

18 Problem of the basal dichotomy of the winged insects

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18.1 INTRODUCTION

There are two main competing hypotheses concerning the basal pterygote dichotomy. The first was proposed by Martynov (1925) and has been since widely supported (Rohdendorf, 1962; Boudreaux, 1979; Kristensen, 1981; Arnett, 1985; Carpenter, 1992; CSIRO, 1992). Currently, it is being most vigorously championed by Kukalová-Peck (1978–1992). This hypothesis infers that the main pterygote dichotomy separates Palaeoptera and Neoptera. The alternative hypothesis is mine (Rasnitsyn, 1976, 1980; Rohdendorf and Rasnitsyn, 1980). It claims that the basic pterygote dichotomy divides the Subclass Scarabaeona (= Pterygota) into Infraclasses Scarabaeones and Gryllones [the reasons for employing these names for higher taxa are explained in Rohdendorf (1977) and Rasnitsyn (1982, 1996)].

18.2 FIRST HYPOTHESIS

Martynov's (1938) hypothesis (Figure 18.1) infers that palaeodictyopteroids (Superorder Dictyoneuridea), mayflies (Superorder Ephemeridea), and dragonflies (Superorder Libellulidea) are symplesiomorphic in that their wings are unfoldable (Figure 18.2), lack the jugal area, and show advanced fluting due to convex MA (Figure 18.3) (wing morphology definitions as in CSIRO, 1992). Neoptera are synapomorphic in possessing an alternative set of character states: wings are foldable backward over the abdomen (Figure 18.4), bear a differentiated jugal area that rocks down in the folded wing (Figure 18.5), and have MA, if differentiated, neutral in its position in relation to the surrounding membrane, and not convex, that is, positioned on a top of a longitudinal convexity of the membrane (Figure 18.6).

This inference, however, is in conflict with various morphological and functional observations. Most important of these is that the permanently outstretched pro-wings and wing pads dramatically limit the mobility of an immature insect. It is particularly so because the wing development was very gradual in ancient insects, resulting in fairly long

wing pads in later, but still non-flying ontogenetic stages. To cope with this problem, some of the immature stages of ancient palaeopterans had their wing pads bent rearward (Figure 18.7), while others acquired the foldable wing pads (Figure 18.8). In a flying, adult insect, permanently outstretched wings obviously hinder it when entering narrow spaces - and hence make the insect permanently exposed to predators, winds and rains. These obstacles are easy to cope with for a good flier, but it can be questioned whether this way of life applied to ancestral pterygotes whose flight necessarily should be weak (Figure 18.9).

Later, Kukalová-Peck (1992) modified her previous claim (Figure 18.10): she agreed that permanently outstretched wings were not a pterygote symplesiomorphy but a synapomorphy of Palaeoptera other than Diaphanopterida (= Diaphanopteroidea, the order that is closely related to other dictyoneurideans but unlike them possesses the foldable wings). However, this hypothesis is still open to criticism. One reason is that the putative palaeopterous apomorphies are prone to independent origin. Unfoldable wings appear in butterflies and various moths (Alucitidae, Geometridae, etc.), in many dipterans (e.g. Bombyliidae), in some hymenopterans (e.g. Cephidae), and so on. The convex MA appears independently from palaeopterans, for instance, in the highly plesiomorphic Permian Homoeodictyon (Figure 18.11), in bittacid mecopterans (Figure 18.12) and in all dipterans (Shcherbakov *et al.*, 1995). In bittacids and dipterans, this vein is called RS4 but represents a branch of MA, because the mecopteroid and neuropteroid RS combines both true RS and MA (Figure 18.13). In addition, Shcherbakov *et al.* (1995) showed that the most archaic Triassic dipteran family, Vladipteridae, has convex developments of both the suggested MA homologues, RS3 and RS4.

Still more significant is the existence of a transition that connects palaeodictyopterans (Figure 18.2 and 18.3) to Paoliidae, which have the least advanced pterygote wings (Figure 18.14). The transition is formed by the order Diaphanopterida (Figure 18.15), and further by

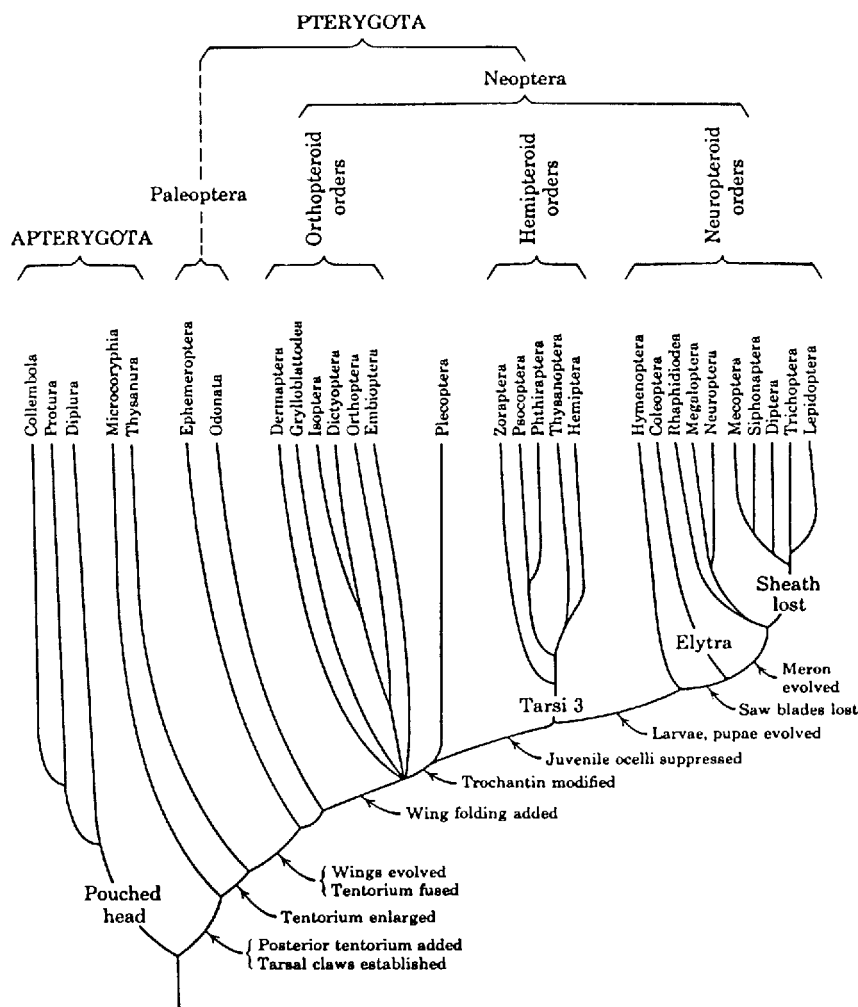


Figure 18.1 Insect phylogeny by Ross (1965) displaying essentially Martynov's view on the basic insect dichotomy.

