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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) galea-lacinia 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) universalism in the antennal flagellum structure, and the non-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 zygodactyly and phylogenetic significance. – Zoologischer Anzeiger 239: 147–178.

**Infraorder relationships**

McCafferty’s (1991) suborders Rectracheata and Piscifoma comprise 3 (namely Vetulata, Lanceolata, and Pannota) and 2 (namely Aretauna and Imprimata) infraorders, respectively. This classification seems to be generally accepted, except for the above mentioned paraphyly of the Piscifoma 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 Veturata by McCafferty (1991) but is left in the Sphilonuroidea-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 Costatergalia a rather paraphyletic status. Similarly, the genus *Pseudiron* (and the respective monotypic family) deserves further critical evaluation, being treated in the otherwise well defined Sphilionuroidea-like lineage (KLUGE 2000, his Brachytergaliae) but in Piscifoma-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 handing with synonymy, e.g., Arthropodae Balthasar, 1937 is definitively not a synonym of Hypogastrinidae Needham, 1901); it is still not applicable to any other insects except for the Ephemeroptera, 37 families have been introduced, which are included. Previous hypotheses for higher-level relationships are discussed and tested in light of these data. In the estimation mayfly phylogenetic relationships. Nearly 100 rDNA, 28S rDNA, 16S rDNA, 12S rDNA, and histone 3) to lysis.

Moreover, as many as 20 suprageneric names (7 of them newly erected as “taxon nov.”) are introduced in this treat- ment (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 Leptophlebioidae, Behningioidea, Ephemerioidea, Caenioidea and Neonephe- merioidea) have been introduced by McCafferty (1991) in addition to the Siphlonuroidea, Baetioidea, and Hepta- genioidea, approximately corresponding to his infraorders Arenata and Imprimata, and the suborder Setisura, respec- tively. Among the 25 superfamilies present, 37 families have been recognized, which include 376 genera and approximately 3,100 species – con- tensively. At present, 37 families have been recognized, which 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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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 ana- lysis. 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).

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 pisci- form mayflies are supported as grossly paraphyletic. Potamanthidae is nested outside the clade Scaphhoodonta (= Ephemerioidea + Leptophlebiidae + Behningiidae) and Behningiidae is nested within the Ephemerioidea, 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 Pseudion and Arthrolepia are nested within this family. The families Baetidae, Leptophlebiidae, Neseameletidae, Oligonuridae, Potamanthidae and Ephemerellidae are sup-