

Classification of Insects and Their Wingbeat Kinematics

The organization and the nomenclature of higher insect taxa used in this book differ substantially from those generally accepted in current entomological literature. Therefore, before describing the diversity of insect flapping-flight kinematics, it is necessary to present a brief account of insect systematics.

1.1. Insect Taxonomy, *by Alexandr P. Rasnitsyn**

Insect systematics, especially at and above the taxonomic level of the order, has undergone continuous reorganization and improvement since Linné (1758). In particular, these changes have affected the content of the class Insecta (which initially corresponded more closely to the current concept of the phylum Arthropoda), the supraordinal taxonomic level, and the content of three of seven Linnean orders: Aptera, Neuroptera, and Coleoptera. The order Hemiptera was divested of thrips and in modern systems often has superordinal rank. The three other orders (Diptera, Lepidoptera, Hymenoptera) persist essentially intact since those remote times.

The revision of the class Insecta was time-consuming. Latreille (1810) separated crustaceans and arachnids from insects in the early nineteenth century and removed myriapods fifteen years later (Latreille 1825). However, it took more than a century to classify the entognathous orders Protura, Collembola, and Diplura as hexapod myriapods rather than true insects (Remington 1955;

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Handschin 1958; Sharov 1966), an inference that remains a subject of debate (cf. Rasnitsyn 1976a; Kristensen 1981b, 1992).

Clearing insect orders of extraneous elements required less time. Considerable progress was achieved by Brauer (1885), who left only two unnatural orders: an Orthoptera that included embiids and a Corrodentia that contained psocids, termites, and lice. Brauer correctly segregated the holo- and heterometabolan orders and, moreover, assembled the future palaeopteran, polyneopteran (except earwigs), paraneopteran, and mecopteroid orders. However, no formal taxa were proposed for these groups, and some of his orders (Orthoptera, Rhynchota, Neuroptera, etc.) are now considered to be superorders.

The next important step was made by Handlirsch (1906–8, 1911, 1925), who established numerous extinct orders, split the rest of the composite extant orders, and diversified the system of intercalary taxa between the subclass Pterygota and its component orders. Many of his new taxa still exist.

The first (and only) system of insects that won worldwide appreciation and incomparable longevity was developed by the Russian entomologist Martynov (1923, 1924a, 1925, 1938). This system, with or without minor modifications, is still in wide (though not universal) use. Martynov proposed that a basic dichotomy of the winged insects (Pterygota) segregates them into two divisions of the highest rank, depending on whether they can fold their wings at rest over their abdomen (Neoptera, comprising the majority of insect orders) or whether they cannot (Palaeoptera, namely, mayflies, dragonflies, and several Paleozoic orders close to Palaeodictyoptera). This idea is incorporated in various contemporary systems, either essentially intact (e.g., Ross 1965; Gillott 1980; Arnett 1993) or with a group discarded because of inferred paraphyly (Palaeoptera in Boudreaux [1979] and Kristensen [1981b, 1992]; Polyneoptera in Kukalova-Peck [1992]; Poly- and Paraneoptera are merged back into Exopterygota by Carpenter [1992]).

Despite the evident advantages of Martynov's system, his intellectual descendants realized a different and more radical trend in higher-level insect taxonomy. This group included students of Rohdendorf, who had studied under Martynov and who inherited and expanded Martynov's laboratory after his death in 1938. Specialized study of the taxonomic diversity of fossil insects, in close conjunction with the taxonomy and evolution of the living forms, prepared them to search for the basal insect dichotomies outside of the traditional approach.

The first step was made by Sharov (1966), who hypothesized that ances-

tral pterygotes (his new order Protoptera) were able to fold their wings at rest, albeit imperfectly. Further incremental development of Sharov's ideas produced an essentially new insect system and phylogenetic scheme (Rasnitsyn 1976a, 1980; Rohdendorf and Rasnitsyn 1980). The main feature of this approach is appreciation of the neopterous nature of ancestral pterygotes. Palaeoptera represent a disparate, polyphyletic group (Rasnitsyn 1997), and the basic pterygote dichotomy segregates Gryllones (Polyneoptera in Martynov's system) and Scarabaeones (the remainder of Pterygota).