Heterologopsis Brauckmann (Figure 18.16). At first glance, *Heterologopsis* seems to be a normal diaphanopterid, with the typically palaeodictyopteroid sucking beak and prothoracic winglets, and with foldable wings. The wings, however, are typical of Cacurgidae, a group related to Paoliidae and venationally the second least advanced group among the winged insects (Figure 18.17).

The above series of taxa may well represent an example of an evolutionary transition from stem pterygotes to the palaeodictyopterans. The problem is that in this series the sucking beak had already originated at the Cacurgid stage (Figure 18.16), that is, long before than the palaeopteran venational synapomorphies appeared. In contrast, in the mayfly–dragonfly clade, the groundplan mouthparts are close to the pterygote groundplan mouthparts (Boudreaux, 1979). Apparently, the dragonflies and mayflies gained their palaeopteran apomorphies independently of dictyoneurideans.

18.3 SECOND HYPOTHESIS

The opposing hypothesis suggests rather that the basic pterygote dichotomy separates the Infraclass Gryllones (= Polyneoptera, or Orthopteroidea in the widest sense) from its ancestral (paraphyletic) Infraclass Scarabaeones. The latter group comprises all the rest of the winged insects, that is, Martynov's Oligoneoptera and Paraneoptera. The first of these two taxa, known also as Holometabola (insects with complete metamorphosis), is typified as the Cohors Scarabaeiformes. Paraneoptera embraces Hemiptera and Psocopteroidea and is typified, jointly with several extinct groups, as the Cohors Cimiciformes (Rasnitsyn, 1980; Rohdendorf and Rasnitsyn, 1980). This hypothesis states that Scarabaeones are sympleisiomorphic in the roof-like repose position of their wings (Figure 18.18), and that in their hind wing the jugal area (Figure 18.5) is small, with the folding line running behind (usually well behind) the vein

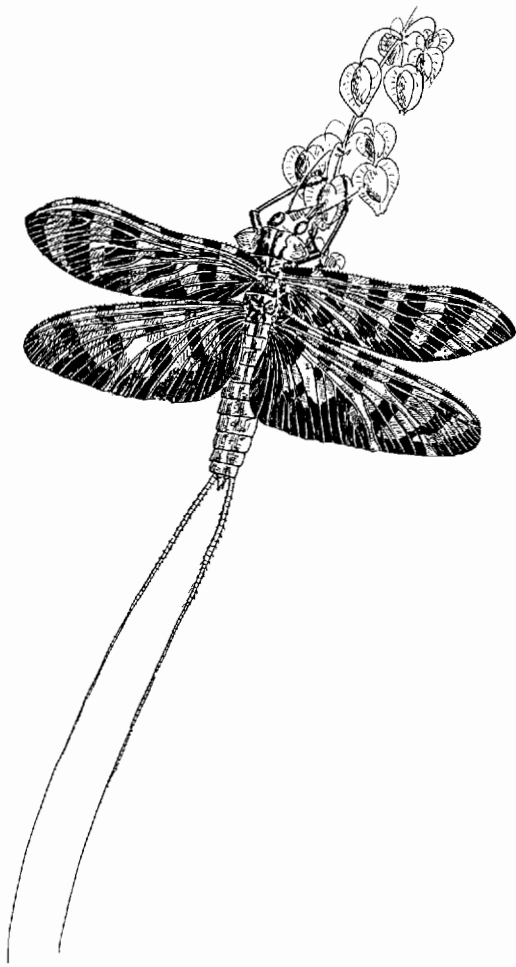


Figure 18.2 *Goldenbergia* sp. (Dictyoneurida) from the Upper Carboniferous of Siberia. Reconstruction by A.G. Ponomarenko. (From Rohdendorf and Rasnitsyn 1980.)

2A (using conservative vein nomenclature; otherwise, if 1A is re-defined as PCu, this vein should be termed 1A). In contrast, Gryllones are synapomorphic in acquiring horizontal wing repose position (Figure 18.4), with their jugal area enlarged in the hind wing, and rocking down before 2A at rest (Figure 18.19).

Under these assumptions, the palaeopteran apomorphies are considered to appear homoplastically on several distinct occasions within the Scarabaeones. One such occasion happened during the course of evolution of the palaeodictyopteroid insects (Superorder Dictyoneuridea), namely, at the appearance of the sister group of Diaphanopterida. This sister group is hypothesized to comprise the orders Dictyoneurida (= Palaeodictyoptera; Figure 18.2) and Mischopterida (= Megasecoptera; Figure 18.20).

The second major independent acquisition of palaeopteran apomorphies defines the Cohors

Libelluliformes, the clade covering mayflies and dragonflies. Unlike my previous opinion (Rasnitsyn, 1980; Rohdendorf and Rasnitsyn, 1980), I now accept the sister group relationships between the Superorders Libellulidea and Ephemeridea based upon synapomorphies in wing morphology. These include the very basal separation of R and RS veins, and the pronounced fluting of their wing surface, so as in the abundantly branching convex vein systems (MA, CuA), the convex primary veins alternate with the concave intercalaries (longitudinal veins with a double, forking base), while in the corresponding concave systems (RS, MP) the concave primary veins alternate with the convex intercalaries. This inference is supported by the wing morphology of the ancient, Carboniferous representatives of both mayflies and dragonflies that lack several of their autapomorphies and thus are overall rather similar (Figures 18.21 and 18.22).

