

THE EPHEMEROPTERA: WHOSE SISTER-GROUP ARE THEY?

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The apomorphies or presumably apomorphic characters of mayflies within the formal Paleoptera are discussed in relation to these hypothetic possibilities: (i) Ephemeroptera + Odonata (= Paleoptera) are sister-group to Neoptera; (ii) Odonata are sister-group to Ephemeroptera + Neoptera and (iii) Ephemeroptera are sister-group to Odonata + Neoptera. Taking into account solely neotological data, the last possibility seems to be parsimonial. However, paleontological data show the paleopteran insect assemblage as a well defined and compact group in comparison with the neopteran orders. A review of principal names applied in higher classification of pterygotes is presented.

INTRODUCTION

The Paleoptera were established more than 70 years ago (MARTYNOV, 1924; CRAMPTON, 1924) to comprise the orders Ephemeroptera, Odonata, and some extinct Paleozoic insect groups. Since then the name «Paleoptera» has been used in different senses to cover different ideas about the actual course of phylogenies. We agree with HENNING (1981) that «...this is unfortunate, because it is essential to avoid misunderstanding by maintaining the greatest possible clarity in the terminology and nomenclature of the group». During the past decade the interrelations of winged insects have been discussed again. The problem was opened with a discovery of new fossil material enabling a quite new interpretation of wing venation (KUKALOVA-PECK, 1989) as well as in connection with new morphological, ultra-structural and molecular biological approaches. The objective of this paper is to review morphological characters important for the definition of apomorphies and to discuss possible sister-grouping(s) of pterygote insects with emphasis on the order Ephemeroptera.

NOTES TO CRITICAL CHARACTERS AND THEIR APOMORPHIC STATE

Antennal flagellum. Antennal flagellum of both the Ephemeroptera and Odonata adults is short and narrow, bristle-like. Since this structure was multisegmented in paleodictyopteroids (more than 30 segments in Permothemistida, 11 segments in fossil mayflies: KUKALOVA-PECK, 1983), the reduction of the flagellum is sometimes considered a synapomorphy within

recent groups (LAMÉÈRE, 1935-1938; BOUTREAU, 1979; HENNING, 1980). However, flagellar reduction obviously developed more than once. In the Ephemeroptera (flagellum always multisegmented in larvae, 1-segmented in adults), the reduction seems to be correlated with general reduction of appendages (mouth parts, sometimes legs). In the Odonata (multisegmented in some larvae, 1-segmented e.g. in Gomphidae; up to 5 segments in adults), the reduction seems to be due to the predatory mode of life in adults or burrowing habits of larvae. Hence, a bristle-like flagellum apparently represents a case of parallelism (cf. KRISTENSEN, 1991).

Compound eyes. The compound eyes in paleodictyopteroids (if preserved in fossils) were uniform. There is no specialization of eyes in Odonata, except for relatively a very high number of ommatidia (up to 10,000) due to predatory habits. Eyes sexually dimorphic in size or eyes divided into dorsal («tubinate») and ventral («normal») parts in mayflies might be considered a trait (autapomorphy?) evolved within the order and related to sexual behaviour.

Mouthparts. Paleodictyopteroids possessed a hypognathous head with a well domed pre-clypeus and 0.5-30 mm long rostrum consisting of 5 stylets interlocking by respective grooves (2 mandibles, 2 lacinio-galeae, 1 hypopharynx) and multisegmented, leg-like maxillary palps (KUKALOVA-PECK, 1991). Ephemeroptera and Odonata have biting-type mouthparts, strongly reduced and vestigial in adults of the latter. The anterior mandibular articulation became universally permanent in the Odonata and

