

## Homologisation of the anterior articular plate in the wing base of Ephemeroptera and Odonatoptera

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In the search for the sister group of modern Ephemera, we used the evolutionary groundplan method to identify synapomorphies in wing articulation. The evolutionary approach is necessary because post-groundplan wing adaptations have obscured the phylogenetically informative higher-level synapomorphies in modern Ephemera, Odonata and Neoptera. Protowing-level sclerites are recognisable fragments of the first limb-derived pleuron, arranged in eight rows above the pathways delivering blood to the eight principal wing veins. Each row includes three sclerites (proxalare, axalare and fulcalare) which articulate with the basivenale (wing blood sinus). Over the course of the pterygote evolutionary history, many row-sclerites have assembled into clusters, plates, or processes, the composition of which can be most clearly recognised by comparison with ancestral Paleozoic fossils. The extant orders Ephemera and Odonata (Palaeoptera: Hydropalaeoptera) share a derived anterior articular plate (AAP) composed of four fused sclerites (two axalaria and two fulcalaria) belonging to the precostal and costal rows. This plate represents a complex and unique synapomorphy. In Neoptera, precostal and costal fulcalaria are fused to basivenalia to form a humeral plate, and axalaria are obscured by the tegula. Palaeoptera include two subdivisions, extant Hydropalaeoptera and extinct Palaeodictyopteroidea.

**Keywords:** Ephemeroptera; Ephemera; Odonata; Hydropalaeoptera; wing articulation

### Introduction

The divisions, lineages and orders of winged insects are easily recognised and differentiated by limb-wing synapomorphies. Therefore, the limb-wing organ system and its character series are the natural first choice for an all-apterygote phylogenetic analysis (Kukalová-Peck 2008). As convincingly established by Hennig (1969, 1981), genuine synapomorphies can be found only when two fundamental rules of systematics are upheld. These are (1) the use of fully homologised character states, which (2) are at the groundplan level in all taxa involved. The groundplan character states in modern higher taxa are those shared by all representatives (usually in a modified version) which are present in their plesiomorphic (concretely found) state

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with respect to the monophyletic pterygote ancestor (for documentation, see Kukalová-Peck 2008).

Obviously, a considerable amount of research is necessary before the search for groundplan character states, and phylogenies, can be launched. This study started by researching the monophyletic organ patterns in Arthropoda, Hexapoda and Insecta - Pterygota, from which all limb-wing character states in Pterygota can be flawlessly derived. All relevant information available in genetics, developmental genetics, ontogeny, physiology, embryology, etc. was gathered and checked for confirmation and compatibility. Gradual changes in the pterygote character state transformation series were recorded from Paleozoic to modern times. The protowing model was constructed from plesiomorphic states (defined as least reduced or unfused), and repeatedly tested by deriving from these states all wing characters found in extant and extinct insect lineages. Then, the same process was repeated in pterygote divisions, lineages and orders. This long-term project has been in progress for over three decades, and frequently verified, improved and updated (Kukalová-Peck 1978, 1983, 1985, 1998, 2008; Kukalová-Peck and Richardson 1983; Riek and Kukalová-Peck 1984; Haas and Kukalová-Peck 2001; Kukalová-Peck and Lawrence 2004).

In this paper, the anterior articular sclerites are evaluated with a unified nomenclature in reference to the common ancestor of the monophyletic Pterygota. The lineage Ephemeroptera was present among early winged insects, and an evolutionary approach shows that the late Paleozoic mayflies †Syntonopterida and †Protereismatida were much closer to the point of divergence of Ephemeroptera from Odonatoptera (and from groundplan-level synapomorphies) than are modern Ephemera. Modern mayflies have developed forewing flight with reduced hind wings functioning as flaps. Therefore, modern mayfly species show a peculiar mix of strong autapomorphies and deep plesiomorphies not found in other living groups.

Knowledge of detailed morphology and physiology of modern limb-wing organ systems, and differences in their expression in fossil ancestors and modern insects clarifies the evolution and phylogeny of extant Pterygota. Wing veins form around blood channels (Arnold 1964). Penetration of channels by tracheae is secondary (Holdsworth 1940, 1941). Eight pathways deliver blood to eight principal wing veins running under eight rows of sclerites. These sclerites are fragments of the first arthropod limb segment flattened into the pleuron (epipleuron) and the mobile wing base ramus bearing muscle insertions (Kukalová-Peck 2008 and before). *Only these original groundplan-level protowing sclerites are shared by all Pterygota.* After diversification into Palaeoptera and Neoptera, most of these individual homologous row-sclerites became differently clustered and fused, *either* into paleopterous plates, *or* into neopterous axillaria, median and humeral plates and the wing processes. These secondary paleopterous and neopterous clusters *cannot be homologised*, because they represent original sclerites and homologous muscle insertions arranged in un-homologous conglomerates!