Because of their thoracic morphology, which is the most plesiomorphic within known Scarabaeones (pterothoracic sterna are not invaginated along the segment midline: no discrimen is developed), dragonflies and mayflies should be considered to be a sister group of the rest of the Scarabaeones. This inference is not yet secure, however, because the body structure is completely unknown for some ancient groups that are highly plesiomorphic in other respects. This applies to the Paoliidae, a group virtually lacking any apomorphy above the pterygote groundplan, but unfortunately known only from their wings (Figure 18.14). Paoliidae have been formerly supposed to represent the ancestral pterygote taxon, Protoptera (Sharov, 1966) or Paoliida (Rohdendorf and Rasnitsyn, 1980). However, as described above, there is a 'smooth' transition connecting them with Diaphanopterida via Cacurgidae (*Heterologopsis*). Diaphanopterida possess the invaginated ptero-thoracic sterna, the same should be hypothesized to *Heterologopsis* and hence to Cacurgidae because of their profound similarity in the body structure. Paoliidae and Cacurgidae are similar enough venationally to deserve attribution to one and the same order (Paoliida). Hence, we should assume that they had similar body morphology, at least until the contrary is proven. However, the discovery of the body of any representative of the Paoliidae may overturn this assumption. The Paoliidae may prove to be an early off-shoot of the pterygote ancestor: either a sister group, or even the ancestral taxon of the rest of the winged insects.

18.4 CONCLUSION

The basal pterygote dichotomy of Palaeoptera and Neoptera can be rejected in favour of that of Scarabaeones and Gryllones. This is based upon functional considerations, and upon fossils whose morphology is congruent with neither monophyly nor paraphyly of Palaeoptera.

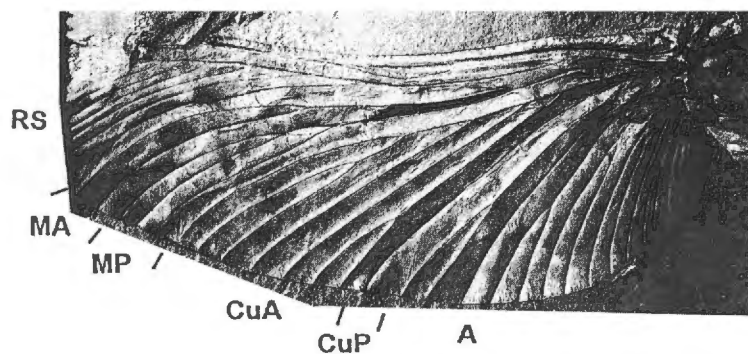


Figure 18.3 Hind wing of *Dunbaria quinquefasciata* (Martynov) (Dictyoneurida) from the Upper Permian (Kungurian) of Tshekarda, Ural Mountains.

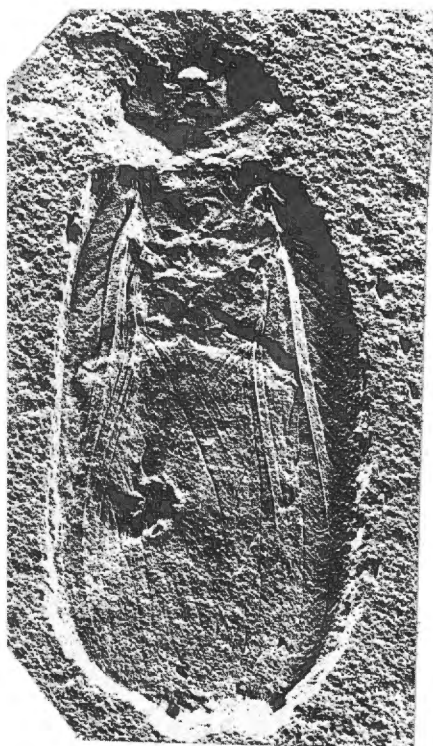


Figure 18.4 *Sylvaphlebia tuberculata* Martynov (Grylloblattida) from the Upper Permian (Kungurian) of Tshekarda, Ural Mountains.

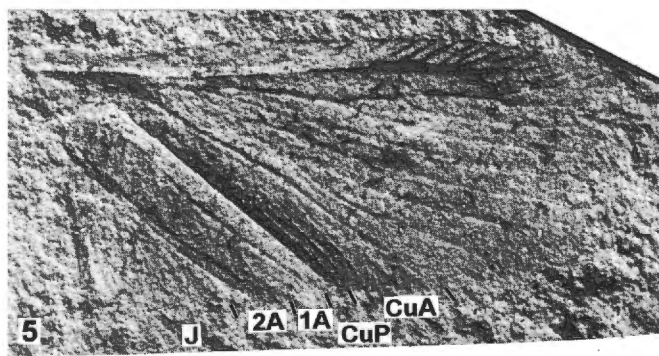


Figure 18.5 *Glaphyrophlebia subcostalis* Martynov (Blattinopseida), the hind wing with unfolded jugum (J), from the Upper Permian (Kazanian) of Soyana, Arkhangelsk Region of Northern Russia.

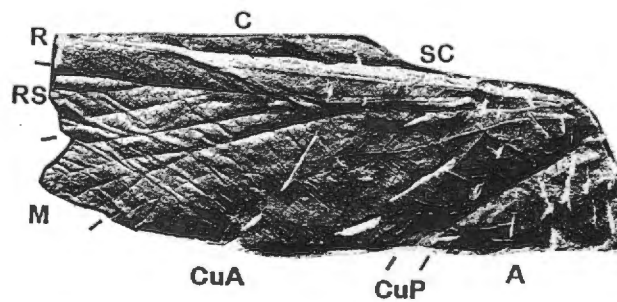


Figure 18.6 Fore wing of *Holasicia vetula* Kukalová (Paoliida) from the lowermost Middle Carboniferous (Namurian C). (From Kukalová, 1958.)

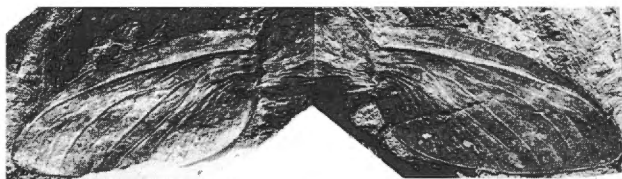
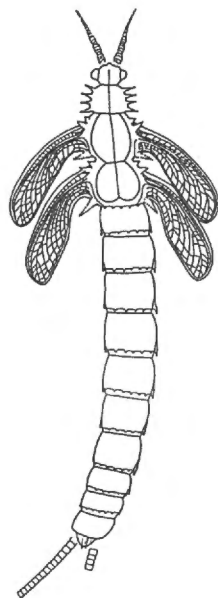


Figure 18.8 Thoracic segment of a nymphal *Tchirkovaea guttata* G. Zalesky (Dictyoneurida) from the Upper Carboniferous of Siberia: aligned photographs of the obverse and reverse parts of the fossil. (From Rasnitsyn, 1980.)