Before presenting an overview of the most recent version of this system, another feature of the present taxonomic proposal should be explained. The difficulties encountered in working with an uncoded nomenclature inspired Rohdendorf's (1977; Rasnitsyn 1982) plan to codify the higher taxa (see also Rasnitsyn 1996), an approach that has been used in the proposed system. Although the following system does not require use of the codified nomenclature, I have little doubt that eventually this fully codified nomenclature will be appreciated. It provides the only way to stabilize the names of the higher taxa in a manner equivalent to that which has already been established with the names of the lower taxonomic ranks.

Class Scarabaeoda Laicharting, 1781 (= Insecta Linné, 1758). Insects.

Subclass Lepismatona Latreille, 1804 (= Thysanura Latreille, 1796, sensu lato). Wingless insects.

Order Machilida Grassi, 1888 (= Archaeognatha Börner, 1904; = Microcoriphia Verhoeff, 1904; + Monura Sharov, 1957). Bristletails. Possibly the sister group to other insects (= Ectognatha Stummer, 1891). Upper or Middle Carboniferous, unless Devonian (Labandeira et al. 1988; Shear et al. 1984), to present; now worldwide (fig. 1.1).

Order Lepismatida Latreille, 1804 (= Thysanura Latreille, 1796; sensu stricto = Zygentoma Börner, 1904). Silverfish. Middle Carboniferous to present; now worldwide.

Subclass Scarabaeona Laicharting, 1781 (= Pterygota Lang, 1888). Winged insects.

Infraclass Scarabaeones Laicharting, 1781.

Cohors Paoliiformes Handlirsch, 1906.

Order Paoliida Handlirsch, 1906 (= Protoptera Sharov, 1966). Middle and Late Carboniferous (mostly Namurian); North America, Europe, rarely in Siberia. Supposedly ancestral to all other winged insects, known only from wings (fig. 1.2).

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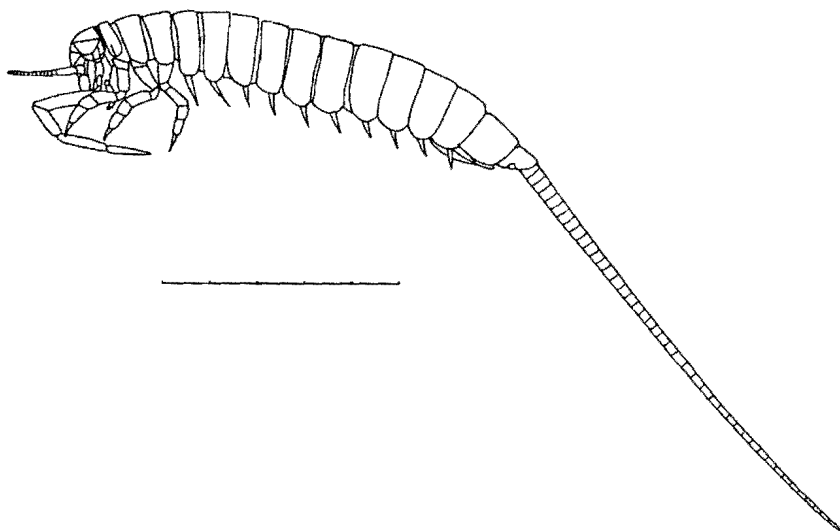


Figure 1.1. *Dasyleptus brongniarti* Sharov (Dasyleptidae), a representative of the Machilida, a proposed sister group of other insects. Upper Permian of southern Siberia. Scale 5 mm. (After Rohdendorf and Rasnitsyn 1980.)

Cohors Libelluliformes Laicharting, 1781 (= Subulicornia Latreille, 1806;
= Hydropalaeoptera Rohdendorf, 1968).

Superorder Ephemeridea Latreille, 1810.

