

Evolution of Odonata, with Special Reference to Coenagrionoidea (Zygoptera)

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> Abstract

A phylogeny including 26 families of Odonata is presented based on data from large and small subunit nuclear and mitochondrial ribosomal RNAs and part of the nuclear EF-1 α . Data were analyzed using Bayesian methods. Extant Zygoptera and Anisoptera are monophyletic. The topology of Anisoptera is ((Austropetaliidae, Aeshnidae) (Gomphidae (Petaluridae ((Cordulegastridae (Neopetaliidae, Chlorogomphidae)) ((Synthemistidae, Gomphomacromiidae) (Macromiidae (Cordulidae s.s., Libellulidae)))))). Each of the major groups among anisopterans is well supported except the grouping of *Neopetalia* with *Chloropetalia*. Lestidae and Synlestidae form a group sister to other Zygoptera, and Coenagrionoidea are also monophyletic, with the caveat that Isostictidae, although well supported as a family, was unstable but not placed among other coenagrionoids. Calopterygoidea are paraphyletic and partly polytomous, except for the recovery of (Calopterygidae, Hetaeriniidae) and also (Chlorocyphidae (Epallagidae (Diphlebiinae, Lestoidinae))). Support for Epallagidae as the sister group of a clade (Diphlebiinae, Lestoideinae) is strong. Within Coenagrionoidea, several novel relationships appear to be well supported. First, the Old World disparoneurine protoneurids are nested within Platycnemididae and well separated from the protoneurine, *Neoneura*. The remaining coenagrionids are divided into two well-supported subdivisions. The first includes Pseudostigmatinae, *stat. nov.*, Protoneurinae, a group of coenagrionids mostly characterized by having an angulate frons, and Argiinae (*Argia*). The second division includes typical Coenagrionidae.

> Key words

Odonata, Zygoptera, Anisoptera, *Epiophlebia*, phylogeny, RNA, Bayesian, parsimony.

1. Introduction

The phylogeny of Odonata has been a matter of controversy for nearly a century and a half. Largely due to the work of BARON DE SELYS-LONGCHAMPS, “the Father of Odonatology”, the families generally recognized today were established as “légions” and first placed in Zygoptera or Anisoptera (1854a,b). Selys treated “légions” as natural groupings and had a sense of their evolutionary position, but the first explicitly phylogenetic or “geneologic” study of Odonata was that of NEEDHAM (1903), followed by MUNZ

(1919; Zygoptera), KENNEDY (1919; Zygoptera) and NEEDHAM & BROUGHTON (1927; Libellulidae), all but that of Kennedy based almost entirely on wing venation. NEEDHAM (1903) proposed, in modern terms, a paraphyletic Zygoptera with Calopterygoidea + *Epiophlebia* sister to a monophyletic Anisoptera and with Aeshnidae the sister of Libellulidae. TILLYARD’S (1917) classification was similar but raised Lestidae to family status, and elevated “legions” now recognized as families of Coenagrionoidea to subfamily status.

KENNEDY'S (1919, 1920) study of zygopteran pines led him to depict modern Zygoptera as a polytomy comprising Calopterygidae (with basal Megapodagrioninae), Hemiphlebiidae, Lestidae, and Coenagrionidae, all arising "by radiation from the primitive lestid or hemiphlebiid stock". TILLYARD (1925) later described *Kennedya mirabilis*, a "small narrow winged" Permian taxon characterized by petiolate wings, two antenodal crossveins, and without the posterior arcular brace. *Kennedya* turned out to be an important taxon, because these wing characteristics caused a reinterpretation of polarities, which led FRASER to propose a new classification system (TILLYARD & FRASER 1938–1940) and finally to FRASER'S (1957) reclassification and phylogeny positing a paraphyletic Zygoptera originating from a *Kennedya*-like ancestor. *Hemiphlebia* was placed at the base of extant Odonata with Coenagrionoidea branching next, followed by Lestinoidea (= Lestoidea), from which in turn arose the Calopterygoidea and its supposed sister taxon, Anisozygoptera + Anisoptera. In the absence of a generally agreed alternative this phylogeny has been widely accepted (DAVIES & TOBIN 1984, 1985; BRIDGES 1994; STEINMANN 1997a,b), despite being explicitly based on putative plesiomorphic character states (FRASER 1954).