Figure 18.7 Nymphal *Mischoptera douglassi* Carpenter and Richardson (Mischoptera) from the Lower Permian (Artinskian) of Illinois, USA. (From Carpenter and Richardson, 1968.)

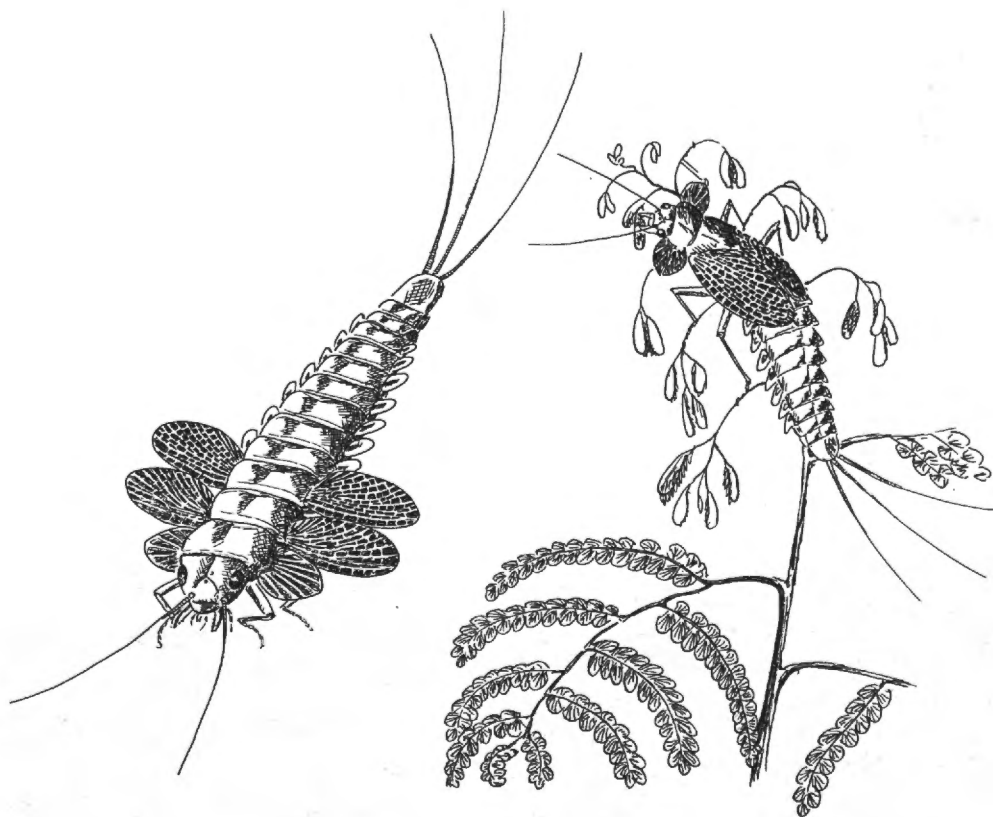


Figure 18.9 Ancestral winged insects. Reconstruction by A.G. Ponomarenko. (From Rohdendorf and Rasnitsyn, 1980.)

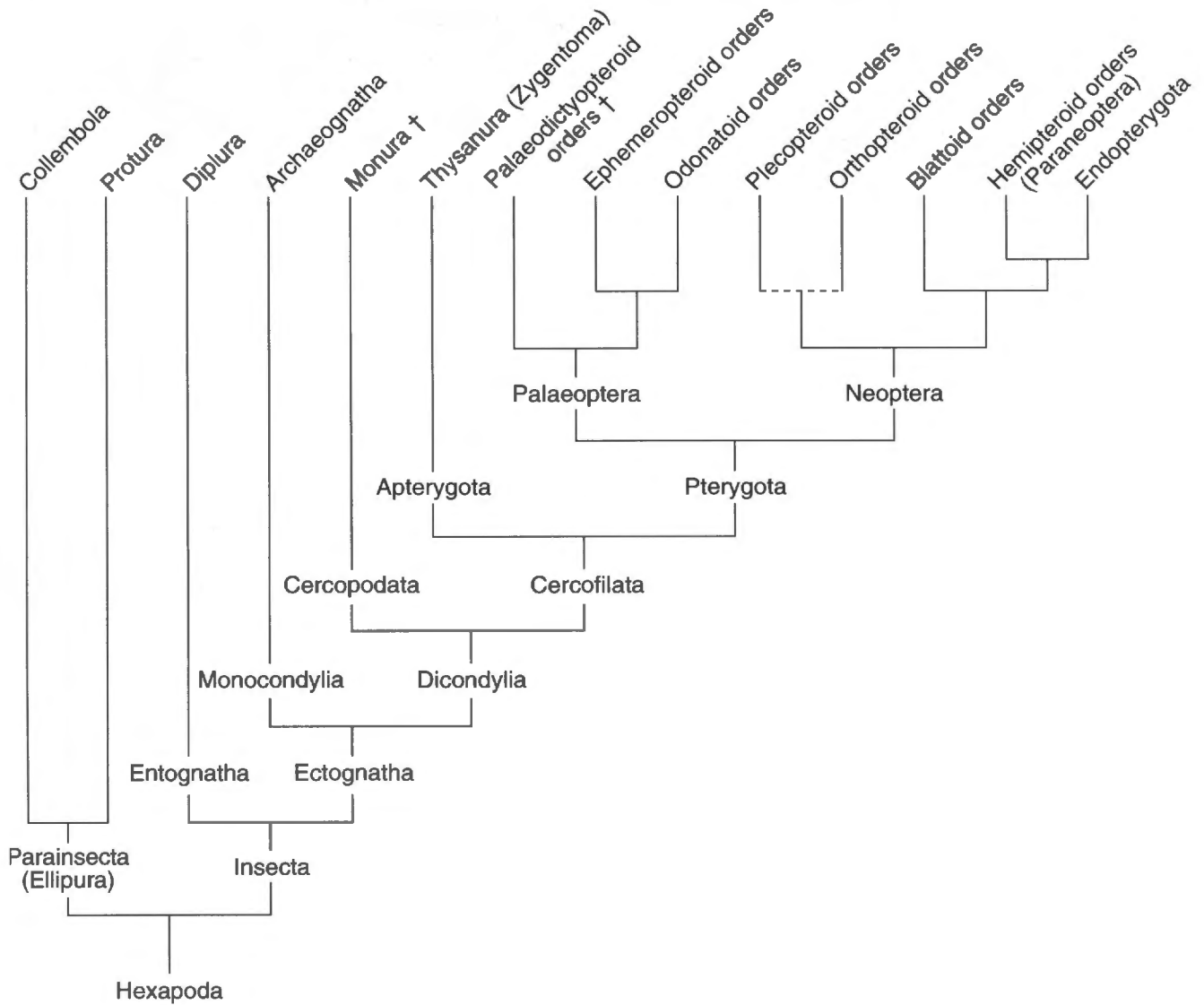


Figure 18.10 Insect cladogram after Kukalová-Peck (1992).