The fully homologisable articular scheme includes eight rows of original pteralia in three columns of articular sclerites (two from the subdivided pleuron, one from the wing-appendage base), each articulated to the fourth column of basivenalia (sclerotised blood sinuses) (Figure 1). Proxalaria (PR) and axalaria (AX) are fragments of the subdivided epicoxal pleuron; fulcalaria (F) are fragments of the exite base (which received muscles); basivenalia (B) are sclerotised veinal blood sinuses. Thus, the wing articulation follows closely the blood flow from the limb into the outer ramus (Figures 1–3). The wing sclerites are aligned in eight rows of wing

veins: precostal (PC), costal (C), subcostal (Sc), radial (R), medial (M), cubital (Cu), anal (A), jugal (J). In extant Ephemeroptera, Odonata and Neoptera, wing pteralia and wing veins are fused, hinged, braced, enlarged, reduced or lost at the species, genus, family, order, lineage and division levels. Of these character states, *only those present at the moment of divergence show clearly the synapomorphies between sister-taxa* (Hennig 1969, 1981).

We homologise the wing articulation in the families of modern Ephemeroptera with that in †Protereismatida, the extinct Paleozoic sister order of Ephemeroptera, extinct and extant Odonatoptera (†Geroptera, †Meganisoptera, †Protanisoptera, Odonata), and with extant Neoptera (Haas and Kukalová-Peck 2001). Previous analyses (e.g. Snodgrass 1935 and the majority of morphologists) compared instead only the large sclerites in modern Ephemeroptera, Odonata and Neoptera while sclerites in fossils and small or weakly sclerotised sclerites were ignored. As a result, solid sclerites and articular plates in mayflies and dragonflies were compared with utterly dissimilar, movably hinged and folding axillaries of Neoptera. This is a fatally flawed method, since all wing sclerites represent an organ system. After diverging from a common ancestral pattern, all sclerites co-evolved to perform a function.

Velma Knox [Mayo] (1935) was first to describe the ‘axillary sclerites’ of mayflies (using methods of comparative morphology and terms for axillaries 1Ax, 2Ax, 3Ax which occur only in Neoptera). She attempted to homologise the wing base of Ephemeroptera with that of Orthoptera (the generalised representative of Neoptera used by Snodgrass 1935). The resulting interpretation showed an illogical, multi-faceted basalare originating under the wing, looping over the wing, and spreading posteriorly. Such a structure would necessarily encompass more than one sclerite, and later researchers tried to rearrange these pieces with little success. However, some entomologists correctly recognised that wing articular sclerites could not be directly homologised (for example Kluge 1994).

In the original description of the oldest known Carboniferous mayfly genus †*Bojophlebia* (order †Syntopterida), Kukalová-Peck (1985) included an interpretation of the modern mayfly wing venation as a composite model representing no family. For more than a decade, we have been trying to refine this work by recording character states of sclerites in all mayfly families with wings large enough to show observable articulation. We present here results concerning the structure of the anterior articular plate. This plate has been derived from the monophyletic pterygote ancestor (protowing: Kukalová-Peck 1983, 1998, 2008; Kukalová-Peck and Lawrence 2004) rather than from extant orthopterans. The anterior articular plate is a compound structure which, among extinct and extant orders, can be homologised only with the anterior articular plate of Odonata.

## Methods

We examined wing bases of specimens of imaginal and subimaginal Ephemeroptera of 43 extant species representing 21 families, 12 named paleontological species and Paleozoic fossils Palaeodictyopteroidea, Ephemeroptera, Odonatoptera and Neoptera from the Museum of Comparative Zoology, Harvard University, Cambridge; Muséum d'Histoire Naturelle, Paris; Russian Academy of Sciences, Moscow; Field Museum, Chicago; Museum of Natural History, London; Národní Museum, Prague; Natal Museum, South Africa; private collections from Mazon Creek area, Illinois, and collection of JKP from Obora, Moravia and Carrizo Arroyo, New

Mexico. Most important for purposes of this paper were *Baetisca rogersi* Berner (and other species of Baetiscidae), *Acanthophlebia cruentata* (Hudson) (Leptophlebiidae), *Siphonurus aestivalis* (Eaton) and *S. columbianus* McDunnough (Siphonuridae) because the visible structures could be compared against good, cleared wing base slides (Figures 7, 9–13). These slides were originally prepared by P.T.P. Tsui using methods appropriate for comparative study of thoracic morphology (Tsui and Peters 1972, 1975).

### ***Nomenclature***

We follow Bechly et al. (2001) in using the names Ephemeroptera and Odonatoptera for lineages, and Ephemerida and Odonata for modern orders. Division Palaeoptera includes superlineages Palaeodictyopteroidea and Hydropalaeoptera. The superlineage Hydropalaeoptera Rohdendorf, 1968 includes lineages Ephemeroptera and Odonatoptera.

### ***Wing homologue***

For an objective morphological analysis, the interpretation of the insect wing *must* be based on the correct homologue in Arthropoda. The protowing evolutionary model of wing articulation was proposed by JKP after an extensive study of extinct and extant insects representing more than 400 million years of wing evolution, and was applied and broadly tested in all modern pterygote orders. All character states described in the text are based on actual specimens. Since details of the protowing articulation pattern given in Figure 1 are beyond the scope of this account, interested readers can find full documentation in the papers by Kukulová-Peck (1983, 1998, 2008).

