Systematic Entomology

Systematic Entomology (2014), **39**, 68–96 DOI: 10.1111/syen.12035

Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata)

KLAAS-DOUWE B. DIJKSTRA[1,2], VINCENT J. KALKMAN[1], RORY A. DOW[1], FRANK R. STOKVIS[1] and JAN VAN TOL[1]

[1]Naturalis Biodiversity Center, Leiden, The Netherlands and [2]University Museum of Zoology, Cambridge, U.K.

Abstract. An extensive molecular phylogenetic reconstruction of the suborder Zygoptera of the Odonata is presented, based on mitochondrial (16S, COI) and nuclear (28S) data of 59% of the 310 genera recognized and all (suspected) families except the monotypic Hemiphlebiidae. A partial reclassification is proposed, incorporating morphological characters. Many traditional families are recovered as monophyletic, but reorganization of the superfamily Coenagrionoidea into three families is proposed: Isostictidae, Platycnemididae and Coenagrionidae. *Archboldargia* Lieftinck, *Hylaeargia* Lieftinck, *Palaiargia* Förster, *Papuargia* Lieftinck and *Onychargia* Selys are transferred from Coenagrionidae to Platycnemididae, and *Leptocnemis* Selys, *Oreocnemis* Pinhey and *Thaumatagrion* Lieftinck from Platycnemididae to Coenagrionidae. Each geographically well-defined clade of Platycnemididae is recognized as a subfamily, and thus Disparoneurinae (i.e. Old World 'Protoneuridae') is incorporated, Calicnemiinae is restricted, and Allocnemidinae (type genus: *Allocnemis* Selys) **subfam.n.**, Idiocnemidinae (type genus: *Idiocnemis* Selys) **subfam.n.** and Onychargiinae (type genus: *Onychargia* Selys) **subfam.n.** and Coperini **trib.n.** (type genus: *Copera* Kirby) are described. Half of Coenagrionidae belongs to a well-supported clade incorporating *Coenagrion* Kirby and the potential subfamilies Agriocnemidinae, Ischnurinae and Pseudagrioninae. The remainder is less well defined, but includes the Pseudostigmatidae and New World Protoneuridae that, with Argiinae and Teinobasinae, may prove valid subfamilies with further evidence. Ninety-two per cent of the genera formerly included in the polyphyletic Amphipterygidae and Megapodagrionidae were studied. Pentaphlebiidae, Rimanellidae and Devadattidae **fam.n.** (type genus: *Devadatta* Kirby) are separated from Amphipterygidae, and Argiolestidae, Heteragrionidae, Hypolestidae, Philogeniidae, Philosinidae and Thaumatoneuridae from Megapodagrionidae. Eight further groups formerly placed in the latter are identified, but are retained as *incertae sedis*; the validity of Lestoideidae, Philogangidae and Pseudolestidae is confirmed. For some families (e.g. Calopterygidae, Chlorocyphidae) a further subdivision is possible; Protostictinae **subfam.n.** (type genus: *Protosticta* Selys) is introduced in Platystictidae. Numerous new combinations are proposed in the Supporting Information. Many long-established families lack strong morphological apomorphies. In particular, venation is incongruent with molecular results, stressing the need to review fossil Odonata taxonomy: once defined by the reduction of the anal vein, Protoneuridae dissolves completely into six clades from five families.

Correspondence: Klaas-Douwe B. Dijkstra, Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, the Netherlands.
E-mail: kd.dijkstra@naturalis.nl

Introduction

Odonata are among the most ancient of winged insects, dating from the Permian (Grimaldi & Engel, 2005). Extant Odonata are considered monophyletic (e.g. Davis *et al.*, 2011) and include two suborders of almost 3000 species each, the Zygoptera or damselflies and the Anisoptera or true dragonflies, and a third suborder, the Anisozygoptera or damseldragons with only four species (Kalkman *et al.*, 2008; Dijkstra *et al.*, 2013). Although wing venation guided classification of Odonata, rampant homoplasy (convergence) obscures relationships, as has been demonstrated in Anisoptera (e.g. Dijkstra & Vick, 2006; Ware *et al.*, 2007; Pilgrim & von Dohlen, 2008; Fleck *et al.*, 2008a; Blanke *et al.*, 2013). The same applies, perhaps more so, in Zygoptera (O'Grady & May, 2003; Carle *et al.*, 2008; Pessacq, 2008), in which systematic challenges remain in groups with the most simplified venation (mostly Coenagrionoidea) and those characterized by the potentially highly homoplasious insertion of supplementary longitudinal veins (mostly Megapodagrionidae).

Although the phylogeny of the Anisoptera has been reasonably well studied and its classification is fairly settled (e.g. Ware *et al.*, 2007; Fleck *et al.*, 2008b), recent studies of Zygoptera rely on rather incomplete molecular datasets (Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010) and one extensive morphological study (Rehn, 2003), although the family Calopterygidae has been studied in detail (Dumont *et al.*, 2005, 2007). Our taxon sampling is the most extensive thus far in Zygoptera, including members of 59% of the 310 genera currently recognized and all (suspected) families, except for the monotypic Hemiphlebiidae. To optimize sampling breadth versus phylogenetic depth, our approach targeted two variable mitochondrial markers [16S, cytochrome c oxidase I (COI)] and a more conserved nuclear one (28S) for many species, rather than more markers for a limited selection. These are among the most commonly applied markers in Odonata and generally provide well resolved and supported trees, at least from species to family level (Hasegawa & Kasuya, 2006; Ballare & Ware, 2011). Moreover, a relatively long section of 28S was sequenced and the combined total extent of 28S + 16S is comparable (84–145%) to several studies with three or more markers (Ware *et al.*, 2007; Bybee *et al.*, 2008; Pilgrim & von Dohlen, 2008; Fleck *et al.*, 2008a,b) and 75% of two studies using four nuclear markers only (Dumont *et al.*, 2005, 2010). For 83% of the studied taxa, COI was sequenced and available sequences surpass previous studies (121–210% and 108%). We focus on the phylogenetic and taxonomic implications of the newly available data (cf. Dijkstra & Kalkman, 2012), particularly for the definition of the families, using Silsby (2001) as the basis of the 'traditional' classification (Dijkstra *et al.*, 2013).

Methods

Specimen acquisition

The study relies on collections assembled in recent years at the Naturalis Biodiversity Center, Leiden, the Netherlands (formerly the National Museum of Natural History and the Netherlands Centre for Biodiversity Naturalis), by the authors, supplemented with donations from our international network (see the Acknowledgements section). Specimens included in the analysis were collected from 43 countries and from all continents, excluding Antarctica. In 34% of cases, one or two legs were removed from a live sample and preserved in 96% ethanol; the specimen was retained as an acetone-dried voucher. In the remaining cases, legs were removed from a specimen previously preserved either in 96% ethanol or by drying with acetone.

DNA extraction and amplification

Genomic DNA was extracted from legs using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Venlo, The Netherlands). Elution was performed in 100 μL elution buffer. Fragments of the nuclear 28S rRNA gene (1346–1532 bp) and the mitochondrial 16S rRNA (522–542 bp) and COI genes (658 bp) were amplified using primer combinations developed with Primer3 (Rozen & Skaletsky, 2000) (Table S1). Twenty-five microlitres of PCR reaction mixes for 16S and COI contained 2.5 μL of 10× CoralLoad PCR Buffer (Qiagen), 1 μL of each primer (10 pM), 1.25 U of Taq DNA Polymerase (Qiagen), 0.5 μL of dNTPs and 1 μL of DNA template. Five microlitres of Q-solution (Qiagen) were added to the reaction mix for 28S. The amplification protocol consisted of 3 min at 94°C followed by 40– 50 cycles of 15 s at 94°C, 30 s at 60°C to 35°C and 40 s at 72°C, and a final 5 min at 72°C. Direct sequencing was performed at Macrogen Europe on an ABI 3730XL sequencer (Applied Biosystems, Carlsbad, CA).

