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Ephemeroptera Phylogeny and Higher Classification: Present Status and Conflicting Hypotheses

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Ephemeroptera relationships to other insects

The order can be characterized by the following principal characters: (1) bristle-like adult antennal flagellum, (2) specific arrangement of tentorial muscles (STANICZEK 2000); (3) ‘sliding’ articulation of mandibles (KUKALOVÁ-PECK 1991); (4) ‘true’ hypopharyngeal superlinguae; (5) galealacinia fusion; (6) unique arrangement of thoracic tracheal trunks (only a single tracheal trunk coming from the leg trachea, corresponding to the trachea of the paranotal lobes of Zygentoma or Archaeognatha; LANDA 1948); (7) universally lacking occlusor muscles of the abdominal spiracles; (8) well developed, long terminal filament in larvae; (9) retention of winged subimaginal stage; (10) fore wings with prominent basal subcostal brace, and (11) anal brace ending on CuP at a bulla; (12) aquatic mode of life; (13) telotrophic ovarioles.

Apparently, some characters are shared with primitive Neoptera, such as Plecoptera (4, 12), and some with Odonata (e.g., 1, 7, 12, partly 10, 11), and one (6) is sometimes considered neotenic.

Three hypotheses on ephemeropteran affinities are available: (a) Ephemeroptera + Odonata (= Paleoptera, perhaps including extinct paleodictyopteran orders) are the sister group of Neoptera; (b) Ephemeroptera are the sister group of Odonata + Neoptera; (c) Odonata are the sister group of Ephemeroptera + Neoptera. The problem still remains open to a general discussion. From the neontological-morphological point of view, hypothesis (b) seems to be most parsimonious (BEUTEL & GORB 2001), but requires, e.g., parallelism in the antennal flagellum structure, and the non-homology of all neopteran hypopharyngeal lobes with superlinguae is perhaps disputable. In contrast, a detailed study of fossil material does lend support to hypothesis (a); according to my opinion this hypothesis is well corroborated by characters of wing venation (e.g., media always with basal stem) and, in general, by the wing-from-leg-base-exite theory (KUKALOVÁ-PECK 1983). Hypothesis (c) seems to be unlikely (see, e.g., discussions by KUKALOVÁ-PECK 1991 and KRISTENSEN 1991).

Suborder relationships

The original subordinal classification by MCCAFFERTY & EDMUNDS (1979), based mostly on thoracic morphology and wing pad position, comprised the holophyletic Pannota and the paraphyletic suborder Schistonota indicating the retention of certain plesiomorphic traits. Later MCCAFFERTY

(1991) suggested a reasonable re-classification into 3 suborders: Rectracheata (including unchanged original Pannota as an infraorder), Setisura, and Pisciforma. Although he used numerous characters including internal anatomy data by LANDA & SOLDÁN (1985), the Pisciforma still required some revision through abandoning the use of plesiomorphic characters.

Since then some progress has been achieved, but it seems to be extremely difficult to reach a parsimonious solution of this problem because some groups (e.g., the superfamily Siphonuroidea) are defined by plesiomorphies, and new characters are hardly available. Independently, N.Yu. Kluge (see KLUGE 2000 for a complete list of his contributions) defined suborders Costatargalia and Furcatargalia on the basis of presence or absence of certain gill structures (therein called “tergalia” to emphasize wing origin; however, ‘gills’ in mayflies might be of a rather different origin). Later, the same author suggested two suborders again: Anteritorna and Posteritorna based on two-fold emergence of anteromorphy. Although partly including clearly holophyletic taxa (e.g., Posteritorna), both subordinal classifications are essentially based on a single character.

