

Carboniferous protodonatoid dragonfly nymphs and the synapomorphies of Odonoptera and Ephemeroptera (Insecta: Palaeoptera)

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Abstract

Three extremely rare fossil protodonatoid dragonfly nymphs are described from the middle Pennsylvanian (Moscovian) of Mazon Creek, Illinois: *Dragonympha srokai* n. gen., n. sp. (Meganisoptera), a large, nearly complete young nymph with an extended labial mask and uplifted wing pads; *Alanympha richardsoni* n. gen., n. sp. (Meganisoptera), a nymphal forewing with two articular plates attached to it; and *Carbonympha herdinai* n. gen., n. sp. (Eomeganisoptera), a detached nymphal forewing. Plesiomorphic states in *Dragonympha* n. gen. indicate homologies unresolved in modern Odonata. The segmented head bears 3rd tergum ventrally invaginated. The extended labial mask still shows limb segments. The prothorax bears a pair of winglets. The short wing pads are fully articulated, twisted, uplifted and streamlined with body. The mesothoracic anepisternum is placed between acrotergite and prescutum. The abdominal leglets form long, segmented, serial gill filaments. In the ontogenesis of modern dragonflies, the wing and articulation disc occurs just above subcoxal pleuron and far from tergum. Wing sclerites are arranged in eight rows protecting eight blood pathways running towards eight wing veins. The sistergroup of Odonoptera has not yet been convincingly resolved with computer cladistic approaches. Reasons are examined and discussed. More accurate, evolution-based character evaluations are shown with examples. The role of a correct model of the pan-arthropod limb and the origin of insect wings is discussed. Groundplan characters in dragonflies and mayflies are compared in their Paleozoic and modern states, their obscurity is clarified and complex synapomorphies are proposed. Palaeoptera is confirmed as a monophyletic group and the following sistergroup relationships are suggested: Pterygota = Palaeoptera + Neoptera; Palaeoptera = Palaeodictyopteroidea + Hydropalaeoptera; Hydropalaeoptera = Odonoptera + Ephemeroptera.

Key words: Pterygota, Palaeoptera, Ephemeroptera, Odonoptera, Meganisoptera, fossil dragonfly nymphs, phylogeny, insect wing, Carboniferous, Mazon Creek.

Zusammenfassung

Drei extrem seltene fossile Larven protodonatoider Libellen werden aus dem mittleren Pennsylvanum (Moscovium) von Mazon Creek in Illinois beschrieben: *Dragonympha srokai* n. gen., n. sp. (Meganisoptera), eine große, nahezu vollständige junge Larve mit ausgestreckter Fangmaske und hochgestellten Flügelscheiden; *Alanympha richardsoni* n. gen., n. sp. (Meganisoptera), ein larvaler Vorderflügel mit zwei ansitzenden Flügelgelenkplatten; und *Carbonympha herdinai* n. gen., n. sp. (Eomeganisoptera), eine isolierte Flügelscheide eines larvalen Vorderflügels. Plesiomorphe Merkmalszustände von *Dragonympha* n. gen. weisen auf unerkannte Homologien zu modernen Odonaten hin. Der gegliederte Kopf weist ein ventral invaginiertes 3. Tergum auf. Die ausgestreckte Fangmaske zeigt noch die Segmentierung von Beinen. Der Prothorax trägt ein Paar Flügelchen. Die kurzen Flügelscheiden sind vollständig gelenkig, gedreht, aufgerichtet und stromlinienförmig mit dem Körper. Das mesothorakale Anepisternum liegt zwischen dem Acrotergit und dem Prescutum. Die abdominalen Beinanhänge bilden lange, segmentierte, serielle Kiemenfilamente. In der Ontogenese moderner Libellen bildet sich die scheibenförmige Embryonalanlage des Flügels und der Flügelgelenkung direkt oberhalb des subcoxalen Pleurons, weit entfernt vom Tergum. Die Flügelgelenkstücke sind in acht Reihen angelegt, welche die acht Blutlakunen schützen, die in die acht Flügeladern verlaufen. Die Schwestergruppe der Odonoptera konnte bislang noch nicht überzeugend mittels computerkladistischer Methoden auffindig gemacht werden. Die Gründe hierfür werden untersucht und diskutiert. Genauere, evolutionsbasierte Merkmalsuntersuchungen werden mit Beispielen vorgestellt. Die Bedeutung eines zutreffenden Modells des ursprünglichen Beins der Pan-Arthropoden und des Ursprungs der Insektenflügel wird diskutiert. Grundplanmerkmale von Libellen und Eintagsfliegen werden in ihren paläozoischen und modernen Ausprägungen verglichen, ihre Unklarheiten werden aufgeklärt und komplexe Synapomorphien werden vorgeschlagen. Die Palaeoptera werden als monophyletische Gruppe bestätigt und folgende Schwestergruppenbeziehungen werden vorgeschlagen: Pterygota = Palaeoptera + Neoptera; Palaeoptera = Palaeodictyopteroidea + Hydropalaeoptera; Hydropalaeoptera = Odonoptera + Ephemeroptera.

Contents

1. Introduction	170
1.1. Morphological concepts and terms	172
1.2. Collecting, fossilization, matrix, and observation methods	174
2. Systematic paleontology	176
Infraclass Palaeoptera MARTYNOV, 1923	176
Order Meganisoptera MARTYNOV, 1932	176
Family incertae sedis	176

Genus <i>Dragonympha</i> n. gen.	176
Genus <i>Alanympa</i> n. gen.	183
Order Eomeganisoptera ROHDENDORF, 1963	186
Family incertae sedis	186
Genus <i>Carbonympa</i> n. gen.	186
3. Discussion	187
3.1. Labial mask	187
3.2. Gill filaments	188
3.3. Thoracic pleuron, pleural inflexions, double wing pivot	189
3.4. Arthropod wing homologue	189
3.5. Articular sclerites follow blood pathways to wing veins	191
3.6. Difference in articulation: Palaeoptera versus Neoptera	192
3.7. Comparative-morphological analysis of the pterygote wing articulation	192
3.8. Homologous muscular insertions	192
3.9. Anterior articular plate	193
3.10. Posterior articular plate	194
3.11. Paleoptery is a derived adaptation	194
3.12. Nymphal winglets in diverse resting positions	195
3.13. Evolution of the veinal system in Odonatoptera and Ephemeroptera	195
4. Conclusion	195
5. References	196

1. Introduction

Three extremely rare protodonate fossil nymphs from Pennsylvanian (Late Carboniferous) nodules at the locality Mazon Creek, Illinois, USA, are described. Protodonate dragonflies from the Late Paleozoic orders †Geroptera, †Eomeganisoptera and †Meganisoptera lived in the tropical belt of Europe, Asia and North America and in the temperate zone of South America. †Meganisoptera had a wingspan of up to 73 cm and specialized in hunting large prey (probably †Palaeodictyoptera and †Megasecoptera). Dragonflies at the Mazon Creek locality were the top aerial predators in luscious moist forests of a large river delta. Adult wing fragments are quite common in Late Carboniferous and Permian freshwater deposits, while bodies are mostly lost to predation or rapid decomposition. Immatures – against all expectation – are almost entirely absent. Besides the three remnants described here, only one poorly preserved and uncertain nymphal wing is known, *Schlechtendaliola nympa* HANDLIRSCH, 1919, from the Stephanian C of Wettin, East Germany (see also HANDLIRSCH 1906–1908). This was later misnamed *Schlechtendaliana* by BRIDGES (1994). BRAUCKMANN & ZESSIN (1989) regarded its position uncertain, but REN et al. (2008) considered it a protodonate. This scarcity of fossil nymphs is inconsistent with their occurrence in aquatic habitats. In contrast, the juveniles of Ephemeroptera and Pleconeoptera are found in many Paleozoic localities and Early Permian sediments at Elmo, Kansas are in places littered with their small, isolated winglets, which became detached from bodies at the articular membrane (winglets never detach in modern nymphs as they are secondarily fused to terga). While conspicuously missing from sediments in the Paleozoic, dragonfly nymphs are relatively

well represented in Mesozoic and Tertiary freshwater deposits. This discrepancy is discussed below.

The Pterygota clade originated with the origin of wings and diversified into divisions, lineages and orders with the adaptation of the wing pairs to different types of flight, wing flexing, wing folding, and other functions. Thus, the relationships between the major lineages with respect to their monophyletic origin from Pterygota are most clearly identified by their veinal systems. The synapomorphies include similarities between the pairs of wings, veinal braces and fusions near wing base, wing areas, fields, flexion lines, and folds, and in fusions and reductions of the wing articular sclerites. As a result, the wing organ-system is a treasure chest of multiple character series, which offer easily observed synapomorphies in the pterygote higher categories: divisions, lineage and orders. Based on the wing organ, for most of the last century systematists consistently classified Odonatoptera as the sister lineage of Ephemeroptera, under the superlineage Hydro-palaeoptera ROHDENDORF, 1968 and the division Palaeoptera MARTYNOV, 1923 (MARTYNOV 1923, 1925; ROHDENDORF 1962; SHAROV 1966; HENNIG 1969, 1981; CARPENTER 1992 and before).

The diversification of the limb-wing organ in Pterygota into divisions, lineages and orders was thematically studied from three decades by this author and co-authors, while following closely the phylogenetic rules and criteria theoretically outlined by HENNIG (1969, 1981): monophyly, full homology, search for the groundplan level of character states in all higher taxa, using this research as background to identify synapomorphies, and turning these into a systematic hierarchy. Over the years, this study repeatedly verified the reality of Palaeoptera and showed Odonatoptera as the sistergroup of Ephemeroptera (KUKALOVÁ-

PECK 1978, 1983, 1985, 1991, 1992, 1998, 2008; RIEK & KUKALOVÁ-PECK 1984; KUKALOVÁ-PECK & BRAUCKMANN 1990; SHEAR & KUKALOVÁ-PECK 1990; HAAS & KUKALOVÁ-PECK 2001; KUKALOVÁ-PECK & LAWRENCE 2004, including the list of modern genera used in systematic considerations).

Evolutionary morphological facts (e. g., in the limb organ system) clearly show Crustacea as the sistergroup of Atelocerata, under Mandibulata (SNODGRASS 1935; KUKALOVÁ-PECK 1998). Entomologists sometimes do not fully realize that, since Crustacea occur in the Cambrian so in all probability did the ancestor of Myriapoda and Hexapoda. This pushes the divergence of Pterygota into divisions (Palaeoptera and Neoptera), superlineages (such as †Palaeodictyopteroidea and Hydropalaeoptera) and even lineages (Odonoptera and Ephemeroptera) way back before the Devonian. It is probably safe to suggest that terrestrial arthropods evolved with first algal mats floating on water and thriving on swampy shores. Ancestral Dicondylia must have had functional outer rami ancestral to wings ever since their divergence, when the vegetation was very short, dense, and surrounded by water. Since freshwater deposits in the Cambrian, Ordovician and Silurian were almost completely destroyed by erosion, positive evidence may never be found. The fact is that all Carboniferous insects known to this author already belong to modern divisions and superlineages, with a single exception: the extinct superlineage †Palaeodictyopteroidea (= †Diaphanopteroidea, †Palaeodictyoptera, †Megasecoptera, †Permethistida).

Within Pterygota, Odonoptera are one of the oldest lineages, and it also bears the most autapomorphic wing organ. This combination of extreme attributes made the full homologization of the wing characters exceptionally confusing. The odonate wing articulation was fully homologized only in 1983 (by this author), and the venation only in 1984 (by RIEK & KUKALOVÁ-PECK). Here, shared characters of articular plates, venational fusions and braces are analyzed in more detail. New, even more complex, synapomorphies are identified, first in the Paleozoic dragonflies and mayflies, and then again in their now obscured state in modern higher taxa.

During the last 20 years, mainstream entomological systematics (concerned mainly with species and genera) has progressed remarkably in accuracy and objectivity with the introduction of computerized systematics. In this, similarities in as many as possible character series are recorded (usually) by classical comparative morphology (SNODGRASS 1935) and then processed by sophisticated computer programs. The programs statistically separate reversals and other secondary variants from genuine (groundplan-level) synapomorphies, and deliver objective, defensible phylogenies in species, genera and in some families. However, when systematists tried to find the re-

lationships in the pterygote higher taxa (orders, lineages, divisions) the resulting phylogenies were uncertain and confusing. First, Odonoptera were shown as the sister of Neoptera (KRISTENSEN 1975, 1981, 1991; many followers), at first mainly because these taxa bear similar broad mandibles manipulated by shearing musculature and a posteriorly shifted hypopharynx, plus some isolated similarities. Surprisingly, the wing organ including by far the largest number of synapomorphies was never properly analyzed, but sidestepped and the existing data supporting Palaeoptera + Neoptera were not refuted, but ignored. The outdated model for the limb organ was the same as used by MANTON (1977, and before). Soon, a different set of similarities and some molecular data showed Odonoptera as the sister of Ephemeroptera + Neoptera. Then, another morphological and molecular data set confirmed their previous classification as the sistergroup of Ephemeroptera. In the last decade, the merits of these three different datasets were intensely scrutinized, but final consensus was never reached (see HOVMÖLLER et al. 2002, OGDEN & WHITING 2003, and WILLKOMMEN 2008 for details and references).

Some entomologists expressed hope that even larger datasets and/or improved molecular data will solve the Odonoptera problem. Others came to believe that the culprit is morphology, which in higher taxa is “incapable” of delivering characters explicit enough to resolve its own morphological phylogenies! If accepted as true, such an embarrassing inability of evolution to leave its marks in the largest animal group (winged insects) is the kind of ammunition creationists are waiting for. The truth is quite different: the problem is not new at all and it had been theoretically analyzed and resolved decades ago by HENNIG (1969, 1981). For a detail review of different systematic problems and solutions in the lower and the higher hexapod taxa, see KUKALOVÁ-PECK (2008).

As generally acknowledged, the synapomorphies of pterygote divisions, lineages and orders in living species are obscured by post-groundplan adaptations. These created convergencies and parallelisms, which cannot be separated from genuine synapomorphies by classical comparative morphology alone. When computers process false data, no matter which programs are used, the results are falsified as well. Since homoplasies in the higher taxa are significantly more frequent than readily recognizable synapomorphies, more data make the situation even worse, and never better. The consensus is that comparative morphology alone is, simply, too limited for the old modern higher taxa! For more information see KUKALOVÁ-PECK (2008).

Arthropods are all legs (SMITH 1970; MARSHALL et al. 1994; RAFF et al. 1991; RAFF 1996; WILLIAMS & CARROLL 1993; SHUBIN et al. 1997; KUKALOVÁ-PECK 2008). As a cautionary tale, remember that 40 years ago the all-arthropod

limb (now presented as polyramous with exites and endites and 11-segmented: KUKALOVÁ-PECK 2008, fig. 1) was interpreted by classical comparative morphology as without rami, and bearing only 6–7 podites (lacking 3–4 podites) (SNODGRASS 1935). Since all arthropod appendages could not be derived from such an impoverished ancestral model, phylum Arthropoda had to be (perfectly logically!) disassembled. The limb appendages most frequently cited were mandibles, erroneously interpreted as one segment (MANTON 1977 and before, references). Instead, all arthropod mandibles include three segments plus two endites, which only may look like one segment! As a result, Hexapoda which actually do show three-segmented mandibles as a plesiomorphy (in modern Archaeognatha) were transferred to a polyphyletic phylum “Uniramia” and it took 17 years to reunite them convincingly back with Arthropoda (KUKALOVÁ-PECK 1992, 1998, 2008; WÄGELE 1993, 1996). In the last two decades, the limited comparative method and its disastrous ancestral “panarthropod” limb model (based on highly derived thoracic legs of grasshoppers!) again sneaked back into the higher taxa of Hexapoda on the coat tails of a genuinely progressive computerized systematic method, only to confuse the understanding of Parainsecta, Diplura (the sister of Insecta), and the basal split of Pterygota (KUKALOVÁ-PECK 1983, 1987, 1991, 1992, 1998, 2008; KUKALOVÁ-PECK & RICHARDSON 1983). As a fact verified then and now again, defensible synapomorphies are found only when the systematic rules outlined by HENNIG (1969, 1981) calling for full homologization at the groundplan level, are followed. The remedy is to approach modern Odonata, Ephemera and Neoptera much more broadly, with evolutionary evidence and with data known in genetics, developmental genetics, ontogeny, physiology, arthropod anatomy, etc., to reach this required level of character attributes.

The purpose of this account is to show, by concrete examples, that this thematic goal is doable, and that it offers objective and repeatable systematic results. Once the all-apterygote protowing ancestor was established (based on a long-term research), the groundplan-level synapomorphies in the limb/wing organ system of Odonoptera and Ephemeroptera are quite clearly recognizable in the Paleozoic ancestors. It is their expression in the modern higher taxa, Odonata and Ephemera, which makes them opaque. Most of them “blend” together as phylogenetically uninformative states and are easily overlooked. However, by applying Hennigian principles, they can be clearly identified with help from fossils.

As a very important step in the phylogenetic research of the higher taxa, all data and identifications in morphological organ systems must be thoroughly crosschecked, supplemented, and scrutinized for support by the evolutionary processes indicated in other biological fields (such as, by dragonfly ontogeny: see evidence below). The natu-

ral urge to trust explicitly the “direct” evidence available in modern fauna to indicate truthfully the grand evolutionary-morphological events is rarely the best choice. As evolutionists use to caution: the adage “seeing is believing” packs lots of visual risks of unbelievable errors.

1.1. Morphological concepts and terms

To avoid possible confusion, the concepts and terms in the limb-wing organ system used in the following text, are shortly reviewed:

Nomenclature. – The higher classification of dragonflies has become quite complex, and is not always reflecting evolution. The internal phylogeny of Odonoptera was significantly improved by BECHLY (1996, 1999) and by BECHLY et al. (2001) and is followed here. Odonoptera and Ephemeroptera is a name used for the lineage. Protodonate dragonflies are considered a grade. Odonate dragonflies are a clade and a synonym for Odonatoclada BECHLY, 1999. Odonatoclada includes the modern order Odonata. Paleozoic Ephemeroptera belong to the order †Syntonopterida and †Prottereismatida. Order Prottereismatida is the sistergroup of the modern order Ephemera.