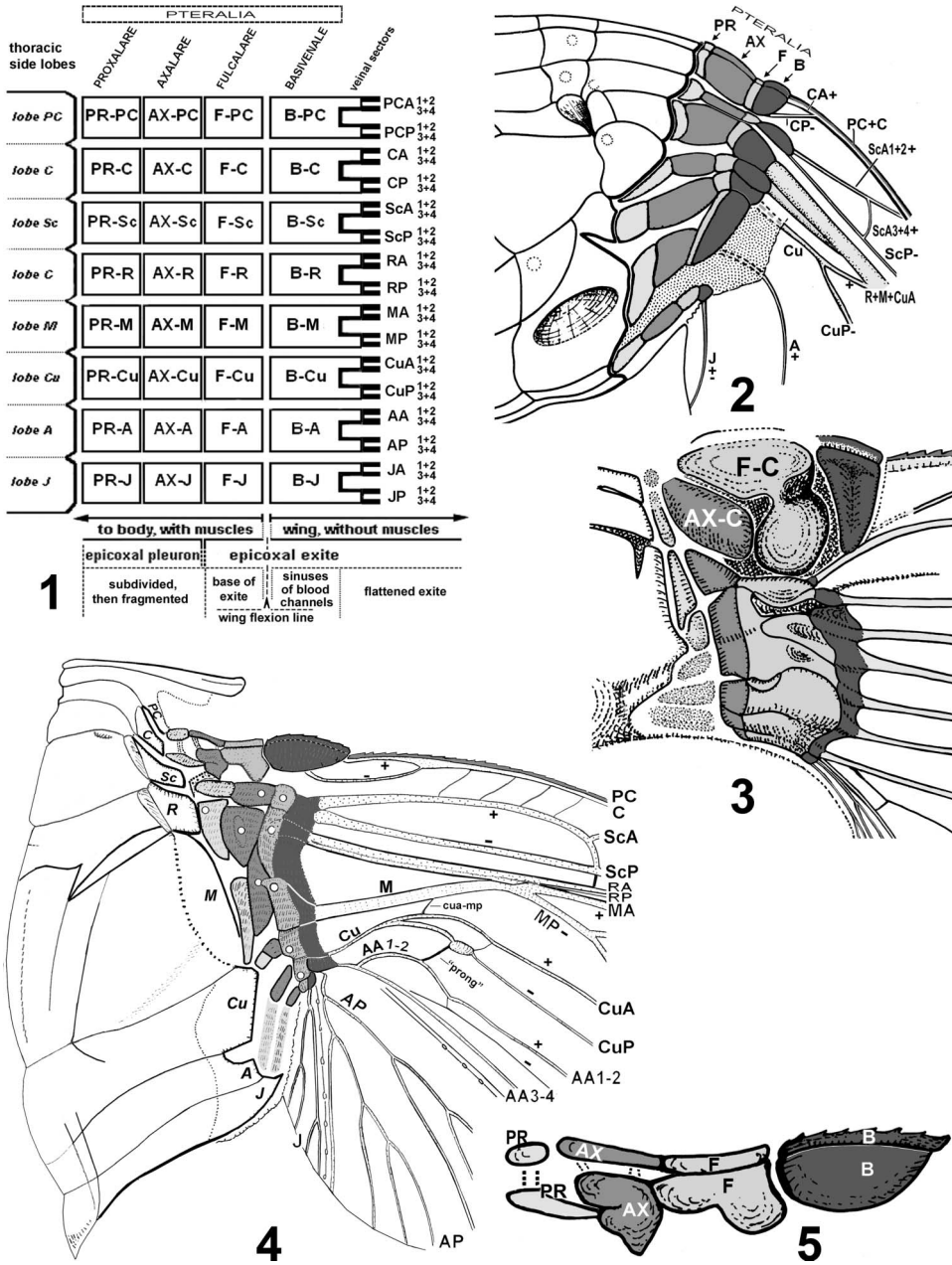
## **Results**

### ***Protowing pattern in Palaeodictyopteroidea and the rise of the paleopterous condition***

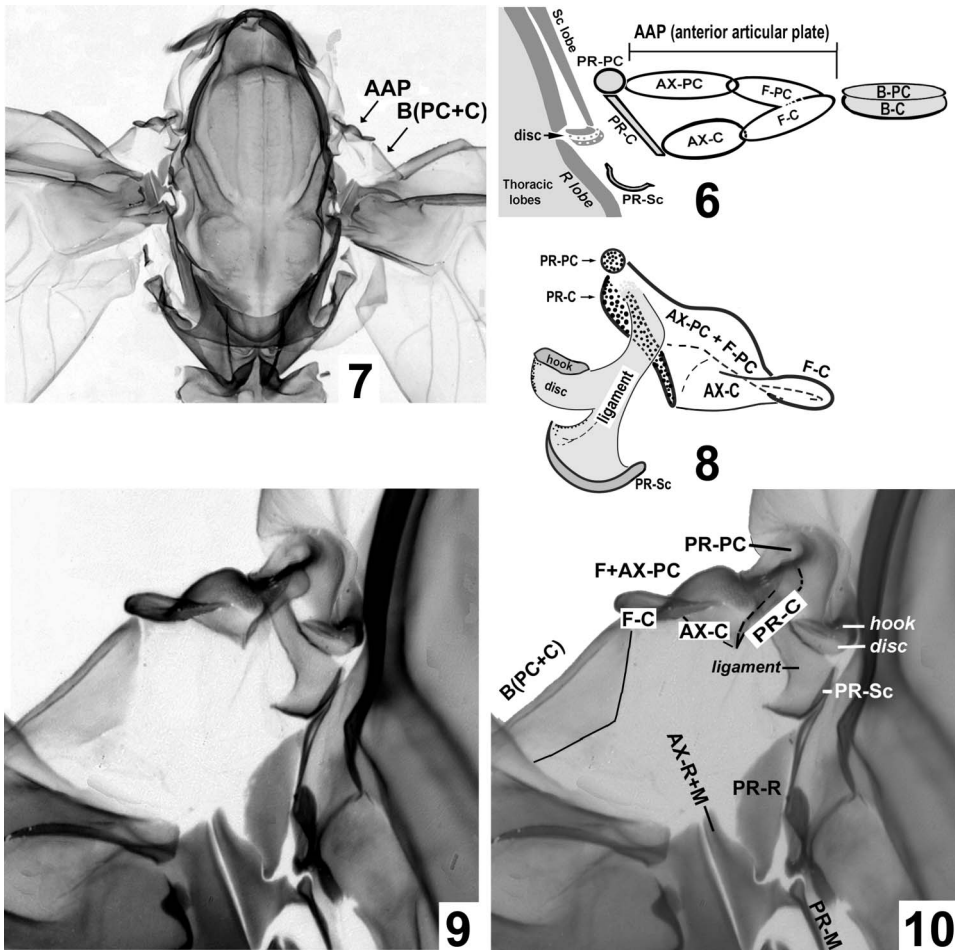
The least derived pterygote wing articulation so far known (regular rows, absence of reductions, very few fusions) is found in the extinct superlineage of rostrate Palaeoptera: Palaeodictyopteroidea, order †Diaphanopteroidea (capable of flexing wings backward, Figure 2). The wing sclerites are arranged in eight regular rows. The only derived states are the fusions between four precostal and costal pteralia, PR-PC and PR-C, AX-PC and AX-C, F-PC and F-C, and B-PC and B-C (an autapomorphy of Palaeodictyopteroidea), showing that rostrate Palaeodictyopteroidea did not have an anterior articular plate. A schematic review of the ancestral pattern is offered in Figure 1 and represents the plesiomorphic states for all pterygote higher taxa.

The groundplan-level proxalaria are free in both Ephemerida and Odonata (Figures 4, 5, 14). In Ephemerida, the axalaria and a part of the fulcalaria are also free (Figures 6, 10, 12) (all plesiomorphies at the protowing level). In Palaeodictyopteroidea, all proxalaria, axalaria and fulcalaria in these rows are fused one to another (Figure 2, an autapomorphy), but Hydropalaeoptera are more derived in other ways. In Odonatoptera, the costal axalaria and fulcalaria evolved from a flexibly connected condition (Figure 3) to a compacted condition and then to fusion without sutures (Figure 14).

Fusions preventing wing flexing are adaptations for energy-efficient flight (they eliminate the muscular pull on the anterior wing margin needed to hold the wings



Figures 1–5. Schematic of pteralia and wing articulation in ancestral insects. (1) Schematic of terms discussed in methods; (2) eight rows of sclerites in Permian Palaeodictyopteroidea: †Diaphanopteroidea (modified from Kukalová-Peck and Brauckmann 1990); (3) articular plates of wing base of plesiomorphic Carboniferous Odonatoptera: incompletely preserved anterior articular plate with sclerites connected by deeply incised grooves (†Geroptera: *Eugeropteron lunatum* Riek, original from specimen, JKP; Museo de la Plata, La Plata, Argentina); (4) wing base of subimago of a Permian Ephemeroptera: †Proterismatida: *Protereisma* sp., the sister order of modern Ephemeroptera, showing thoracic lobes, rows and columns of sclerites, wing base with complex subcostal and anal brace (improved from Kukalová-Peck 1991); (5) same specimen, detail of pteralia in precostal and costal row; costal fulcalare (F-C) bears two large lobes as in the anterior plate of †Geroptera (3).