Nevertheless, several different phylogenetic hypotheses have been suggested more recently. CARLE (1982), using a wide variety of morphological characters, concluded that Anisoptera and Zygoptera are each monophyletic, with Gomphidae the sister to remaining Anisoptera. Chlorogomphidae, usually placed in Cordulegastridae previously, was raised to family status and both families were considered basal Libelluloidea. CARLE & LOUTON (1994) later modified this scheme, placing the newly defined Austropetaliidae as sister to Aeshnidae, and Neopetaliidae (*Neopetalia* only) immediately basal to Chlorogomphidae, and CARLE (1995) separated Gomphomacromiidae from Corduliidae. PFAU (1991) placed Aeshnidae as sister to all other Anisoptera based principally on detailed studies of genitalic functional morphology. Cordulegastridae, Petaluridae, and Gomphidae formed a new superfamily, Petaluroidea. PFAU (2002) also supported the paraphyly of Zygoptera based on morphology of caudal appendages and their muscles. TRUEMAN (1996) presented a computer-assisted phylogeny, based strictly on wing venation, very similar to Fraser's, including *Hemiphlebia* as the sister taxon to the rest of Odonata, but with Petaluridae basal to Austropetaliidae and with many families, especially in Zygoptera, paraphyletic. BECHLY (1995), utilizing inferred ground plans and manual cladistic analysis, inferred a monophyletic Zygoptera (Calopterygoidea ((Coenagrionoidea, Megapodagrionidae) (Hemiphlebiidae, Lestoidea))), and monophyletic Anisoptera with Petaluridae sister

to other extant Anisoptera and Gomphidae sister to Libelluloidea. LOHMANN (1996) proposed a phylogeny for Anisoptera much like Bechly's but with Aeshnidae as sister to other Anisoptera, in accord with Pfau's arguments. CARLE & KJER (2002), also based in part on the work of Pfau, proposed yet another arrangement of Anisoptera, ((Austropetaliidae, Aeshnidae) (Gomphidae (Petaluridae, Libelluloidea))). The most recent computer-implemented morphological study (REHN 2003) utilized diverse characters and again found monophyletic Zygoptera and Anisoptera. Rehn's results placed *Philoganga* or *Philoganga* + *Diphlebia* as sister to other Zygoptera, with Amphipterygidae and Megapodagrionidae (both sensu FRASER 1957) forming a paraphyletic assemblage branching basal to Calopterygoidea, which in turn was sister to a monophyletic Lestoidea (with *Hemiphlebia* branching at its base) plus a monophyletic Coenagrionoidea. Rehn's Anisoptera form a pectinate array with Petaluridae and Gomphidae, successively, as sister to remaining Anisoptera.

Previous molecular studies of Odonata as a whole include those of HOVMÖLLER et al. (2002), OGDEN & WHITING (2003), SAUX et al. (2003), KJER (2004), KJER et al. (2006), and HASEGAWA & KASUYA (2006). All but KJER (2004), KJER et al. (2006), and HOVMÖLLER (2002) recovered a paraphyletic Zygoptera with *Lestes* as sister to a monophyletic Anisoptera. KJER (2004) discussed the weakness of his hypothesis, which recovered a paraphyletic Anisoptera. The molecular based topologies of HOVMÖLLER et al. (2002) and KJER et al. (2006) come closest to the phylogeny we present in this paper. In all molecular studies, however, much of the phylogenetic diversity of Odonata is left unsampled. Almost the only features of odonate phylogeny that currently enjoy consensus are the monophyly of Anisoptera with *Epiophlebia* as its sister taxon, and the deeply nested position of Libellulidae within Anisoptera. Here we suggest a revised phylogeny of Odonata, with particular emphasis on new conclusions about relationships among the Coenagrionoidea.

