

<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 Neoephe-meroidea) 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.

Acknowledgements

My sincere thanks are due to Klaus-Dieter Klass and Niels P. Kristensen for valuable comments on the manuscript.

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-

ported as monophyletic groups. While our analysis is in its preliminary stages, it represents the first formal cladistic analysis across the major lineages of Ephemeroptera.

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The Phylogenetic Relationships of the Three Extant Suborders of Odonata

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The order Odonata includes three extant suborders (Zygoptera, Anisozygoptera: Epiophlebiidae, and Anisoptera) with totally 5538 described species. The fossil record is relatively well documented with more than 600 fossil species and reaches from Tertiary representatives of extant families back to primitive protodonates of the lowermost Upper Carboniferous (320 mya).

The system of Odonata is still largely based on the typological classification by FRASER (1957), but within the last two decades there have been several attempts towards a phylogenetic system of odonates (CARLE 1982; TRUEMAN 1996; LOHMANN 1996; BECHLY 1999; REHN 2003). Differences between the results of these attempts are based on different selection of characters or even more so on different methodological approaches (e.g., traditional Hennigian Phylogenetic Systematics versus computer-based numerical analysis).

There is a broad consensus that Epiophlebiidae and Anisoptera are both monophyletic, while 'Anisozygoptera' is a paraphyletic assemblage of Epiophlebiidae and fossil stemgroup representatives of Anisoptera.

The monophyly of Anisoptera is supported by numerous morphological autapomorphies (sperm vesicle developed as copulatory organ, wing venation with hypertriangle, triangle, subtriangle and anal loop, larval locomotion by jet-propulsion) and this is also the case for Epiophlebiidae (hamuli posteriores developed as copulatory organ, interocellar lobe, ovoid pedicel, hairy eye tubercle, larval stridulation organs). It is also undisputed that Epiophlebiidae is the sister group of Anisoptera, because there are several good synapomorphies (discoidal cell distally distinctly widened in hindwing, male hindwing with anal angle, males with a secondary epiproctal projection, synthorax with the dorsal portion of the interpleural suture suppressed, larvae with anal pyramid).

Concerning Zygoptera, most recent authors considered them as monophyletic, while TRUEMAN (1996), in a cladistic analysis of wing venational characters, suggested that Zygoptera is a highly paraphyletic group, as already indicated in FRASER (1957). However, the monophyly of Zygoptera is supported by several strong putative autapomorphies, such as the transverse head, the more oblique pterothorax, abdominal sternites with triangular cross-section and longitudinal keel, formation of an ovipositor-pouch by the enlarged outer valves (valvula 3 = gonoplacs) of the 9th abdominal sternite, and of course the highly specialized ligula that is developed as copulatory organ. The presence of caudal gills, even though uniquely present in Zygoptera among extant odonates, has been demonstrated to be a symplesiomorphy by the finding of a fossil dragonfly larva. This larva has wing sheaths that clearly show the characteristic veinal features of the isophlebiid stemgroup representatives of Anisoptera, but still possesses three caudal gills.

A detailed phylogenetic system of fossil and extant odonates with all synapomorphies, based on my results, is available at <http://www.bechly.de/phylosys.htm>.

A recent cladistic study of 122 morphological characters by REHN (2003) basically confirmed this phylogeny; this includes the sistergroup relationship of Tarsophlebiidae and crown-group Odonata, the monophyly of Zygoptera, a lestinoid + coenagrionoid clade which is sister group to Calopterygoidea, the position of the relict damselfly *Hemiphlebia* at the very base of lestinoid zygopteres, the position of Petaluridae at the base of Anisoptera, and the sistergroup relationship of African Coryphagrionidae to the Neotropical Pseudostigmatidae. The only clear differences concern the positions of amphipterygid and megapodagrionid damselflies, which REHN (2003) proposes to represent a paraphyletic basal grade towards the lestinoid + coenagrionoid clade. However, the wide separation of the zygopteran genera *Diphlebia* and *Philoganga* in this phylogeny appears doubtful, because these two genera are united by very strong larval synapomorphies and some synapomorphies of the imagines.

Recent molecular studies on the higher phylogeny of odonates (MISOFF & RICKERT 1999a, b) did not resolve the Zygoptera problem and did partly even conflict with monophyla like Cavilabiata (including Cordulegastridae, Neopetaliidae, Chlorogomphidae and libelluloids) that are very well-established by morphological evidence beyond reasonable doubt. Methodological artefacts like long-branch-attraction and noise seem to be prevalent.

The interpretation of the three different types of secondary copulatory organs as autapomorphies of the three extant suborders respectively is based on a groundplan reconstruction of the male secondary genital apparatus. This ground plan includes small hamuli anteriores and posteriores, a small unsegmented ligula and an undifferentiated vesicula spermalis. This hypothetical reconstruction has been confirmed by the discovery of a well-preserved male specimen of Tarsophlebiidae, the putative fossil sister group of all extant odonates, which shows exactly this type of genitalia (Fig. 1). Consequently, none of the substructures was suited as intromittent organ for sperm transfer in the ground plan, so that there still must have been a mechanism involving external spermatophores. This is confirmed by the finding that the primitive protodonate *Namurotypus sippeli* from the Carboniferous of Germany did not yet possess a secondary male genital apparatus, but primary genitalia that are most similar to those of *Zygentoma*, which deposit spermatophores. The curious odonate mating wheel probably evolved by attaching the spermatophore on the sternites of the basal male abdomen.

Concerning the phylogenetic position of the order Odonata in the tree of insects the evidence is ambiguous. Fossil evidence and some morphological and molecular characters support the monophyly of Palaeoptera (= Palaeodictyopteroidea + Ephemeroptera + Odonata), while rather strong characters of the extant head morphology (STANICZEK 2000) and some molecular data support the monophyly of Metapterygota (= Odonata + Neoptera). Consequently, this issue still has to be considered as more or less unresolved.