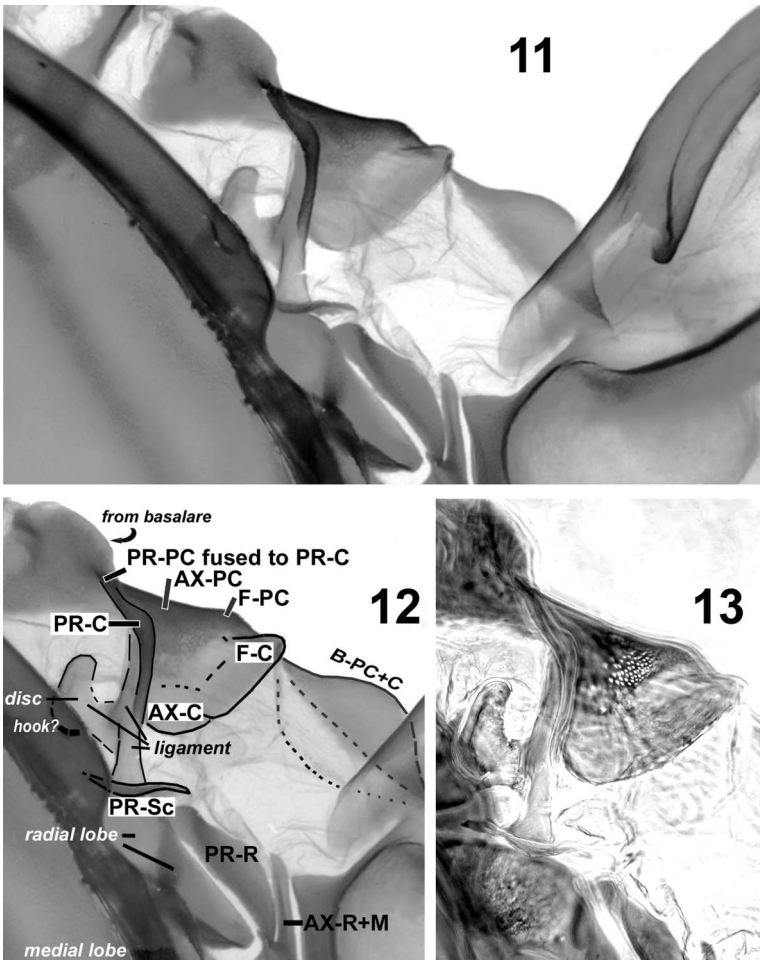


Figures 6–10. (6) Schematic of terminology applied to the anterior articular plate (AAP). (7–10) *Acanthophlebia cruentata*, (7) dorsal view of thorax and wing bases of male imago; (8) outline of right AAP with proxalaria (PR) of PC, C, and Sc rows and hook/disc structure; (9, 10) left AAP and adjacent structures as photographed (9) and labelled (10).

open). In modern Palaeoptera, fusions between sclerites on the thoracic and wing side of the flexion line (between fulcalaria and basivenalia) prevent the wings from flexing and create a long lever which rests and rocks on pleural pivots. Flight in Odonatoptera is extremely autapomorphic. Odonatoptera also differ from all other Pterygota in that the basalare has become ventrally fused to the anterior plate, and overlaps it anteriorly to form a narrow rim.

### *Odonatoptera, fossils*

The oldest preserved wing articulation of an Odonatoptera (†Geroptera, Figures 3, 14) shows part of the posterior arm of the anterior articular plate, with a large, bi-lobed costal fulcalare (F-C) narrowly separated from the costal axalare (AX-C) by a deeply incised groove-like suture. In the sister group Odonatoclada (including the



Figures 11–13. *Baetisca rogersi*, right articular plate of male imago. (11) Photograph; (12) same with labels; (13) same photographed in phase-contrast.

rest of fossil orders plus modern Odonata) the anterior plate becomes much more compact and the groove becomes a suture in †Meganisoptera and †Protanisoptera and disappears in modern Odonata. The proximally prominent projection (‘nose’) on the costal axalare is still prominent in †Meganisoptera, small in †Protanisoptera, and hardly noticeable in Odonata (Figure 14).

***Ephemeroptera, fossils***

The oldest wing articulation in Ephemeroptera known to date is that of an Early Permian subadult of †Protereismatida (Figures 4 and 5). The proxalaria and axalaria of the precostal and costal rows are separate (two protowing plesiomorphies previously mentioned). This fossil is from white dolomitic limestone (Elmo, Kansas) and the dark brown preserved colouration of connections between PR-PC and PR-C may be an anterior projection on PR-C or a ligament. More connections between