2. Methods

DNA was extracted, amplified, and purified using standard techniques. Amplification products from both strands were generated, purified, and used as templates for cycle sequencing using Applied Biosystems BigDye ReadyMix; fragments were sequenced on both ABI slab gel and capillary sequencers. Forward and reverse sequences were edited and consensus se-

quences created as in KJER et al. (2001). Consensus sequences were evaluated and contaminated sequences removed, based on BLAST searches, overlapping sequence fragment identities, and phylogenetic analyses of individual fragments. Sequences of rRNA were aligned manually utilizing secondary structure models (GUTELL et al. 1994) and compensatory substitutions according to KJER (1995, 2004). Ambiguously aligned regions are excluded from analyses according to the criteria presented in KJER et al. (2007). Portions of the large and small subunit nuclear ribosomal RNA's (28S and 18S rRNAs; 6228 aligned nts.), EF-1 α (1074 exon nts.), mitochondrial rRNA's (12S and 16S; 1181 aligned nts.) were selected for analysis. Protein coding genes were length invariant, and alignment was trivial. Introns in EF-1 α were identified in comparison to mRNA-generated sequences taken from GenBank. Outgroup taxa, taken from GenBank, included *Tricholepidion*, *Ctenolepisma*, *Lepisma* (Thysanura = Zygentoma), *Calibaetis*, *Hexagenia*, *Caenis*, *Stenonema* and *Centroptilum* (Ephemeroptera), and the neopterans, *Gromphadorhina* (Blattodea), and *Isoperla* (Plecoptera). The GenBank accession numbers for all included taxa and genes are given in the Electronic Supplement.

Two independent analyses were simultaneously performed with MrBayes (HUELSENBECK & RONQUIST 2002). Each of the analyses consisted of 5,000,000 iterations, each with 4 chains, 1 cold, 3 hot. All parameters for the Bayesian analysis can be found in the Nexus file available on Kjer's website, and the journal's online website. The program MODELTEST (POSADA & CRANDALL 1998) was used to select a model from the combined data under the Akaike criterion. The GTR+I+G model (TAVARÉ 1986; YANG 1994; YANG et al. 1994; GU et al. 1995) was used with each of the three data sets (i.e., EF-1 α nuclear rRNA, and mitochondria rRNA) unlinked, and free to vary under their own characteristics. Plots of the likelihood scores from the MrBayes ".p" files were examined with Tracer (RAMBAUT & DRUMMOND 2003) to determine the appropriate "burn-in", and after discarding the burn-in (the first 1000 trees from each run), all near optimal trees were pooled. Posterior probabilities were recorded from this pooled treefile from a majority-rule consensus tree, calculated in PAUP (SWOFFORD 1999). In order to illustrate a phylogram, the most likely of all trees was identified, and imported into the Treeview (PAGE 1996) program.

Data are available on GenBank, and voucher specimens are deposited in the Rutgers Entomological Museum. Alignments and Nexus files are available on Kjer's website <http://www.rci.rutgers.edu/~insects/indexpersonnel.htm>, and the journal's website <http://globiz.sachsen.de/snsd/publikationen/ArthropodSystematicsPhylogeny/>.

3. Results

Anisoptera and Zygoptera were found to be monophyletic. Results are further summarized in Fig. 1. The relationship of Odonata to other Pterygota is still unresolved (WHITFIELD & KJER 2007; KLASS 2007), and our results provide no further resolution to the Palaeoptera question. The placement of Epiophlebiidae was unstable, with support for a sister taxon relationship with other Odonata, Zygoptera, or Anisoptera. We present a basal trichotomy (Fig. 1). Nevertheless, our data recover, with very strong support, a monophyletic Zygoptera, in agreement with CARLE (1982), BECHLY (1994, 1995), and REHN (2003). The anisopteran topology in Fig. 1 is very similar to that reported by CARLE & KJER (2002), based on morphology. It supports placement of *Neopetalia* in Libelluloidea, Austropetaliidae as sister to Aeshnidae as in CARLE & LOUTON (1994) and the monophyly of Synthemistidae + Gomphomacromiidae. The zygopteran topology is similar to that proposed by KENNEDY (1919), with the superfamily Lestoidea (not to be confused with the unrelated genus *Lestoidea* Tillyard) as sister to all other Zygoptera. Calopterygoid phylogeny remains obscure. Based on this limited taxon sample, only the (Hetaerinidae, Calopterygidae), and (Epallagidae (Diphebiinae, Lestoideinae)) groups are well supported. Isostictidae is monophyletic but often recovered within Calopterygoidea or as sister to coenagrionoids with less than 50% probability.