Data analysis

Sequences were edited with SEQUENCHER 4.10.1 (Gene Codes Corporation, Ann Arbor, MI) and assembled using BIOEDIT 7.0.9.0 (Hall, 1999). GENEIOUS PRO 5.6.4 (Biomatters Ltd, Auckland, New Zealand) (Drummond *et al.*, 2011) was used to check for stop codons. All sequence data and additional geographic and ecological data as well as photographs of the specimens were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham & Hebert, 2007). Sequences were also deposited in GenBank. Barcode index numbers (BINs) and GenBank accession numbers are provided in Table S2. The number of unique site patterns was 635 for 28S, 452 for 16S and 359 for COI.

Phylogenetic analyses

Multiple sequence alignments were performed using MAFFT (Katoh *et al.*, 2009) under default parameters. After exploration of all molecular data with neighbour joining analysis using MAFFT, a selection was made for in-depth analysis of specimens for which both 16S and 28S sequences were available. As a rule, we included two individuals per genus, preferably representing distant species, or two for each distinct clade if the genus appeared not to be monophyletic. The subset included 356 specimens, representing at least 322 species placed in 184 genera. For 295 of these specimens, COI sequences are available as well. Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the individual datasets of 28S (additional taxa: *Amazoneura*, *Dolonagrion*, *Megapodagrion*) and 16S (adding *Coeliccia dinoceras* Laidlaw, *Xiphiagrion*), as well as the combined 28S + 16S and 28S + 16S + COI datasets. MP analyses were performed in TNT (Goloboff *et al.*, 2008) by heuristic search with 10 000 random-taxon-addition replicates, TBR branch swapping, maxtrees set to 1000 with auto-increase. All characters were treated as equal and unordered. Gaps were treated as missing data. Node support was established with a bootstrap analysis of 500 replicates. ML analyses were run with RAXML (Stamatakis *et al.*, 2008) using a Gamma model of rate heterogeneity, with each fragment treated as a separate partition. For the BI, the best-fitting nucleotide substitution model for each of the individual fragments was assessed using hierarchical likelihood ratio tests in MRMODELTEST 2.3 (Nylander, 2004). For 28S and 16S, a general time reversal (GTR + I + G) model (nst = 6) was selected, whereas for COI the Hasegawa–Kishino–Yano model (nst = 2) was used, all with a proportion of invariable sites and a gamma distribution for rates across sites (rates = invgamma). For each dataset, two independent Monte Carlo Markov Chain simulations were run in MRBAYES 3.2.1 (Huelsenbeck & Ronquist, 2001) with four chains, for 4 000 000 generations and a sample frequency of 2000 at a temperature of 0.05, providing > 10 000 trees for the consensus after an average standard deviation of split frequencies < 0.01 had been reached. Several anisopterans were tested as outgroup, leading to similar topologies, and thus only results using *Aeshna juncea* (Linnaeus) of Aeshnidae are shown.

Morphology

Specimens in the Naturalis Biodiversity Center (Leiden) and University Museum of Zoology (Cambridge) and numerous publications (e.g. Bechly, 1996; O'Grady & May, 2003; Rehn, 2003; Gassmann, 2005; Bybee *et al.*, 2008; Pessacq, 2008; van Tol *et al.*, 2009; Garrison *et al.*, 2010; Yu & Bu, 2011b) were examined for morphological characters of the lineages identified by molecular analysis.

Results

The phylogenies reconstructed on the 28S + 16S and 28S + 16S + COI datasets are presented in Figs 1–3. Support for important clades is summarized in Table S3 and, where relevant, is discussed for separate partitions in the following sections. Of the generally accepted families, many were recovered as monophyletic with good support in (almost) all analyses: Calopterygidae, Chlorocyphidae, Euphaeidae, Isostictidae, Lestidae, Lestoideidae, Platystictidae and Polythoridae. Coenagrionidae was monophyletic if the Pseudostigmatidae and New World Protoneuridae were included, as was Platycnemididae if the Old World Protoneuridae were included, although seven genera had to be moved between the two families (see Discussion for details). Amphipterygidae and Megapodagrionidae were found to be highly polyphyletic, although the latter revealed several large and sometimes well-supported groups of genera. The remaining families are either monogeneric (Philogangidae, Pseudolestidae) or nearly so with only one taxon sampled (Dicteriadidae). Perilestidae and Synlestidae were paraphyletic in many analyses but in BI/ML 28S + 16S + COI, the two combined were monophyletic with low support and a well-supported monophyletic Perilestidae was embedded in Synlestidae.

Although family-level clades often were well supported and the internal topology of these clades was frequently resolved, generally limited support was found for family interrelationships. However, the clade combining Coenagrionidae, Platycnemididae, Pseudostigmatidae and the entire Protoneuridae was well supported. BI/ML 28S + 16S recovered Isostictidae as their sister group, but with low support. Lestoidea (including Lestidae, Perilestidae and Synlestidae) was well supported consistently as the sister group of all remaining Zygoptera, as was Platystictidae as the sister group of the remainder. No nearest relatives could be identified for the families Calopterygidae, Chlorocyphidae, Philogangidae, Polythoridae and Pseudolestidae, as well as for the clades that formerly constituted Amphipterygidae and Megapodagrionidae. Only Euphaeidae and Lestoideidae appeared consistently as sister groups with good support, but their further relationships remained unclear. The results and their implications are detailed in the following section for each family and/or well-supported clade.

Discussion

Molecular and morphological studies indicate that Zygoptera are monophyletic (Bechly, 1996; Rehn, 2003; Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010), although Trueman (1996, 2007) questioned this based on an analysis of wing venation. Given our focus on that suborder and the often low support of higher-level relationships found within it, our dataset is unsuited for this issue. Our analyses supported the prevailing family classification for 72% of all genera and 80% of all species of Zygoptera. Therefore recognition at the family level of equally well-supported but previously unrecognized clades, particularly within the 'family' Megapodagrionidae, should be considered. Proposed taxonomic consequences are discussed in the following sections, starting with the relatively well defined smaller sister groups of remaining Zygoptera (the superfamilies Lestoidea and Platystictoidea), followed by the 'crown' radiation of the Coenagrionoidea, which encompasses three-fifths of all damselfly species. The discussion concludes with the problematic remainder, grouped strictly for convenience in the probably paraphyletic 'Calopterygoidea'.