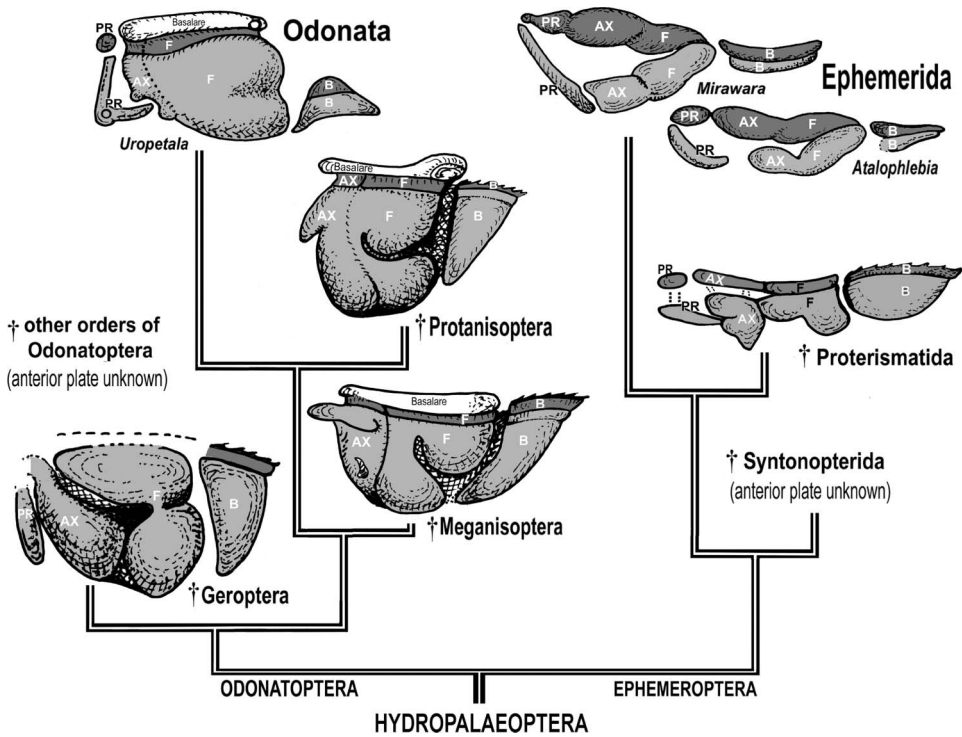


Figure 14. Evolutionary transformations of the anterior articular plate in Ephemeroptera and Odonatoptera. Although composition remains identical and both groups show similar lobes and projections, AAP in dragonflies is more compact. Later fusions replaced hinges, and lobes and projections were almost erased; in modern Ephemeroptera and Odonatoptera this complex synapomorphy went unnoticed (modified from Kukulová-Peck 1998 and the text above).

sclerites (probably ligaments) are shown as dotted lines in Figures 4 and 5 (these eventually change into fusions in Odonatoptera). The anterior articular plate includes two arms (anterior and posterior), with the axalare fused to the fulcalare of each arm. The anterior arm of the plate is narrow, and the posterior arm contains a nose-like projection on the costal axalare and two prominent lobes on the costal fulcalare. It is of great interest that these character states are found also in the Paleozoic Odonatoptera (Figures 3 and 14) but are later obscured. Thus, the anterior articular plate composed of the fused axalare and fulcalare of PC and C (a synapomorphy at the Hydropalaeoptera level) is easily recognised in the Paleozoic representatives, but quite dissimilar in the modern representatives.

### *Ephemeroptera, modern*

In the modern order Ephemeroptera, here considered the sister group of †Proterismatida, the articular plate is proximally open like a 'V'. Both arms are about of the same width and the 'nose' of the axalare and lobes of the fulcalare are weakly indicated only in some genera (Figure 14). The unfused proxalare, axalare and part of the fulcalare are at the protowing level. The articular plate is always sclerotised and distinct. Figure 7 shows the leptophlebiid mayfly *Acanthophlebia cruentata* with



the wing bases stained, spread and mounted so that their position is clear. Basally, the proxalaria of PC and C are fused or connected by a short ligament. The costal proxalare (PR-C) is connected by a strong ligament to the subcostal proxalare (PR-Sc) near the lateral wall of the thoracic tergum (Figures 8–10). Referring back to Figure 4, we recognise that the thorax is weakly subdivided into lobes which align laterally with the pteralia. The thickened lateral portion of what is treated here as a lateral extension of radial lobe has been termed the ‘suralare’ by Kluge (1994), and the proxalare of Sc is adjacent to this. The structure here termed the ‘hook’ (= apex of PAB:PA of Kluge 1994) fits into a small concavity in the radial thoracic lobe. This ‘hook’ probably represents a detached fragment of the subcostal thoracic lobe; it is not always distinct and may be absent in some groups (Kluge 1994).

Figures 8–10 are different views of the anterior articular plate (AAP) of the specimen in Figure 7. Figure 8 diagrams the right AAP from Figure 7 and its associated proxalaria, ligaments, and the hook/disc structure. Figures 9 and 10 are the same view of the left anterior wing base with different degrees of contrast given without and with labelling. Particularly clear in these figures is the strong, knob-like distal fusion of F-PC with F-C. This is always present in Ephemeroidea, but not always as distinct as shown here because the plate shifts and rotates with motion of the wing. Figures 11–13 show the structure of the AAP of the family Baetiscidae from a slide of *Baetisca rogersi*. Details of AAP and associated structures are labelled in Figure 12 and photographed again in phase contrast (Figure 13).

The wing base in modern Ephemeroidea is a moveable, three-dimensional structure and the proxalaria, being closest to the tergum, are often turned vertically; this is especially true for PR-C and PR-Sc. In some derived genera PR-Sc appears fused to the tergum, and in other families (particularly members of the Ephemeroidea), the ligament between PR-C and PR-Sc is enlarged and puffed up dorsally so that the underlying plate is obscured; in further derivations of Ephemeroidea, AX-PC may be reduced or desclerotised. In other families, the pieces of AAP may be indistinguishable so they appear as only a single plate. There are more variations, but the contributions of the anterior plate to the phylogeny of extant families are beyond the scope of this paper. Instead, we demonstrate here the groundplan of Ephemeroidea, which serves as a reference scheme of plesiomorphic states for character evaluations.