Coenagrionoidea are here more extensively sampled and the framework of a phylogeny with some strongly supported features is apparent. Two striking results are suggested. First, Protoneuridae appear not to be monophyletic (e.g. REHN 2003). The three disparoneurines (*Chlorocnemis*, *Nososticta*, and *Prodasi-neura*) are grouped with Platycnemididae. This grouping is morphologically supported by a distinctly transverse adult head and small labial cleft. New World Protoneuridae, which possess an angulate frons (represented here by *Neoneura*), is part of a morphologically diverse group including *Argia moesta*, several presumed coenagrionoids mostly characterized also by having the frons angulate (KENNEDY 1919; DEMARMELS 1985; O'GRADY & MAY 2002), and Pseudostigmatidae, also with an angulate frons. Second, this latter group is well differentiated from a third group comprising other more typical Coenagrionidae that lack an angulate frons, including *Coenagrion* and the large genera, *Enallagma*, *Ischnura*, and *Pseudagrion*, among others.

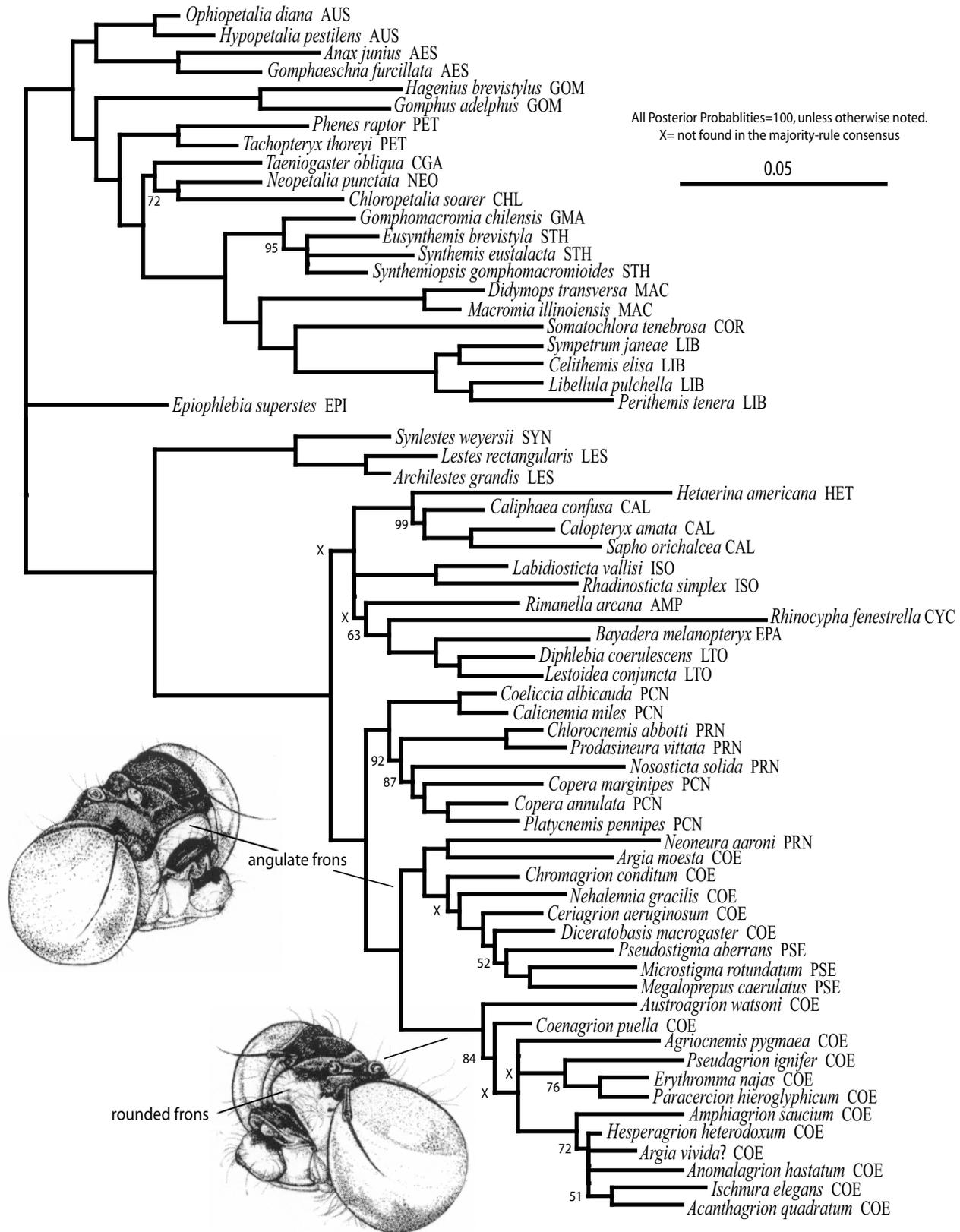


Fig. 1. Likelihood phylogram from the Bayesian analysis; all posterior probabilities are 100% unless given to the left of a node. This was the most likely tree from among many trees in the distribution, therefore there are some nodes, indicated by an “X”, on this “best” tree that are not present in the majority-rule consensus from which posterior probabilities were calculated. Conventional family groupings are indicated with the following abbreviations: AES – Aeshnidae, AMP – Amphipterygidae, AUS – Austropetaliidae, CAL – Calopterygidae, CGA – Cordulegastridae, CHL – Chlorogomphidae, COE – Coenagrionidae, COR – Corduliidae, CYC – Chlorocyphidae, EPA – Epallagidae, EPI – Epiophlebiidae, GMA – Gomphomacromiidae, GOM – Gomphidae, HET – Hetaerinae, ISO – Isostictidae, LES – Lestidae, LIB – Libellulidae, LTO – Lestoideidae (Lestoideinae + Diphlebiinae), MAC – Macromiidae, NEO – Neopetaliidae, PCN – Platycnemididae, PET – Petaluridae, PRN – Protoneuridae, PSE – Pseudostigmatidae, STH – Synthemistidae, SYN – Synlestidae.