Monophyly. – The Hennigian evolutionary phylogenetic approach and the groundplan systematic method (KUKALOVÁ-PECK 2008) are followed. The wing organ system in a monophyletic Pterygota must be flawlessly derivable from a single protowing model and by using exactly the same criteria for separating plesiomorphies from apomorphies. The limb/wing character states used here were homologized and evaluated with respect to a single all-arthropod limb model and the all-apterygote protowing (KUKALOVÁ-PECK 2008, figs. 1, 17). Reliable synapomorphies shared by divisions, lineages and orders are found only in their groundplan character states (HENNIG 1969, 1981). For a review of evolutionary models and the application of the groundplan method, see KUKALOVÁ-PECK (2008, figs. 1–21).

Protowing. – The first evolutionary model of the pre-flight pterygote protowing was reconstructed in 1983, by this author. This was based on the step-wise transformation series of veinal systems recorded in all pterygote lineages, from the Paleozoic to modern times. The least modified (fused, reduced) states in eight principal veins were selected from a significant sample in each higher taxon, compared, and the least modified reconstructed into a single protowing shared by all Pterygota. Against expectation, this protowing model was later found in fossil prothoracic wings, which were never used in powered flapping flight! These shared similar plesiomorphic veinal system in Carboniferous Odonoptera and Palaeodictyoptera, which bear very different meso- and metathoracic

flying wings. Thus, the protowing model used here is based both on the extremely broad data from modern insect orders, and on the evidence from fossil record (KUKALOVÁ-PECK 1983, figs. 13–15; 2008, fig. 17). The plesiomorphic wing articulation arranged in separate rows following blood pathways was found in Palaeodictyopteroidea: †Diphanopteroidea. This also was verified against significant samples from all modern lineages (KUKALOVÁ-PECK 1998; 2008, fig. 18). The pteryogote articulation models used here include articular sclerites in their least fused and reduced state.

Articular sclerites. – These are fragments of the muscled epicoxal pleuron (= first arthropod limb podite flattened and imbedded into the pleural membrane) (KUKALOVÁ-PECK 2008, fig. 17). This is articulated dorsally to the tergum and ventrally to the subcoxa (shaped either as a cylindrical podite (in mouthparts and male genitalia) or as a pleuron (on thorax and on pregenital abdominal segments) (KUKALOVÁ-PECK 1991, 2008). Horizontally, the sclerites are arranged in rows protecting the limb blood pathways, delivering blood to principal veins of the wing ramus (Figs. 6A, 11–15). Each of the eight rows, named after their veins include three sclerites: proxalare (PR), axalare (AX), and fulcalare (F). The fulcalare always articulates with the same wing basivenale (B). Vertically, wing sclerites form columns (proxalar, axalar, fulcalar, and basivenal). Proxalaria and axalaria originated from subdivided epicoxal pleuron, and fulcalaria, probably from the muscled base of the wing ramus. On the wing-side from the wing flexion line, which runs distad from fulcalaria, basivenalia (B) are the sclerotized blood sinuses of the eight principal veins. Wing basivenalia have no muscular insertions. Wings are moved by muscles attached to the thoracic epicoxal sclerites and indirectly, by the movement of thoracic segments.

These evolutionary conditions indicate that wing sclerites, which are articulated in rows, inserted with muscles and arranged in regular columns are ancestral to all Pterygota and thus plesiomorphic. Fusions between sclerites, either in rows, in columns, between columns, to the tergum, to the subcoxal pleuron, or to basivenalia are derived and thus offer higher-level synapomorphies. Paleopterous articular plates and composite sclerites, and neopterous mobile axillary sclerites, wing processes, and medial and humeral plates are identified below as non-homologous clusters composed of different row-sclerites. Therefore, they are derivable only from the shared common ancestral model (the muscles are homologous, but the sclerite clustering is different).

The comparative morphological interpretation based directly on the modern fauna is quite different. Wing sclerites are seen as irregularly distributed cuticular fragments, which are mostly considered directly homologizable. Much effort over many years has been spent to find a

convincingly shared pattern (WILLKOMMEN & HÖRN-SCHEMEYER 2007; WILLKOMMEN 2008, and for references), but no consensus was reached.

Articulation symmetry and blood flow. – The relationship between the limb blood flow into the wing appendage and the alignment of articular sclerites with wing basivenalia and veins was researched by the insect physiologist ARNOLD (1964) (KUKALOVÁ-PECK 1978, 1983). The original row-sclerites are still clearly visible in fossil dragonflies (Figs. 5, 6B, 13), fossil and modern mayflies (Figs. 11, 12), and in most parts of the neopteran articulation (Fig. 14) (HAAS & KUKALOVÁ-PECK 2001). In all lineages of modern Palaeoptera and Neoptera, the row arrangement is retained and can be recognized (KUKALOVÁ-PECK & LAWRENCE 2004, figs. 29–33; KUKALOVÁ-PECK 2008, figs. 18, 19). This shows that all modern lineages, no matter how modified their wing articulation may be, retained the underlying row arrangement of sclerites.

Venation system. – At the wing base, each blood channel forms a sclerotized blood sinus called a basivenale (B), which gives rise to a pair of separate veinal sectors, each dichotomously branched two to three times (each vein is a fully dichotomous branching system adapted to fill out the space). The protowing shows a slightly reinforced anterior wing margin (indicating motion), but completely lacks the veinal fusions and braces (which are necessary for powered flight; these were added later and are not shared by all Pterygota). But, even the precosta bears two veinal sectors (in some modern Ephemeroidea: personal communication by T. SOLDÁN). This ancestral model rules that the veinal stems, crossvein braces and veinal fusion braces, which characterize modern higher taxa, are all derived and potentially synapomorphic. Note that braces close to the wing base mark the diversification of early flight, and deliver clear and testable division- and lineage-level synapomorphies (see below). Example: The division Palaeoptera shares two veinal stems (the stem of M and of Cu), while the division Neoptera does not share any veinal stems, which can be found in all lineages! For the history of fully homologized venation in Odonatoptera wings, see RIEK & KUKALOVÁ-PECK (1984), KUKALOVÁ-PECK (1983, 1991, 1992, 1998, 2008), HAAS & KUKALOVÁ-PECK (2001), KUKALOVÁ-PECK & LAWRENCE (2004), and the text below.

Groundplan character states in higher taxa. – In modern higher taxa, groundplan character states are those which are the least derived (with respect to the protowing) and present in a significant sample of all representatives (living and fossil). This requires some explanation. A taxon without a groundplan cannot exist (HENNIG 1981). Groundplan characters are always present, either visibly or obscured (most often by reductions, e. g., in size) and fusions. In the higher taxa the groundplan-

level fusions never become “unfused” and reductions “un-reduced” (reversals are completely absent; any changes in the groundplan would change the taxon itself). However, post-groundplan adaptations added at the family, genus and species levels are often impossible to eliminate without evolutionary clues (see examples below). Therefore, since only the groundplan characters contain reliable synapomorphies, their convincing separation and identification is crucial for unveiling the relationship between the higher taxa.

Predictability of the wing character transformation series. – With reversals absent in the higher taxa (HENNIG 1969, 1981; KUKALOVÁ-PECK 1983 to 2008), and the ancestral protowing lacking fusions, braces, and reduction between wing veins and wing sclerites, all these later adaptation can only be added, but never removed. This predictability is the Rosetta stone of higher-level phylogenetic analysis, because it provides the systematic tool for an objective recognition of the plesiomorphic, apomorphic and synapomorphic states. They stand out when the specimens are compared with the protowing. This so-called groundplan method (KUKALOVÁ-PECK 2008), applied in a significant representative sample, is first used to identify the groundplan character states in all higher taxa (of Pterygota), and second to select the reliable synapomorphies which they share (see examples below). If it appears to be a long-term, labor-intensive process, this impression is correct. But, the foundation has been finally established and now it is time for fine-tuning. Comparative morphology approach in the limb/wing organ system based on modern and close to modern fauna is a very considerable shortcut, but it does not resolve phylogeny of the modern higher taxa with Paleozoic origin.

1.2. Collecting, fossilization, matrix, and observation methods

Mazon Creek nodules. – The middle Pennsylvanian (Moscovian) fauna of Mazon Creek offers three-dimensional remnants of terrestrial and aquatic arthropods with well-preserved delicate morphological details. The decomposing organisms attracted iron ions percolating in mud, and these formed around them hard ironstone nodules composed of pyrite and limonite. An insect remnant is found in about every 115 nodules. Freshly excavated nodules cannot be split open without severely damaging the fossil. They should be kept submerged in water in buckets for two or more winters, subjected to repeated freezing, and only then are they ready to split into two perfect halves along the plane of weakness occupied by a fossil. This lengthy process makes casual collecting unproductive, and the abandoned mining area is rapidly disappearing under vegetation and new housing development.

Dr. E. S. RICHARDSON, the legendary former custodian of the Chicago Field Museum, met the challenge by recruiting help from more than 100 volunteers living near the coal mining area. For three decades, these amateur paleontologists spent their free time collecting and processing Mazon Creek nodules. The fossils were then brought to the Field Museum, where they were expertly prepared, identified and catalogued. Dr. RICHARDSON provided instructions and encouragement, organized meetings and exhibits, and arranged lectures by visiting scientists. Private collectors competed with each other in making important discoveries. When Dr. RICHARDSON was active, almost all private collections were donated or willed to the Field Museum. Later, many specimens were sold abroad or ended up in other museums willing to interact with collectors. During my frequent visits, I was able to study fossil insects in private homes. Large homoiopterid Palaeodictyoptera (KUKALOVÁ-PECK & RICHARDSON 1983, figs. 3–6) opened the path towards the full homologization of the wing articulation in Odonatoptera, Ephemeroptera and Neoptera (KUKALOVÁ-PECK 1983, 1985, 1998). The owner refused to donate or sell this historical holotype, which was later knocked down by a cat and broken. Good casts made by Dr. RICHARDSON as insurance, are available in the Field Museum as well as in my collection.

Preservation of fossil insects. – The rare attribute of Mazon Creek fossils is that they are preserved more or less three-dimensionally, with appendages in a nearly natural position (NITECKI 1979). Mouthparts, antennae, legs, leglets, and genitalia are usually buried in the matrix and must be dug out. Heads and bodies were often desclerotized and deformed by pressure before petrification, and then thinly coated with strongly adhering white kaolinite. The splitting plane often runs partly outside and partly through the middle of insect bodies, so that the imprint and counter-imprint do not exactly match (labial mask of the dragonfly nymph described here is preserved only in one half of the nodule). Genitalia are often seen in dorsal view, from inside the abdomen. Exiters, endites and vesicles are delicate features smaller than the grains of matrix, yet they are sometimes distinctly preserved. Desclerotization makes some structures semi-transparent and visible through the skeleton. There is often some free space around fossils, with protruding patches of kaolinite and lumps of pyrite. These occur on the natural inner surface and not as the sign of in-depth preparation, as some paleontologists hypothesize without attempting hands-on preparation of Mazon Creek nodules.

Preparation and coating. – Mazon Creek fossils have yielded fine details of limb morphology, wing articulation, genitalia, cercopods, head structures and mouthparts, which may not have been otherwise homologized correctly in modern insects (KUKALOVÁ-PECK 2008). Minute limb podites, exiters, endites, sclerites and sutures

are usually coated with kaolinite glued to cuticle. When chipped away, it often scalps carbonized chitin so that features look “artificially sculptured”. The hard matrix is best removed by a heavy-duty vibro-engraver with a chisel-shaped sharp iridium point. Preparation of a good specimen is slow and usually takes more than one day. Small debris constantly conceal newly uncovered sutures and morphological details and must be brushed away with a fine brush and cleaned. Brush strokes almost instantly produce a reflective sheen. This does not harm the fossil but is unsightly and lowers the visibility of the details under a microscope. Application of a light (grey) coating of ammonium chloride completely solves the problem and enhances fine details. The coating is hygroscopic and must be washed off by water after each session to prevent formation of hydrochloric acid. Preparation of hard matrix requires considerable practice, a morphological background and lots of patience since fine details are easily “prepared off” rather than out.

Illumination and observation. – Fine details in fossil insects are best seen when illuminated at a very low angle from 10 o'clock and/or from 2 o'clock, and by two gooseneck illuminators, which are used one at a time. For best results, the fossil is held in the hand, turned slowly around 360 degrees, and rocked back and forth to catch the best light. Sunlight should be always used as well, as it sometimes brings out colour shades and a significant visual enhancement. An exact angle of light is often needed to make visible the weakly preserved exites, mouthparts, segmentation in the head and leglets, etc., which tend to be overwhelmed by the grainy, uneven and reflective matrix. Observers not familiar with Mazon Creek fossils often need help with illumination. Individuals with a naturally low ability to distinguish details on the uneven surface, or lacking stereoscopic vision, may miss fine details altogether. Unshakeable belief in faulty panarthropod limb model (with 6–7 segments and no rami) appears to lessen observation abilities as well. A correct limb model is absolutely crucial for full homology and evaluation of the limb-derived appendages, which deliver by far the largest, most informative dataset for arthropod-insect phylogenies. It is unfortunate that insect specialists are often not familiar with the complexity and phylogenetic importance of the old arguments about how many muscled segments, exites and endites are included in the ancestral pan-arthropod limb. Hence, they often overlook the epicoxal pleuron, exites, prefemur, patella and basitarsus rather often visible in Paleozoic insect palps, legs, leglets and gonostyli. The sole reason is that they are not expected to be there! But, surprisingly, they are still retained in some modern insects and are unrecognized (see a review by this author, 2008). Unfortunately, a denial of their presence is fatal for realistic arthropod and insect phylogenies.

Museum specimens and posterity. – After the surface of *Dragonympha srokai* n. gen., n. sp. became reflective, the Field Museum authorities decided to treat it with ultra-sound to remove the sheen so that the holotype would be in good shape when returned to the Illinois State Museum in Springfield. In a split second, the ultrasound dulled the irreplaceable, finely preserved morphological details and almost completely erased the weakly imprinted labial mask. During a later visit to Springfield, I obtained permission and removed the thin, dulled surface layer with some success, but the sheen returned. The red flag is out that the ultra-sound technique is extremely harmful to the Mazon Creek fossil, and should be completely avoided.

The purposes of keeping insect collections in the museums are multiple and complex. The dilemma is to which extent should specimens be preserved for posterity in a pristine original state? Should they be, ever, exposed to a potentially harming preparation and dissections by competent specialists? In 2001, F. HAAS (the world foremost functional morphologist in earwig wing folding) and I (with two decades of evolutionary study of the pterygote wing articulation and wing base braces on my credit) co-authored a detailed phylogenetic analysis of the earwig wing base. Yet, we were not allowed to open the wings of earwig specimens from two rare families for fear that they may be damaged! The opportunity that two narrow specialists in two extremely broad fields meet again to completely analyze the utmost complex insect wing folding from an all-apterygote evolutionary view, may not repeat itself any time soon. Since posterity now has four vials of completely undamaged earwigs, the pertinent question is – for which better purpose? In the specimen of *Dragonympha srokai* n. gen., n. sp., the preparation uncovered unique scientific evidence. This was later diminished for a parallel reason – so that posterity had a better-looking holotype.

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2. Systematic paleontology

Infraclass Palaeoptera MARTYNOV, 1923
 Hydropalaeoptera ROHDENDORF, 1968
 Superorder Odonatoptera MARTYNOV, 1932
 Order Meganisoptera MARTYNOV, 1932
 Family incertae sedis

Genus *Dragonympha* n. gen.

Typus generis: *Dragonympha srokai* n. sp. This genus is monotypic and is known only from the holotype (obverse and reverse).

Derivatio nominis: From dragon (English) as in dragonfly, and nympha (Latin); feminine.

Diagnosis. – Young nymph of a large adult. Head: Segmentation distinct. Antennae moderately long and heavy, with relatively long joints. Labial mask with very narrow basal portion, centrally incorporating a long and narrow sternum; prementum includes serrated, very broad paraglossae (almost as long as palps), and slender and pointed labial palps (glossae not preserved). Thorax: Protergum large and complete, with acrotergite, prescutum, and reduced prothoracic wings fused to it laterally. Prothorax equally long as mesothorax but shorter than metathorax. In the mesothorax, the acrotergite and prescutum distinctly preserved. In the mesothorax and metathorax, the pleural sulcus associated with a pleural inflexion running parallel to it anteriorly, and dissecting katepisternum. Another parallel dorso-ventral inflexion dissects epimeron. Ventral wing process (VWP) distinctly developed, two-pronged. Wings: Nymphal wings articulated, at rest held in uplifted position. The size is relatively much larger than in any modern nymph of a comparable developmental stage. Wing veins distinct, veinal system protodonate and bearing short intercalated branches as in Meganisoptera. Basalar and subalar sclerites are sclerotized. Thoracic legs long, robust, with patella (PAT) separated from tibia (TI) by a deeply incised suture. Abdomen is similar as in adults, slender and much longer than in modern nymphs. Abdominal terga flanked by lateral ridges (epicoxal pleura fused to terga?) followed by long and narrow plates representing subcoxal-to-trochanteral pleura (exact homology uncertain). Last pleural plate bears serial posteriorly articulated leglets, elongated and adapted as respiratory filaments. Abdominal leglets (incomplete) composed of tubular, movably articulated podites.

Relationship. – *Dragonympha* n. gen. is a young nymph of a large adult, which bears articulated and fully movable wings with protodonate veinal system, a long and slanted CuP crossing, and veinal branches with short veinal supplements. These character states occur in the gigantic †Meganisoptera, which is the most probable order of provenance. The wings and the abdomen of *Dragonympha* n. gen. are morphologically much closer to those of adults

than are those in the nymphs of modern Odonata. The labial mask is strongly autapomorphic. These two character states exclude the nymph from Odonatoclada (which include modern Odonata).

Remarks. – In Paleozoic †Palaeodictyopteroidea and Ephemeroptera, the abdominal epipleura form ridged side-lobes separated from the terga by deeply incised sutures. In †Diaphanopteroidea, which are closest to the all-apterygote groundplan, ridged abdominal epicoxal pleura are followed by three flattened coxopodal pleura: the subcoxal (SCX), coxal (CX) and trochanteral (TR) pleuron. Abdominal leglets (telopodites) are articulated distally to the trochanteral pleuron (KUKALOVÁ-PECK 1983; 1991; 1992, figs. 27, 37; 2008, figs. 15, 20). But, in *Dragonympha* n. gen., there is no suture separating the epicoxal pleuron from the tergum and there are probably only two pleural plates, to the second of which the gill filament is articulated; therefore, an accurate homologization of the abdominal pleuron probably includes pleural fusions and is uncertain.