The suggested reclassification of Zygoptera based on this discussion is provided in Appendix 1, including the authorities

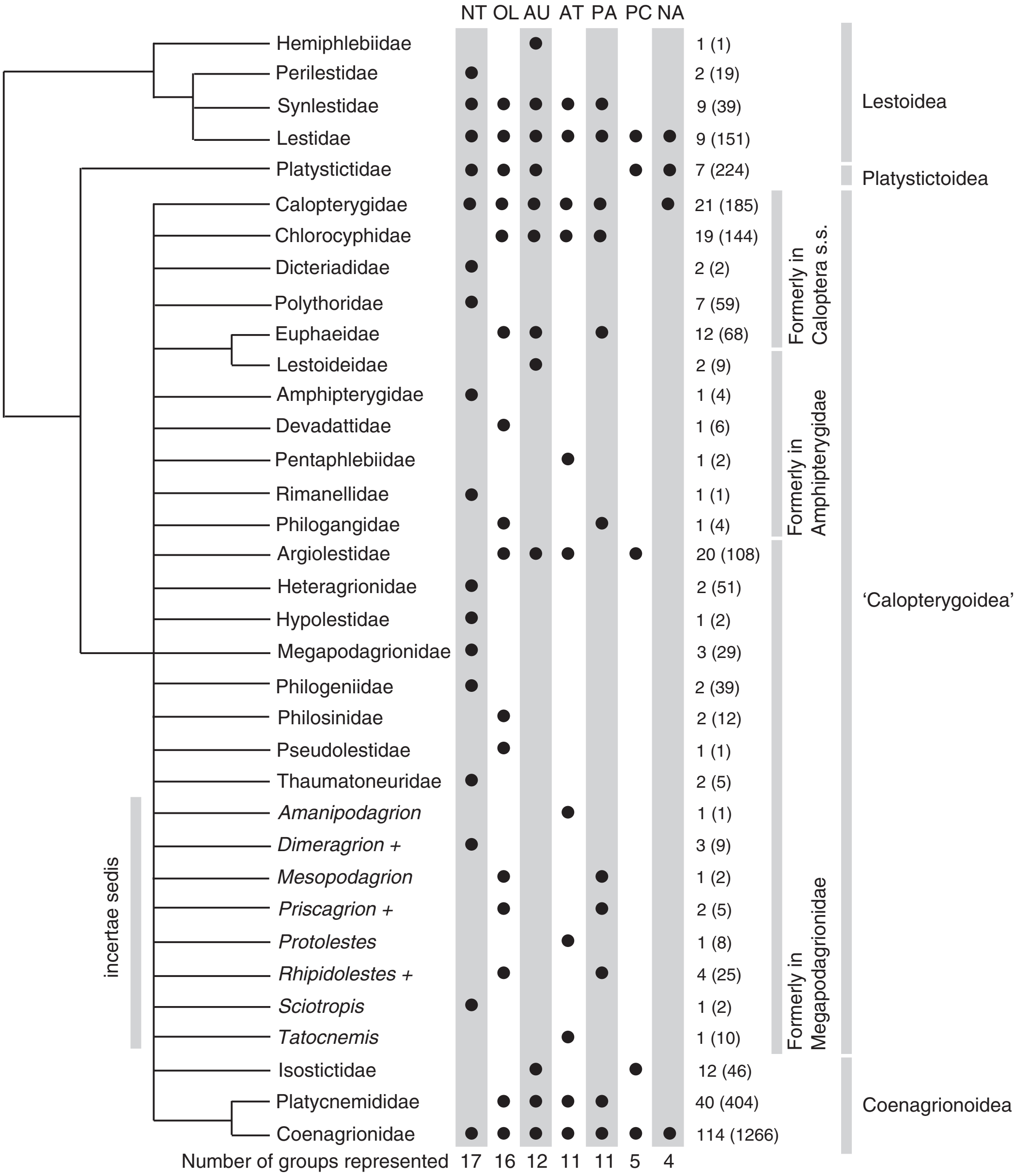


Fig. 1. Summary of Zygoptera phylogeny, based on Figs 2, 3 and the Discussion section. Only reasonably supported dichotomies are shown. The classification follows Appendix 1 (see for other genera placed near *Dimeragrion*, *Priscagrion* and *Rhipidolestes*) and the fate of some traditional taxa is indicated. For each recognized damselfly lineage, the known numbers of genera and species (in brackets) are shown, as is their occurrence in the Afrotropical (AT), Australasian (AU), Nearctic (NA), Neotropical (NT), Oriental (OL), Pacific (PC) and Palaearctic (PA) regions.

for all genus- and family-group names. Diagnoses of new or revised family groups are given in Appendix 2 and a summary of proposed taxonomic changes, including new combinations, is given in Table S4.

Superfamily Lestoidea

All analyses confirmed that the over 200 species of Lestoidea (not to be confused with the unrelated genus *Lestoidea*) form the sister group of all the other 93% of damselflies (cf. Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010; Davis *et al.*, 2011). Contrary to Rehn (2003), the position of the superfamily Lestoidea suggests that the narrowed external edge of the labial palp is an apomophy of remaining Zygoptera, rather than that the expanded edge arose convergently in Lestoidea and Anisoptera. With the exception of *Hemiphlebia*, Lestoidea possesses distinctly modified secondary genitalia with a reduced apex of the genital ligula (the functional penis) and triangular anterior hamules (Rehn, 2003; Garrison

