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; REIN 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 stem-group 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, inter-ocellar 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 ovispositor-pouch by the enlarged outer valves (valvula 3 = gonoplaques) 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 venal 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/phyl sosys.htm.

A recent cladistic study of 122 morphological characters by REIN (2003) basically confirmed this phylogeny; this includes the sistergroup relationship of Tarsophlebiidae and crown-group Odonata, the monophyly of Zygoptera, a lestidoin + coenagrionid clade which is sister group to Calopterygoidea, the position of the relict damselfly Hemiplhebia at the very base of lestidod zygopterans, the position of Petaluridae at the base of Anisoptera, and the sistergroup relationship of African Coryphagriaidoideae to the Neopterous Pseudostigmatidae. The only clear differences concern the positions of amphiptyrgid and megapodagrionid damselflies, which REIN (2003) proposes to represent a paraphyletic basal grade towards the lestid + coenagrionid clade. However, the wide separation of the zygopteran genera Diplebia 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 (MISO & RICKERT 1999a, b) did not resolve the Zygoptera problem and did partly even conflict with monophyla like Cavaliabata (including Cordulegasteridae, Neopteroidae, 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 spermali. 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 to mistakely be placed into the stemgroups of the zygopteran genera Zygoptera and Anisoptera, but is still highly specialized in 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 (= Palaeodictyopteroida + Ephemeroptera + Odonata), while rather strong characters of the extant head morphology (STANICKZI 2000) and some molecular data support the monophyly of Metapterygota (= Odonata + Neuroptera). Consequently, this issue still has to be considered as more or less unresolved.

References

References


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.

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 characteristics 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 epiprocts 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