Figure 18.11 Fore wing of *Homoeodictyon elongatum* Martynov (?Hypoperlida) from the Upper Permian of Kargala, Southern Ural Mountains, showing convex MA stem.

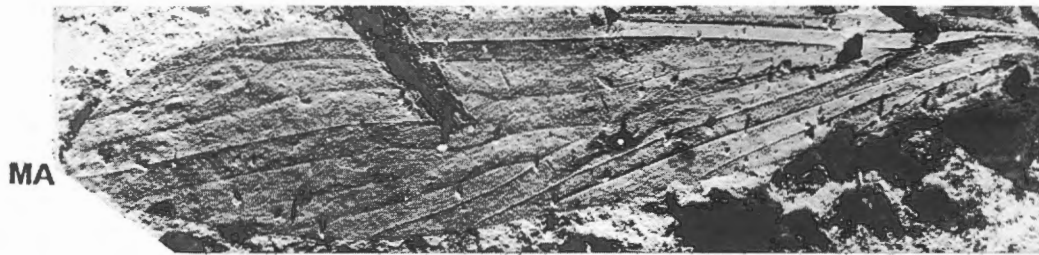


Figure 18.12 Fore wing of the Bittacid scorpionfly *Neorthophlebia robusta* Martynov (Panorpida) from the Lower Jurassic of Kirghizia (vicinity of Shurab), the fore wing with convex hind MA branch (= RS4). (From Martynov, 1937.)

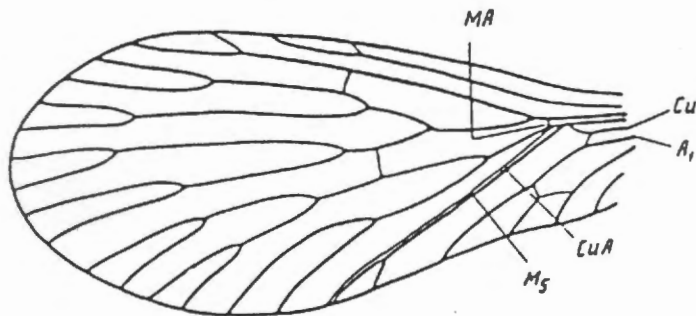


Figure 18.13 Hind wing of the Kaltanid scorpionfly *Altajopanorpa pilosa* O. Martynova (Panorpida) from the Upper Permian (Ufimian) of Kuznetsky Basin, S. Siberia, showing MA base. (From Novokshonov, 1992.)

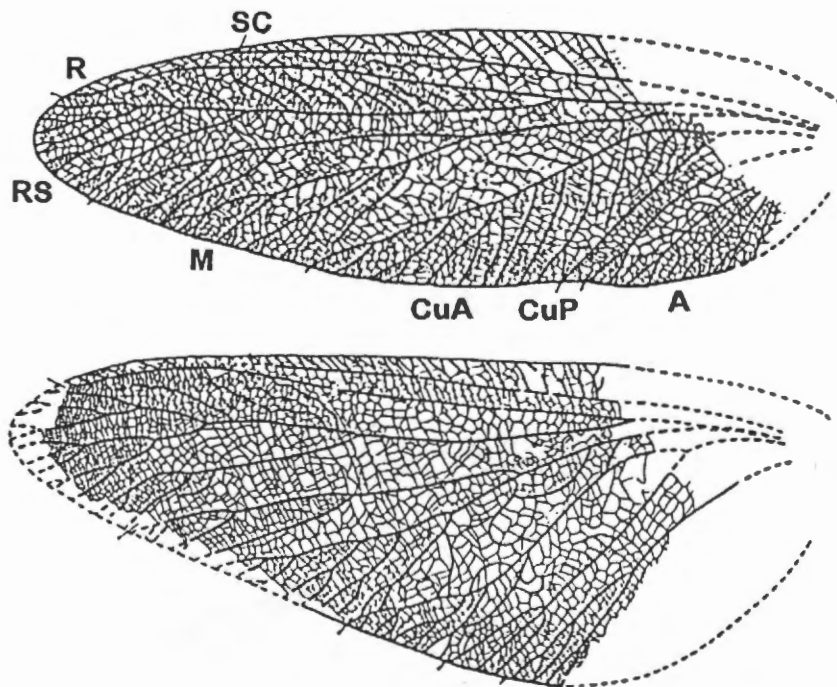


Figure 18.14 Wings of *Zdenekia grandis* Kukalová (Paoliida) from the lowermost Middle Carboniferous (Namurian C) of Czech Republic. (From Kukalová, 1958.)



Figure 18.15 *Uralia maculata* Kukalová-Peck and Sinitshenkova (Diaphanopterida) from the Upper Permian (Kungurian) of Tshekarda, Ural Mountains. Reconstruction by A.G. Ponomarenko. (From Rohdendorf and Rasnitsyn, 1980.)

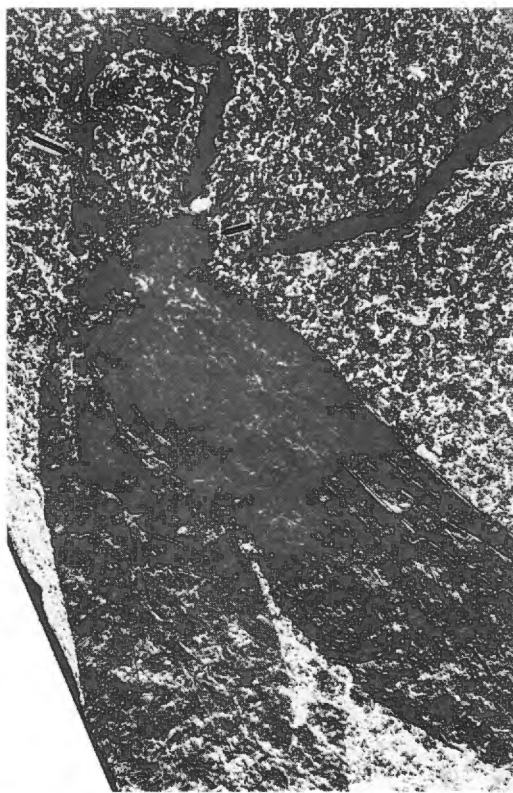


Figure 18.16 *Heterologopsis ruhrensis* Brauckmann and Koch (?Paoliida) from the lowermost Middle Carboniferous (Namurian) of Germany (Brauckmann *et al.*, 1985). Arrows indicate the beak and prothoracic winglet.