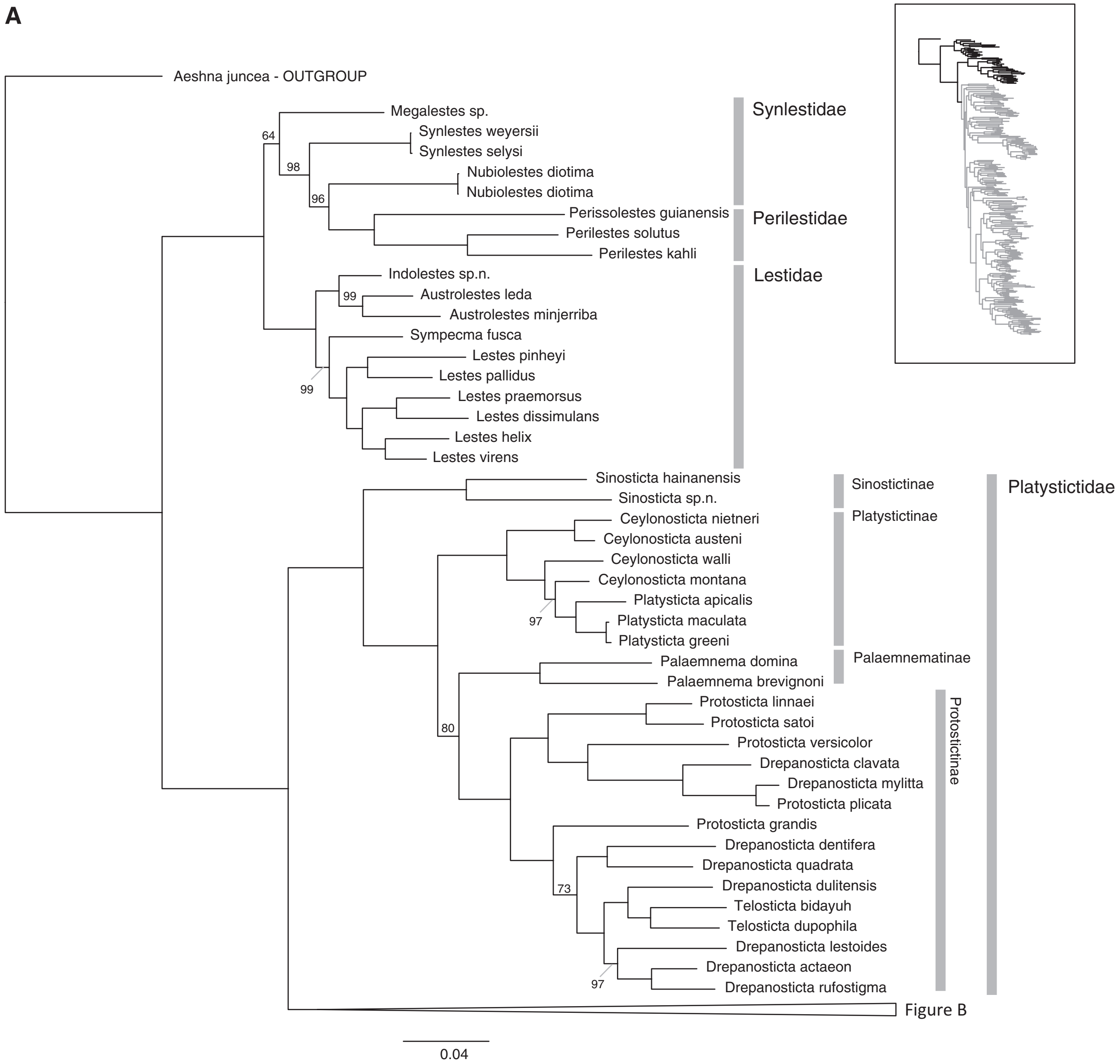
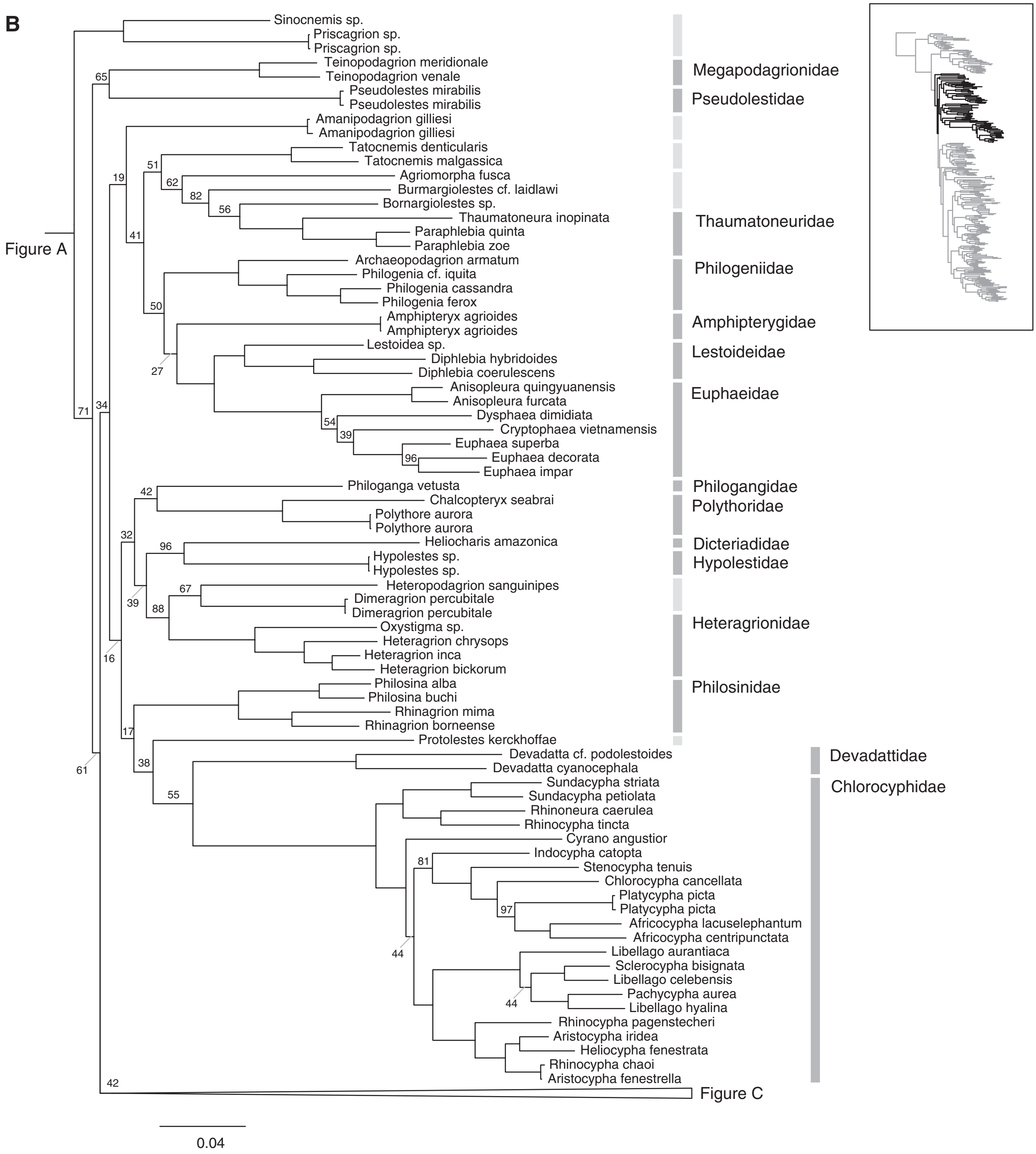


Fig. 2. Phylogenetic reconstruction for 295 specimens from the combined Bayesian analysis of 28S, 16S and COI. Posterior probabilities are shown (as percentages) only if below 100%. Species names and classification as proposed are shown. (a) Lestoidea and Platystictoidea; (b, c) various groups; (d) Platycnemididae; (e) Coenagrionidae.

et al., 2010). The monotypic Hemiphlebiidae from south-eastern Australia and Tasmania was not studied, but is the sister group of remaining Lestoidea according to previous studies (Rehn, 2003; Dumont *et al.*, 2010; Davis *et al.*, 2011).

Just over a quarter of the Lestoidea species are placed currently in the Perilestidae and Synlestidae. We found no support for the monophyly of the latter family, but in BI/ML 28S + 16S + COI the two combined were monophyletic with low support, as was Perilestidae with high support. The last is expected given the morphological similarity of the Neotropical *Perilestes* and *Perissolestes*. The monotypic *Nubiolestes* from central Africa has been considered the only non-American perilestid, but formed the sister group of the American genera only in BI/ML 28S + 16S + COI, although with low support. However, we had difficulty amplifying COI for many synlestids and BI, ML and MP of 28S and 28S + 16S recovered *Nubiolestes* as the sister group of the southern African *Chlorolestes*. Neotropical Perilestidae share mid-dorsal spines on the larval abdomen, a two-toothed ovipositor, very short pterostigmata, anal veins reduced basally (or shifted distally) allowing the quadrilateral cells to reach the wing margins, and a distinctive layout of markings and appendages (Garrison *et al.*, 2010). The anal vein and ovipositor dentition of *Nubiolestes* are intermediate to *Chlorolestes* and other features