Dragonympha srokai n. sp.

Figs. 1–3

Holotype: Specimen No. ISM 004 ab, Illinois State Museum, Springfield, Illinois, USA.

Derivatio nominis: In recognition of paleontologist Dr. STEVEN D. SROKA, who found the unique nymph and generously donated it to the collection of the Illinois State Museum in Springfield, Illinois.

Stratum typicum: Pennsylvanian (Moscovian).

Locus typicus: Mazon Creek area, Will-Kankakee County, Francis Creek shale, Pit 11, Peabody Coal Company, Illinois, USA.

Diagnosis. – Same as genus (monotypic).

Preservation. – The holotype of *Dragonympha srokai* n. gen., n. sp. is preserved in an ironstone nodule with some free space left inside, containing crystals of pyrite, limonite, and kaolinite. The nodule split in two halves along the plane of weakness containing the fossil. The holotype is slightly 3-dimensional, with the exo-skeleton softened and deformed before petrification. The imprint and counter-imprint do not match. Head segmentation, antennae, tergal sclerites, abdominal pleura, and abdominal gill filaments are preserved in both halves, thoracic pleura are much better preserved in the reverse, and the labial mask occurs only on the obverse half of the nodule. Note that because of these differences, some photographs do not fully match with the figures. To provide full interpretation, a figure was made on transparent paper, flipped back and forth, and the details were drawn in two colors. This method allows one to decide which detail in which half is better preserved, and to combine them into one drawing as accurately as possible. This is a customary, practical procedure for Mazon Creek 3-dimen-

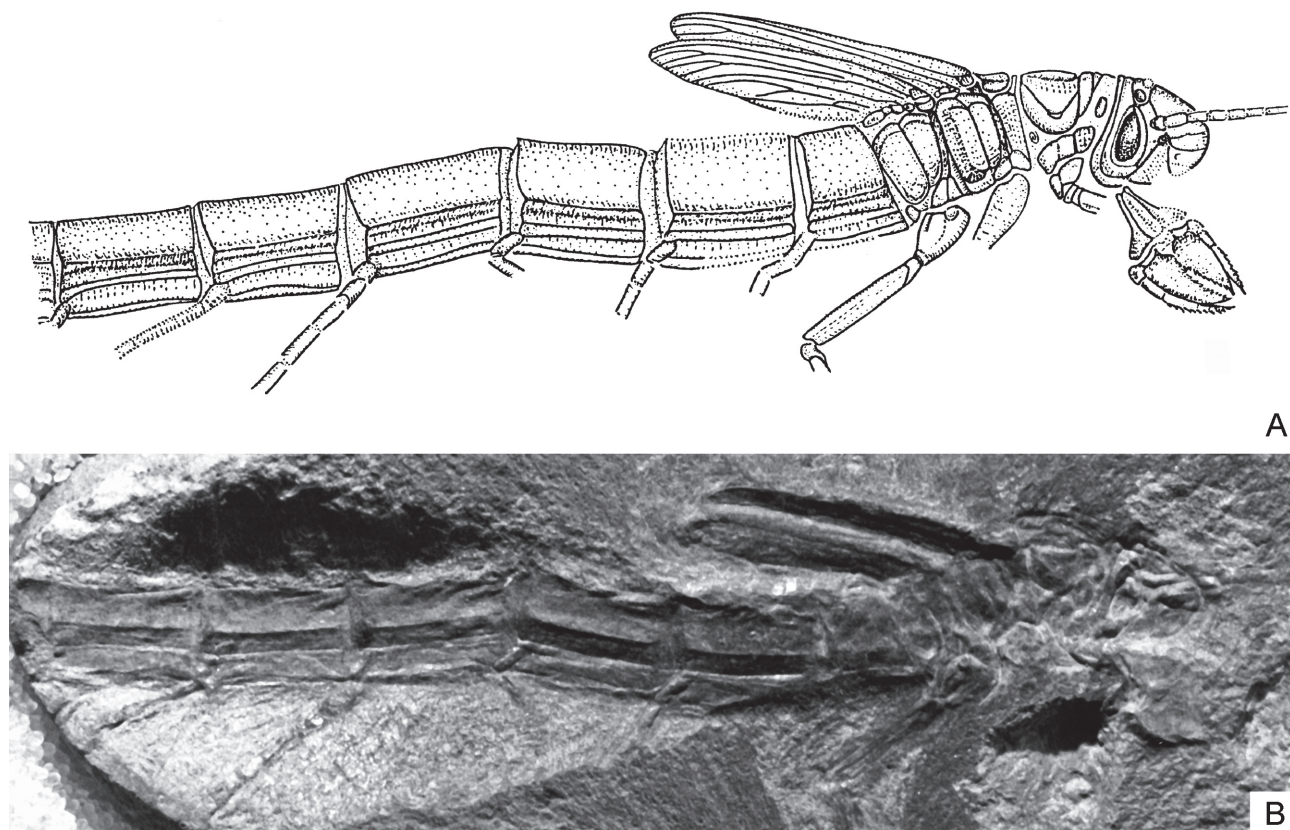


Fig. 1. *Dragonympha srokai* n. gen., n. sp., holotype (†Meganisoptera). Young nymph of a large adult. Labial mask extended, wings uplifted (flexible, not fused to body) and streamlined with body, abdominal gills derived from segmented leglets, thorax with multiple reinforcements, anepisternum not expanded. Pennsylvanian (Moscovian), Mazon Creek, Illinois, USA. – **A.** Composite figure, obverse and reverse combined. **B.** Obverse of the holotype, uncoated, the end of abdomen missing. – Length of the remnant without antennae = 38.1 mm. Original.

sional fossils. Consequently, the photographs of both halves do not completely match with the combined figure! In the past, some of my combined figures were unjustly criticized as “inexact” and “controversial” (repeatedly by A. G. RASNITSYN), even when the figured structures still exist in living insects. Combined figures are much more accurate and user-friendly than two non-matching mirror images accompanied by a verbal interpretation. Figs. 1A and 2 are composite presentations of all morphological features in obverse and reverse halves, combined.

Description. – Young nymph in full lateral view preserved on two halves of an ironstone nodule shows a segmented head, antenna, extended labial mask, thorax with incompletely preserved legs, and seven abdominal segments with posteriorly articulated filamentous gills. The shape of the head, extended labial mask and the presence of respiratory abdominal filaments prove that *Dragonympha srokai* n. gen., n. sp. is a true protodonate nymph and not a newly emerged adult in which the wings have not yet expanded.

Dimensions: Length without antennae 38.1 mm; head, length 3.3 mm, height 3.8 mm; prothorax, length 2 mm; pterothorax, length 4.8 mm, height 4 mm; abdomen, length of the fragment 28 mm; 2nd abdominal segment, length 4.7 mm, height 3.4 mm.

For better clarity, the description of features below is immediately followed by remarks, which offer broader interpretations and additional evidence.

Head, cranium: For an updated evolutionary reference model of insect head see KUKALOVÁ-PECK (2008, fig. 6). The epipleuron (= the first flattened segment of the limb-derived mouthparts in Arthropoda) is fused to the ventral end of all head terga. The labrum, mandible, maxilla and labium in Hexapoda are formed by the entire coxopodite; this is articulated to epipleuron by its subcoxa and bears two endites (coxal and trochanteral) (SHEAR et al. 1998; KUKALOVÁ-PECK 1998, 2008, figs. 6, 12). Acron (a flap bearing sensory organs, not a segment) shifted far dorsally and into tergum I and II, which became reduced to a thin rope loop running around the eyes (as a ring) and

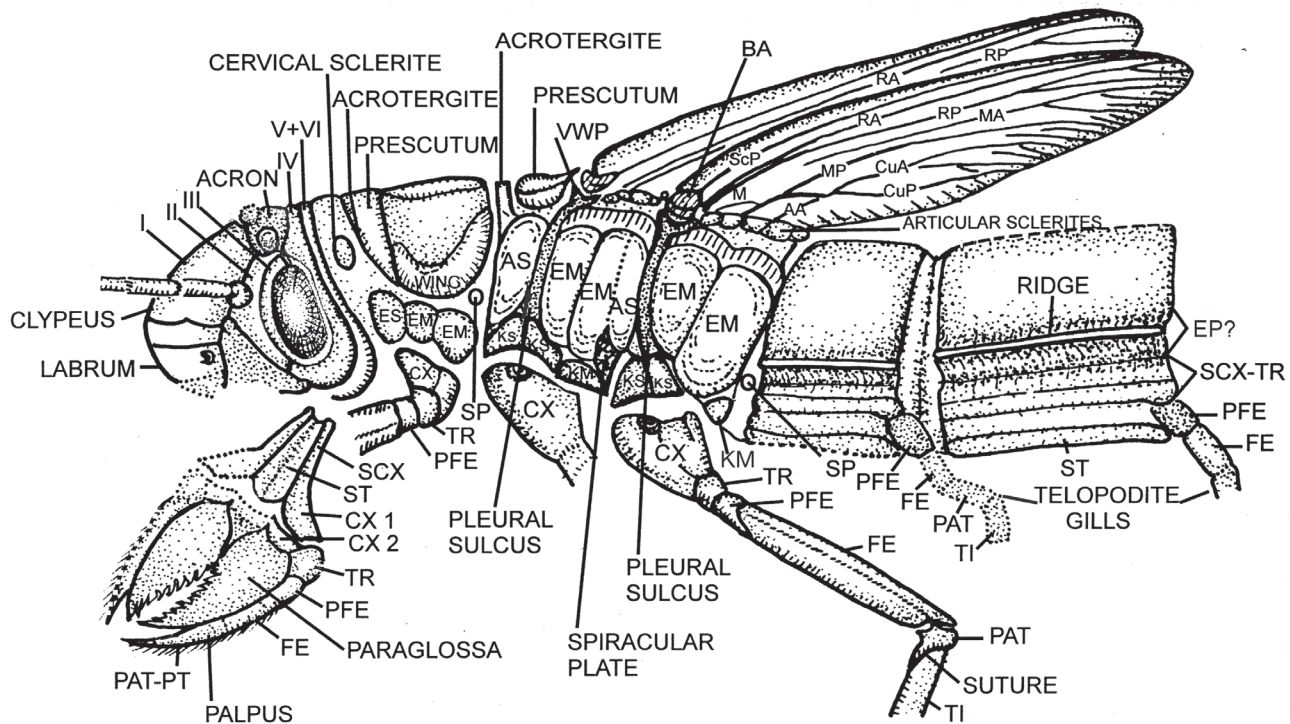
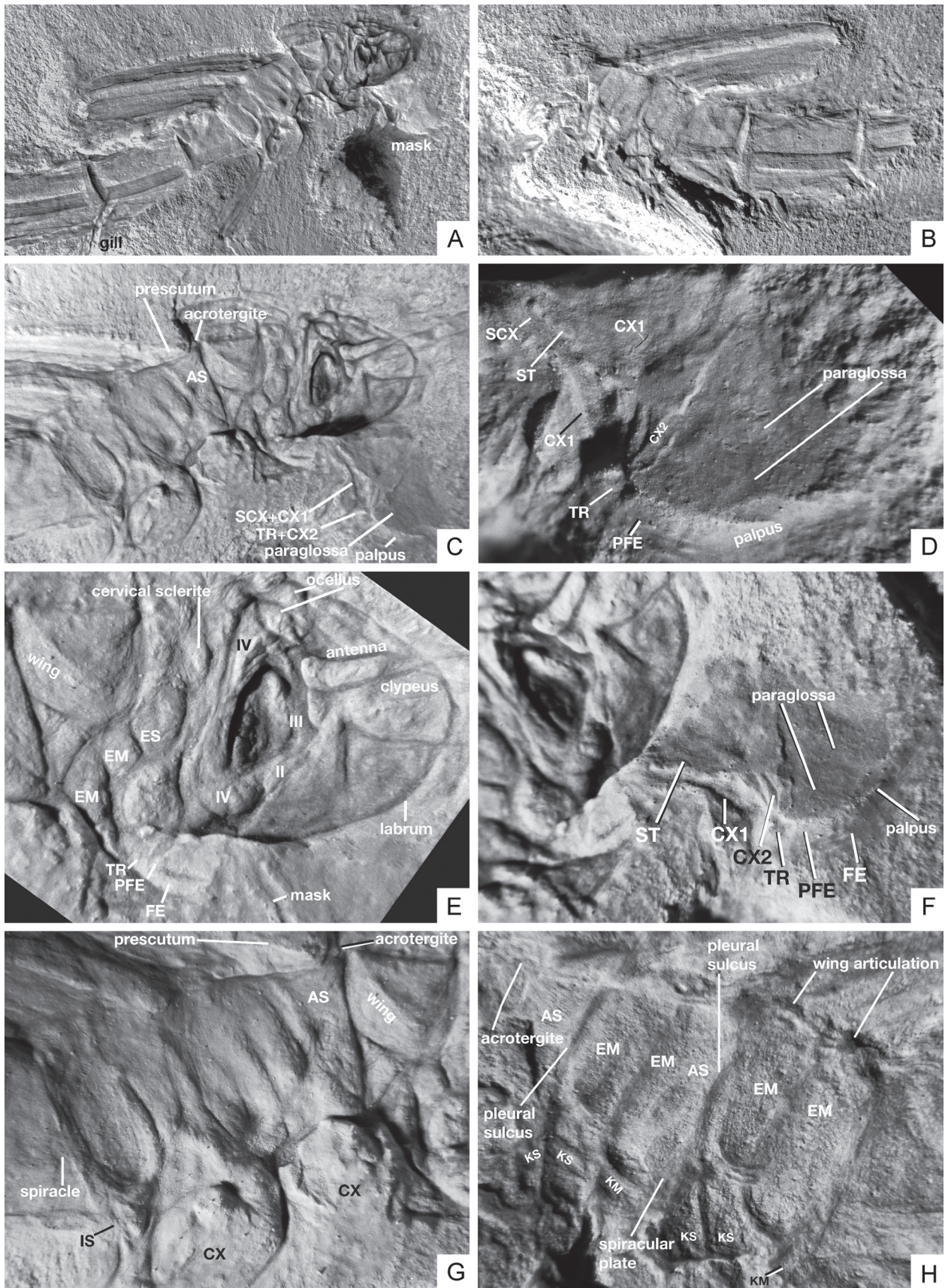


Fig. 2. *Dragonympha srokai* n. gen., n. sp., holotype (†Meganisoptera), morphological interpretation. Head tergum I, II, III forming a strip surrounding the eye, tergum III not delimited above the eye, epipleuron III invaginated to bear hypopharynx, tergum+epipleuron II and IV meet at the invagination scar. Labial mask: subdivision of CX into CX1 and CX2 serving as a hinge; ST VI flanked by SCX fused to CX1; CX2 narrow, flanked by a protruding TR; telopodite-based palpus narrow, pointed and barbed; very broad paraglossae with small even teeth, glossae unknown. Mesothorax: anepisternum (AS) placed between acrotergite and prescutum; pleural sulcus subdivides katepisternum (KS); parallel pleural inflexion subdivides epimeron (EM); wings articulated and uplifted; thoracic legs with distinct TR, PFE slanted and fused to FE, PAT slanted and fused to TI. Abdomen: boundaries between abdominal pleural plates (EP to TR) uncertain; telopodites (PFE to PT) with movable podites serving as respiratory filaments. – Symbols: AS = anepisternum; BA = basalare; CX, CX1, CX2 = coxa, subsegment 1 and 2; EP = epipleuron; ES = episternum; FE = femur; KM = katepimeron; KS = katepisternum; PAT = patella; PFE = prefemur; PT = pretarsus; SCX = subcoxa; SP = spiracle; ST = sternum; TI = tibia; VWP = ventral wing process. Original.

the dorsal acron, above which they leave no noticeable trace. Acron small and clearly delimited, bearing three ocelli close to each other and eyes. Eyes are middle sized, laterally placed and broadly framed by tergum III. Ventral ends of tergum I meet ventrally from acron, abut laterally, and fuse one to another (this fusion also brings together epicoxal pleura and coxopodites I, fused into labrum). Tergum I forms a large clypeus, dorsally extended and ventrally fused to labral epipleura. Coxopodites I fuse laterally one to another and into the labrum. Antennal appendage shifted upward into the ventral portion of tergum

II. It bears a very short scape (SCX), slightly longer pedicel (CX), and narrower flagellum (TR through PT is flagellated). Antennae are probably medium long, much more robust than in modern fauna. Eye pushed deep into the tergum III, which forms around it a distinctive strip, broader anteriorly and above, narrower posteriorly, and invaginated ventrally. Dorsal portion of tergum III is not delimited and is possibly fused to tergum IV without a suture. Ventrally, epicoxal pleuron fused to tergum III invaginates inside the head and its limb appendages fuse together to form hypopharynx. Tergum II and tergum IV

Fig. 3. *Dragonympha srokai* n. gen., n. sp., holotype (†Meganisoptera) coated with ammonium chloride. Symbols as in Fig. 2. – **A.** Obverse showing labial mask, but head originally covered by matrix. **B.** Reverse lacking head and not matching obverse. **C.** A close-up of 3A with light at a different angle. **D.** Labial mask: narrow palpus is steeply slanted towards horizontal paraglossa. **E.** Head: eye surrounded by tergum I, II, III; tergum III narrowing into a suture ventrally from the eye; prothoracic pleuron with three invaginated sulci. **F.** Labial mask in a different light angle than in 3D (protruding parts falsely appear as sunken). **G.** Obverse of meso- and metathorax: acrotergite, bulging prescutum, and three pleural inflexions distinctly preserved. **H.** Reverse of meso- and metathorax: Sulci shown in different light angle. Katepisternum (KS) dissected by an inflexion parallel to pleural sulcus. – Abbreviations as in Fig. 2. Original.



fuse together ventrally with a deep scar under tergum III, marking invagination of epipleuron III with hypopharynx. Tergum IV is narrow dorsally, encircling posterior part of the eye, broadened ventrally and extended proximally to meet epicoxal pleuron II at an invagination scar of epicoxal pleuron III. Tergum V + VI fully fused without a suture (a synapomorphy of Dicondylia), sinuous, very narrow dorsally but broadening latero-ventrally and ventrally.