Neoptera (synapomorphy). Other groups, namely paleodictyopteroids and both extant and fossil Ephemeroptera usually possess non-permanent, «sliding» anterior mandibular articulation with an ample articular membrane which permits considerable freedom of movement (KUKALOVA-PECK, 1981, 1991). However, the situation in recent Ephemeroptera is complicated and yet to be studied. The lateral (middle) articulation is lacking in some Siphonuridae (SCHÖNMANN, 1981) but in most other groups the mandibles seem to correspond in position to the anterior condyle of commonplace dicondylous mandibles. However, this arrangement does not support the homology. The mandibular base fits a concavity in the cranial margin in mayflies while «normally» (in Odonata and Plecoptera) the reverse is true (KRISTENSEN, 1991). This condition in the Ephemeroptera thus appears to be autapomorphic. Some authors (CRAMPTON, 1924; HENNIG, 1981) consider the fusion of the maxillary galea and lacinia into a single lobe in the Ephemeroptera and Odonata a derived character in common. Similar trends to this fusion seems to be apparent in some other pterygotes as well. This character thus seems to be conceived as a shared derived one with the Neoptera. On the other hand, the structure of the larval hypopharynx singles the Ephemeroptera out from any other extant insects. Hypopharyngeal lobes of Odonata or Neoptera may never be true superlinguae (DENIS & BITSCH, 1973) also these structures in some Plecoptera remains debatable (cf. ZWICK, 1980). Dragonfly prelabium/palp complex («mask» of larvae) used to be considered a prominent autapomorphy within this order. However, the meganeurid larvae belonging to extinct order Protodonata already possessed a mask with prominent raptorial paraglossae and short palps (KUKALOVA-PECK, 1991). A further common character shared by Odonata and Neoptera is the reduction of all tentorio-mandibular muscle bundles but one, the tentoriolacinial muscle. The same probably concerns some pterothoracic muscles as well (KRISTENSEN, 1991).

Thorax. PFAU (1986) stressed the unique (autapomorphic) arrangement of the dragonfly thorax: pterothoracic segment with strong

backward slant, terga small, mesepisterna almost meeting mid-dorsally in front of wings. Oclucosor muscles of abdominal spiracular sclerites are present in some Odonata as well generally in the Neoptera but lacking in mayflies, as in the primarily apterous insects. Ephemeroptera only have a single tracheal trunk coming from the leg trachea and corresponding to the trachea of paranotal lobes in *Zygentoma* or *Archaeognatha* (LANDA, 1948; WEBER, 1949). This is considered as a neotenic trait by BOUDREAUX (1979) but it is yet to be studied. In Odonata and Neoptera the tracheation of each wing and pterothoracic leg includes a component connected with the spiracle of the following segment (synapomorphy).

Thoracic legs. Only primitive pterygote features (synplesiomorphy) are retained within the «paleopterygotes»: the absence of muscled trochantin (a sternal fragment) and the elimination of thoracic coxal endites (KUKALOVA-PECK, 1991). Anteriorly articulated fore legs of paleodictyopteroids supported the rostrum during feeding (sucking of plant juices); legs of the Protodonata and Odonata (especially hind ones) are oriented postero-ventrally for grasping large prey; fore legs of males in the Ephemeroptera are usually (not always) elongated in tarsal parts for grasping females during mating flight.

Wings and wing venation. There is no doubt that the Ephemeroptera and Odonata are alone amongst the recent Pterygota in being unable to flex their wings back over the abdomen. Most of the authors believe this character to be primitive (e.g. WEBER, 1949; BOUDREAUX, 1979; HENNIG, 1981 and others). However, in fossil *Diaphanopteroidea* the wing could be flexed backwards at least by a simple mechanism due to unfused articular sclerites and in some advanced Permian forms the wing even completely overlapped (KUKALOVA-PECK, 1991). Also band-like wing articulation (small sclerites densely crowded into a primitive band continuing under the wing as several basalaria and subalaria) is regarded as retained primitive pterygote feature (KUKALOVA-PECK, 1985, 1987). However, there are only two large

sclerites in the basal articulation of the wing in Odonata usually called the humeral (costal) plate and the axillary (radio-anal) plate (SNODGRASS, 1958). This morphological arrangement is connected with the direct mode of wing movements. The dorsal longitudinal muscles are small or absent and dorsoventral ones are divided by the wing process (fulcrum) into laterally attached depressors and mesally attached elevators (SHVANVICH, 1943; SNODGRASS, 1958; PFAU, 1986). Quite different, indirect mode of wing movements occurs in mayflies and Neoptera. The wing upstroke is due to the depression of the notum by notosternal or vertical muscles, downstroke results from contraction of the longitudinal dorsal muscles (lengthwise compression and arching of notum). According to KUKALOVA-PECK (1986, 1991) synapomorphies of the ephemeropteran-odonata lineage plus extinct paleodictyopteran orders are as follows. The media always possesses a basal stem, veins are strongly fluted and venial ridges are expressed mostly only in one membrane (dorsal or ventral). In the Odonata and Ephemeroptera, the venation is rich in prominent y-shaped intercalaries and there is a very similar formation of a basal wing brace through an anastomosis of the anterior anal vein with the posterior cubitus (apomorphy). The latter character is manifested by a composite anal brace ending either on CuP at a secondarily desclerotized bulla in Ephemeroptera or at a kink in CuP in Odonata + Protodonata. Articulated, sometimes movable prothoracic wings and rich, dichotomously branched archidictyon with anal area braced against buckling by sclerotisation in the basal corner are shared only within paleodictyopteroids orders. There is probably only one true autapomorphy within the Ephemeroptera: the anastomosis of the strongly arched ScA+ forms a conspicuous subcostal brace in the fore wings. Hind wings, markedly smaller or missing in mayflies, are attributed to apomorphy (cf. BOUDREAUX, 1979). However, besides numerous cases of this phenomenon within neopteran lines, this character is shared e.g. with extinct Permothemistida. Similarly, the absence of a common radial stem in some Ephemeroptera was considered uniquely apomorphic within primitive winged insects,

