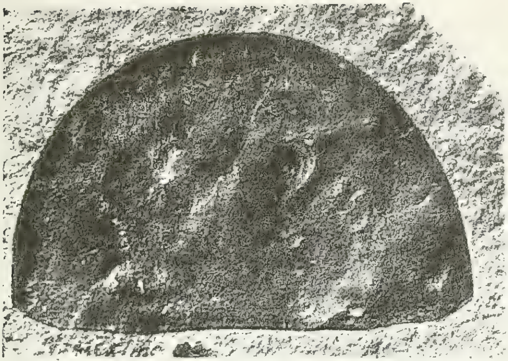
PLATE XX

Family Eurypteridae

Figs. 1–2. *Erieopterus microphthalmus microphthalmus* (Hall), 1859. 1—prosoma, × 1.2; 2—fragment of prosoma with coarse irregular 'bubblelike' ornamentation, × 3; Silurian, North America (New York) (Kjellesvig-Waering, 1958).

Figs. 3–5. *Erieopterus microphthalmus eriensis* (Whitefield), 1882; 3—prosoma with third walking leg and anterior part of mesosoma, × 2.8; 4—prosoma (ventral view), × 2; 5—opisthosoma, × 1.3; Silurian, North America (Ohio) (Kjellesvig-Waering, 1958).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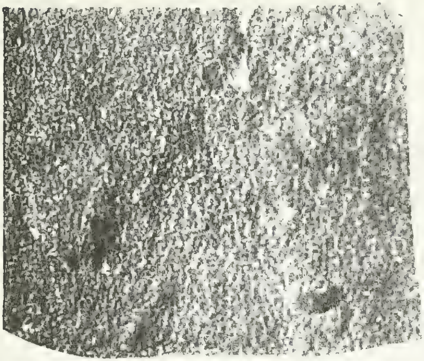
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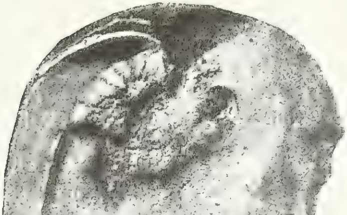
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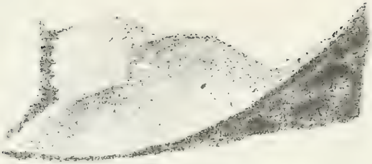
PLATE XXI

Family Hibbertopteridae

Figs. 1–3. *Camylocephalus oculatus* (Kutorga) 1838; 1—prosoma, 1/3 natural size; 2—left posterior corner of prosoma, natural size; 3—fragment of right side in which the posterior corner is absent, natural size; Upper Permian, Bashkiviya (Kutorga, 1838).

2



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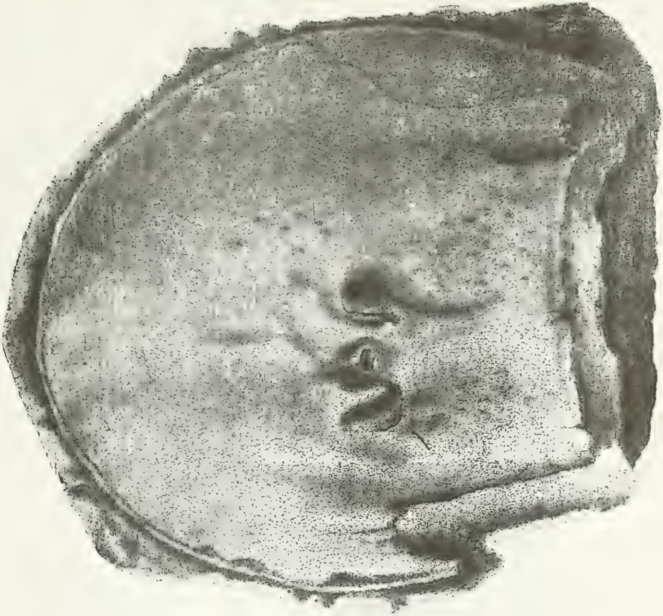