Remarks. – The strip-like portion of tergum III anteriorly from the eye was first noticed and figured (without interpretation) in the Permian Ephemeroptera (KUKALOVÁ-PECK 1985, fig. 34B) and †Diaphanopteroidea (KUKALOVÁ-PECK 1985, fig. 33B). Later, the strip was recognized as part of tergum III (by KUKALOVÁ-PECK 2008, figs. 6, 7). *Dragonympha srokai* n. gen., n. sp. is the first fossil, which shows that the tergum III actually makes a full loop under the eye. A conspicuous, broad, crescent-shaped tergum III also occurs ventrally and anteriorly from the eye in †Monura (Insecta: †Monocondylia, the sister-order of Archaeognatha) (SHAROV 1966; KUKALOVÁ-PECK 1998, 2008, fig. 7). In all Hexapoda, the epicoxal pleuron III (fused to head tergum III, with limb appendages III articulated to it) invaginated into the head capsule under the eye and fused together into the hypopharynx. Only interpreting correctly the coxopodites forming labrum, mandible, maxilla and labium (rather than calling them – incorrectly – “coxae”) makes their characters useful in phylogeny. In predatory Odonatoptera, mandibles must generate strong bite. For this adaptation, they are broad and hypopharynx is shifted posteriorly to make place; a strong, permanent, socketed anterior articulation is formed, for shearing and opening sideways like a door on two pivoting condyles; and, some muscles are strengthened and other reduced. This adaptation yielded in Odonatoptera five convergencies shared with Neoptera, which group evolved similar shearing mandibles to chew hard vegetation (see “Conclusion” below). In contrast, in the maxillary coxopodite separate coxal and trochanteral endites (inner rami: lacinia and galea) are shared by all Arthropoda. In all Palaeoptera = (†Palaedictyopteroidea) + (Odonatoptera + Ephemeroptera) they are uniquely fused together into lacinio-galea. In Neoptera and other Hexapoda, these endites are separate (a symplesiomorphy: KUKALOVÁ-PECK 2008, figs. 6, 10, 11).

Like all other Palaeoptera, *Dragonympha srokai* n. gen., n. sp. has prominent eyes. This attribute doubtlessly coevolved with the prominently paleopteran trend of the time toward improving flight. The head is attached to prothorax, which is relatively short to very short, never elongate. These are the Palaeoptera groundplan characters. Therefore, a very small head with miniscule eyes on a long prothorax, that WILLMANN (1999) interpreted as belonging to a very large Carboniferous Ephemeroptera: †Syntonop-

terida: *Lithoneura lameerei*, is a neopteran remnant (possibly a young gerarid; see rebuttal continued below).

Mouthparts and antennae: The clypeo-labrum formed by limb appendages of tergum I, consisting of two epicoxae I and two coxopodites I fused along their lateral margins. Clypeo-labrum is transversely subdivided by secondary sulci and turned postero-ventrally, as in modern odonate nymphs. Limb appendage II (antenna) is heavier and much longer than in modern dragonflies (total length unknown). Antennae bear a small scape (SCX), long pedicel (CX), and slightly shorter flagellated antennal articles (seven articles preserved). Appendage III (hypopharynx) fully invaginated with epicoxae III under the eye, invisible. Appendage IV (mandible) includes coxopodite IV articulated by SCX (in Hexapoda, the mandibular telopodite is reduced); mandible is broad and extended obliquely antero-dorsally towards the secondary permanent clypeo-tentorial condyle (an autapomorphy of Odonatoptera). Appendage V (maxilla) is not preserved. Appendages VI (labium) are fused with labial sternum into a labial mask. This is divided into basal portion and prementum by a transverse hinge. The hinge runs through the labial coxae, subdividing them into two subsegments, CX1 and CX2: CX1 is part of the basal portion, CX2 of the prementum. Basal portion of the labial mask includes a long labial sternum in the middle. This is flanked on each side by a narrow subcoxa (SCX) fused without a suture with long CX1. Basal portion is very narrow proximally and broadening abruptly distally. Prementum bears a very short and thickened base composed of fused coxal subdivisions CX2, flanked by two short trochanters (TR). Labial palp (= telopodite VI) articulated to trochanter (TR) includes a long prefemur (PFE), weakly indicated femur (FE), a patella (PAT) fully fused to tibia (TI) through pretarsus (PT), ending in a pointed spike. Palp is equipped with dense lateral spines. Glossae (coxendites VI) not preserved. Paraglossae (trochendites VI) almost as long as palps, very broad, seemingly flat and with a sinuous inner margin equipped with about ten teeth. Paraglossae and palps appear to be partially fused.

Remarks. – The labial mask is extended, detached from the head and partially decomposed along the coxal subdivision into CX1 and CX2, which functioned as a hinge. Horizontal subdivisions in limb segments subcoxa and coxa (marked by sutures) may be plesiomorphic (Note that in pterygote thorax, the epicoxal pleuron is horizontally subdivided into the proxalar and axalar column of pteralia, and the subcoxal pleuron may be also subdivided.). Mandibles of Archaeognatha bear a coxa distinctly subdivided by a suture (KUKALOVÁ-PECK 1998, fig. 19.1; 2008, figs. 11, 12). All Arthropoda share the serially homologous (= homonomous) polyramous limb-derived appendages articulated to the epicoxal pleuron: the mouthparts (including labrum), antennae, legs, leglets, gonostyli,

cerci, wings, winglets, vesicles, and genitalia. By monophyly, these are all flawlessly derivable from a single ancestral polyramous limb model shared by all Arthropoda (KUKALOVÁ-PECK 2008, fig. 1). Evolutionary steps by which they are derived (fusions, reductions, modifications) provide numerous reliable higher-level arthropod and hexapod synapomorphies in the morphological system (KUKALOVÁ-PECK 1998).

Prothoracic spiracle: The placement of this non functional spiracle in the intersegmental membrane (rather than on a plate within the mesothorax) is considered here a plesiomorphy.

Prothorax and prothoracic winglets: Lateral cervical sclerite large. Prothoracic acrotergite and prescutum crescent shaped, also relatively large. Pronotum is large and well sclerotized, with a protruding medial ridge. Narrow prothoracic winglets fully fused to pronotum, separated from it by a deeply incised suture. Prothoracic pleuron very small, bearing a narrow episternum and an epimeron about twice as broad as episternum. Pleural sulcus simple, not accompanied anteriorly by pleural inflexion. Katepisternum and katepimeron are missing.

Remarks. – Prothoraces in Paleozoic Palaeoptera nymphs often bear small crescent-shaped prothoracic winglets, which in adults become larger and fully veined. These may occasionally retain all principal veinal sectors, branched and lacking any fusions and braces, as in the ancestral protowing venation shared by all Pterygota (KUKALOVÁ-PECK & LAWRENCE 2004, fig. 1). At the groundplan level, sister lineages Odonoptera and Ephemeroptera share a short, winged prothorax, in nymphs as well as in adults. The large Carboniferous mayfly *Lithoneura lameerei* (†Syntonoptera; interpreted by KUKALOVÁ-PECK 1985, figs. 11–13) bears a short prothorax with relatively large wings preserved only in outline. WILLMANN (1999) erroneously replaced it with a narrow neopteran prothorax, which accidentally settled nearby, and provided an inadequate figure of this well preserved fossil. However, the veinal fusions and braces, exactly as figured by me in 1985, are recognizable in good photographs that WILLMANN (1999) published with his emendation, but obviously did not recognize himself. These are all shared with another syntonopterid mayfly published in the same 1985 paper, *Bojophlebia prokopi*. *Bojophlebia* was accepted by WILLMANN (2007) as the oldest known mayfly without any doubt. Basal Carboniferous mayflies are very important for an understanding of Odonoptera since they help to pinpoint and verify the groundplan characters (see the analysis of sistergroup below). Large prothoracic winglets, such as those present in *Lithoneura*, were until 1985 erroneously believed to be present only in †Palaeodictyoptera. The 1985 paper introduced them for the first time as present in several nymphs and adults. Perhaps, this novelty

alone is the reason that a well-preserved and phylogenetically important mayfly showing clearly all groundplan character states of Ephemeroptera and Syntonoptera, is being introduced in some publications as an “unresolved” specimen. In any case, it is always the groundplan that matters (HENNIG 1969, 1981). In quite the same line of logic, yet another syntonopterid, the gigantic nymph very probably of *Bojophlebia prokopi* (also with prothoracic winglets and also perfectly fitting the Ephemeroptera groundplan) was redescribed by KLUGE (1994) erroneously as a “silverfish” named after this author. The *Bojophlebia* nymph died belly up, showing ventral abdomen ending in three characteristically thin “tails”, bearing serial leglets and very large and rounded (after preparation) abdominal winglets with strong anterior margins, stacked like card one upon another so that they are mostly shown only as crescent-shaped slivers (unless prepared out). These, in spite of being obviously transparent and rounded in my photographs (the matrix is too coarse to show venation), were misinterpreted as “solid” tergal outgrowths pointed as in trilobites (!). The groundplan of silverfish (distinctly expressed in all Carboniferous silverfish: KUKALOVÁ-PECK 1987, fig. 16; 1991) includes serial abdominal leglets plus four vesicles (endites) on each pregenital segment, narrow tergal sidelobes, and very chunky tails with cerci oriented sideways. In contrast, gigantic *Bojophlebia* nymph shows the complete reduction of pregenital abdominal vesicles, which is the groundplan feature typical for Palaeoptera, plus the complete set of mayfly groundplan character states.

Evolutionary morphology shows that seriality of limbs, endites and wings is plesiomorphic in all arthropod higher taxa. Therefore, a more complete expression of seriality in fossils should be expected and exploited for a better understanding of modern morphology. In phylogeny, it is the groundplan state that counts (HENNIG 1969, 1981).

An evolutionary biologist/systematist must keep an open mind for finding unexpected plesiomorphies in fossils, or else they are overlooked! In †Palaeodictyopteroidea, quite rarely, prothoracic winglets were found detached from the protergum, which indicates that they remained articulated (KUKALOVÁ 1970, fig. 32). The adults of basal Carboniferous orders, †Geroptera in dragonflies and †Syntonoptera (*Lithoneura lameerei*: KUKALOVÁ-PECK 1985, fig. 11) in mayflies bore large prothoracic winglets supported by original wing venation. This venation occurs also in syntonopterid nymphs (KUKALOVÁ-PECK 1985, figs. 17–21) (serial homology was much more complete). In †Geroptera (Fig. 7), prothoracic winglets are “frozen” in an oblique uplifted position, which also indicates original movability. Prothoracic winglets continue to occur in more derived Paleozoic orders, e. g., in †Eomeganisoptera and †Protereismatida, but they are significantly smaller and their venation loses its protowing integrity. They are

firmly fused to the protergum in most, but not all known Hydropalaeoptera (KUKALOVÁ-PECK in: WOOTTON & KUKALOVÁ-PECK 2000, fig. 10; WOOTTON et al. 1998: 599; BECHLY et al. 2001, fig. 14; KUKALOVÁ-PECK & LAWRENCE 2004, fig. 1B; KUKALOVÁ-PECK 2008). In the much more derived nymph *Dragonympha srokai* n. gen., n. sp., the prothoracic winglets are fused and strongly reduced but pterothoracic wings are mobile and can be lifted up. The above facts seem to indicate that the (unknown) nymphs of the earliest Odonatoptera may have been capable of lifting up all three pairs of winglets! In the plesiomorphic adults, the prothoracic winglets eventually “froze” in an uplifted position, but in the more derived juveniles and adults, they became reduced to narrow, leathery sidelobes. In Neoptera, the plesiomorphic prothoracic winglets are fused to terga, their articulation is reduced to a crescent-shaped ridge, and the winglet is reinforced by a dense network, which forms from the wing membrane; true venation was not found (possibly an autapomorphy at the Neoptera level) (KUKALOVÁ-PECK 1985, figs. 4, 7, 8, 11, 17–19, 23, 28–32; 1991, fig. 6.14).

P t e r o t h o r a x : Mesothorax about as long as prothorax and about a quarter of its length shorter than metathorax. Acrotergite short, but distinct. Prescutum is relatively large, bulging. Sclerites of mesopleuron and metapleuron alike, differing only slightly in size and shape. Mesothoracic episternum II reaches about half the width of epimeron II (EM). Metathoracic episternum III about three times narrower than epimeron III (EM). In both thoracic segments, episternum subdivided into anepisternum (AS) and small, crescent-shaped katepisternum (KS). Anepimeron incompletely subdivided by a dorsoventral invagination. Katepimeron (KM) crescent-shaped in mesothorax, small, triangular and detached in metathorax. Pleural sulcus (with VWP) open (i. e., not invaginated as in Odonata), in its ventral part posteriorly bent, more strongly in metathorax. Pleural inflexion parallel to pleural sulcus running closely anteriorly from it and ventrally dividing the crescent-shaped katepisternum (KS) in half. Mesothoracic spiracle resting in membrane anteriorly from mesothorax. Metathoracic spiracle resting on a plate. Suture between mesothorax and metathorax weak and incomplete. Mesothoracic and metathoracic ventral wing process and basalaria (fused to ventral side of the anterior articular plate) well sclerotized and distinct. Subalaria composed of several small sclerites, less distinct than basalaria.

R e m a r k s . – *Dragonympha srokai* n. gen., n. sp. shows that the position of the acrotergite in Odonatoptera is unchanged and that the anepisternum was positioned ventrally in-between the acrotergite and prescutum. This indicates that the dorsally expanded anepisternum in adult dragonflies became wedged between the acrotergite and the prescutum.

W i n g s : Compared to living nymphs, the fore and hind wing are relatively large, fully articulated and held in a parallel uplifted resting position, as in modern damselflies and in mayflies. Wing articulation seems more advanced in development than wing venation. Hind wing is broadest in the proximal third, quickly tapering distally. Anterior wing margin gently curved, posterior wing margin slightly concave. Venation not fully formed, but showing clearly the branching and braces of protodonate type. The slanted CuP crossing, the shape of M, a long anal brace, and added secondary branches and intercalary sectors are similar as in the wings of †Meganisoptera.

N y m p h a l w i n g p o s i t i o n a n d f e e d i n g a d a p t a t i o n : Juveniles of basal Paleozoic Palaeoptera and Neoptera with fully articulated or partly fused wings (secondary fusion to the terga started already in the Carboniferous) are known from many localities. A novel discovery is that in *Dragonympha* n. gen. the wing articulation and musculature were strong enough to lift the wings up into a position streamlined with the body, possibly for easier movement on dry land. *Dragonympha* n. gen. was probably semiaquatic and may have climbed up and down the stems of aquatic vegetation or search of prey by walking through thick waterlogged undergrowth. Far too short for powered flight, the strongly articulated winglets give an impression of being functional before they became tucked away over the back. Perhaps, they were originally propelling the nymphs forward when sitting on water surfaces as envisaged by MARDEN (2003). Possibly, young dragonflies were hunting Parainsecta, Archaeognatha, †Monura and †Cercopoda, as they were walking, jumping and bouncing across the water surface, and catching them with a rapid flick of their hinged labial mask.

T h o r a c i c l e g s : Coxa (CX) and short trochanter (TR) are typically odonatoid. A slightly larger slanted prefemur (PFE) is fused to femur (FE) (an autapomorphy). Patella (PAT) is distinctly separated from tibia (TI) by a deeply incised oblique suture (a symplesiomorphy shared by all Palaeoptera).

R e m a r k s . – Slanted prefemur (PFE) fused with femur (FE) is a derived condition occurring also in †Diaphanopteroidea (a parallelism) (KUKALOVÁ-PECK 2008, figs. 4, 18). Gigantic †Meganisoptera bore long and strong legs with long spines, articulated far anteriorly and under the head (Fig. 4). Two pairs were held spread sideways and the third pair backward, to grasp very large prey (†Palaeodictyoptera, †Megasecoptera). In contrast, modern Odonata have weak legs directed downwards, and feed on small prey. Some modern juveniles retained plesiomorphic fully articulated trochanter and femur (a plesiomorphy at the Hexapoda and Arthropoda level). Since fused limb-podites at the ordinal level do not un-fuse, this plesiomorphy indicates two assumptions: the ancestral Odonatoptera were adapted to catch small, fast moving prey; and, modern

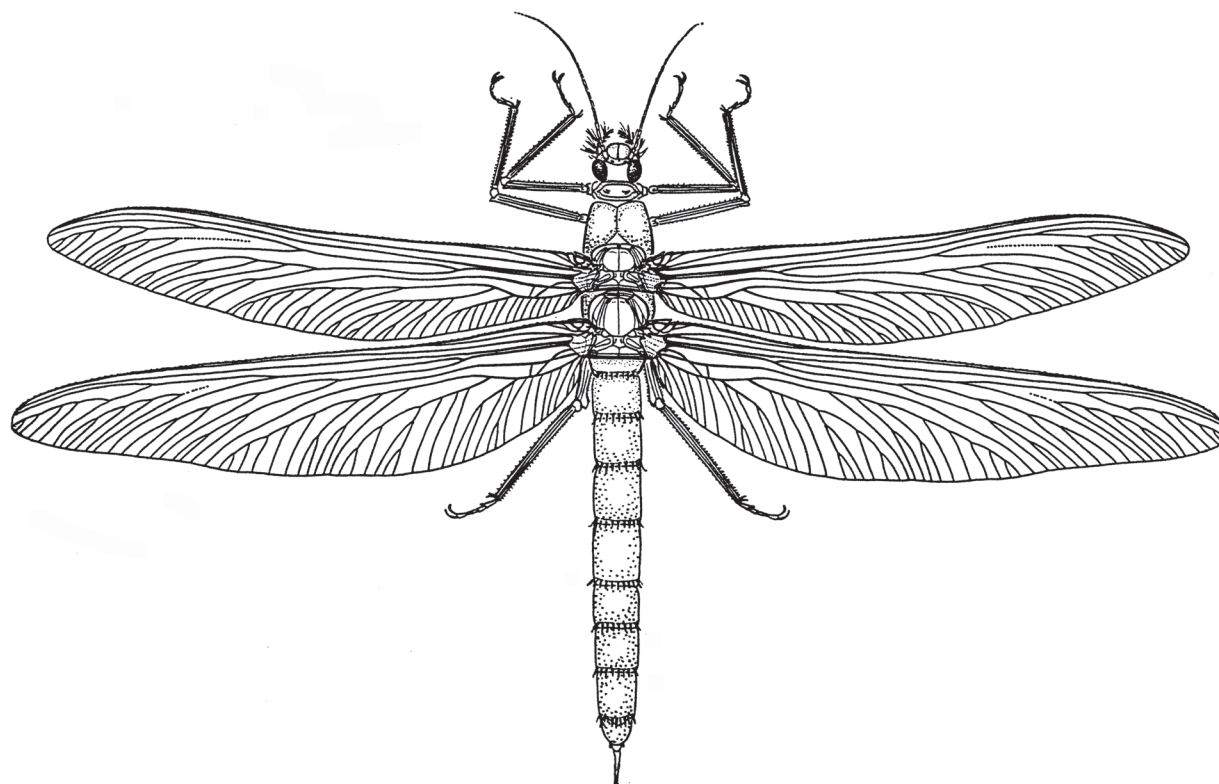


Fig. 4. †Meganisoptera – gigantic dragonflies: adult, maximum wing span 73 cm. Reconstruction based on *Meganeurula selysii* (head, pteroterga, wings, legs); *Meganeurula* sp. # 1422 (legs, abdomen); “*Titanophasma fayoli*” (= *Meganeura* sp.) (the length of body, protergum, end of abdomen). Uncertain: fusion of mesothoracic anepipleura. Late Pennsylvanian of Commentry, France. Muséum national d’Histoire naturelle, Paris. Cubital cell no more functional, anal brace mildly concavely arched, extended distally by a triple fusion (AA+CuP+CuA) as in *Alanympa* n. gen. Note long and powerful raptorial legs with prothoracic coxae shifted far forward and under the eyes, and metathoracic legs extended posteriorly, long curved tarsi and large curved unguis, adapted for catching very large prey on the wing. – Original reconstruction.