### *Hydropalaeoptera* = *Ephemeroptera* + *Odonoptera*

Overall, the above transformation series of the articular plate in Odonoptera and Ephemeroptera show a classical evolutionary divergence in sister group structures. While the anterior plates of Carboniferous †Geroptera and Permian †Protereismatida share hinged and fused sclerites with peculiar features (lobes, nose-like projections) and ligament connections between rows and projections, these are later gradually modified. Quite clearly, modern Odonata show little similarity in important details to modern Ephemeroidea. However, constituent sclerites remain homologous in both orders, and function as a single, well-sclerotised plate (a complex synapomorphy at the Hydropalaeoptera level). This plate is absent in Palaeodictyopteroidea (Figure 2), as well as in Neoptera (in which axalaria are replaced by a tegula and fulcralia are fused without a suture to basivenalia in the humeral plate (Haas and Kukalová-Peck 2002, Figure 1; Kukalová-Peck 2008, Figure 19). Together with an equally complex subcostal and anal brace (composed of three and five veinal elements, respectively: Kukalová-Peck 1998, 2008), the wing

organ system shows Ephemeroptera as the sister group of Odonoptera under Hydropalaeoptera.

## Discussion

The relationship between the three basal pterygote groups, Ephemeroptera, Odonoptera and Neoptera, has been intensely debated by systematists for almost two decades, most recently in these proceedings (Willkommen 2009). No consensus has been reached in spite of the fact that the wing organ system in these groups is very different and morphologically complex, and thus predisposed to offer distinctive higher-level synapomorphies. Two major obstacles prevented using this organ in phylogeny: the difficulty of full homology of all character states, and the recognition of groundplan-level states which alone include reliable synapomorphies.

It is a difficult task to make sense out of a modern mayfly wing base which appears composed of random bits and pieces, some with muscles and some with ligaments and some appearing to float in the membrane. The pioneering work of Knox (1935) using comparative morphology of modern insects recognised some pteralia and confused others. Such errors occurred because attempts to homologise extant orders without deriving the character states from the monophyletic ancestral structure are flawed. We employed an alternative, groundplan method. This is an evolutionary approach that examines concrete transformations of morphological character states and shows in which direction and by which steps character state series evolved. In the sister groups of higher taxa, only the groundplan-level synapomorphies can be clearly recognised and separated from homoplasies (convergences, parallelisms) which bedevil modern insect species. The fact that the Late Paleozoic representatives of Ephemeroptera, Odonoptera and Neoptera are some 300 million years closer to the crucial groundplan state facilitates precise homology and identification of the groundplan states in the extant higher taxa.

The present interpretation of wing pteralia has been developed over more than 25 years of thematic study of wing character transformation series in all pterygote lineages from Paleozoic to modern times. Its application to the modern order Ephemera was cross-checked by us for more than 10 years in a study including most extant and all Paleozoic genera and new complex synapomorphies were found. Ephemera cannot be treated as a sister group of Neoptera because they share all synapomorphies in the pterygote limb-wing organ system only with Odonata and Palaeoptera. Some of these synapomorphies are highly complex, such as the anterior articular plate (involving four sclerites), the posterior articular plate, the subcostal brace, and the anal brace (Kukalová-Peck 1998, 2008). Other clearly expressed synapomorphies are at the Hydropalaeoptera and Palaeoptera level. In all, 65 differences (!) in the wing organ system have been published marking the basal split of Pterygota into Palaeoptera and Neoptera (Haas and Kukalová-Peck 2001; also Kukalová-Peck 1983, 1985, 1998; Riek and Kukalová-Peck 1984; Kukalová-Peck and Lawrence 2004).

This account is concerned with only one complex synapomorphy, the anterior articular plate (Figures 7–13) which is elaborated upon and improved following its introduction in 1998. The anterior articular plate is shared by Ephemeroptera and Odonoptera, but it is absent in Neoptera. In Ephemera, the basalare is connected by a ligament to PR-PC, either alone or also to PR-C. These proxalaria articulate with both arms of the V-shaped anterior articular plate. In Odonata, which have

highly autapomorphic flight mechanics, the basalare is fused ventrally to the anterior plate and overlaps it anteriorly. The anterior plate is composed by fusion of the same four sclerites as in Ephemeroptera, but the precostal and costal rows are fully fused. Thus, the plate has the same composition, but it is more compact.

Sutures, which mark fusions between two previously separate sclerites, are clear in many modern genera of Ephemerida (Figures 7–13). In Odonatoptera, they are visible as open hinges in †Geroptera, and as sutures in the Paleozoic orders (Figures 3 and 14). In Palaeodictyopteroida, sutures between the precostal and costal PR, AX, F, B are quite clearly visible (Kukalová-Peck and Richardson 1983). In Neoptera, the veins and basivenalia of PC and C are always fused. The fused neopteran proxalaria (PR-PC and PR-C) are usually small and inconspicuous (but occasionally enlarged, Kukalová-Peck and Lawrence 2004, figures 29 and 30), and a sensory organ (tegula) is located in the position of the precostal and costal axalaria (AX-PC and AX-C). Unique to Neoptera is a powerful ligament connecting the basalare to the humeral plate to keep wings open during flight (Snodgrass 1935). In the present interpretation (Kukalová-Peck 1998, 2008; Haas and Kukalová-Peck 2001) this humeral plate is composed of F-PC and F-C and B-PC and B-C fused together without a suture. In all Palaeoptera including modern Ephemerida and Odonata, only the precostal and costal basivenalia are fused (with a suture), and the basivenalia are never connected to the basalare. In itself, this strong character also distinguishes Palaeoptera from Neoptera.