Order Triplosobida Handlirsch, 1906 (= Protephemerida Handlirsch, 1906).

Late Carboniferous of Europe. Poorly known group.

Order Syntonopterida Handlirsch, 1911. Lower Middle Carboniferous to
Lower Permian of Europe and North America. Includes Syntonopteridae
and Bojophlebiidae. Archaic ancestors of mayflies (fig. 1.3).

Order Ephemerida Latreille, 1810 (= Ephemeroptera Haeckel, 1896). Mayflies.
Lower Permian to present; worldwide.

Superorder Libellulidea Laicharting, 1781 (= Odonata Fabricius, 1792, s.l.;
+ Geropteroidea Brodsky, 1994). Dragonflies.

Order Eugeropterida Riek & Kukalova-Peck, 1984 (= Geroptera Brodsky,
1994). Carboniferous of Argentina. Very archaic, known only from wings.

Order Meganeurida Handlirsch, 1907. Lowermost Middle Carboniferous
to Lower Cretaceous; worldwide, but prefer warm climates. Probably
ancestral to Libellulida (fig. 1.4).

Order Libellulida Laicharting, 1781 (= Odonata Fabricius, 1792; sensu stricto

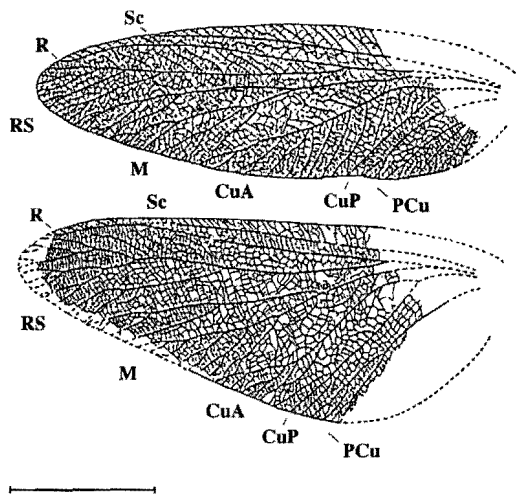


Figure 1.2. *Zdenekia grandis* Kukalova (Paoliidae), a representative of the proposed ancestors of winged insects, known only by fossil wings. Lowermost middle carboniferous of Czechia. For designations of veins see section 4.2.1 and figure 4.5. Scale 20 mm. (After Kukalova 1958.)

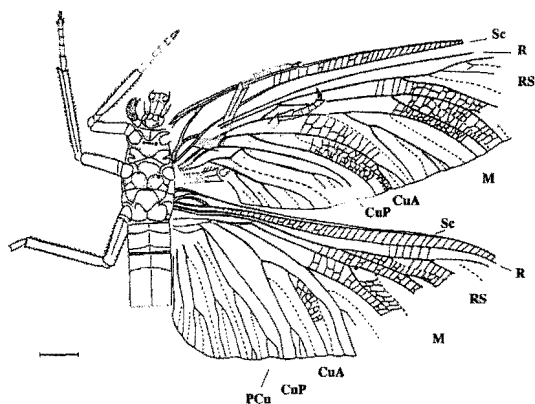


Figure 1.3. *Bojophlebia prokopi* Kukalova-Peck (Bojophlebiidae), a representative of the ancestors of mayflies. Middle carboniferous of Czechia. Designations as in figure 1.2. Scale 20 mm. (After Kukalova-Peck 1985.)

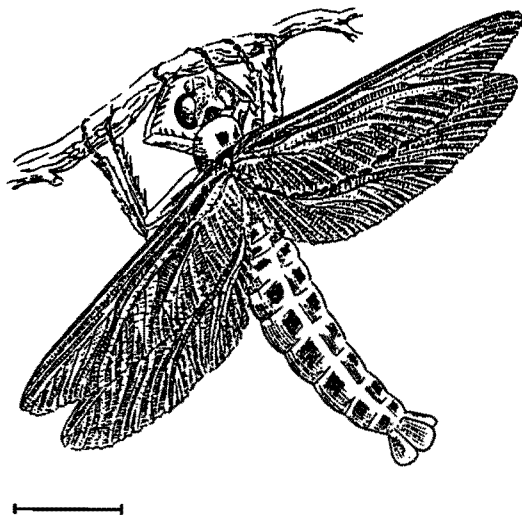
= Neodonata Martynov, 1938). True dragonflies and damselflies. Late Triassic to present; worldwide.