Odonata come from an ancient stock, of which †Meganisoptera is an early side branch.

Abdomen: Abdominal segments long and slender like in modern damselfly adults. First segment reaches about half the length of the second segment. Abdominal terga flanked by lateral protruding ridges. Abdominal winglets reduced. Abdominal pleura include two narrow plates. The ventral plate articulates posteriorly with the abdominal leglet (telopodite, PFE through PT). Telopodites are serial, tubular, greatly elongated, bending along articular planes, and serving as respiratory filaments.

Remarks. – Laterally protruding ridges may be homologous to the crested abdominal epipleura smoothly fused to terga, present in other Palaeoptera. Fossil Ephemeroptera bear prominent epipleural sidelobes to which abdominal winglets articulate, but they are separated from terga by deeply incised sutures. Two narrow pleural plates in the dragonfly nymph are in the same position as three pleural plates in †Diaphanopteroidea (sub-coxal, coxal and trochanteral plate: KUKALOVÁ-PECK 1992,

figs. 27–35; 2008, fig. 20). But, this comparative evidence appears insufficient and full homologization is left open.

Genus *Alanympa* n. gen.

Typus generis: *Alanympa richardsoni* n. sp. This genus is monotypic and is only known from the holotype.

Derivatio nominis: From ala (Latin) = wing and nympha (Latin); feminine.

Diagnosis. – *Alanympa* n. gen. differs from *Dragonympha* n. gen. mainly in a broader cubito-anal area and a smaller MA area. *Alanympa* n. gen. differs from *Carbonympha* n. gen. in following attributes: Wings with a sinuous posterior margin. RP– forks proximally from the fork of MA+. The stem of M is fused at length with the stem of Cu and also with the basal portion of CuA. Cubito-anal area is longer and narrower. Cubito-medial and anocubital stems are almost perfectly straight and running parallel to each other. CuP crossing is oblique, concave

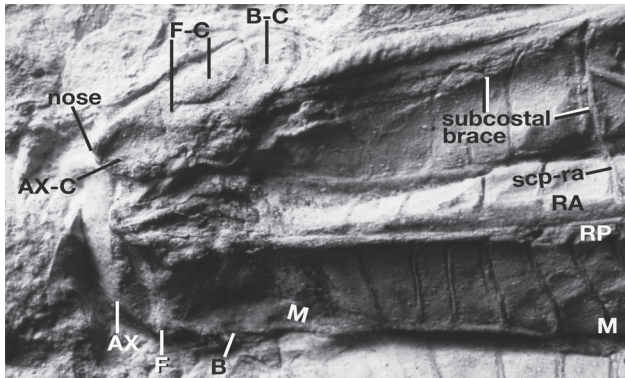


Fig. 5. *Megatypus schucherti* TILLYARD, 1925 (†Meganisoptera), adult hind wing, Early Permian (Kungurian) of Elmo, Kansas. Maximum width of wing base 35 mm. Forewing base of a gigantic dragonfly showing anterior articular plate with a typical protruding “nose,” large lobe on F-C and an obliquely oriented B-C; posterior articular plate shows the rows and columns of articular sclerites marked by sutures. – After KUKALOVÁ-PECK (1985), veinal symbols updated.

and distinct. CuA crossing is weak, perpendicular and not distinguishable from regular crossveins. Cubital cell lost its frame and function. Anal brace long, almost straight, composed of AA, plus AA1+2, plus the kink in CuP, plus the kink in CuA, plus a long fusion AA1+2 + CuA + CuP. Veinal supplements present in the CuA and CuP area.

Relations. – The absence of nodus and arculus in the wing is characteristic for all protodonate dragonflies. *Alanympha* n. gen. contains the following combination of characters: Radial sectors RA and RP basally adjacent. The stem of M fuses close to base with Cu and CuA and its remaining portion is long and wavy. MA crossing towards RP reduced. Radial, medio-cubital and anal veinal stems near base are almost straight and run close and in parallel to each other. CuP crossing is distinct and oblique but CuA crossing is very weak and cubital cell is absent. Anal brace straight, including a long kink in CuP, kink in CuA and a fusion CuA+CuP, by which it is elongated much further distally than in †Geroptera or †Eoanisoptera. All these character states are typical for †Meganisoptera. In the wing articulation, the anterior plate and the posterior plate are identical to those recorded previously by this author in adult †Meganisoptera (Figs. 4, 5) (KUKALOVÁ-PECK 1985, 1991, 1998).

Alanympha richardsoni n. sp.

Fig. 6

Synonymy: Odonopteran nymphal wing. – KUKALOVÁ-PECK, 1991, fig. 6.15 H; veinal homologization in Fig. 6A is updated.

Holotype: Specimen No. PE 29407, Field Museum of Natural History, Chicago, USA.

Derivatio nominis: In honor of Dr. EUGENE S. RICHARDSON, curator in the Field Museum of Natural History in Chicago, who organized the collection of unique Carboniferous fossils from the Mazon Creek mining district and saved it for posterity.

Stratum typicum: Pennsylvanian (Moscowian).

Locus typicus: Mazon Creek area, Illinois, USA.

Diagnosis. – Same as genus (monotypic).

Description. – The forewing of a probably middle-aged nymph without apex, detached from tergum and bearing two axillary plates. Only the obverse half of the ironstone nodule is known. Venation and articulation well preserved. Veins are broader than in adult wings and less clearly defined. Broad costal area indicates a forewing.

Wing: Forewing fragment, length 30 mm; probable total length 34 mm; maximum width 10.6 mm. The wing is about 3.3 times as long as broad. Anterior margin convexly bent beyond the end of ScA+. Sinuous posterior margin bent concavely between wing base and the end of CuP and convexly at the CuA area. Precostal strip PC is broad and serrated (a synapomorphy at the Palaeoptera level). CP– is short and simple, joining CA+ close to base. ScA+ forming a prominent recurrent subcostal brace (a synapomorphy shared with Ephemeroptera). ScA+ relatively short, forked into a ScA1+2 branch fused with the anterior margin well before ¼ of wing length, and a recurrent branch ScA3+4, antero-posteriorly oriented and ending on ScP. RA and RP abutted at length to each other, running in parallel with the stem of Cu and M, and with anal brace (a synapomorphy of †Meganisoptera shared with Odonatoclada). RP– forked beyond mid-wing. RP area is narrower than in adult wings but longer and broader than in *Carbonympha* n. gen. The convex stem of M starting half way between RP+ and Cu–, arched and fused with the stem of Cu– and with the basal portion of CuA, then continuing distally for about an equal distance and dividing into MA and MP. MA crossing towards RP is not distinguishable from crossvein (a synapomorphy of †Eo-meganisoptera + †Meganisoptera + Odonatoclada). MA+ diverging from RP+ shortly before the first third of the wing length. MA+ forked between mid-wing and the distal third of the wing length. Base of CuA slightly arched. CuA distally from anal brace long and undulated. CuP– is long, strong and oblique. CuA+ bears probably eight, CuP– six, and AA+ seven terminal branches with veinal supplements. CuP crossing is strong, oblique, CuA crossing weaker, resembling a crossvein. Anal brace is basally very slightly concavely arched. Anal brace forming a long and almost straight ridge, composed of AA+, plus the basal portion of AA1+2, fused at length with the kink in CuP, plus more distally with the kink in CuA and almost reaching ⅓ of the total wing length. AP– is long, simple, highly oblique and distinctly concave. Jugal vein J+ is

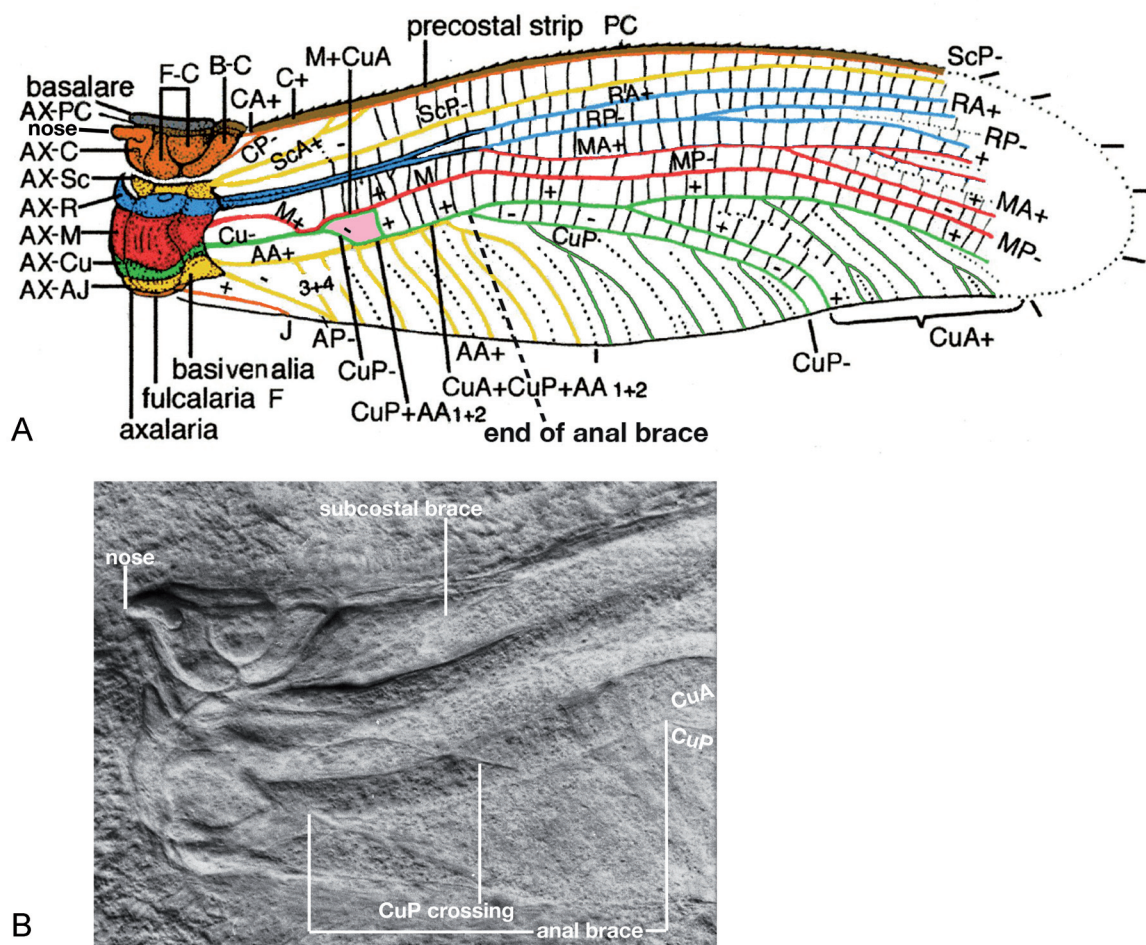


Fig. 6. *Alanympa richardsoni* n. gen., n. sp., holotype (†Meganisoptera). – **A.** Nymphal forewing with anterior and posterior articular plate. Length 30 mm. **B.** Same, wing base only. Derived features: Free M basally short, its fusion brace to cubitus longer. Cubital cell (colored pink) incompletely framed, not functional, CuAc reduced to a crossvein. Anal brace extended further distally by a tripple fusion of AA1+2 + CuP + CuA; almost straight; running in parallel with the veinal stems of Cu, M, R. AA1+2 enriched by secondary intercalary branches. Anterior plate with a large, half-circular F-C lobe, and a narrow, obliquely arched basivenale B-C. Posterior plate showing the row-sclerites fused together with sutures. – Symbols: AX = axalare; F = fulcalare; B = basivenale. Original figure and photograph.

single, convex. CuA, CuP and AA areas bear many veinal supplements. Numerous, fine, almost regular crossveins present.

Wing articulation: Nymphal anterior plate and posterior plate closely resemble those of adult †Meganisoptera previously homologized and figured by KUKALOVÁ-PECK (1985, 1991, 1998), but are shorter. Precostal and costal axalaria and fulcalaria fused into a single composite anterior articular plate (AX-PC+F-PC + AX-C+F-C), which is fused ventrally to basalare. Basalare is overlapping the anterior plate and forms a slightly protruding anterior rim of the plate, fused and separated by a deeply incised suture. Precostal row-sclerites AX-PC and F-PC are long, narrow and fused to each other. Costal row-sclerite AX-C is short and broad, fused to a lobate F-C along a

weakly indicated suture, and bearing proximo-anteriorly a nose-like projection; row-sclerite F-C partially subdivided into a smaller proximal lobe fully fused to AX-C, and a larger distal lobe. Larger distal lobe of F-C is positioned obliquely antero-proximally with respect to the much narrower proximal lobe; it is semi-circular and separated from the proximal lobe by a deeply incised, arched and flexible furrow. Anterior plate is distally articulated to the precostal-costal basivenale B-PC+B-C. This is elongate, narrow, arched and strongly slanted, to articulate at length with the semi-circular distal lobe in F-C.

Remarks. – This belongs to a nymph with a large adult stage. The wing probably belongs to a middle-age nymph, more mature than that of *Carbonympha herdinai* n. gen., n. sp. It is relatively longer and narrower, bears a

less convex anterior and a deeply sinuous posterior margin, more sclerotized veins, broader RP area and a more developed venation in the apical third, while MA diverges from RP more distally from the wing base. Since the wing apparently belongs to a more mature instar but is smaller, the corresponding adult was probably also significantly smaller.

Order Eomeganisoptera ROHDENDORF, 1963
Family incertae sedis

Genus *Carbonympha* n. gen.

Typus generis: *Carbonympha herdinai* n. sp. This genus is monotypic and is only known from the holotype.

Derivatio nominis: After the Carboniferous Period, and nympha (Latin); feminine.

Diagnosis. – The forewing of *Carbonympha* n. gen. differs from that of *Alanympha* n. gen. as follows. The posterior wing margin is almost straight. RP fork placed distally from MA fork. M fused very shortly only with CuA (instead of a longer fusion with Cu and CuA). Cubital cell fully framed, small. CuA and CuP fusing only very shortly, distally from the cubital cell, then separate again. Anal area short, with few anal branches. Anal brace composed of four elements: concavely arched AA, plus AA1+2 spot-fused with the kink in CuP, plus brace cup-aa1+2 (absorbed in spot-fusion), plus the kink in CuP shortly fused with the kink in CuA. *Carbonympha* n. gen. differs from *Dragonympha* n. gen. in a longer stem of M fused to CuA (rather than fused to the stem of Cu), shorter CuP crossing closer to wing base, and in a shorter and broader cubital and anal area (all plesiomorphies).