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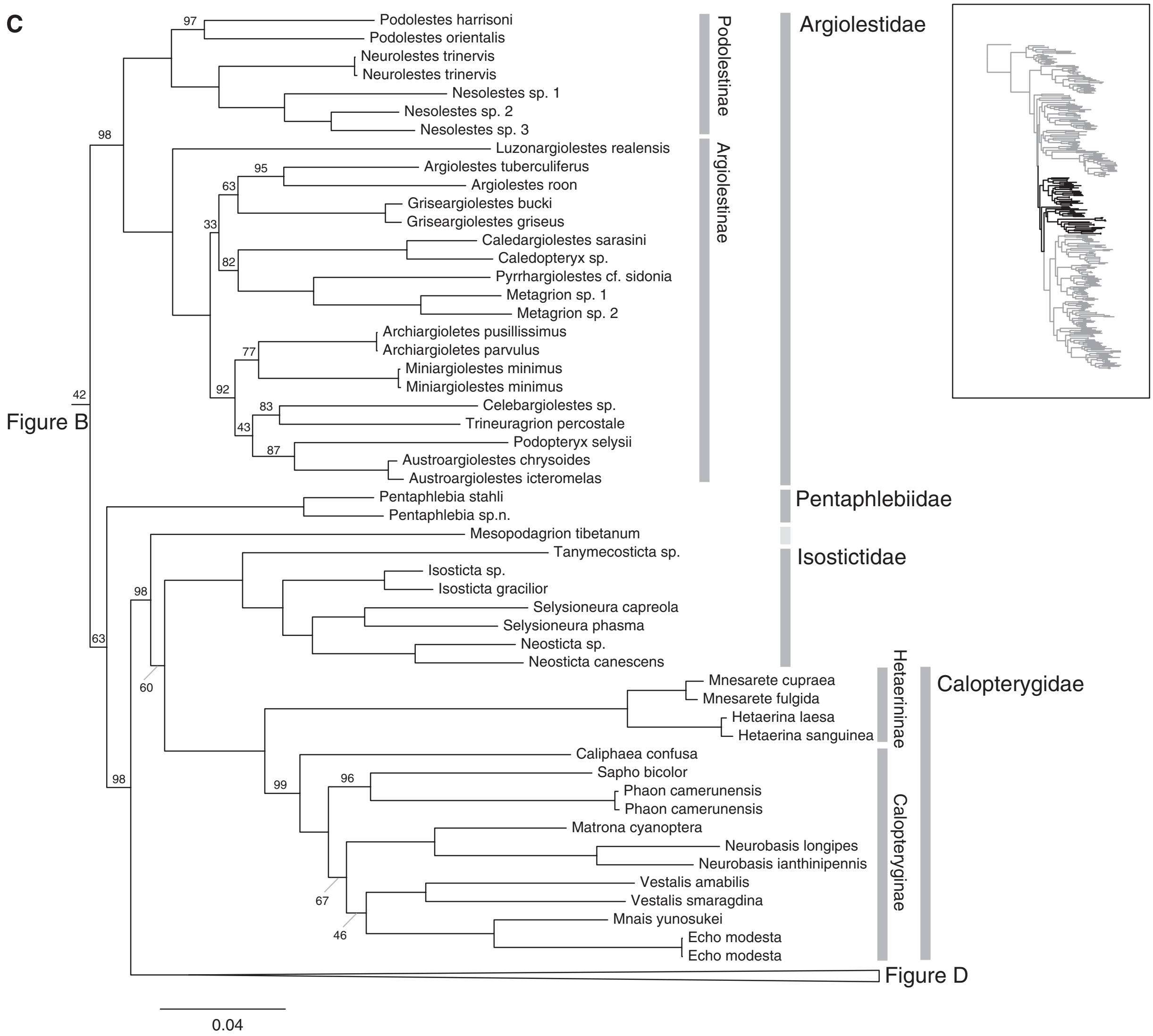
are closer to the latter. Interestingly, the Synlestidae from South Africa (*Chlorolestes*, *Ecchlorolestes*) never grouped together, nor did those from Australia (*Episynlestes*, *Synlestes*). We did not sample the problematic genera *Phylolestes* from Hispaniola, *Sinolestes* from China and *Chorismagrion* from Australia. The last, sometimes placed in the Chorismagrionidae (Bechly, 1996), was recovered within Synlestidae by Bybee *et al.* (2008) and Dumont *et al.* (2010). May *et al.* (unpublished data in Dijkstra *et al.*, 2013) found Synlestidae to be monophyletic if *Nubiolestes* was included, but morphological apomorphies for the group remain to be identified. Given the discussed problems, we retain Perilestidae and Synlestidae as



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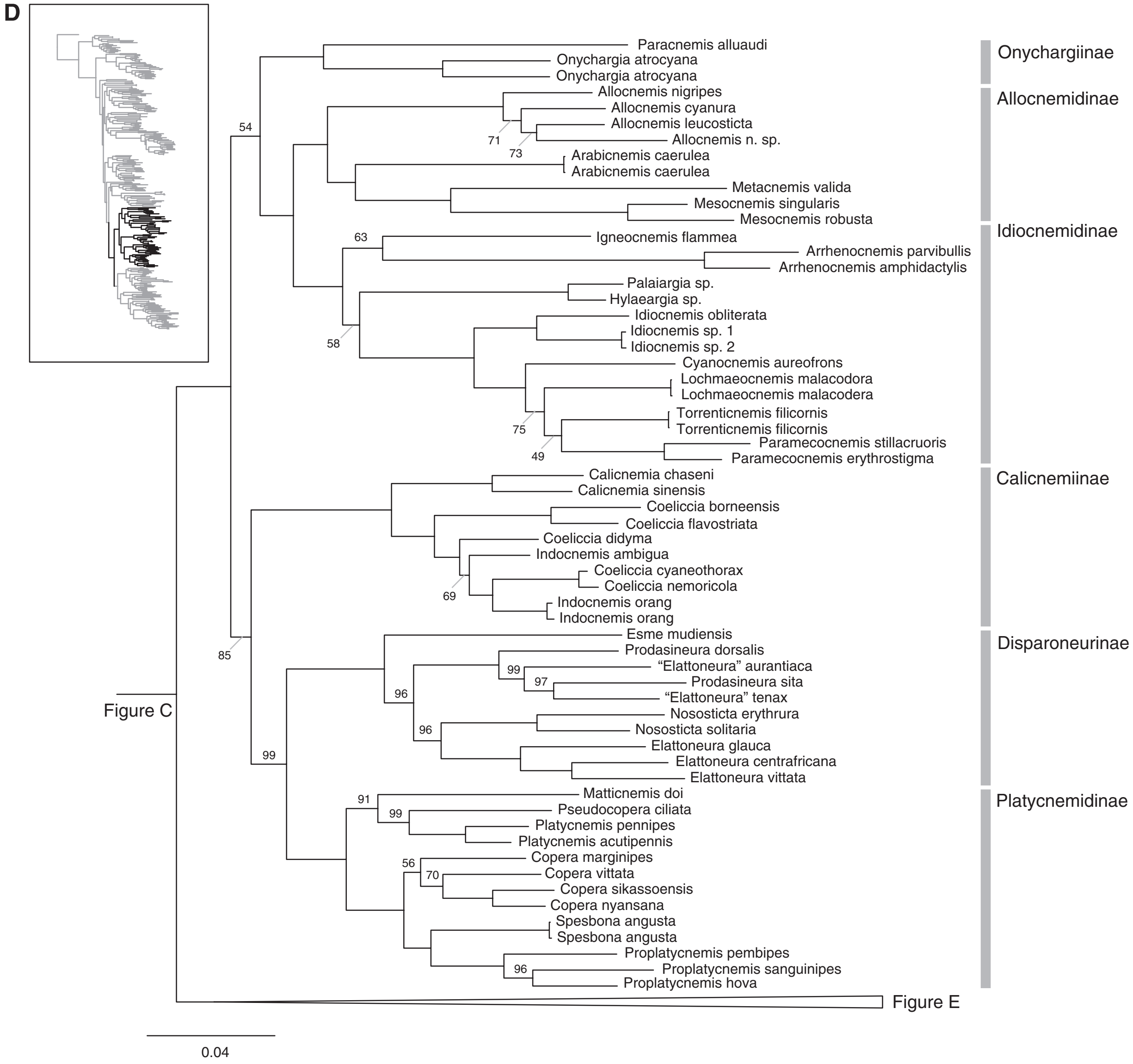
currently recognized, only transferring *Nubiolestes*, although Synlestidae may still prove not be monophyletic and the two families might eventually be merged or divided. Lestidae was monophyletic in all analyses (cf. Rehn, 2003; Bybee *et al.*, 2008; Dumont *et al.*, 2010). *Austrolestes* and *Indolestes* are sister groups, but were never monophyletic with *Sympecma*, which also closes its wings at rest, and thus no support for the subfamily Sympecmatinae was found. *Sympecma* was recovered in *Lestes* in ML 28S + 16S: over half the species of Lestidae are currently placed in *Lestes* and this heterogeneous and cosmopolitan genus is likely to be subdivided in the future.