Infraorder relationships

MCCAFFERTY’S (1991) suborders Rectracheata and Pisciforma comprise 3 (namely Vetulata, Lanceolata, and Pannota) and 2 (namely Arenata and Imprimata) infraorders, respectively. This classification seems to be generally accepted, except for the above mentioned parphyly of the Pisciforma and the position of some ‘critical’ genera. For instance, the genus *Oniscigaster* (and the respective monotypic family) requires more attention showing, e.g., dramatic autapomorphic increase in ventral tracheal anastomoses. It is treated in the monotypic infraorder Vetulata by MCCAFFERTY (1991) but is left in the Siphonuridae-like taxa in his Tridentiseta by KLUGE (2000), probably on the basis of the mouthpart “dentisetae” synapomorphy and bordered gills of this genus, which gives to Kluge’s Costatargalia a rather paraphyletic status. Similarly, the genus *Pseudiron* (and the respective monotypic family) deserves further critical evaluation, being treated in the otherwise well defined Setisura-like lineage (KLUGE 2000, his Brachytergaliae) but in Pisciforma-Arenata by MCCAFFERTY (1991). A rather different higher classification using “consistently non-ranking taxonomy” has been developed by KLUGE (2000, see therein for earlier citations, and on

<http://www.bio.pu.ru/win/entomol/KLUGE/EPH/Contents.htm> for more details). I am definitively not in a position to evaluate the scientific invention of this undoubtedly sophisticated classification, but there are some evident restrictions concerning its general acceptance: in many respects, it interferes with the ICZN (for instance, rather arbitrary handling with synonymy, e.g., Arthropleidae Balthasar, 1937 is definitively not a synonym of Heptageniidae Needham, 1901); it is still not applicable to any other insects except for the Ephemeroptera; and it seems to be extremely complicated to be used in other than strictly taxonomic papers (I do not understand why to use “*Turbaniculata Anteropatellata Baetis/fg7 Acentrella/gl*” instead of simply the genus (subgenus) name *Acentrella* of the family Baetidae, e.g., in faunistic lists and ecological papers). Moreover, as many as 20 suprageneric names (7 of them newly erected as “taxon nov.”) are introduced in this treatment (KLUGE 2000) and to trace their relationships to widely used sub- and infraordinal, super- and subfamilial, familial or even generic names requires a long time and maximal concentration.

Superfamily and family relationships

Contrary to the situation in the sub- and infra-ordinal ranks, there is a general consensus in the definition of taxa of (super-)family rank as well as in the application of taxon names. Five superfamilies (namely Leptophlebioidea, Behningioidea, Ephemeroidea, Caenoidea and Neoephemeroidea) have been introduced by MCCAFFERTY (1991) in addition to the Siphonuroidea, Baetoidea, and Heptagenioidea, approximately corresponding to his infraorders Arenata and Imprimata, and the suborder Setisura, respectively. At present, 37 families have been recognized, which include 376 genera and approximately 3,100 species – contrary to 20 families defined, e.g., by MCCAFFERTY & EDMUNDS (1979). However, taxonomic changes at this level are restricted mostly to formal shifts in rank (from subfamily to family status). As far as I know, only the genus *Siphuriscus* (originally incertae sedis within the Siphonuroidea) will be treated in a separate family soon.

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Phylogeny of Ephemeroptera: Molecular Evidence

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Mayflies are unique among insects by the presence of a non-reproductive winged stage (subimago) that molts to become the reproductive adult. Phylogenetic relationships among mayfly families are poorly known, and current hypotheses are based on untested scenarios of character evolution, which lack any sort of rigorous phylogenetic analysis.

In our ongoing study we use data based on five genes (18S rDNA, 28S rDNA, 16S rDNA, 12S rDNA, and histone 3) to estimate mayfly phylogenetic relationships. Nearly 100 genera of mayflies, representing the majority of lineages, are included. Previous hypotheses for higher-level relationships are discussed and tested in light of these data. In the following explanations the use of taxon names refers to the classification of MCCAFFERTY (1991).

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Our analysis supports the family Baetidae as sister to all other mayflies, though this result is sensitive to outgroup and optimization alignment parameter selection. The pisciform mayflies are supported as grossly paraphyletic. Potamanthidae is nested outside the clade Scaphodonta (= Ephemeroidea + Leptophlebiidae + Behningiidae) and Behningiidae is nested within the Ephemeroidea, rendering this group of burrowing mayflies non-monophyletic. These results suggest that mandibular tusks were gained on multiple occasions with a secondary loss in the lineage Behningiidae. Additionally, the large family Heptageniidae is not supported as monophyletic because the genera *Pseudiron* and *Arthroplea* are nested within this family. The families Baetidae, Leptohiphidae, Nesameletidae, Oligonuridae, Potamanthidae and Ephemerellidae are sup-