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### References

- Arnold, J.W. (1964), 'Blood circulation in insect wings', *Memoirs of the Entomological Society of Canada*, 38, 3–49.
- Bechly, G., Brauckmann, C., Zessin, W., and Groning, E. (2001), 'New results concerning the morphology of the most ancient dragonflies (Insecta: Odonatoptera from the Namurian of Hagen-Vorhalle (Germany)', *Journal of Zoological Systematics and Evolutionary Research*, 39, 209–226.
- Haas, F., and Kukalová-Peck, J. (2001), 'Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta)', *European Journal of Entomology*, 98, 445–509.
- Hennig, W. (1969), *Die Stammesgeschichte der Insekten*, Frankfurt am Main: Kramer.
- Hennig, W. (1981), *Insect Phylogeny*, New York: John Wiley and Sons.
- Holdsworth, R. (1940), 'Histology of the wing pads of the early instars of *Pteronarcys proteus* Newman', *Psyche*, 47, 112–120.
- Holdsworth, R. (1941), 'The wing development of *Pteronarcys proteus* Newman', *Journal of Morphology*, 70, 431–461.
- Kluge, N.J. (1994), 'Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics', *Bulletin de la Société entomologique de France*, 99, 41–61.
- Knox, V. (1935), 'The body-wall of the thorax', in *The Biology of Mayflies: With a Systematic Account of North American Species*, eds. J.G. Needham, J.R. Traver, and Y.-C. Hsu, Ithaca, NY: Comstock, pp. 135–149.
- Kukalová-Peck, J. (1978), 'Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record', *Journal of Morphology*, 156, 53–126.
- Kukalová-Peck, J. (1983), 'Origin of the insect wing and wing articulation from the arthropodan leg', *Canadian Journal of Zoology*, 62, 1618–1669.

- Kukulová-Peck, J. (1985), 'Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera)', *Canadian Journal of Zoology*, 63, 933–955.
- Kukulová-Peck, J. (1991), 'Phylogeny of extant hexapods', in *The Insects of Australia: A Text Book for Students and Research Workers* (Vol. 1, 2nd ed.), Melbourne: Melbourne University Press, pp. 125–140.
- Kukulová-Peck, J. (1998), 'Arthropod phylogeny and 'basal' morphological structures', in *Arthropod Relationships*, eds. R.A. Fortey and R.H. Thomas, London: Chapman Hall, pp. 249–268.
- Kukulová-Peck, J. (2008), 'Phylogeny of higher taxa in Insecta: Finding synapomorphies in the extant fauna and separating them from homoplasies', *Evolutionary Biology*, 35, 4–51.
- Kukulová-Peck, J., and Brauckmann, C. (1990), 'Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany', *Canadian Journal of Zoology*, 68, 1104–1111.
- Kukulová-Peck, J., and Lawrence, J.F. (2004), 'Relationships among Coleopteran suborders and major neopteran lineages: Evidence from hind wing characters', *European Journal of Entomology*, 101, 95–144.
- Kukulová-Peck, J., and Richardson, E.S., Jr. (1983), 'New Homiopteridae (Insecta: Palaeodictyoptera) with wing articulation from Upper Carboniferous strata of Mazon Creek, Illinois', *Canadian Journal of Zoology*, 61, 670–687.
- Riek, E., and Kukulová-Peck, J. (1984), 'A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings', *Canadian Journal of Zoology*, 62, 1150–1166.
- Rohdendorf, B.B. (1968), 'Direction in the phylogenetic evolution of insects (Insecta Pterygota)', *Journal of General Biology*, 29(1), 57–66 (in Russian).
- Snodgrass, R.E. (1935), *Principles of Insect Morphology*, New York: McGraw-Hill.
- Tsui, P.T.P., and Peters, W.L. (1972), 'The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera)', *Journal of Zoology, London*, 168, 309–367.
- Tsui, P.T.P., and Peters, W.L. (1975), 'The comparative morphology and phylogeny of certain Gondwanian Leptophlebiidae based on the thorax, tentorium, and abdominal terga (Ephemeroptera)', *Transactions of the American Entomological Society*, 101, 505–595.
- Willkommen, J. (2009), 'The tergal and pleural wing base sclerites – homologous within the basal branches of Pterygota?', in *International Perspectives in Mayfly and Stonefly Research. Proceedings of the 12th International Conference on Ephemeroptera and the 16th International Symposium on Plecoptera, Stuttgart 2008*, ed. A.H. Staniczek, *Aquatic Insects*, 31 (Suppl. 1), 443–457.