

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 = gonoplags) 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 (MISOF & RICKERT 1999a, b) did not resolve the Zygoptera problem and did partly even conflict with monophyla like Cavilabiata (including Cordulegastridae, Neopetaliidae, Chlorogomphidae and libelluoids) 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.

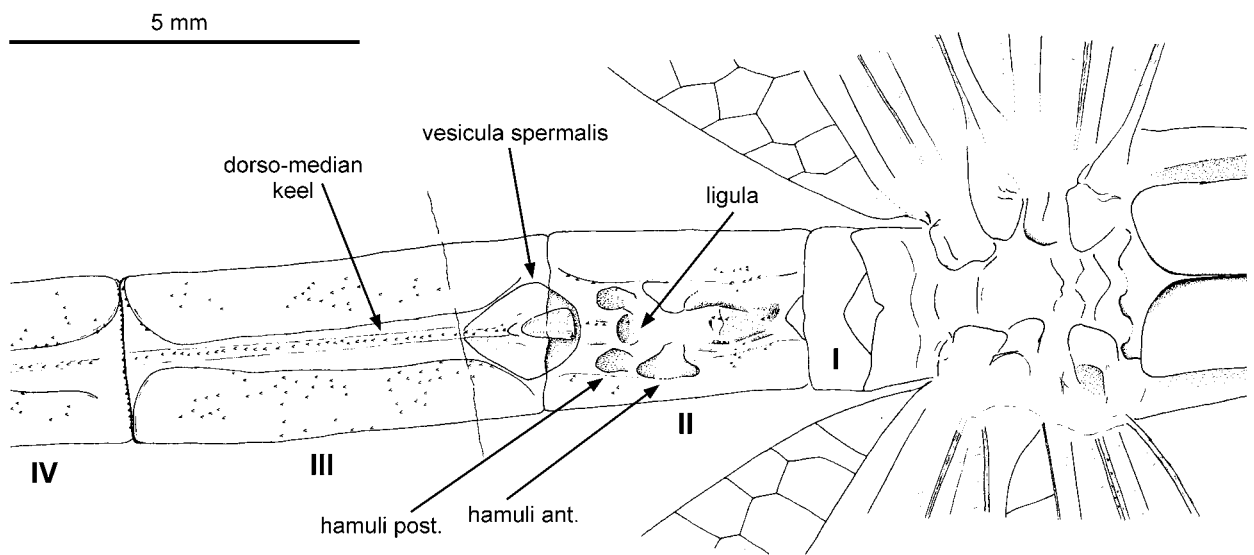


Fig. 1. *Tarsophlebia eximia*, Upper Jurassic Solnhofen Limestone, male specimen no. SOS 1720 at the Jura Museum in Eichstätt (Germany), camera lucida drawing of ventral side of abdomen with secondary genital apparatus.

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Morphological Support of the Major Clades of Plecoptera

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The monophyly of the order Plecoptera is beyond doubt, but the position of Plecoptera among the Neoptera continues to be debated. Ordinal apomorphies are few: the loop-shaped gonads, loop-shaped seminal vesicles, absence of an ovipositor, presence of a cercus heart, and oblique intersegmental musculature supporting the laterally (!) undulating larval swimming movements.

Since the earliest studies, two clades were distinguished within Plecoptera, at various levels between genus (*Perla* versus *Nemoura*) and suborder (Setipalpia versus Filipalpia, or Systellognatha versus Holognatha) (KLAPÁLEK 1905; ENDERLEIN 1909). The competing suborder designations reflect differences of opinion that were actually formalistic and marginal; the disagreement is easily overcome by consistent phylogenetic methodology.

Contemporary systems are based on a large number of characters of external and internal morphology that were studied across all families of the order, and by some cytological and behavioural characters (ZWICK 1973, 2000). The

relationships of the four endemic southern hemisphere families had previously not been satisfactorily recognized. Several of the traditionally recognized major taxa proved to be monophyletic and persist in the present classification. The Systellognatha are supported, among other, by the reduction of the adult mandibles, by a complex set of gills in particular positions on the thorax, complicated male epi-procts involving numerous movable components, and profound modifications of abdominal tergite 10; variations can be followed across all families. Eggs are hard-shelled, with a suction-disk-like attachment organ, the anchor, at the posterior pole. The first larval instar lives on yolk remains in the gut, only the 2nd instar is actively feeding. The female receptacle carries a number of accessory glands along its stalk-like base. The vast majority of all Systellognatha belong to the Perloidea, which share carnivorous larvae with a modified, slender type of mandible (some adults in this group with secondarily functional mandibles possess the same derived type of mandible), tiny glossae that are