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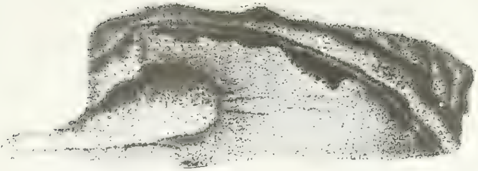
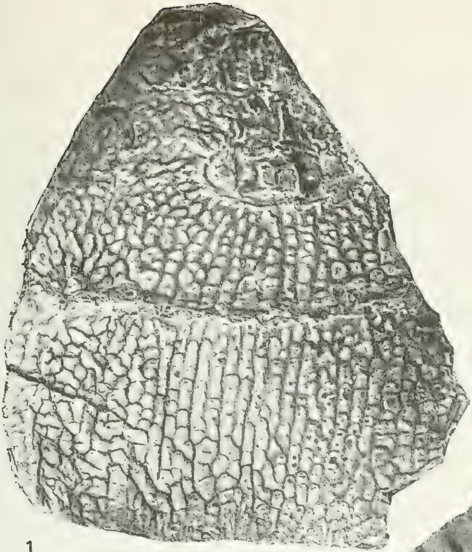


PLATE XXII

Family Mycteropidae

Figs. 1–3. *Mycterops ordinatus* Cope, 1886: 1—prosoma and first tergum of mesosoma with right side broken; 2—fragment of left side of prosoma; 3—fragment of posterior ? tergum with scaly ornamentation. All specimens are shown to natural sizes. Pennsylvanian Division (Alleganian Formation), North America (Pennsylvania) (Kjellesvig-Waering, 1959).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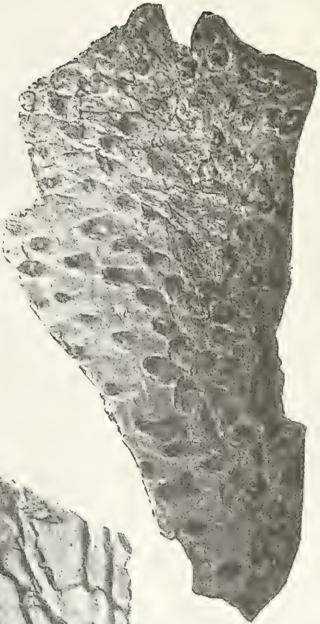
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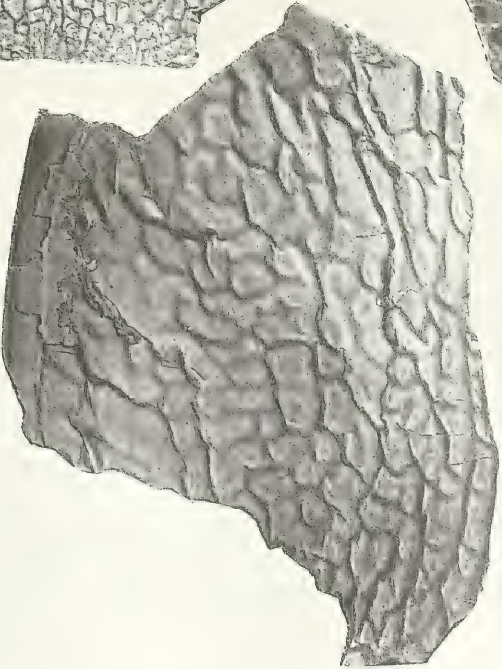
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ALPHABETIC INDEX OF LATIN NAMES OF TAXA[1]

Pages with descriptions of specific taxonomic groups or genera are given in italics bold print. Pages with illustrations of representative forms of genera are marked with an asterisk (*).

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[1] Reproduced from the Russian original. Russian page numbers appear in the left-hand margin in the text—General Editor.

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