Cohors Cimiciformes Laicharting, 1781. Former Paraneoptera and related archaic orders.

Superorder Caloneuridea Handlirsch, 1906. Suggested ancestral group to both Paraneoptera (via Hymenoptera) and Oligoneoptera.

Order Cnemidolestida Handlirsch, 1906 (= Cnemidolestidae Handlirsch, 1906; sensu Handlirsch, 1937; = Gierarida Handlirsch, 1906; sensu Rohden-

Figure 1.4. *Arctotypus* sp. (Meganeuridae), a representative of the proposed ancestors of damselflies and dragonflies. Upper Permian of northern Russia. Scale 40 mm. (After Rohdendorf and Rasnitsyn 1980.)



dorf, 1977). Middle to Late Carboniferous; Europe and North American (equatorial belt of the Carboniferous).

Order Blattinopseida Bolton, 1925. Middle Carboniferous to Late Permian; Eurasia and North America.

Order Caloneurida Handlirsch, 1906 (= Caloneurodea Martynov, 1938).

Middle Carboniferous to Late Permian; Eurasia and North America.

Order Zorotypida Silvestri, 1913 (= Zoraptera Silvestri, 1913). Miocene to present; worldwide but patchy in warm climates, including oceanic islands. Supposedly a sister group of holometabolous insects (Rasnitsyn, forthcoming).

Superorder Hypoperlida Martynov, 1928.

Order Hypoperlida Martynov, 1928. Uppermost Lower Carboniferous to Upper Permian of Eurasia and North America. A suggested ancestral group to both Paraneoptera and Palaeodictyopteroidea (fig. 1.5).

Superorder Dictyoneuridea Handlirsch, 1906 (= Palaeodictyopteroidea Rohdendorf, 1961).

Order Cacurgida Handlirsch, 1906 (former Paoliida without Paoliidae and Evenkidae). Lower Middle to Upper Carboniferous of Europe and North America. Supposedly ancestral to the rest of the superorder.

Order Dictyoneurida Handlirsch, 1906 (= Palaeodictyoptera Goldenberg, 1854). Lower Middle Carboniferous to Late Permian, with highest abundance during Middle and especially Late Carboniferous; widespread in

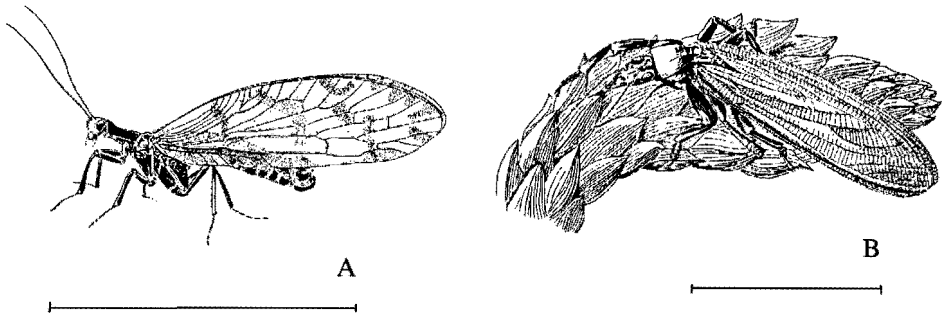


Figure 1.5. A, *Tshekardobia osmylina* Rasnitsyn (Ampelipteridae); B, *Synomaloptila longipennis* Martynov (Synomaloptilidae), suggested ancestors of rhynchote and paleodictyopteroid insects. Lower Permian of Urals. Scale 20 mm. (After Rohdendorf and Rasnitsyn 1980.)