Superfamily Platystictoidea and family Platystictidae

Platystictidae is monophyletic in all analyses and the sister group of all Zygoptera, excluding Lestoidea, in BI and ML of 28S + 16S and 28S + 16S + COI (cf. Bybee *et al.*, 2008; van Tol *et al.*, 2009; Dumont *et al.*, 2010; Davis *et al.*, 2011). The group possesses a peculiar combination of venation characters, including a reduced anal vein abutting (when present) the quadrilateral cell, a supplementary basal cross-vein and a very basally positioned node, and is also characterized by the ridges on the occiput and postgenae (Rehn, 2003; Garrison *et al.*, 2010). Currently the over 220 species are placed in just seven genera, a higher ratio than in any other family. This is due to the highly polyphyletic nature of the Oriental genera *Protosticta* and *Drepanosticta* (van Tol *et al.*, 2009). The recently described genus *Telosticta* is monophyletic, but further generic revision is required (Dow & Orr, 2012). Wilson (1997) erected the subfamily Sinostictinae for the distinct genus *Sinosticta* from southern China, which was the sister group of remaining Platystictidae with high support. The Sri Lankan Platystictidae were found to be the sister group of all platysticids except



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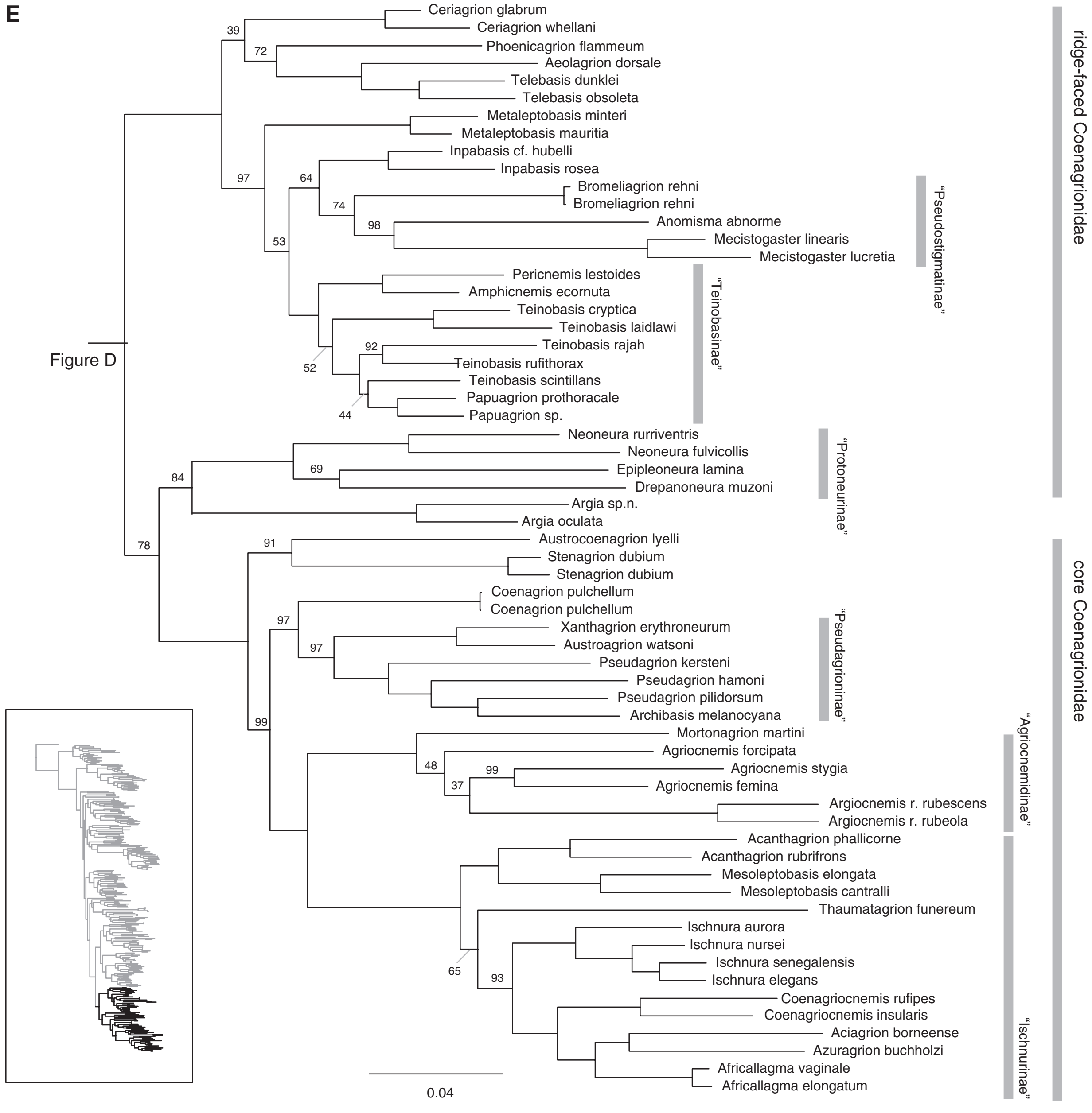
Sinosticta in BI 28S + 16S and BI/ML 28S + 16S + COI, and of the Neotropical genus *Palaemnema* (sole member of the subfamily Palaemnematinae) in BI/ML 28S and ML 28S + 16S, making the Oriental Platystictinae paraphyletic. Therefore we limit Platystictinae to the Sri Lankan group and erect Protostictinae **subfam.n.** for the remaining Asian Platystictidae. The genus *Ceylonosticta* is reinstated for the Sri Lankan species placed in the mainland genus *Drepanosticta*, although this genus appears paraphyletic relative to the endemic *Platysticta* and must be revised (Table S4).

Superfamily Coenagrionoidea

A monophyletic group including Coenagrionidae, Platycnemididae, Protoneuridae and Pseudostigmatidae *sensu* Silsby (2001), was well supported by BI/ML 28S +16S/ 28S + 16S + COI (cf. Bybee *et al.*, 2008; Carle *et al.*, 2008). Isostictidae is the sister group of this assemblage according to Bybee *et al.* (2008), a relationship we recovered only with low support in BI/ML 28S + 16S. All aforementioned families are retained in the superfamily Coenagrionoidea, including almost three-fifths of all damselfly species. They are characterized by the larval prementum, which has an (almost) entire anterior border and palps bearing setae, although palpal setae also occur in the Lestidae (Bechly, 1996; Rehn, 2003).

Coenagrionoid classification has been unsettled by the discovery of non-monophyly of its long-recognized families. As detailed in the following, our extensive sampling allows reconfiguration of the superfamily into three families, of



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which Isostictidae includes less than 3% of species and Platycnemididae 24%. The Old World 'protoneurids' (Disparoneuridae in Kalkman & Orr, 2012) are not closely related to the true New World Protoneuridae (Pessacq, 2008), being either the sister group of Platycnemididae (Bybee *et al.*, 2008; van Tol *et al.*, 2009; Dumont *et al.*, 2010) or falling within that family (Rehn, 2003; Carle *et al.*, 2008). In BI/ML 16S/28S + 16S/28S + 16S + COI, Platycnemididae forms the sister group of remaining Coenagrionoidea (excluding Isostictidae) and Disparoneuridae is the sister group of its subfamily Platycnemidinae. The remaining Platycnemididae (previously considered as subfamily Calicnemiinae) are paraphyletic, as demonstrated previously based on morphology (Gassmann, 2005). Our analyses show that they form several geographically well-defined clades. Stability is served by expanding the family to incorporate the Disparoneuridae and recognizing each of these clades as a subfamily. The latter family-group name is favoured over Caconeuridae, introduced simultaneously (Fraser, 1957), because *Caconeura* belongs to a distinctive southern Indian radiation, while *Disparoneura* has more in common with the widespread elements of this group. The complex systematics of the remaining 73% of Coenagrionoidea is discussed under Coenagrionidae.