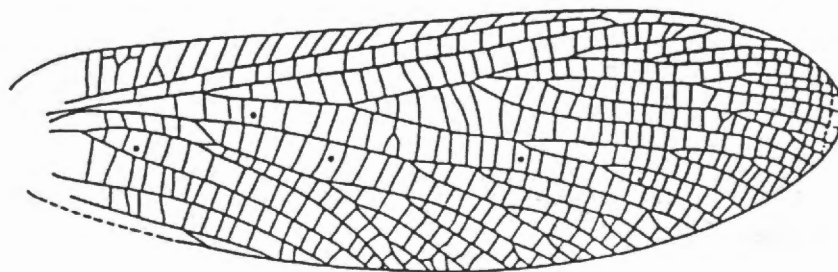


Figure 18.17 Fore wing of *Heterologus langfordorum* Carpenter (?Paoliida) from the Lower Permian (Artinskian) of Illinois, USA. (From Carpenter, 1944.)

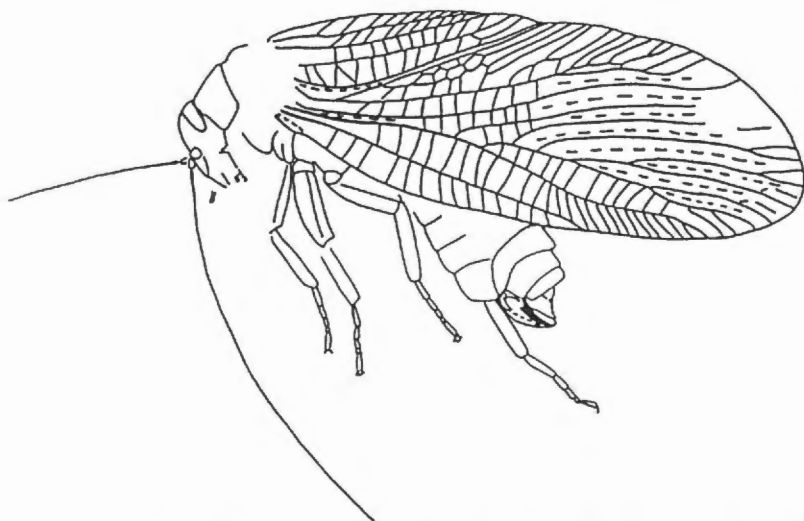


Figure 18.18 *Glaphyrophlebia uralensis* (Martynov) (Blattinopseida) from the Upper Permian (Kungurian) of Tshékarda, Ural Mountains. (Rasnitsyn, 1980), habitus drawing to show the roof-like wing repose position.

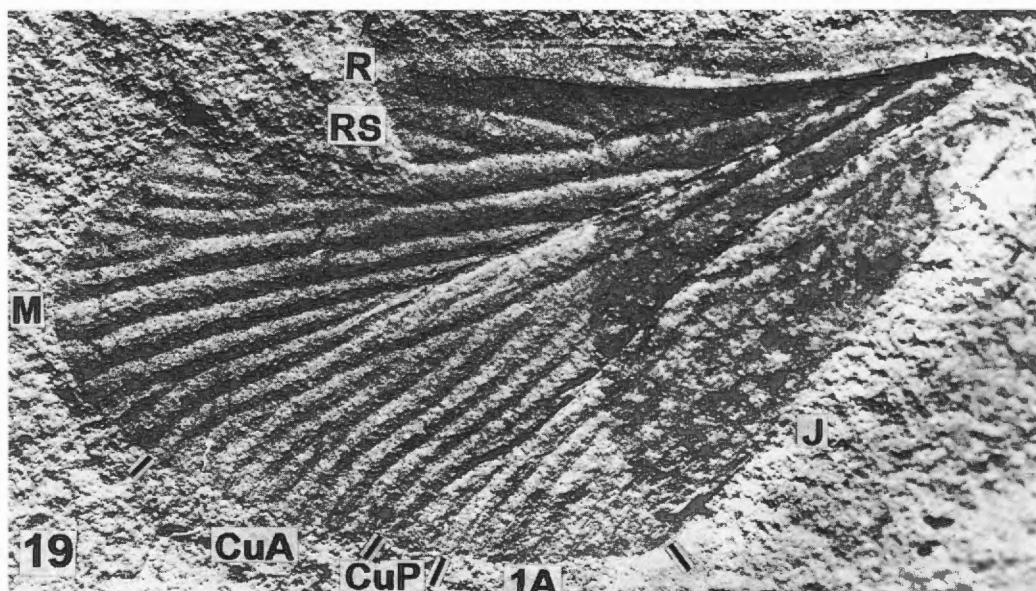


Figure 18.19 Hind wing of the roach *Phyloblatta?* sp. (Blattida) from the Upper Permian (Kazanian) of Soyana, Arkhangelsk Region of Northern Russia, to show semicircular jugum (J) bent down along the flexion line behind 1A.