Relations. – Complex braces (nodus and arculus) are absent in *Carbonympha* n. gen. and in protodonate orders †Geroptera, †Eomeganisoptera and †Meganisoptera (a symplesiomorphy), but they are present in Odonatoclauda (a synapomorphy) (BECHLY et al. 2001). In †Geroptera, RA and RP are basally separated one from another (a plesiomorphy at the protowing level), but in *Carbonympha* n. gen., †Eomeganisoptera, and †Meganisoptera, they are fused laterally with each other since the wing base. In †Geroptera, MA crossing is retained (a plesiomorphy), but in *Carbonympha* n. gen., †Eomeganisoptera, †Meganisoptera, and Odonatoclauda, MA crossing is reduced (a synapomorphy). In †Geroptera, M is relatively long and braced with CuA by a crossvein or a spot fusion (= individual variation). In *Carbonympha* n. gen. and †Eomeganisoptera, M is also long but its brace with CuA is a short fusion (an autapomorphy). In Meganisoptera, the stem of M is significantly shorter and M+CuA fusion is long. In †Geroptera, anal brace is short, concavely curved, AA+AA1+2 is connected to the kink in CuP by a short crossvein aa1+2-cup, and the kink in CuP is connected to

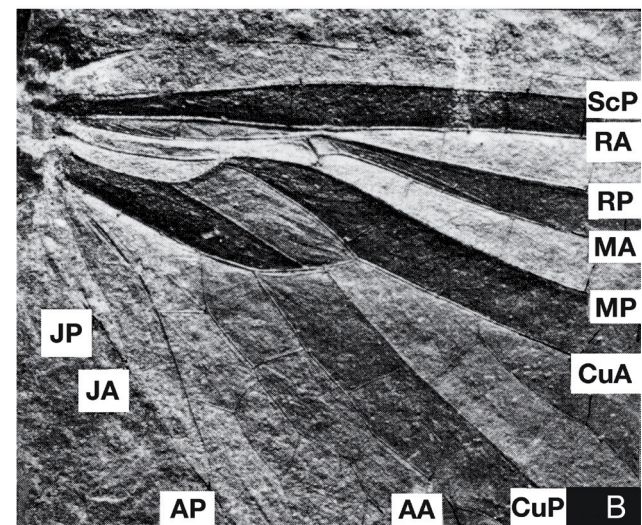
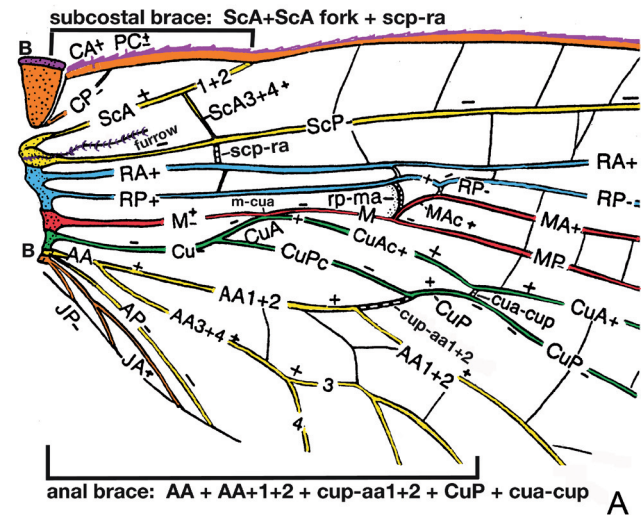


Fig. 7. †Geroptera: Eugeopteridae, with venation system very close to the Odonatoptera groundplan. ?Late Mississippian, locality Malanzan, La Rioja, Argentina. Synapomorphies shared with Ephemeroptera (Fig. 11) include: the extended recurrent subcostal brace $ScA + ScA3+4 + scp-ra$; RA and RP basally at the same level; strong brace $RP + MA$; the stem of M formed; the stem of Cu formed; brace $M + CuA$; cubital cell (colored pink) framed by five identical veinal elements: CuA, CuAc, CuPc, anal brace; anal brace composed of five identical veinal elements: AA, AA1+2, cup-aa1+2, kink-or-hinge & bend in CuP, cua-cup. Crossvein or spot-fusion braces become longer in modern dragonflies, but are partly desclerotized in modern mayflies (Fig. 12). – A. *Eugeopteron* sp., the right forewing of a complete adult dragonfly (WOOTTON & KUKALOVÁ-PECK 2000, fig. 10). A flexion line (furrow) in subcostal area also occurs in Ephemeroptera (Fig. 12); microengineering cubital cell (colored pink) is framed as in Protoreisomatida (Fig. 11); it becomes reduced to a hinge (pink dot) while cup-aa1+2 is extra long in Ephemeroptera (Fig. 12). Original figure, KUKALOVÁ-PECK. Length of section 10 mm. B. *Eugeopteron lunatum* RIEK, 1984, hind wing. Note RA and RP only touching, MA crossing to RP retained but weak, double rp-ma crossvein brace, ultra-short mp-cua crossvein brace, and anal brace ending on CuA by a relatively long cua-cup crossvein as in Ephemeroptera. – After RIEK & KUKALOVÁ-PECK (1984, fig. 14). Length of section 14 mm.

CuA by a crossvein cua-cup (four plesiomorphies of Odonoptera). In *Carbonympha* n. gen. and †Eomeganisoptera, anal brace is longer and straighter, AA1+2 spot-fused to the kink in CuP, and this is fused at length to the kink in CuA (Fig. 8) (an apomorphy). In †Meganisoptera and Odonatoclada, anal brace is longer and much more straight. AA1+2 is fused at length with the kink in CuP and with the kink in CuA (a synapomorphy). In †Geroptera and †Eomeganisoptera including *Carbonympha* n. gen., the veinal supplements typical for large wings are, as far as known, absent. Thus, a short, broad and irregular cubito-anal area occurs only in †Geroptera and †Eomeganisoptera (a symplesiomorphy). The character states above refer *Carbonympha* n. gen. to the order †Eomeganisoptera, possibly to a new family.

The order †Eomeganisoptera includes the medium-sized species *Erasipteron larischi* PRUVOST, 1919 (Fig. 8D). Compared to *Carbonympha* n. gen., *Erasipteron* has a narrower cubito-anal area, and bears longer and more parallel CuA and CuP crossings, delimiting a larger and more obliquely rectangular cubital cell. This flight important cell is most prominent and longest in the plesiomorphic order †Geroptera (Fig. 7). In wing experiments, this cell operated as a sophisticated “micro-engineering” flight device lowering the trailing posterior wing margin and preventing it from fluttering and tearing (like a flag in the wind) (WOOTTON et al. 1998). Cubital cell gradually disappears in derived dragonfly taxa. In Protanisoptera (Odonatoclada), it is small and still noticeable, but probably afunctional. Remarkably, modern Odonata: Anisoptera contain an analogous flight-important cell called arculus, which has a similar function. Instead of being placed between CuA and CuP sectors, it occurs between MA and MP sectors (WOOTTON et al. 1998).

Carbonympha herdinai n. sp.

Figs. 8A, B, C

H o l o t y p e: Specimen No. PE 31972, Field Museum of Natural History, Chicago, USA.

D e r i v a t i o n o m i n i s: Named in recognition of Mr. JERRY HERDINA, amateur paleontologist and one of the most active and productive collectors of arthropods in the Mazon Creek area, who discovered the holotype. Mr. HERDINA collected under the auspices of Dr. EUGENE S. RICHARDSON and generously donated his entire excellent collection to the Field Museum of Natural History in Chicago.

S t r a t u m t y p i c u m: Pennsylvanian (Moscovian).

L o c u s t y p i c u s: Mazon Creek area, Will-Kankakee County, Francis Creek shale, Pit 11, Peabody Coal Company, Illinois, USA.

D i a g n o s i s. – Same as genus (monotypic).

D e s c r i p t i o n. – An almost complete forewing of a young nymph that was detached from wing articulation before undergoing fossilization, and was preserved in an

ironstone nodule as obverse and reverse halves. Veins broad, not fully defined on reverse half, barely distinguishable on obverse half. Broad costal area indicates a forewing.

D i m e n s i o n s: Forewing length 36.5 mm, probable length 37.5 mm; maximum width 12.8 mm.

W i n g: Anterior margin strongly convexly bent. Posterior margin is almost straight, with a slightly convex bend close to wing base. Wing about three times longer than broad, quickly tapering in the distal third. Subcostal brace angled, with recurrent ScA3+4 oblique and weak. RA and RP are basally adjacent one to another. RP branches are not distinguishable and occupy a very small area. RP– fork placed distally from the first fork in MA+. MA crossing between M and RP reduced, not distinguishable from crossveins. The stem of M fused shortly with CuA+ before dividing into MA crossing (reduced) and MP. MA area showing six, CuA ten, CuP seven, and AA six branches. MA, CuA, CuP, AA branches with many veinal supplements. The stem of Cu is short and concave. The strong, slightly oblique CuA crossing and the strong, oblique, and slightly arched CuP crossing are almost parallel, enclosing a short and obliquely quadrangular cubital cell. MA, CuA, and CuP area enlarged, supported by numerous veinal supplements. Anal brace relatively short, composed of the concavely arched AA, plus AA1+2 spot-fused with the kink in CuP, plus the kink in CuP, reaching the kink in CuA and shortly fused with it. AP– is short, simple, distinctly concave. J+ is short, simple, convex. Crossveins are dense, weak and slightly irregular.

The wing pad of *Carbonympha* n. gen. belongs very probably to a young instar of a species with large adults. This is indicated by its convexly arched costal margin, broad and quickly tapering wing, veinal branching weakly developed in the apical area, principal veins diverging close to wing base, and by numerous veinal supplements in MA, CA, and CuP area.

3. Discussion

3.1. Labial mask

Extensive evidence now exists that all aquatic insect immatures (in Odonata, Ephemera, Plecoptera, Hemiptera, Coleoptera, Megaloptera, Trichoptera, etc.) entered water from the terrestrial habitat, independently and at different times (KUKALOVÁ-PECK 2008). The labial mask of Odonata is formed by the limbs of head segment VI and sternum VI, and was present in the Paleozoic as well as in modern Odonoptera. This shows it to be a groundplan structure. Hexapod nymphs were originally terrestrial and *Dragonympha* n. gen. was probably still semiaquatic. This suggests that the labial mask probably originated as an adaptation to capture terrestrial prey out of water.

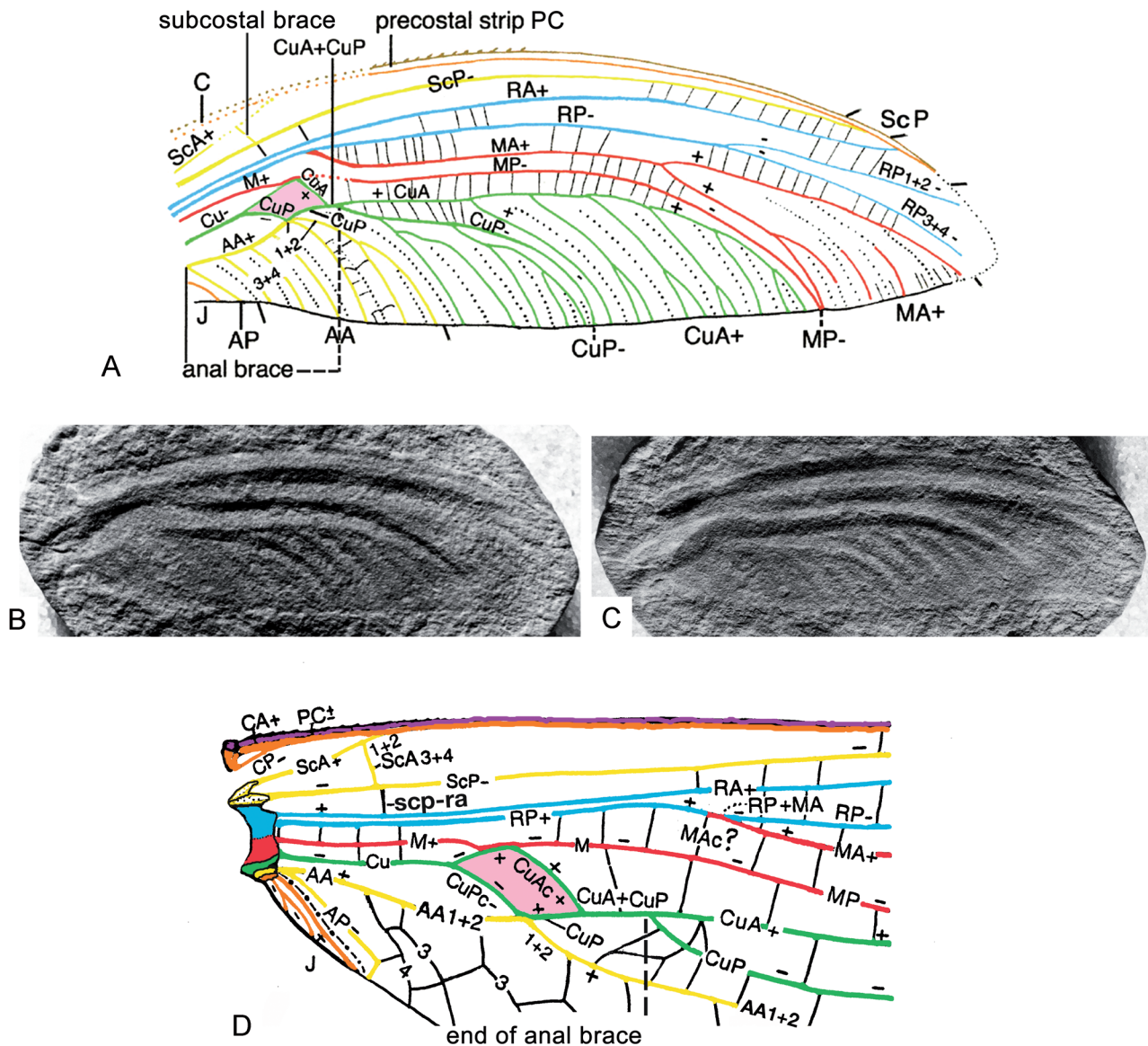


Fig. 8. †Eomeganisoptera: Erasipteridae, nymph and adult. – **A.** *Carbonsympha herdinai* n. gen., n. sp., nymphal wing, holotype. Interpretation of forewing of a young nymph from a near-basal order, detached from body. Length 36.5 mm. Plesiomorphies close to †Geroptera: M long, fusion brace M + CuA short; micro-engineering cubital cell (pink) small but still fully framed by cubital fork; the kink in CuP proximally absorbing cup-aa1+2 brace and meeting AA1+2, distally very shortly fused to CuA; fusion brace distal from cubital cell short, including CuA + CuP; anal brace still concavely arched but elongated by a CuA + CuP fusion. **B.** Reverse of the holotype. **C.** Obverse of the holotype. **D.** *Erasipteron larischi* PRUVOST, 1919, adult forewing, holotype. Total length 54 mm. Early Pennsylvanian (Bashkirian) of Moravia. Interpretation of forewing, showing identical fusion braces as in *Carbonsympha* n. gen.; fusion between the kinks in CuA and CuP longer. – Symbols: CuAc = CuA crossing; CuPc = CuP crossing (towards anal brace). All originals from holotypes. *Erasipteron*: after KUKALOVÁ (1964), symbols updated. Length 20 mm.

3.2. Gill filaments

The abdomen of *Dragonympha srokai* n. gen., n. sp. is similar to that of modern Zygoptera but relatively longer. It bears serial abdominal leglets – telopodites – adapted as gill filaments and composed of flexibly articulated podites. Similar filamentous gills occur in modern damselflies

Euphaeidae (= Epallagidae) and Polythoridae on up to seven pregenital segments. These were morphologically analyzed for position, articulation and musculature and identified as limb telopodites by NORLING (1982). Modern juvenile Plecoptera and Megaloptera, which also bear long leglet-based gill filaments, wander around through waterlogged vegetation (e. g., *Stenoperla* in New Zealand; per-

sonal observation). The hexapod groundplan-level abdomen includes nine pairs of serial winglets and leglets (segment X has no appendages). The full double series was found only in the nymphs of Paleozoic Ephemeroptera and Pleconeoptera; in all other pterygotes it was variously reduced (KUKALOVÁ-PECK 1978, figs. 28–30, 35; 1985; 1991, figs. 6.13, 6.14, 6.17; 1992, figs. 27–35; 2008, figs. 13, 15, 18, 20; CARPENTER 1992, fig. 61). All limb-derived appendages in Hexapoda have their origins in Proterozoic Arthropoda. Note that all reductions and fusions of limb podites at the groundplan level of the higher taxa are permanent (i. e., muscled limb podites cannot be “un-reduced” or “un-fused”) (HENNIG 1981; RAFF 1996; KUKALOVÁ-PECK 2008). If abdominal winglets and leglets are retained in some Palaeoptera and Neoptera, their homologues must have been present in the Mandibulata, Crustacea, Atelocerata, Hexapoda, Insecta, Dicondylia, and Pterygota. This logic of continuity rules the landscape of evolution and must be kept in mind when dealing with unusual structures, which might otherwise be coined to be “neoformations”.

3.3. Thoracic pleuron, pleural inflexions, double wing pivot

The pterygote pleural sulcus is a dorso-ventral inflexion in the subcoxal pleuron (= subcoxal podite flattened and inserted into pleural wall as a plate called the pleuron), which dorsally provides the main ventral pivot (VWP) for the wing, and ventrally, the articulation for the coxa. It serves as structural reinforcement of the subcoxal pleuron, necessary especially in insects with a very high pterothorax. In modern Odonata, the pleural sulcus is deeply invaginated and obscured, but in protodonates it is externally visible and flanked by an additional anterior pleural inflexion (PRITYKINA in: RIEK & KUKALOVÁ-PECK 1984), which provided the high slanted pleuron with additional structural support. This inflexion doubtlessly also occurred in modern Odonata, in which it added the second wing pivot. In modern odonates, the “double” pleural sulcus of protodonate dragonflies probably fused into one, and then became externally obscured, while the autapomorphic double wing pivot persisted (BECHLY 1996). Ancestral features in *Dragonympha* n. gen. support this interpretation. In *Dragonympha srokai* n. gen., n. sp. the primary pleural sulcus is bent postero-ventrally as in Odonata: Anisoptera, but the added anterior pleural inflexion is straight and ventrally it dissects the crescent-shaped katepisternum. As a new and surprising feature found in *Dragonympha* n. gen., the pleuron in epimeron II and III is strengthened by yet another, previously unknown, dorso-ventral epimeral pleural inflexion.

3.4. Arthropod wing homologue

Identifying the correct wing homologue in Arthropoda is not a merely theoretical evolutionary problem. Like the full (not impoverished) pan-arthropod limb model, its outcome fundamentally changes the character evaluations in the higher taxa and opens or closes the access to the groundplan-level synapomorphies. With classical comparative morphological method, wing is interpreted as part of tergum. Therefore, the wing articular sclerites are erroneously interpreted as irregular skeletal fragments shared by Odonatoptera, Ephemeroptera and Neoptera. With the groundplan method, wing is the mobile exite of the first pan-arthropod limb segment flattened into pleuron. Therefore, the sclerites are interpreted as the fragments of epicoxal pleuron, arranged into rows above blood pathways and running from the limb into the appendage (to nourish veinal ridges supporting the wing blade). In the first interpretation, wing sclerites are compared on a one-to-one basis and searched for similarities. In the second, the sclerites in Odonatoptera, Ephemeroptera and Neoptera must be first individually flawlessly derived from the row-sclerites in the shared ancestral protowing pattern, and only then compared one with another (see following paragraphs for details and fundamentally different results).