Northern Hemisphere, but common only in Eurameria, most probably owing to its warmer climate; absent on southern continents. Ancestral to the following orders:

Order Mischopterida Handlirsch, 1906 (= Megasecoptera Brongniart, 1893; + Archodonata Martynov, 1932). Middle and Upper Carboniferous, Lower and very rare in Upper Permian; worldwide although rare, except in Eurameria and westernmost Angarida.

Order Diaphanopterida Handlirsch, 1906 (= Diaphanopteroidea Handlirsch, 1906). Lowermost Middle Carboniferous to Lower Permian; North Eurasia and North America.

Superorder Psocidea Leach, 1815 (= Psocopteroidea Rohdendorf, 1961).

Order Psocida Leach, 1815 (= Psocoptera Shipley, 1904; = Copeognatha Enderlein, 1903). Booklice. Lower Permian to present; worldwide with particular diversity in tropics. Ancestral to lice and birdlice, as well as to thrips.

Order Nymida Leach, 1815 (= Mallophaga Nitzsch, 1818). Birdlice. Worldwide; no fossil record.

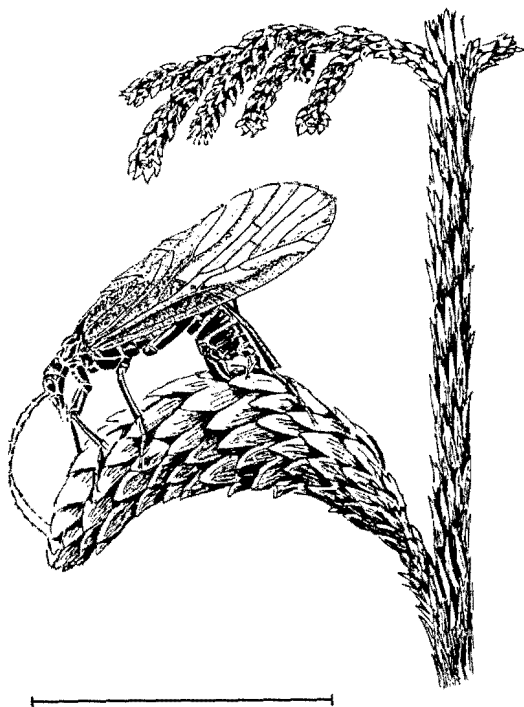
Order Pediculida Leach, 1815 (= Anoplura Leach, 1815; = Siphunculata Latreille, 1825; = Phthiraptera Haeckel, 1896). Lice. Worldwide; recorded since Eocene.

Superorder Thripidea Fallén, 1814.

Order Thripida Fallén, 1814 (= Thysanoptera Haliday, 1836). Thrips, including Lophioneuridae. Lower Permian to present; worldwide.

Superorder Cimicidea Latcharting, 1781 (= Rhynchota Burmeister, 1835).

Figure 1.6. *Palaeomantina pentamera* Rasnitsyn (Palaeomantiscidae), a representative of the supposed ancestors of endopterygote insects. Lower Permian of Urals. Scale 10 mm. (After Rasnitsyn 1980.)



Order Cimicida Laicharting, 1781 (= Hemiptera Linné, 1758; = Homoptera Leach, 1815; + Heteroptera Latreille, 1810). Lower Permian to present; worldwide.

Cohors Scarabaeiformes Laicharting, 1781 (= Holometabola Burmeister 1835; = Endopterygota Sharp, 1899; = Oligoneoptera Martynov, 1925).

Superorder Palaeomanteidea Handlirsch, 1906.

Order Palaeomanteida Handlirsch, 1906 (= Miomoptera Martynov, 1927).

Upper Carboniferous to Upper Jurassic; North Eurasia and North America, rarely also in Australia and South Africa. Supposedly ancestral group to all other holometabolans (fig. 1.6).

Superorder Scarabaeidea Laicharting, 1781 (= Coleopteroidea Handlirsch, 1903).