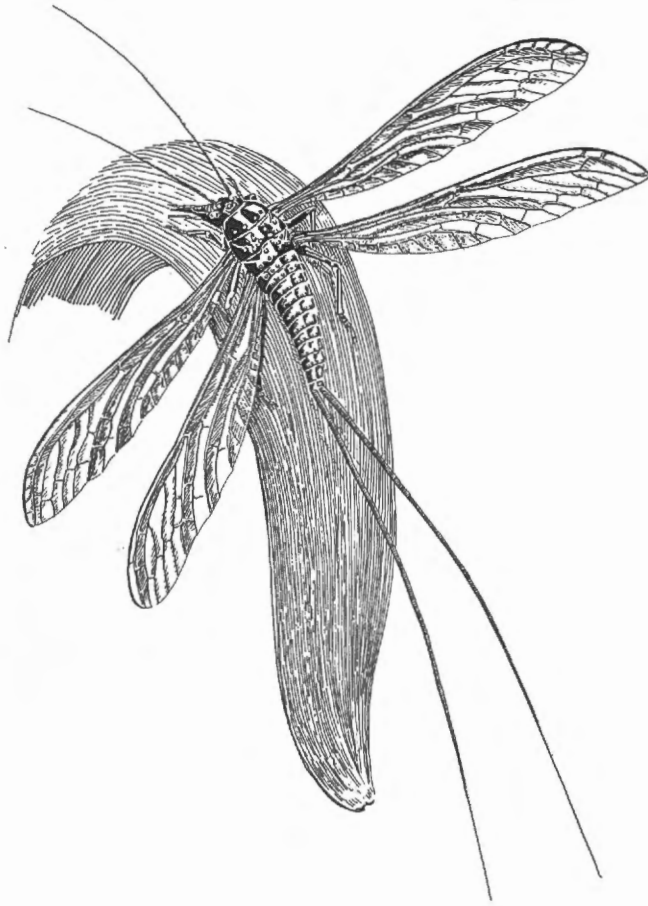


Figure 18.20 *Sylvothymen* sp. (Mischopterida) from the Upper Permian (Kungurian) of Tshekarda locality, Ural Mountains. Reconstruction by A.G. Ponomarenko. (From Rohdendorf and Rasnitsyn, 1980.)

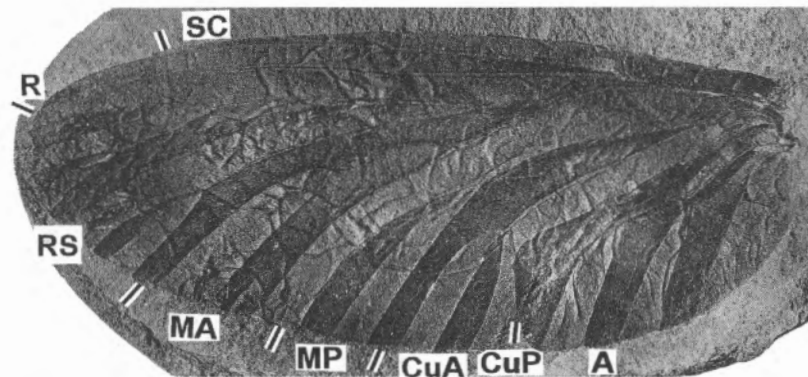


Figure 18.21 Fore wing of the archaic mayfly *Lithoneura mirificum* Carpenter (Syntonopterida) from the Lower Permian (Artinskian) of Illinois, USA. (From Carpenter, 1944.)

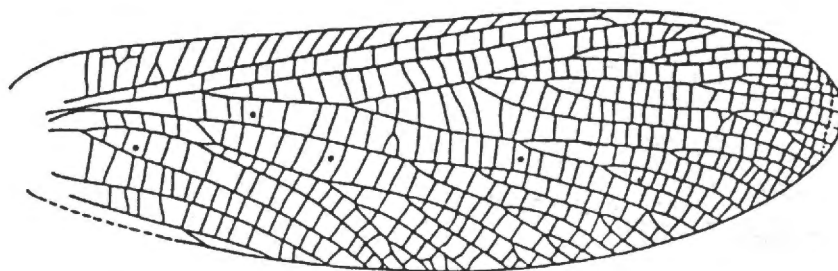


Figure 18.17 Fore wing of *Heterologus langfordorum* Carpenter (?Paoliida) from the Lower Permian (Artinskian) of Illinois, USA. (From Carpenter, 1944.)

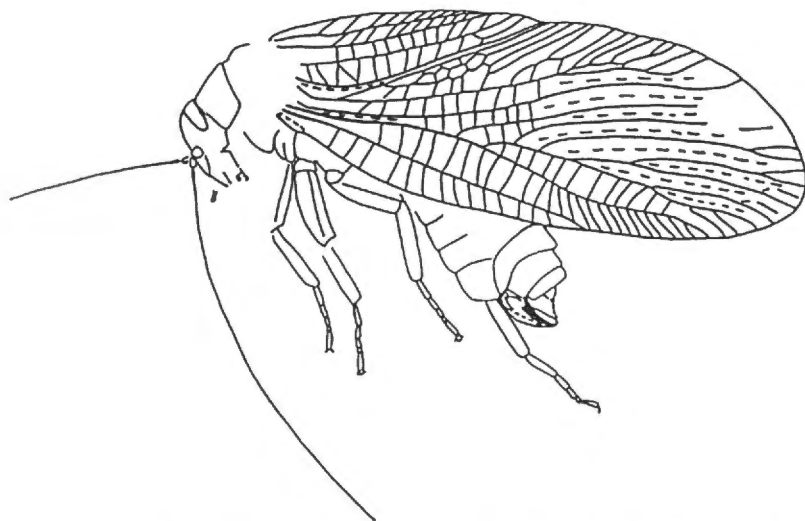


Figure 18.18 *Glaphyrophlebia uralensis* (Martynov) (Blattinopseida) from the Upper Permian (Kungurian) of Tshekarda, Ural Mountains. (Rasnitsyn, 1980), habitus drawing to show the roof-like wing repose position.