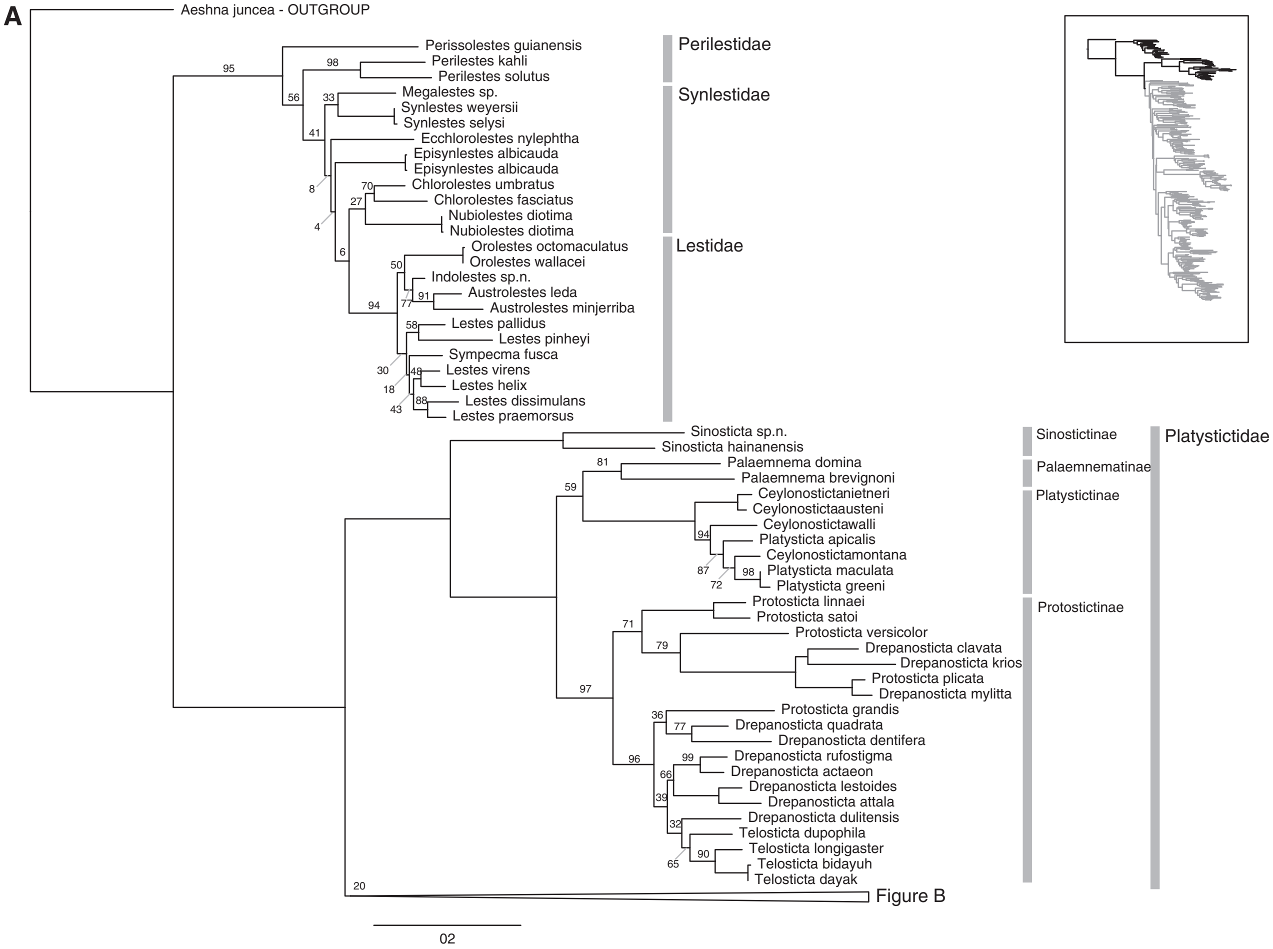


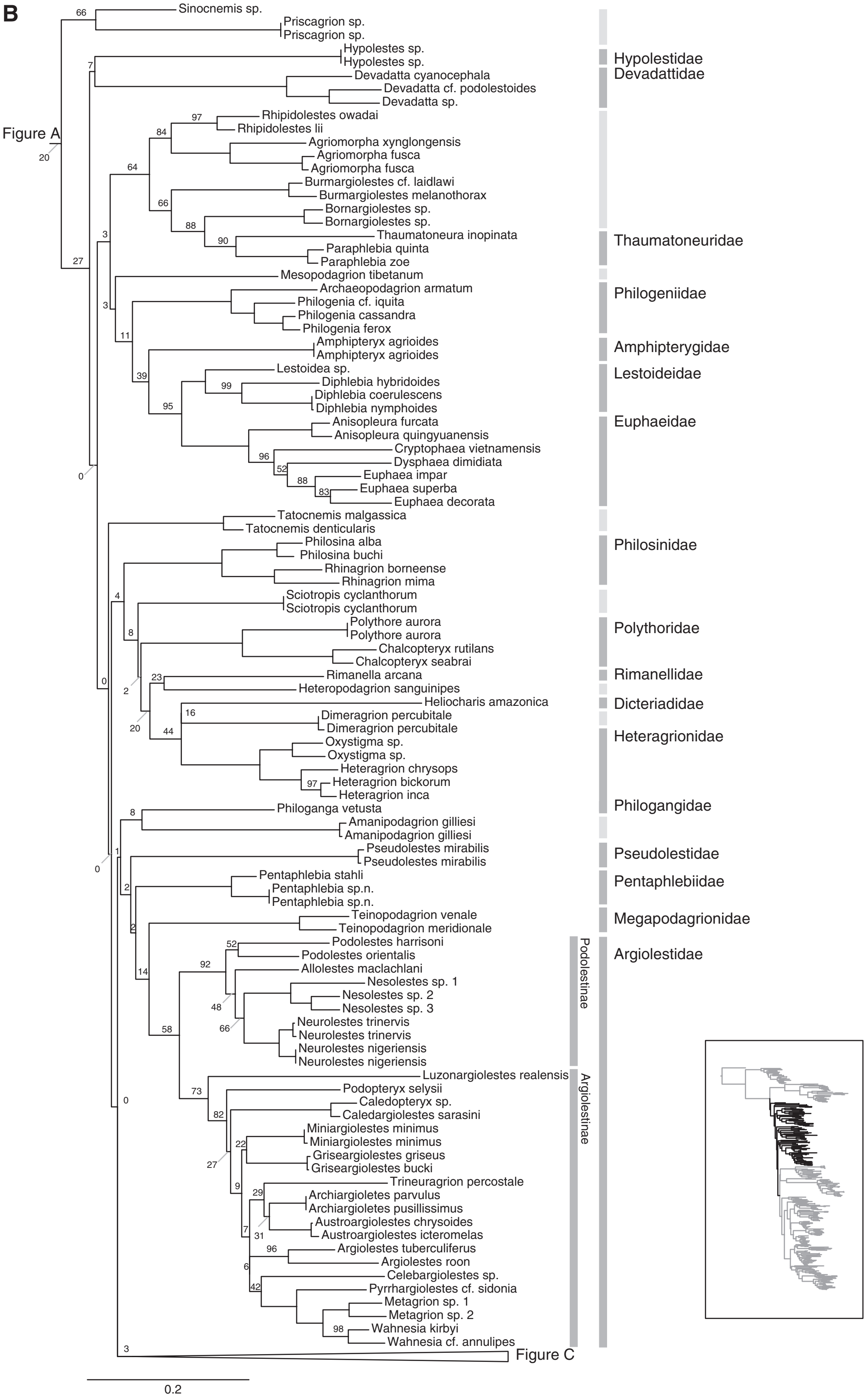
Fig. 3. Phylogenetic reconstruction for 356 specimens from the combined maximum likelihood analysis of 28S and 16S. Bootstrap values are shown only if below 100. Species names and classification as proposed are shown. (a) Lestoidea and Platystictoidea; (b, c) various groups; (d) Platycnemididae; (e) Coenagrionidae.