Order Scarabaeida Laicharting, 1781 (= Coleoptera Linné, 1758). Beetles. Lower Permian to present; worldwide. The largest (richest in species number) order of living beings.

Order Stylopida Stephens, 1829 (= Strepsiptera Kirby, 1813). Eocene until

- present; worldwide. Relationship to beetles is questionable (cf. Kristensen 1992).
- Superorder Myrmeleontoidea Latreille, 1802 (= Neuropteroidea Handlirsch, 1903).
- Order Raphidiida Latreille, 1810 (= Raphidioptera Navas, 1918). Snakeflies.
Lower Jurassic to present; after Lower Cretaceous not found at southern continents.
- Order Corydalida Leach, 1815 (= Megaloptera Latreille, 1802). Alderflies and dobsonflies. Upper Permian to present; worldwide. Fossils only in Eurasia, except for a single South African Triassic finding.
- Order Myrmeleontida Latreille, 1802 (= Neuroptera Linné, 1758). Lacewings and ant lions. Lower Permian to present; worldwide.
- Order Jurinida M. Zalesky, 1928 (= Glosselytroidea Martynov, 1938). Lower Permian to Middle Jurassic; worldwide. Jurassic fossils found only in Asia. This order and Palaeomanteida are the only extinct holometabolous orders.
- Superorder Papilionidea Laicharting, 1781 (= Mecopteroidea Martynov, 1938).
- Order Panorpida Latreille, 1802 (= Mecaptera Packard, 1886; = Mecoptera Comstock & Comstock, 1895; + Paratrachoptera Tillyard, 1919a; + Paramecoptera Tillyard, 1919b). Scorpion flies. Lower Permian to present; worldwide, but with most living groups extratropical.
- Order Phryganeida Latreille, 1810 (= Trichoptera Kirby, 1813). Caddisflies.
Lower Permian to present; worldwide but more abundant in temperate climate.
- Order Papilionida Laicharting, 1781 (= Lepidoptera Linné, 1758). Butterflies and moths. Lower Jurassic to present; worldwide.
- Order Muscida Laicharting, 1781 (= Diptera Linné, 1758). Flies. Middle Triassic to present; worldwide.
- Order Pulicida Billberg, 1820 (= Aphaniptera Kirby, 1826; = Siphonaptera Latreille, 1825). Fleas. Eocene to present; true fleas are worldwide. Questionable fossils from the Upper Jurassic and Lower Cretaceous of East Asia and Australia indicate the sister-group relationship of fleas to the other Papilionidea (Rasnitsyn 1992b).
- Superorder Vespeidea Laicharting, 1781 (= Hymenopteroidea Handlirsch, 1903).
- Order Vespida Laicharting, 1781 (= Hymenoptera Linné, 1758). Wasps, bees,