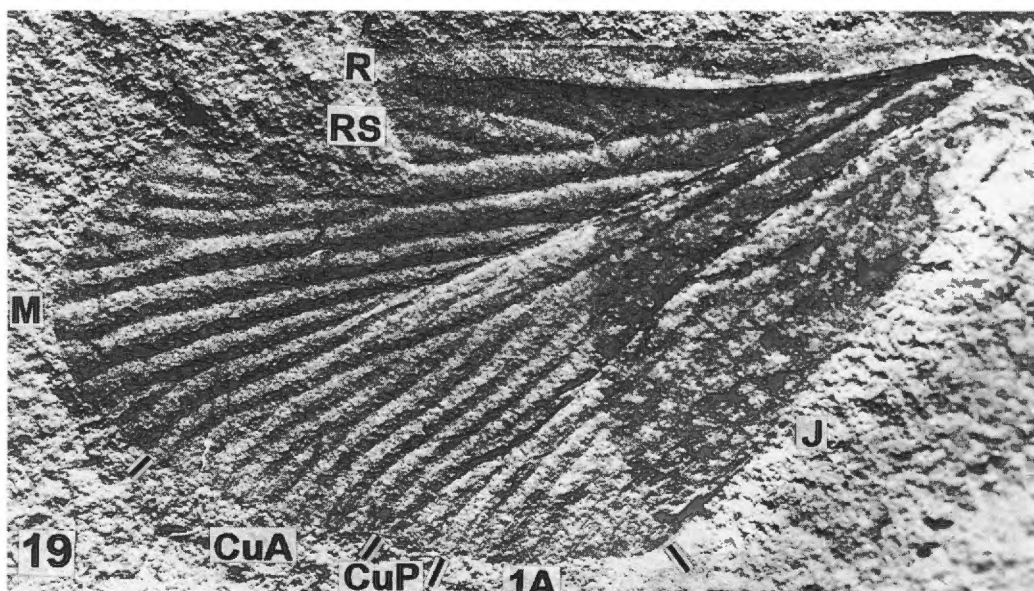


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Figure 18.22 Fore wing of the archaic dragonfly *Eogeropteron arcuatum* Riek (Meganeurida) from the Carboniferous (Malanzan Formation) in Paganzo Basin, Argentina (Riek and Kukalová-Peck, 1984). The counterpart of the fossil shows the wing from below, with convex and concave veins being mirrored compared with the usual appearance.

REFERENCES

- Arnett, R.H. (1985) *American Insects. A Handbook of the Insects of America North of Mexico*, Van Nostrand Reinhold Co., New York.
- Boudreaux, H.B. (1979) *Arthropod Phylogeny: with Special Reference to Insects*, John Wiley & Sons, New York.
- Brauckmann, C., Koch, L. and Kemper, M. (1985) Spinnentiere (Arachnida) und Insekten aus den Vorhalle-Schichten (Namurium B; Ober-Karbon) von Hagen-Vorhalle (West-Deutschland) *Geologie und Paläontologie in Westfalen*, 3, 1–132.
- Carpenter, F.M. (1944) Carboniferous insects from the vicinity of Mazon Creek, Illinois. *Illinois State Museum, Scientific Papers*, 3, 1–20.
- Carpenter, F.M. (1992) *Treatise on Invertebrate Paleontology*. Pt. R. Arthropoda 4. Vol. 3, 4. Superclass Hexapoda. Geological Society of America, Boulder, Colorado, and University of Kansas, Lawrence, Kansas.
- Carpenter, F.M. and Richardson, E.S. (1968) Megasecopterous nymphs from the Pennsylvanian concretions of Illinois. *Psyche*, 75, 295–309.
- CSIRO (ed.) (1992) *The Insects of Australia*, 2nd edn, Melbourne University Press, Melbourne.
- Kristensen, N.P. (1981) Phylogeny of insect orders. *Annual Review of Entomology*, 26, 135–57.
- Kukalová, J. (1958) Paoliidae Handlirsch (Insecta – Protorthoptera) aus dem Oberschlesischen Steinckohlenbecken. *Geologie*, 7, 935–59.
- Kukalová-Peck, J. (1978) Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *Journal of Morphology*, 15, 53–126.
- Kukalová-Peck, J. (1983) Origin of insect wing and wing articulation from the arthropodan leg. *Canadian Journal of Zoology*, 61, 1618–69.
- Kukalová-Peck, J. (1992) Fossil history and the evolution of hexapod structure, in *The Insects of Australia*, 2nd edn. (ed. CSIRO), Melbourne, Melbourne University Press, pp. 144–82.
- Martynov, A.V. (1925) über zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. *Zeitschrift für Ökologie und Morphologie der Tiere*, 4, 465–501.
- Martynov, A.V. (1937) Liassic insects of Shurab and Kizil-Kiya. *Transactions of the Paleontological Institute, Academy of Sciences of USSR*, 7, no. 1, Izdatelstvo AN SSSR, 232 pp. (in Russian, with English summary).
- Martynov, A.V. (1938) An essay on the geological history and phylogeny of the insect orders (Pterygota). Pt. I. Palaeoptera and Neoptera-Polyneoptera. *Transactions of the Paleontological Institute, Academy of Sciences of USSR*, 7, no. 4, Izdatelstvo AN SSSR, 148 pp. (in Russian, with French summary).
- Novokshonov, V.G. (1992) Early evolution of caddisflies (Trichoptera). *Zoologicheskii Zhurnal*, 71, 58–67 (in Russian).
- Rasnitsyn, A.P. (1976) On the early evolution of insect and the origin of Pterygota. *Zhurnal Obshchey Biologii*, 37, 543–55 (in Russian with English summary).
- Rasnitsyn, A.P. (1980) Origin and evolution of Hymenoptera. *Transactions of the Paleontological Institute, Academy of Sciences of USSR*, 174, Nauka Press, Moscow, 192 pp. (in Russian).
- Rasnitsyn, A.P. (1982) Proposal to regulate the names of taxa above the family group. *Bulletin of Zoological Nomenclature*, 39, 200–7.
- Rasnitsyn, A.P. (1996) Conceptual issues in phylogeny, taxonomy, and nomenclature. *Contributions to Zoology*, 66, 3–41.
- Riek, E.F. and Kukalová-Peck, J. (1984) A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62, 1150–66.
- Rohdendorf, B.B. (ed.) (1962) *Osnovy paleontologii. Chlenistonogiye. Trakheinye i khelitserovaye*, Izdatelstvo Akademii Nauk SSSR, Moscow, 560 pp [in Russian, translated into English as Rohdendorf B.B. (ed.) (1991) *Fundamentals of Paleontology*. Vol. 9, Arthropoda, Tracheata, Chelicerata. New Delhi, Amerind Co., 894 pp.]
- Rohdendorf, B.B. (1977) The rationalization of names of higher taxa in zoology. *Paleontologicheskii Zhurnal*, no. 3, 11–21 [in Russian, translated into English in *Paleontological Journal*, 11, 149–55 (1977).]
- Rohdendorf, B.B. and Rasnitsyn A.P. (eds). (1980) Historical development of the class Insecta. *Transactions of the Paleontological Institute, Academy of Sciences of USSR*, 175, Nauka Press, Moscow, 269 pp. (in Russian).
- Ross, H.H. (1965) *A Textbook of Entomology*, 3rd edn, John Wiley & Sons, New York.

Sharov, A.G. (1966) On the position of the orders Glosselytrodea and Caloneurodea in the system of Insecta. *Paleontologicheskii Zhurnal*, no. 3, 84-93 (in Russian).

Shcherbakov, D.E., Lukashevich, E.D. and Blagoderov, V.A. (1995) Triassic Diptera and initial radiation of the order. *Dipterological Research*, 3, 75-115.