4. Discussion

The monophyly of Anisoptera has never been in question, but the phylogenetic arrangement of included groups has been a source of major disagreement (eg. CARLE 1995; BECHLY 1996; PFAU 2005). PFAU (1991, 2005) proposed his unique Petaluroidea comprising Gomphidae, Petaluridae, and Cordulegastridae, based largely on his reconstruction of the evolution of the penis. The molecular evidence, however, strongly indicates that Pfau's Petaluroidea is paraphyletic, with Cordulegastridae sister to all other Libelluloidea, as also inferred by most other authors (e.g., FRASER 1957; CARLE 1982; MISOF et al. 2001; REHN 2003). This result implies that the biphasic function of the distal penile chamber is a plesiomorphy within Libelluloidea, with subsequent development of a single phase pump in the monophyletic synthemistid (incl. gomphomacromiini), macromiid, corduliid, libellulid group. Placement of *Neopetalia* in Libelluloidea and establishment of Austropetaliidae as basal aeshnoids (CARLE & LOUTON 1994) is supported by both morphological and molecular results. Consequently, similarities between Austropetaliidae and Neopetaliidae are either plesiomorphies (abdominal color pattern, separated compound eyes), or convergences (reddish wing spots, quadrate epiproct). Additionally, similarities between Aeshnidae and Libellulidae, including the elongate male epiproct, contiguous compound eyes, hoodlike interocellar lobe, well developed median and radial planates, elongate double anal loop, and lateral abdominal carina, are due to convergence (contra NEEDHAM 1903; CARLE 1982). Loss of an endophytic ovipositor apparently is an independent autapomorphy of Gomphoidea and Libelluloidea (contra BECHLY 1994; LOHMANN 1996; REHN 2003). However, shifts in ovipositor form and function has perhaps enhanced coevolution of male and female genitalia leading to the independent numerical dominance of Gomphidae and Libellulidae in comparison to their near sister groups as shown in Fig. 1.