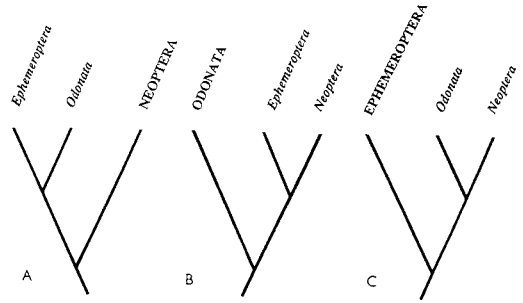


Fig. 1. Scheme of three theoretical possibilities of sister-grouping of the Pterygota: A - monophyly of Paleoptera (Ephemeroptera + Odonata), B - monophyly of Ephemeroptera + Neoptera, C - monophyly of Odonata + Neoptera; sister-groups in italics.

but RIEK & KUKALOVA-PECK (1984) found the same condition in fossils of Odonata and paleodictyopteran orders.

Abdomen. Short abdominal leglets were sometimes present in both nymphs and adults of paleodictyopteroids. In their terrestrial nymphs, the abdominal exites fused with the epicoxa sidelobes. Nymphs of fossil Ephemeroptera had small prothoracic winglets, 2 pairs of articulated wings (secondarily fused with nota in recent groups) and 9 pairs of abdominal wings. With the exception of a single species with 8 pairs of abdominal wings (ZIMMERMANN & BRAASCH, 1979) 7 or less pairs are retained in extant representatives of the order. Abdominal appendages of extant pterygotes are strongly reduced. A long terminal filament of mayflies is considered an unique character occurring nowhere in pterygotes. However, the homology (and hence plesiomorphy) of the posteromedian gill filament in some Austroperlidae (Plecoptera) remains questionable (ZWICK, 1980; KRISTENSEN, 1991). Accessoric genitalia of Odonata probably represent an apomorphy. The paired female gonopores in some mayfly females, originally considered uniquely primitive within pterygotes, are now probably correctly regarded as a secondary feature (BOUDREAUX, 1979; BITSCH, 1979). The presence of a median vestibulum into which the anterior parts of the gonoducts open (Heptageniidae, Oligoneuriidae) is considered primitive, recalling conditions in non-ptyergote insects (BITSCH, 1979). Similarly,

Table 1. Survey of higher classification of the Pterygota (opinions treating major clades as independent groups not included).