Broad evidence from biological fields and paleontology supports the origin of the insect wing from an articulated outer ramus (exite) on the first pan-arthropod limb

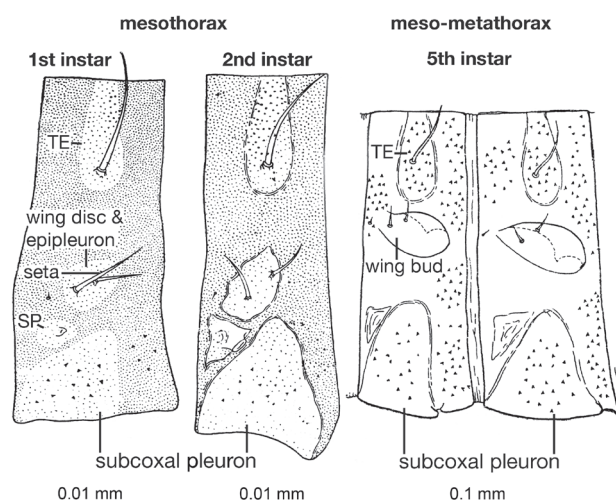


Fig. 9. Origin of insect wings from epipleural exites. Early pleural wing development in modern *Libelulla quadrimaculata* L. Wing Anlage (wing plus epipleural articulation) occurs in the position of the epipleuron, close to subcoxal pleuron and above spiracle. Wing disc in 1st and 2nd instar; wing bud in 5th instar. Wing shifts upward with each instar, evaginates before the tergum is reached and fuses secondarily to tergum in the 8th instar. – After BOCHAROVA-MESSNER (1959), captions altered.

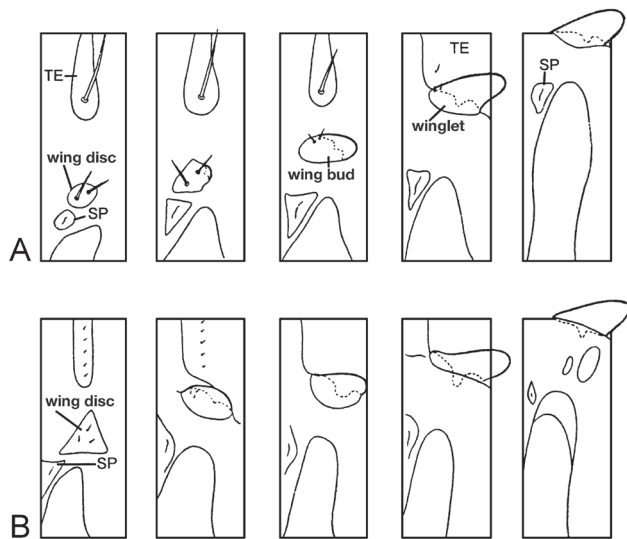


Fig. 10. Wing ontogeny in basal and somewhat derived Anisoptera. – **A.** Libellulidae: *Libellula quadrimaculata* L. **B.** Aeshnidae: *Aeshna grandis* L. In derived Pterygota, the secondary fusion of the wing pad to the tergum occurs in ever-younger instars. Merging of instars occurs especially in early stages. Modern ontogenetic series are jumbled and nymphal wings falsely resemble tergal outgrowth. The erroneous paranotal theory of wing origin and the concept of “plesiomorphic” paleoptery stand mostly on this false impression. – After BOCHAROVA-MESSNER (1959), captions modified.

podite (epicoxa) (KUKALOVÁ-PECK 1983; KINGSOLVER & KOEHL 1994). In all Arthropoda, the epicoxa flattened and changed into the epicoxal pleuron, articulated dorsally with the tergum and ventrally with the subcoxal podite. The evidence is as follows: In *Drosophila*, the wing Anlage separates from the limb Anlage (GARCIA BEILLIDO 1975; RAFF et al. 1991). In the ontogeny of modern Odonata, the wing Anlage includes wing disc plus the articular sclerites (STENZHORN 1974). Combined disc occurs in the pleural membrane just above subcoxal pleuron and far from the tergum (Figs. 9, 10) (TOWER 1903; BOCHAROVA-MESSNER 1959). Genetically, insect wings are homologues of the (epicoxal) gills in modern basal Crustacea (AVEROV & COHEN 1997; PAGANIBAN et al. 1995). Wing veins form around the blood pathways, and their channels are entered by tracheae only after they were formed (HOLDSWORTH 1940, ARNOLD 1964). Some articular plates in Paleozoic and modern Palaeoptera show that they are composed of rows of sclerites (Figs. 6B, 11–13) (see KUKALOVÁ-PECK 1983, 1991, 2008 for a review). Evidence from the biological fields above supports origin of the wing from the limb, and its close ties with the blood flow. In contrast, there is no biological evidence at all indicating that the insect wing originated from tergal skeletal fragments. Short-cut observations concluding that the wing pads in modern nymphs resemble simple tergal expansions and thus must be prim-

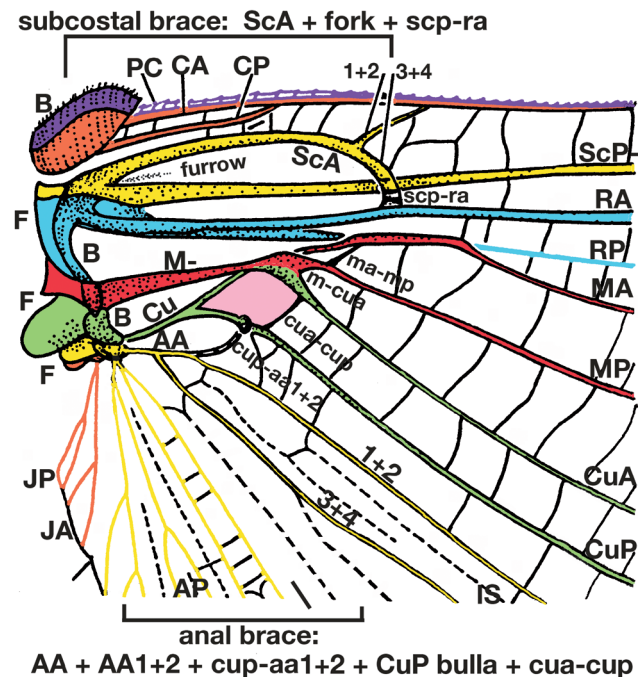


Fig. 11. Ephemeroptera: order †Protereismatida: *Protereisma latum* SELLARDS, 1907, hind wing. Early Permian of Kansas. Total length 20 mm. The wing shows eight flight-important, synapomorphic fusions and braces, some highly complex, shared with †Geroptera (see legend to Fig. 7A, B). Crossveins precede fusions. Cubital cell (colored pink) has a bulla (hinge) followed by a small bend in CuP where †Geroptera have a sharp kink. Note a long reinforced cua-cup brace enclosing the synapomorphic cubital cell. Posterior plate is composed of the same basivenalia and fulcalaria as in dragonflies (which equally create rocking wing base and prevent wing flexing), but axalaria are not included. – After RIEK & KUKALOVÁ-PECK (1984, fig. 10), updated. Length of section 5 mm.

itive, or that the gliding flight must be plesiomorphic because it is the simplest kind of flight, are directly falsified by many facts. Examples: 1, the presence of fully mobile, articulated wings in many Paleozoic nymphs (such as in *Dragonympha srokai* n. gen., n. sp.: a plesiomorphy at the Arthropoda level); 2, Odonatoptera, Ephemeroptera, Neoptera at the groundplan level show the first column of articular sclerites (proxalaria) fully articulated to tergum. This condition still persists in all extinct and extant Odonatoptera and in all fossil Ephemeroptera. Exceptions: In modern Ephemera with nearly dipterous flight, the anajugal proxalare becomes very long, strong and it sometimes secondarily fuses to tergum. In modern Neoptera, only the proxalaria in rows PC, C, A, J engaged in the anterior and posterior wing process are either separate from tergum (a plesiomorphy) or fused to it (an apomorphy); 3, gliding in nature is known as a dead-end adaptation (“once a glider – always a glider”). All wings capable of powered (flapping) flight, are based without exception on articu-

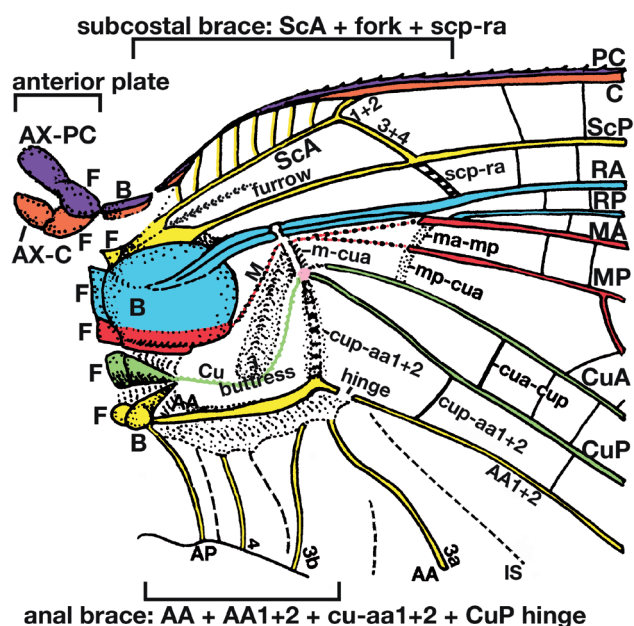


Fig. 12. Order Ephemera: Siphuriscidae: *Siphuriscus chinensis* ULMER, 1920, the species of living mayflies with most plesiomorphies. Compared to 16 synapomorphies which fossil mayflies (Figs. 11, 15) visibly share with dragonflies (Figs. 6–8, 13), only the subcostal brace, laterally adjacent radial sectors and fusion brace RP+MA can be reliably recognized. In contrast, the stems of M and of Cu are desclerotized, cubital cell and part of the anal brace reduced, anal brace is angled and its proportions changed, anterior plate V-shaped instead of lobate, posterior plate misses the cubital and anal row and lost inner sutures, and a large membranous field attached to it is supported by a buttress formed by stiffened membrane. Shared characters are disguised and obscured, but only when modern Ephemera alone are studied. Original figure from a specimen in collection at Florida Agricultural and Mechanical University (FAMU).

lated, muscled, mobile limb-derived appendages. In juveniles, fusion of winglets to tergum started in Pennsylvanian (in cockroaches), but is always secondary. Fusions took place independently (and therefore somewhat differently) in all paleopterous and neopterous lineages (a parallelism). Flight adaptations in Odonoptera and other Palaeoptera were discussed by WOOTTON & KUKALOVÁ-PECK (2000), WOOTTON et al. (1998), and KUKALOVÁ-PECK et al. (2009).

3.5. Articular sclerites follow blood pathways to wing veins

In a physiological study of insect blood flow, ARNOLD (1964) showed that the wing articular sclerites (pteralia) are arranged into rows (protecting the limb blood pathways to the wing ramus). This discovery launched a better understanding of the articular and veinal ancestral pattern

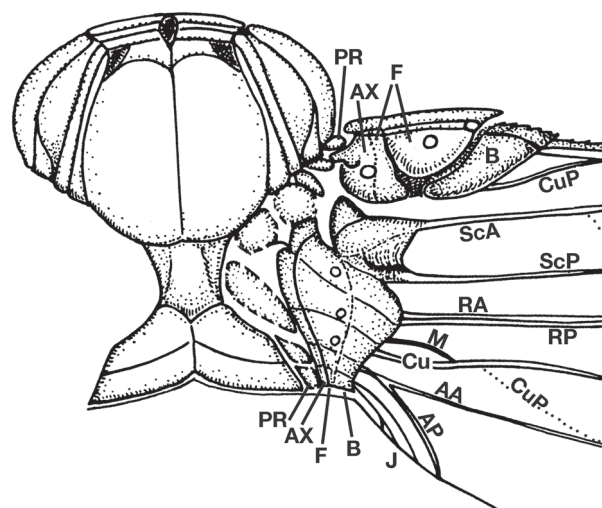


Fig. 13. Meganeuroptera: Meganeurida: *Meganeura monyi* BROGNIART, 1893, holotype. Late Pennsylvanian, Commeny, France. Muséum national d'Histoire naturelle, Paris. Muscle attachments seen through skeleton marked by circles. Proxalaria (PR) free, preserved only as shapeless “bumps”. All axalaria (AX) fused to fulcralia (F). Anterior plate and posterior plate similar to those in Figs. 5 and 6A, B, row-sclerites above blood pathways fused with sutures. – After KUKALOVÁ-PECK (1991, fig. 6.15D), updated. Total wing length about 30 cm.

(KUKALOVÁ-PECK 1978, 1983, 1991, 2008). There are eight pathways and eight rows of sclerites, always aligned with the same eight basivenalia of eight principal pairs of the veinal sectors (KUKALOVÁ-PECK 1983, 1998, 2008). This alignment between sclerites and veins is permanent (unchangeable by adaptations) because it reflects the pterygote monophyletic pattern of blood flow through the limb and into the wing. The ancestral, ridged and entirely dichotomously branched blood veins (starting as dichotomous from each of the basivenalia) were adapted to fill out and nourish the entire mobile blade and to provide support for movement. They are not unique within the Arthropoda. Analogous, also veined and movement promoting uropods in some marine decapod crustaceans resemble surprisingly closely the densely dichotomously branched tegmina of cockroaches (e. g., in Florida lobsters). Veinal stems and braces are adaptations necessary for powered forward flight. They are very different in Palaeoptera and Neoptera and again in all their superlineages and lineages because all these groups evolved a different kind of flight. Palaeoptera and Neoptera share only the protowing elements, because diversification in Pterygota started not after flight began, but in the process of its development. This consideration is important and could probably be supported by experiments.

The above facts indicate that: 1. On the wing side, the plesiomorphic state includes two principal veinal sectors (= veinal ridges) branching dichotomously immediately

from their basal blood sinus (= sclerotized basivenale) and then another two to three times. Hence, the three central veinal stems (of R, M, and Cu formed by fusion of veinal sectors) are always derived. Any other fusions and braces are also always derived. 2. On the thorax side, sclerites arranged in regular rows, articulated to each other, to the tergum, and to the basivenale, are plesiomorphic. Any hinges or fusions between sclerites from different rows are always derived. Row-sclerites combined into clusters or plates are derived. Since the monophyly of Pterygota rests on the homology of the ancestral row-sclerites, there is no reason to shoehorn clusters and plates in Odonoptera, Ephemeroptera and Neoptera into being homologous. A detail observation in modern Palaeoptera provides fast verification that the plates are partly homologous and partly independently formed. But, when compared to Neoptera, any plates in living and extinct Palaeoptera are non-homologous in every aspect!

Predictability is the cornerstone requirement for identifying groundplan character states in the higher taxa, which include synapomorphies. In systematic practice, it was first necessary to identify the proxalare (PR), axalare (AX), fulcalare (F), and basivenale (B) in one row after another, in a significant sample of the representatives. The least reduced and fused sclerites were recorded in the evolutionary model, which was gradually built up and improved as the study proceeded. Fusions with sutures are considered less derived than fusions without sutures. The final version of the reconstructed groundplan should include only the least derived states found in the taxon, and identified as such with respect to the protowing. Only after similar research was done in all pterygote lineages, it was time to start looking for the reliable synapomorphies, which the groundplans include. If this appears to be a mammoth-sized long-term project, this impression is completely justified. But, so far no shortcuts have brought positive and defendable results. The phylogenetic scheme is now open to improvements, verification in other biological fields, and additional data. The generalized procedure, which is called the groundplan method, was used in biology instinctively for a century, but HENNIG (1969, 1981) added an excellent theoretical structure to it, which is easy to follow (KUKALOVÁ-PECK 2008).

3.6. Difference in articulation: Palaeoptera versus Neoptera

In Palaeoptera, the row-sclerites remained arranged in rows and columns, and the differences are only in fusions, desclerotizations, size, and reductions. Fossils usually show rows and columns much more distinctly than living species, especially in Odonoptera (see above). Note that in Neoptera, sclerites are also arranged in rows and col-

umns, except in two central axillary sclerites, 1Ax and 2Ax (Fig. 14). In these, three row-sclerites acquired autapomorphic oblique connections with the anteriorly placed sclerites from the next distal column: in 1Ax, PR-M became connected to AX-R, and AX-R to AX-Sc; in 2Ax, AX-M became connected to F-R (Fig. 14). The resulting oblique “arms” wrap around 3Ax when it rotates and collapses to lock the wing at rest (HAAS & KUKALOVÁ-PECK 2001, fig. 1A–C; KUKALOVÁ-PECK 2008, fig. 19). Note that in the basal paleopterous order †Diaphanoptera, the wings are also flexed backward over the abdomen but in a plesiomorphic way reminiscent of protowing: the posteriorly placed sclerites and veins are simply crowded together (KUKALOVÁ-PECK 2008, fig. 18).

3.7. Comparative-morphological analysis of the pterygote wing articulation

Many (about 60) such analyses were published over the last century. In these, only large sclerites, clusters and plates were dealt with, while small and weakly sclerotized sclerites within the same system (!) were ignored. Remaining sclerites were then presumed to be homologous skeletal fragments scattered in the articular pleural membrane, and different in size, shape and location. Therefore, homologization was proposed based on the similar shape, location, and the insertion of homologous muscles.

The fact that some neopterous sclerites (1Ax, 2Ax, 3Ax) bear highly flexible hinges, while all paleopterous plates and sclerites are solid or with only slightly bendable grooves, was for unknown reasons not considered a homologization problem. Differences in function and horizontal or slanted position were not confronted, and sutures were ignored. The presumption rooted in the classical comparative morphology that the articular plates (called sometimes incorrectly “axillaries”) and the true axillaries must be directly homologous was obviously stronger than the concrete morphological evidence. But, some systematists did recognize that the wing sclerites in Ephemera are not homologous with those in Neoptera (KLUGE 1994; WILLKOMMEN & HÖRNSCHEMEYER 2007; WILLKOMMEN 2008). Yet, these and similar data were used in advanced computer analyses in hope that very large datasets will “solve” the relationship of Odonoptera! Not surprisingly, basal phylogenies of the pterygote higher taxa remained unresolved now for almost two decades (OGDEN & WHITING 2003).