- and ants. Middle or Upper Triassic to present; worldwide. Supposedly a sister group of other holometabolans excluding Palaeomanteida.
- Infraclass Gryllones Laicharting, 1781 (Polyneoptera Martynov, 1923).
- Superorder Blattidea Latreille, 1810 (= Dictyoptera Clairville, 1798).
- Order Eoblattida Handlirsch, 1906. Middle and Upper Carboniferous of Britain, France, and the United States; probably confined to the warmest climate. Supposedly ancestral to other blattidean orders.
- Order Blattida Latreille, 1810 (= Blattodea Brunner, 1882). Roaches. Lower Middle Carboniferous to present; worldwide but most abundant in warm climates. Possibly ancestral to both termites and praying mantids.
- Order Termitida Latreille, 1802 (= Isoptera Brullé, 1832). Termites. Early Cretaceous to present; warm temperate, subtropic, and especially tropic zones (generally within 40° north and south) of all continents.
- Order Manteida Latreille, 1802 (= Mantodea Burmeister, 1835). Praying mantids. Lower Cretaceous to present; living mantids are termophilous. For the oldest fossils, see Gratshev and Zherikhin (1993).
- Superorder Perlidea Latreille, 1802 (= Plecopteroidea Martynov, 1938).
- Order Grylloblattida Walker, 1914 (= Notoptera Crampton, 1915; = Grylloblattodea Brues & Melander, 1932; + Protorthoptera Handlirsch, 1906; = Paraplecoptera Martynov, 1925; + Protoperlaria Tillyard, 1928). Middle Carboniferous to present; worldwide in Paleozoic, now amphi-Pacific relicts in Holarctic. Ancestral to other perlidean orders (fig. 1.7).
- Order Perlida Latreille, 1810 (= Plecoptera Burmeister, 1835). Stoneflies. Upper Lower Permian to present; worldwide although rare in warmer climates.
- Order Forficulida Latreille, 1810 (= Dermaptera DeGeer, 1773; + Protelytroptera Tillyard, 1931). Earwigs. Lower Permian to present; worldwide.
- Order Embiida Burmeister, 1835 (= Embioptera Shipley, 1904). Web spinners. Oligocene (or, possibly, Upper Cretaceous, if this is the age of the Burmese amber) to present; living embiids are worldwide in warmer climates.
- Superorder Gryllidea Laicharting, 1781 (= Orthopteroidea Handlirsch, 1903).
- Order Gryllida Laicharting, 1781 (= Orthoptera Olivier, 1789). Grasshoppers and crickets. Upper Carboniferous to present; worldwide.
- Order Phasmatida Leach, 1815 (= Phasmatodea Burmeister, 1835). Stick insects. Late Permian to present; fossils comparatively rare, found in Eurasia and Australia only. Living forms common in all tropic regions, rare in warm temperate ones.

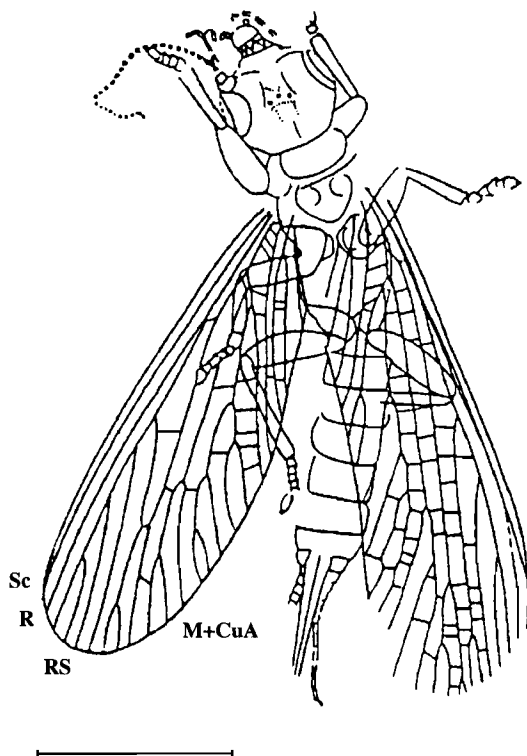


Figure 1.7. *Blattogryllus karata vicius* Rasnitsyn (Blattogryllidae), the ancestor of stoneflies and related orders. Upper Jurassic of southern Kazakhstan. Designations as in figure 1.2. Scale 10 mm. (After Rasnitsyn 1976b.)

Order Mesotitanida Tillyard, 1925 (= Titanoptera Sharov, 1968). Middle and Late Triassic only; Central Asia, Australia, and eastern Europe.

1.2. Classification of Insect Wing Kinematics

The identification of insect orders relies considerably on features of the wings. Insects can have one or two wing pairs, with one pair larger than the other (either fore- or hindwings can be longer, depending on taxon). The wings can be hardened (elytra), membranous or leathery, fringed, scaled or hairy; veins and cells can be numerous or strongly reduced. From this, one is able to suggest that the wings—and flying, as their main function—played quite an important role in the evolution of insects. Indeed, after its origination, flight evolved in almost all insect orders. The historical change of flight imposed constraints on the general appearance of subordinate taxa, thus considerably channeling their evolution. Hence, the traditional classification and nomenclature of insect orders was based mainly on features of wing appa-

Form and Function of Insect Wings

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