Name applied	Author	Orders or groups included	Note
Archipterygota	Börner, 1909	Ephemeroptera	coordinated with Metapterygota to form Pterygota
Metapterygota	Börner, 1909	Odonata + Neoptera	coordinated with Archipterygota to form Pterygota
Paleoptera	Martynov, 1924	Ephemeroptera + Odonata + ancestors	5 extinct orders corresponding to "paleodictyopteroid group" included; coordinated with Neoptera to form Pterygota
Archipterygota	Crampton, 1924	Ephemeroptera + Odonata	coordinated with Neopterygota (= Neoptera)
Subulicornia	Laméere, 1935-38	Ephemeroptera + Odonata	defined on the basis of bristle-like flagellum
Paleoptilota	Laméere, 1935-38	Ephemeroptera + Odonata	coordinated with Neoptilota (= Neoptera)
Opisthoptera	Lemche, 1940	Ephemeroptera + Neoptera	coordinated with Plagioptera to form Pterygota
Plagioptera	Lemche, 1940	Odonata	coordinated with Opisthoptera to form Pterygota
Chiastomyaria	Shvanvich, 1943	Ephemeroptera + Neoptera	coordinated with Orthomyaria to form Pterygota
Orthomyaria	Shvanvich, 1943	Odonata	coordinated with Chiastomyaria to form Pterygota
Paleodictyoptera	Boudreaux, 1979	Paleodictyoptera + Megasecoptera	subsection of section Plagiopterata (= Plagioptera Lemche, 1940)
Odonatoptera	Boudreaux, 1979	Protodonata + Odonata	subsection of section Plagiopterata (= Plagioptera Lemche, 1940)
Ephemerata	Boudreaux, 1979	Ephemeroptera and its ancestors ("Protephemerida")	subsection of section Opisthoptera (= Opisthoptera Lemche, 1940)
Ephemeriformes	Rasnitsyn, 1980	Ephemeroptera + ancestors	monotypic cohort of infraclass Scarabeones
Libellulones	Rasnitsyn, 1980	Odonata + ancestors	infraclass category, coordinated with infraclasses Scarabeones and Gryllones
Dictyoneuridea	Rasnitsyn, 1980	Paleodictyoptera + Megasecoptera + Permothemistida	superorder of cohort Cimiciformes of infraclass Scarabeones
Diaphanoptera	Rasnitsyn, 1980	Diaphanopteroidea	superorder of cohort Cimiciformes of infraclass Scarabeones

the arrangement of ovarioles is now regarded to be modified, having only remote relations to the original ovarian metamery (ŠTYS *et al.*, 1993).

Metamorphosis and «aquatic mode of life». The subimaginal stage of the Ephemeroptera undoubtedly represents an ancient condition (cf. EDMUNDS & McCAFFERTY, 1988). BOUDREAUX (1979), on the contrary, explains it as a secondary specialization. Absence of this instar in Odonata + Neoptera supports their monophyly. Besides the prometaboly of most recent mayflies, the secondary hemimetaboly (suppressed imaginal instar in females) is observed in some families (EDMUNDS & McCAFFERTY, 1988). Ametaboly universally occurred in paleodictyopteroids (and may have occurred also in the Paleozoic Protodonata). Larvae of at least some Paleozoic groups were terrestrial with gradual development of articulated wings; some of them were able to fly (KUKALOVA-PECK, 1991). The aquatic lifestyle, previously considered to be derived (synapomorphy of Ephemeroptera + Odonata) seems disputable now although it might be connected with a presumably aquatic origin of the tracheal system (cf. ŠTYS & SOLDÁN, 1980).

DEFINITION OF THE SISTER-GROUPS AND HIGHER CLASSIFICATION OF PTERYGOTE INSECTS

As already pointed out by HENNIG (1981) there are three theoretical possibilities how to define monophyly within the extant existing pterygote lineage. These are as follows.

(i) Ephemeroptera + Odonata are the sister group to remaining pterygotes, the Neoptera (Fig. 1A). This classical conception is based mainly on four presumable synapomorphies: (a) bristle-like adult antennal flagellum, (b) arrangement of intercalary veins (interpreted as a modification of archedictyon) and wing flexing, (c) fusion of galea and lacinia, and (d) aquatic mode of life of larvae (cf. HENNIG, 1981). On this basis pterygote insects were classified into Paleoptera (= Archipterygota, Subulicornia, Paleoptilota) consisting of the Ephemeroptera and Odonata, and Neoptera (Table 1). However, these characters represent either parallelism (a) or are at least disputable (c, d) and this sister-grouping is currently rejected by the most recent authors (BOUDREAUX, 1979; RASNITSYN, 1980; KRISTENSEN, 1981, 1992). On the other hand, there are some

arguments supporting, from the paleontological point of view, the concept of a monophyletic taxon Paleoptera. KUKALOVA-PECK (1985, 1991) managed to find, based on her interpretation of wing venation, clear synapomorphies of ephemeropteran-odonate plus the extinct paleopteroid lineage (media always with basal stem and anal-crossing or bulla in the anastomosis areas). Moreover, her wing-from-leg-base-exite theory (KUKALOVA-PECK, 1983) provides parsimonious explanations of a number of primitive pterygotes evolutionary events. Despite some evident autapomorphies of paleodictyopteroids (mouthparts modified into sucking proboscis; suppressed medial caudal filament: BOUDREAUX, 1979) wing-venation characters strongly support the idea of a compact Paleoptera. Contradictions between neontological and paleontological points of view urgently need more attention.