The question of whether Zygoptera is monophyletic has been perhaps the principal unresolved issue in higher level phylogeny of Odonata. As noted in the introduction, several authors have supported a paraphyletic Zygoptera. Each of these analyses suffers, however, from limited taxon or character sampling or, in the case of Fraser's work, by prephylogenetic systematic methods. Our results provide strong independent validation of zygopteran monophyly from a large taxon sample and extensive molecular data, and they agree in this respect with the most detailed morphological analyses performed using modern systematic principles (CARLE 1982; BECHLY 1994, 1995; REHN 2003; KLASS 2008).

Our hypothesis for Zygoptera includes support for Lestoidea as sister to other Zygoptera, as in HOVMÖLLER et al. (2002), and KJER (2004), and as implied by KENNEDY (1920). The position of *Hemiphlebia*, not included here, is still unclear. In his text FRASER (1957), too, suggests a basal branching of Lestoidea from other Zygoptera (and indeed from all extant Odonata). The accompanying tree and Fraser's description of it, however, makes Coenagrionoidea the sister to other Zygoptera. This appears to be a consequence of his view that Megapodagrionidae, Pseudolestidae and Amphipterygidae are "annectant" between Lestoidea and Calopterygoidea and that the latter are sister to or even progenitors of Anisoptera. Such an arrangement forces Coenagrionoidea to a position as sister to the other taxa.

Our data strongly refute the placement of Calopterygoidea as related to Anisoptera. If Isostictidae, the position of which is unstable, is excluded, the Calopterygoidea (inc. Amphipterygida sensu BECHLY 1995) form the sister group of Coenagrionoidea. However, traditional calopterygoids are not recovered as monophyletic but are intermingled in a paraphyletic assemblage with taxa generally placed within Amphipterygida and possibly also including Isostictidae. This region of the phylogeny is characterized mostly by long terminal branches and short deeper internodes, so it is likely that considerably more taxon sampling, and possibly use of additional genes and/or more appropriate models, will be required to resolve this group. DUMONT et al. (2005) provide a detailed analysis of Calopterygidae which agree exactly with the results presented here. Our results also justify family rank for Isostictidae as proposed by LIEFTINCK (1975) and indicate that it is not phylogenetically close to Protoneuridae. The group (Epallagidae (Diphlebiinae, Lestoideinae)) is strongly supported and indicates that a close relationship between Polythoridae (not included in this study) and Epallagidae proposed by KENNEDY (1919) may be due to the convergent acquisition of larval lateral abdominal gills.

Coenagrionoidea excluding Isostictidae (ie. Coenagrionidae, Platycnemididae, Protoneuridae, and Pseudostigmatidae; all sensu FRASER 1957, except that Protoneuridae excludes Isostictidae), reveal several unexpected but well supported relationships. Protoneuridae appears to be polyphyletic, with New World protoneurids (*Neoneura*) closely associated with *Argia*, the angulate-frons Coenagrionidae (the *Nehalennia-Telebasis* Series of KENNEDY 1920), and Pseudostigmatidae. *Nososticta*, *Chlorocnemis*, and *Prodasineura*, placed by FRASER (1957) in Disparoneurinae, are recovered within Platycnemididae (Fig. 1). Fragmentary data (not shown) from other New World protoneurids place them with *Neoneura*. The strong molecular differences between protoneurines and disparoneurines are