3.8. Homologous muscular insertions

Pterygote limb musculature is shared by Palaeoptera and Neoptera (a symplesiomorphy). Homologous muscles

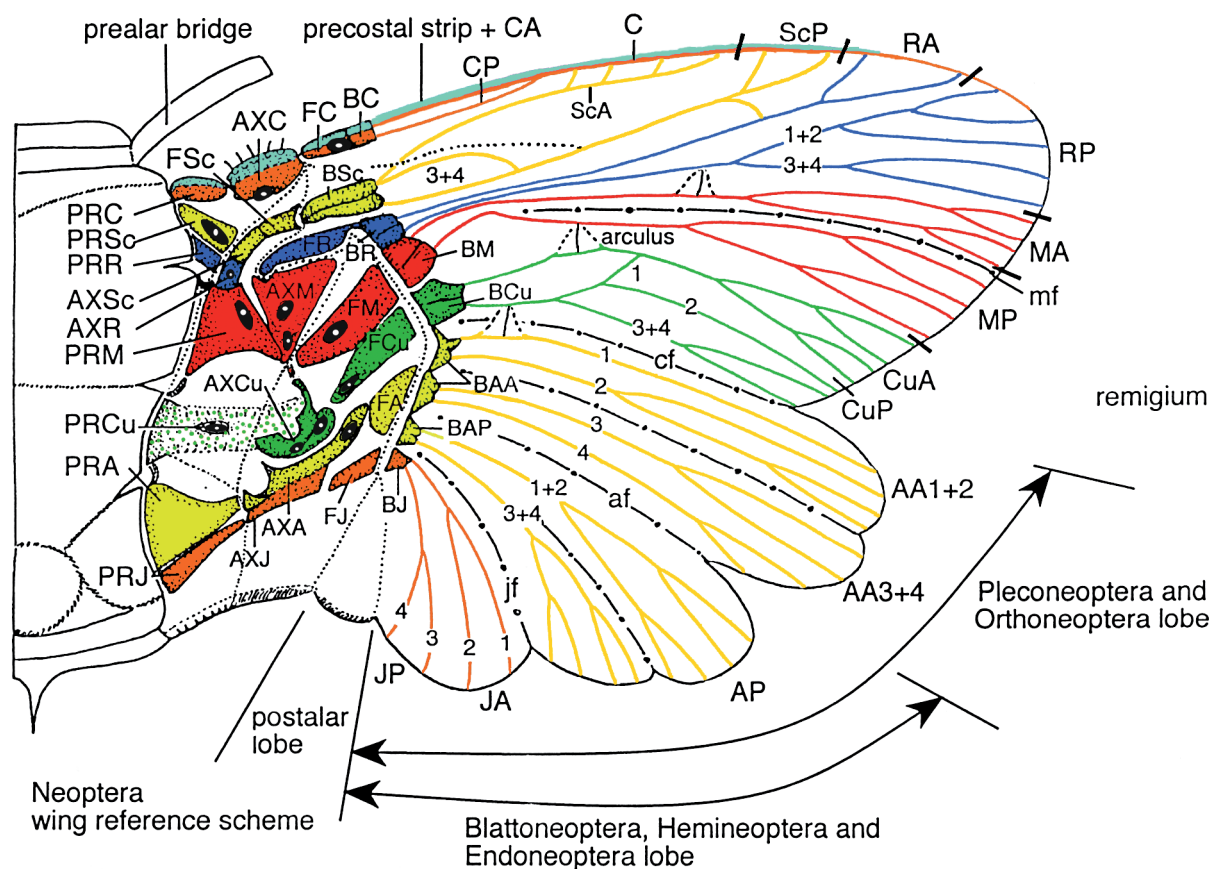


Fig. 14. Neoptera: the groundplan reference scheme includes the least fused and reduced character states of the sclerites, muscular attachments and venular sector, found in all lineages after a broad search. The wings can be flexed backward and locked so that the narrower tegminous forewings protect the broader, thinner and foldable hind wings, which are the main flying pair. Frequently occurring braces and fusions (a parallelism) are dotted. The arrangement of sclerites in rows, precosto-costal, medial, cubital, anal and jugal, is undisturbed. However, in the first and second axillary, 1Ax and 2Ax, there are derived connections between the subcostal, radial and medial proxalaria, axalaria and fulcalaria, which form two narrow parallel oblique arms. When the third axillary (3Ax) folds, rotates, and collapses along articular planes between its five sclerites, these oblique arms wrap around the vortex. All row-sclerites, some muscles, and all venular sectors are shared with Palaeoptera, but not a single composite sclerite, venular stem, or brace is shared at the division groundplan level. – After KUKALOVÁ-PECK in HAAS & KUKALOVÁ-PECK (2001, fig. 2), updated.

usually stay attached to the same row-sclerites even after they become part of differently composed clusters. Example: In Neoptera, the wing flexing muscle is attached to the cubital axalare AX-Cu (the goblet) which is part of 3Ax. In Odonata, it is attached to AX-Cu or F-Cu, while this part of cubital row is fused into the composite posterior plate (TANNERT 1958; BRODSKY 1994; KUKALOVÁ-PECK 1983, 1998). In Ephemera, the cubital row is still retained separate, and AX-Cu and F-Cu with muscular attachments are articulated to each other (a plesiomorphy) (BRODSKY 1994; WILLKOMMEN 2008). Thus, homologous wing musculature does deliver phylogenetically important facts, but it can be correctly interpreted only within a broader evolutionary context! Without it, the phylogenetic significance of muscle insertions in the organ system is uncertain, and reliable supporting information is tossed

around without much impact. Again, comparative morphology alone is quite helpless to resolve problems in modern higher taxa with deep Paleozoic roots.

3.9. Anterior articular plate

In the ancestral Hydropalaeoptera, this plate shared by mayflies and dragonflies (Figs. 5, 6, 12, 13, 15) had probably only three fusions: precostal axalare to precostal fulcalare (AX-PC + F-PC); costal axalare to costal fulcalare (AX-C + F-C), and precostal fulcalare and costal fulcalare (F-PC + F-C) fused together by their distal ends. The unusual feature of this plate is a large, bilobed costal fulcalare (F-C). In the Permian †Protoreismatida (Fig. 11), these lobes are far apart, but in Odonatoptera they are close to-

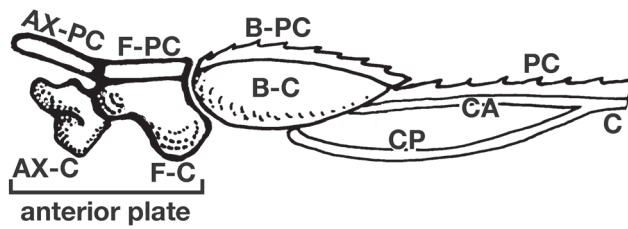


Fig. 15. Ephemeroptera: †Prottereisma: *Prottereisma* sp., forewing, young subimago. Early Permian (Kungurian), Elmo, Kansas. The anterior plate articulated to basivenale, serrated precosta (PC) fused to costal sector CA+ and the costal sector CP-. The costal axalare AX-C with a projecting “nose”, two large lobes in fulcalare F-C, and a large basivenale B-C broadly articulated with F-C are closely reminiscent of the anterior plates in early dragonflies (Figs. 5, 6, 13). – After KUKALOVÁ-PECK (1998, fig. 19.7c), interpretation updated. Length of section 2 mm.

gether and separated by a deep, probably flexible furrow, while the larger distal lobe is placed antero-proximally with regard to the smaller proximal lobe (Figs. 6B, 13). In modern Odonata, the groove between lobes became a shallow and barely noticeable depression (KUKALOVÁ-PECK 1983, fig. 16 B; 1998, fig. 19.7c). In modern Ephemera the ancestral anterior plate is more strongly sclerotized than the surrounding sclerites and V-shaped (Fig. 12), so that it is superficially dissimilar from the rounded plate of Odonata. The homologous composition was discovered only in 1998 by this author. It offers a complex synapomorphy of Hydropalaeoptera, unique under Pterygota (KUKALOVÁ-PECK et al. in press 2009).

3.10. Posterior articular plate

In the ancestral Hydropalaeoptera, the posterior plate almost certainly included fusions in the same row, between the subcostal, radial, medial, cubital, anojugal fulcalaria (on the thorax side) and basivenalia (on the wing side). These fusions elongated and stiffened the wing base, so that it rested and rocked on pleural pivots. It also probably included fusions between the central rows, subcostal + radial + medial, which are fused in all so far known Hydropalaeoptera (Figs. 5, 6, 11–13). Note that in Ephemera (Fig. 12), the cubital and the anojugal row are not part of this posterior plate since they are still separated from each other by membranous gaps. In the extinct sister order †Prottereisma (Fig. 11) these gaps are closed and their presence is uncertain. In dragonflies the posterior plate is larger than in mayflies and much more compact. All rows including cubital and anal row are firmly fused together, and the column of axalaria (AX) is added to the plate (Figs. 6A, 13). As shown in fossils, rows inside the

plate were originally marked with sutures (Figs. 5, 6B, 11–13). In modern Odonata only remnants of the original symmetry can be seen. These include the incision between the subcostal and radial row, the groove between the ancestral plate and the axalar column, and the cubital row (F-Cu + B-Cu) strongly slanted posteriorly as in modern Ephemera.

3.11. Paleoptery is a derived adaptation

In the rostrum-bearing Palaeoptera: Palaedictyopteroidea: †Diaphanoptera, the fusions between rows of sclerites were minimal and occurred only between four precostal + costal sclerites (PR, AX, F, B). Therefore, they could move their wings in all directions and flex them backward and over the abdomen. The other orders of the same rostrum-bearing lineage, Palaedictyoptera, Megasecoptera, and Permothemistida could not flex their wings backward, because they developed fusions between basivenalia and fulcalaria in the subcostal-to-jugal row. This shows that paleoptery is a secondary state, not a primary condition.

The posterior articular plate is an energy-saving device, which keeps the wings permanently in the extended position. In Neoptera, wings have to be kept extended during flight by the basalar muscle, which costs extra energy. The sizes and the flexion lines and grooves inside paleopterous posterior plates differ at the ordinal level, and their function during flight is poorly known. Example: †Palaedictyoptera seem to have the posterior plate too large to be able to manoeuvre the wings in flight, which obviously does not make much sense (see a good photograph of this ancient plate by KUKALOVÁ-PECK & RICHARDSON 1983, figs. 1, 3, 4, 6). While all early Palaeoptera (predatory or imbibing open fructifications) show a strong evolutionary trend toward flight improvement, the main survival strategy in early Neoptera (feeding on hard plant matter) was not to fly away from predators but to hide, as quickly as possible. They were slow fliers (see KUKALOVÁ-PECK 1991 for figures) and they escaped predation by keeping their thinner and broader hind wings under the protection of narrower and thicker tegmina firmly locked above them, and by hiding in narrow spaces. Probably, they reflexively fell down from their perch like modern beetles, or they hopped away and into dense vegetation, like grasshoppers. Neopterous flight blossomed only in the Mesozoic, with membranized forewings and hind wings reduced and/or hooked to them in tandem (as in Hymenoptera and Diptera). Evolutionary morphological differences between Palaeoptera and Neoptera are precipitous and start right from the protowing. It can be said with confidence that the sister relationship of either Odonoptera or Ephemeroptera with Neoptera is not morphologically possible.

3.12. Nymphal winglets in diverse resting positions

All known aquatic nymphs of Paleozoic Ephemeroptera have thoracic winglets movably articulated with the posterior plates. These were held laterally extended like in adults, but were strongly curved backward for easier forward movement (CARPENTER & RICHARDSON 1968, 1971). The curve straightened gradually in each instar, and it took several subimagos to fully straighten the wings (KUKALOVÁ-PECK 1978, 1991, 1998; SHEAR & KUKALOVÁ-PECK 1990). Two detached winglets of juvenile Odonoptera described here (Figs. 6, 8) are also curved, but they are almost straight in the young *Dragonympha* n. gen. (Figs. 1, 2). In this, they are lifted up and oriented obliquely backward, so that they are streamlined with the body. This adaptation obviously facilitated forward movement, perhaps up and through vegetation along shorelines. Fully aquatic nymphs typically have their wings laying flat on the back, an adaptation enabling crawling through mud-covered debris on the river bottom. How to interpret these differences?

The adaptation to lift up the wings is relatively simple since the posterior plate is inserted by limb muscles (BRODSKY 1994; WILLKOMMEN & HÖRNSCHEMEYER 2007; WILLKOMMEN 2008). It is also wide open to parallelism. In adult Paleozoic †Protereismatida and many modern Ephemera, wings uplifted at rest protrude high above body and the wind sways them like sails. Adult damselflies also lift up their narrow wings at rest, but hold them at an oblique angle streamlined with the body with the help from dorsally extended anepisterna. In *Dragonympha* n. gen., the winglets are also streamlined with the body, but the difference is that the anepisternum is not yet extended dorsally (Figs. 1, 2). In the mayfly sister orders, the uplifted wing position may be a synapomorphy. In the dragonfly orders, it more probably evolved independently and in parallel. More information is needed. Note that Paleozoic Palaeoptera and Neoptera had several subimagos (KUKALOVÁ-PECK 1978, 1983, 1991, 2008). No fossil record of dragonfly subimagos exists but in the modern Odonata, submarginal instars are replaced by the teneral state. This may show posteriorly curved wings similar to those described in the subimagos of †Megasecoptera (SHEAR & KUKALOVÁ-PECK 1999) (personal observation on the shore of the Lake Huron). Thus, the presence of subimagos is a plesiomorphy, and not an autapomorphy separating Ephemeroptera from the rest of Pterygota, as repeatedly misinterpreted in comparative morphological datasets! For the rich fossil record on multiple subimagos in Palaeodictyoptera, Megasecoptera and Ephemeroptera and the parallel origin of the metamorphic instar in modern pterygotes see KUKALOVÁ-PECK (1974, 1978, 1983, 1985, 1991, 2008; SHEAR & KUKALOVÁ-PECK 1999).

3.13. Evolution of the veinal system in Odonoptera and Ephemeroptera

Wing articulation and veinal systems identify all pterygote higher taxa and their sistergroups (HAAS & KUKALOVÁ-PECK 2001; KUKALOVÁ-PECK & LAWRENCE 2004; KUKALOVÁ-PECK 1991, 2008; this paper). Venational characters are fully homologized and evaluated with respect to the protowing. The groundplan level character states, including reliable synapomorphies, are the character states least fused and reduced with respect to protowing, found in a significant sample of each higher taxon. Fossils offer invaluable help in homologization and in the search for groundplans, especially in the oldest modern lineages, in which these states are most difficult to recognize. In the oldest taxa Odonoptera, Ephemeroptera and Neoptera, the probable time distance from their divergence in the Silurian or even Ordovician (some 400 m. y.) is too long to preserve synapomorphies in their original clear-cut shape. Instead, they are overwhelmed by convergencies and parallelisms from which they are visually inseparable, and cannot be recognized.

In the analysis above, the intention was to show, by concrete examples, how much the synapomorphic character states have become obscured in modern fauna. The wing base of the Carboniferous order †Geroptera (the side line closest to protowing) is compared with the wing base of Carboniferous Odonatoclauda: †Eoanisoptera (the basal order in the taxon which includes modern Odonata), and these two plesiomorphic dragonfly groups are compared with their counterparts in mayflies. The wing base of Carboniferous †Syntonopterida (KUKALOVÁ-PECK 1985) and Permian †Protereismatida (both close to protowing) is compared with the wing base of modern Ephemera (represented by the plesiomorphic living species).

4. Conclusion

Late Paleozoic dragonflies and mayflies may be more than 100 m. y. distant from their probable time of lineage divergence in the early Paleozoic, while for modern Odonata and Ephemera, this distance is believed to be some 400 m. y. or more. Thus, fossils are much closer to lineage-level groundplans and, quite naturally, offer many more evolutionary clues to relationships than living species. Compared to this, e.g. modern Lepidoptera are much younger, and diverged only about 170 m. y. ago. Therefore, their modern basal species offer many more evolutionary clues than those of the much older orders and lineages. This shows that all modern higher taxa do not start at the same time in an analysis of their characters. This important aspect is often underestimated or forgotten.

As an example, when the foremost lepidopterist – comparative morphologist N. KRISTENSEN (1975, 1981, 1991) compared the modern species of Odonata with those of Ephemera and Neoptera (separated for about 400 m. y.), he obtained five similarities in the limb-derived shearing mandible, which Odonata “shared” with Neoptera. These appeared to offer much more convincing synapomorphies than the single, fused lacinio-galea in the maxilla, shared by Odonata and Ephemera. But, the history of the evolution of this organ is the catch, and the documentation provided by fossils, paints a different picture.

In Insecta, the permanent anterior condyle (formed by changing the sliding mandibular groove into a tight socket), strong muscles (for opening sideways) and necessary adjustments regarding the hypopharynx (dictated by increased width of the mandible) is a relatively late albeit important adaptation occurring only in the plant chewing Neoptera, and in the predaceous Odonoptera. In contrast, maxilla includes two independent CX and TR endites which are serially homonomous and used by arthropods including insects mainly for eating and copulating. Therefore, they occur originally in all limbs and are part of the Arthropoda groundplan, believed to be of Proterozoic origin. The fusion of maxillary endites took place much later at the Palaeoptera level, is unique, and it occurs both in †Palaeodictyopteroidea with sucking and Hydropalaeoptera with chewing mouthparts. These attributes make the fusion of maxillary endites a very strong synapomorphy shared by the division Palaeoptera (a unique apomorphy), and absent in the division Neoptera (a plesiomorphy). This pattern of age and occurrence shows quite clearly that the shearing mandible originated twice (and independently), first in Neoptera and then again in Odonoptera (a convergence). Very broad approach to diversification of the wing organ system using arthropod anatomy, and all relevant data from other biological fields and paleontology provided so far 65 differences between Palaeoptera and Neoptera, which can be readily observed and verified in modern fauna (HAAS & KUKALOVÁ-PECK 2001).

Limb organ system in Arthropoda and wing organ system in Pterygota appear to be the natural first choice in defensible phylogenetic analysis of the higher taxa. In the protowing organ system basal for Pterygota, all differences between the divisions Palaeoptera and Neoptera are autapomorphic. Therefore, these two veinal systems can be derived only from the common ancestral protowing. The only morphologically possible split of Pterygota is into divisions Palaeoptera + Neoptera. The other two erroneous but repeatedly proposed schemes, Pterygota = Ephemeroptera + (Odonoptera + Neoptera) and Pterygota = Odonoptera + (Ephemeroptera + Neoptera) are morphologically quite impossible and were reached either by using non-homologous character states, or states which were not at the groundplan level of these higher taxa (Hen-

nigian systematic principles were violated). These schemes should be abandoned.

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