(ii) Odonata are the sister-group to Ephemeroptera + Neoptera (Fig. 1B). This concept is originally based on some odonatan apomorphies in flight apparatus arrangement («direct» mode of wing movements, wing articulation morphology and the ontogenetic development of wing pads in larvae). These characters led e.g. LEMCHE (1940) or SHVANVICH (1943) to separate the order Odonata from other pterygotes on the basis of the Ephemeroptera + Neoptera monophyly (Table 1). This idea is also accepted by RASNITSYN (1980) who, taking into account some paleontological evidences, classifies the Odonata even into the separated infraclass (Table 1). The ephemeropteran/neopterian synapomorphies are pointed out also by BOUDREAUX (1979). His principal arguments are based on the «indirect» sperm transfer of Odonata and the presence of accessoric genitalia on the anterior abdominal segments. Consequently, the «direct» (gonopore-to-gonopore) mode of sperm transfer could be considered a shared apomorphy of Ephemeroptera and Neoptera although there are several cases of accessoric genitalia presence in the latter. This concept of sister-grouping, discussed in detail by KRISTENSEN (1981), has not received general acceptance and is believed more disputable than the others.

(iii) Ephemeroptera are the sister-group to Odonata + Neoptera (Fig. 1C). Contrary to prominent ordinal autapomorphies of the

Odonata, mayfly autapomorphies are not so obvious. However, many characters isolating the Ephemeroptera from other pterygote insects have been defined, most important of them as follows: (a) «sliding articulation» of mandibles, (b) arrangement of tentorialacinal muscles, (c) true hypopharyngeal superlinguae present, (d) unique arrangement of thoracic tracheal trunks, (e) universally lacking occlusor muscles of the abdominal spiracles; (f) well developed, long terminal filament in larvae and (g) fore wings with prominent basal subcostal brace or (h) anal brace ending on CuP at a bulla in adults. Naturally, these characters are of a different value as far as the apomorphic state is concerned. Some of them appear to be autapomorphic (a, g), some are shared with primitive Neoptera and some Odonata (e, and partly h), others might have homological structures in Plecoptera (c, f) and one is considered neotenic (d). Clearly autapomorphic within the recent pterygotes is a retention of the subimaginal state within recent Ephemeroptera, however secondarily reduced in females of some families. Reduced mouthparts in mayfly adults represent a secondary trait, these are functional in the Paleozoic representatives. The same is probably true for some characters of genitalia and their ducts. The character state of compound eyes and male fore legs arrangement is not fully understood and yet to be examined.

The sister-grouping Ephemeroptera and Odonata + Neoptera is strongly supported by some recent ultrastructural findings. The ovarioles of mayflies are surprisingly of the telotrophic type (GOTTANKA & BÜNING, 1992). In this respect, mayflies occupy a quite isolated position among primitive pterygotes since this ovarial type otherwise occurs only in some Megaloptera, Raphidioptera, Hemiptera and Coleoptera-Polyphaga. Also the ultrastructure of mayfly spermatozoa is unique with a 9+9+0 axoneme pattern and only one mitochondrial derivative (BACCETTI *et al.*, 1969). Shape diversity of spermatozoa is worth our attention as well: some groups (e.g. the family Leptophlebiidae) possess quite derived, extraordinarily small, rounded spermatozoa without flagellum (SOLDÁN, 1979). WHEELER (1989) demonstrated that sequences of bases in the ribosomal DNA are quite different in the Ephemeroptera but related in Odonata + Neoptera.

To conclude, the above arguments seem to support the monophyly of Odonata + Neoptera and their respective sister-grouping to the Ephemeroptera seems to be parsimonial. However, the proper reconstruction of phylogeny and higher classification of pterygote insects remain still open due to numerous contradictions and disputable circumstances concerning fossil representatives. Some authors (e.g. MATSUDA, 1981; KUKALOVA-PECK, 1983; RIEK & KUKALOVA-PECK, 1984; PFAU, 1986) believe that the views of recent dissenters cannot be reconciled with modern systematic arguments. Consequently, all major pterygote clades can be treated as independent groups, three paleopterous (ephemeroids, odonatoids and the Paleozoic plant-sucking paleodictyopteroids) and one neopterous.

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