supported by several morphological characters; for example, platycnemidids and disparoneurines have the adult frons rounded, tibial spurs long, labial cleft shallow, and head transversely elongate, while in protoneurines, the frons is angulate, the spurs short, the labial cleft deep, and the head not unusually elongate transversely. Possession of an angulate frons, short tibial spurs, and a deep labial cleft appear to be synapomorphies of Protoneuridae (*sens. nov.*) while the transversely elongated head, at least, unites Platycnemididae + Disparoneurinae. Thus it appears that protoneurines and disparoneurines have been hitherto placed in one family due mainly to convergent similarity resulting from reduced venation, but they are not actually close relatives. We lack sequence data for Caconurinae, but they share the same morphological characteristics as noted for disparoneurines. Note, too, that the shape of the discoidal cell evidently has little if any systematic significance above the subfamily or tribal level.

The coenagrionoid group comprising *Neoneura* through *Megaloprepus* in Fig. 1 includes a number of taxa that have not commonly been associated by most recent workers, and the suggestion that protoneurines and *Argia* belong here has not, to our knowledge, been considered previously. Most of these species are distinguished from typical coenagrionids by their angulate frons (*Argia* is a notable exception), and in many, the larval caudal lamellae are very strongly nodate, or pedunculate. SANTOS (1966), however, suggested that Pseudostigmatidae may have been derived from coenagrionids similar or identical to *Leptagrion* (a genus with the frons angulate), based on their common larval habitat of phytotelmata, especially leaf axils of bromeliads. RAMÍREZ (1997), too, based on larval morphology, argued for evolution of Pseudostigmatidae from within Coenagrionidae, although he noted that similarity in larval caudal lamellae among species inhabiting phytotelmata may be due to convergence. DEMARMELS (1985, 2007) elaborated this idea in two papers that have received less attention than they deserve. His morphological analysis based on larval and adult characters, although not including *Neoneura* and *Argia*, is fully consistent with our conclusions. He recognized the validity of Kennedy's subdivision of the *Nehalennia-Telebasis* Series into a "*Chromagrion-Nehalennia-Teinobasis* Series", characterized principally by an articulated ventrobasal spur on each male cercus, a structure absent in the "*Ceriagrion-Telebasis-Metaleptobasis* Series". The former is represented in our phylogeny by a group comprising *Chromagrion* and *Nehalennia*. Note that, although clearly placed in this subgroup by virtue of their articulated cercal spur, the frons of *Bromeliagrion*, *Chromagrion* and *Pyrhosoma* is rounded, with vestigial angulation only in the median frontal emargination of the latter two. The

Ceriagrion-Telebasis group is paraphyletic (as also found by DEMARMELS 2007) relative to Pseudostigmatidae and is represented here by *Ceriagrion* and *Diceratobasis*; the larval habitat of *Diceratobasis* is again in bromeliad axils.

In summary, we suggest that Disparoneurinae be regarded as a subfamily of Platycnemididae, pending further analysis to confirm its monophyly. Pseudostigmatinae *stat. nov.* are considered highly autapomorphic Coenagrionidae related to the angulate-frons coenagrionid taxa, including Teinobasini Tillyard (DEMARMELS 2007), the "*Ceriagrion-Telebasis-Metaleptobasis* Series" (KENNEDY 1920), and probably the Protoneuridae and Argiinae, although the distinctive morphological features of the last group suggest the need for further study. We note the placement of a supposed *Argia vivida* among the Coenagrionidae s.s. The latter data were obtained from GenBank and we did not verify the specific identification of the voucher specimen.

The topological positions of narrow winged Zygoptera suggest that Kennedy's narrow wing ancestor theory for Zygoptera is more plausible than ever. The narrow wing and stalked wing base appear likely to be a synapomorphy of *Kennedyia* + extant Odonata. So, too, may be possession of two antenodal crossveins, although CARLE (1982) points out that the frequent lack of alignment of "primary antenodals" in Protozygoptera may imply that these are not homologous with the costal braces of extant Odonata. Certainly our results suggest independent evolution of unstalked wing bases and numerous antenodal crossveins in Anisoptera and Calopterygoidea.

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