Family Isostictidae

All analyses confirmed that Isostictidae is monophyletic, although its position is problematic and it may not belong in Coenagrionoidea (cf. Bybee *et al.*, 2008; Carle *et al.*, 2008). The family incorporates less than 50 damselfly species confined to Australia, New Guinea, New Caledonia and neighbouring islands. Larvae have unique gills that are strongly constricted medially and somewhat swollen basally in most genera. Adults are peculiar with laterally compressed heads, recalling some Coenagrionidae such as *Amphicnemis*, *Ceriagrion* and *Neoneura*, with wide and deep labial clefts, and have rather forcipate and often toothed or serrate cerci, lack bright colours and are generally very slender.

Family Platycnemididae

Incorporating Disparoneuridae, this family includes over 400 species confined to the Old World, mostly to tropical streams and rivers. Despite being long recognized as a family and genetically well defined, no clear morphological apomorphies are known, although the species always lack spines on the genital ligula shaft (Pessacq, 2008; Kalkman *et al.*, 2010), while these are present in at least 53% of 103 examined coenagrionid genera. Adults often have laterally expanded heads (with usually shallow labial cleft and no trace of postfrontal suture) and tibiae with dense long spines (Rehn, 2003; Carle *et al.*, 2008). A consistently recovered clade comprised the small Oriental genus *Onychargia* and the Madagascan *Paracnemis*: we consider this as the subfamily Onychargiinae **subfam.n.** It was the sister group of remaining Platycnemididae in ML 28S + 16S/28S + 16S + COI, but of the combined African and Papuan clades (see later) in BI 28S + 16S/28S + 16S + COI. *Onychargia* was placed previously in Coenagrionidae, but its spineless genital ligula, long leg spines, markings (most notably the transverse pale band across vertex) and cerci with long internal tooth (concealed in tenth tergite) fit Platycnemididae better. The two genera have quite similar markings and share notably short cerci, as well as their swampy habitats



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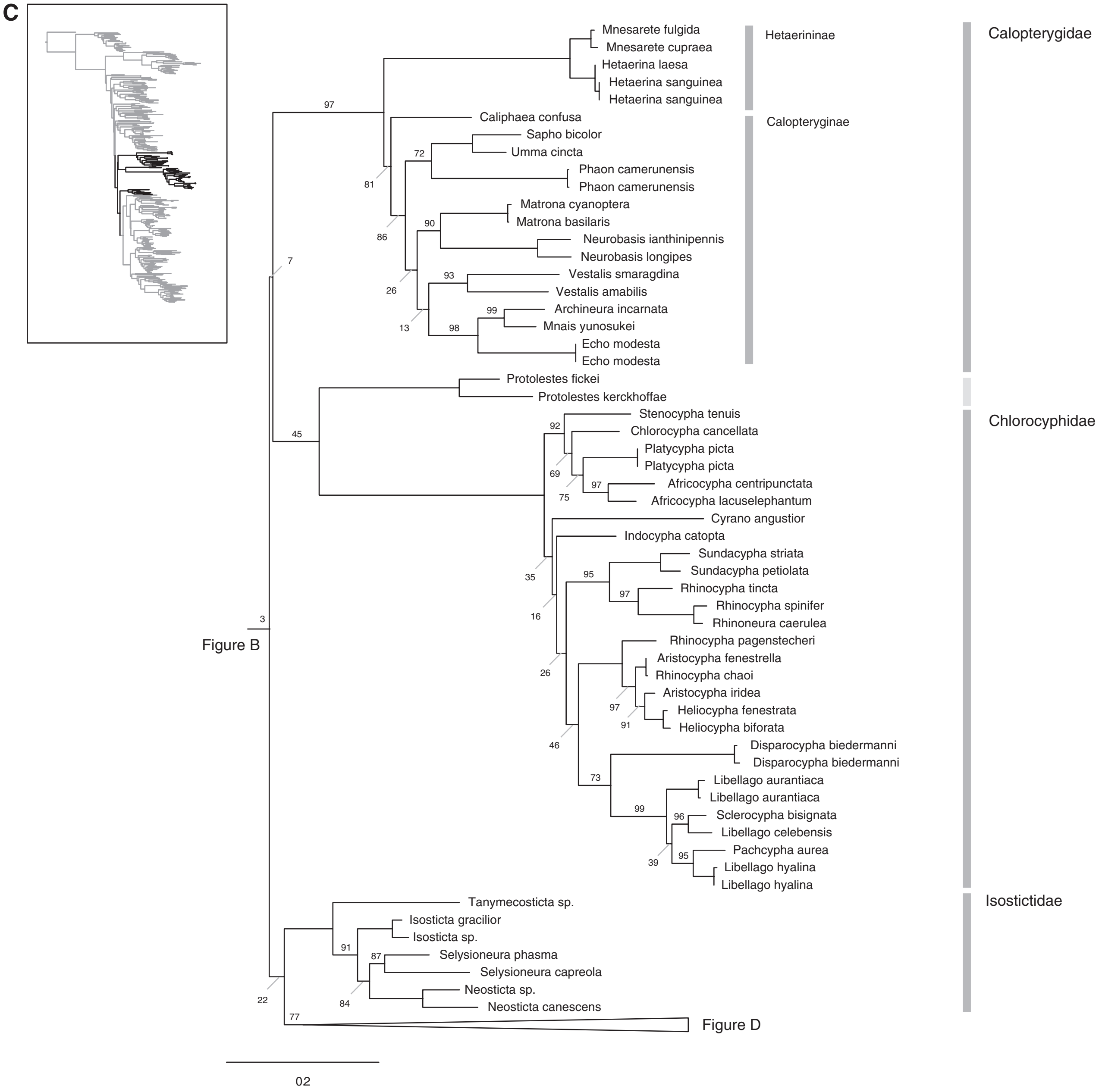

Fig. 3. Continued.

(K. Schütte, *in litt*.), which is unusual for the family. *Paracnemis* is monotypic, although '*Metacnemis*' *secundaris* Aguesse (known only from the holotype from Madagascar) is unlike that South African genus and closer to *Paracnemis*, most notably by markings, and is placed there until its rediscovery allows a better assessment (Table S4).

Another clade represents almost 30 species restricted to tropical mainland Africa (*Allocnemis*, *Mesocnemis*, *Metacnemis*, *Stenocnemis*) plus the endemic monotypic genus from adjacent Arabia *Arabicnemis*, which we consider as the subfamily Allocnemidinae **subfam.n.** Although this group is well defined geographically, their morphology is heterogeneous, the robust *Mesocnemis* and *Metacnemis* having been previously associated with 'argiine' Coenagrionidae. Distinguished only by the relative length of the anal vein, the genera *Allocnemis*, *Chlorocnemis* Selys and *Isomecocnemis* Cowley (the latter two were formerly in Protoneuridae for this reason) are intermixed and all species should be treated under the first name (Table S4). *Metacnemis* should be restricted to *M. valida* (Hagen in Selys), as both species added to that genus later appear not to be related (see discussion both earlier and later in this paper). This African clade is the sister group of

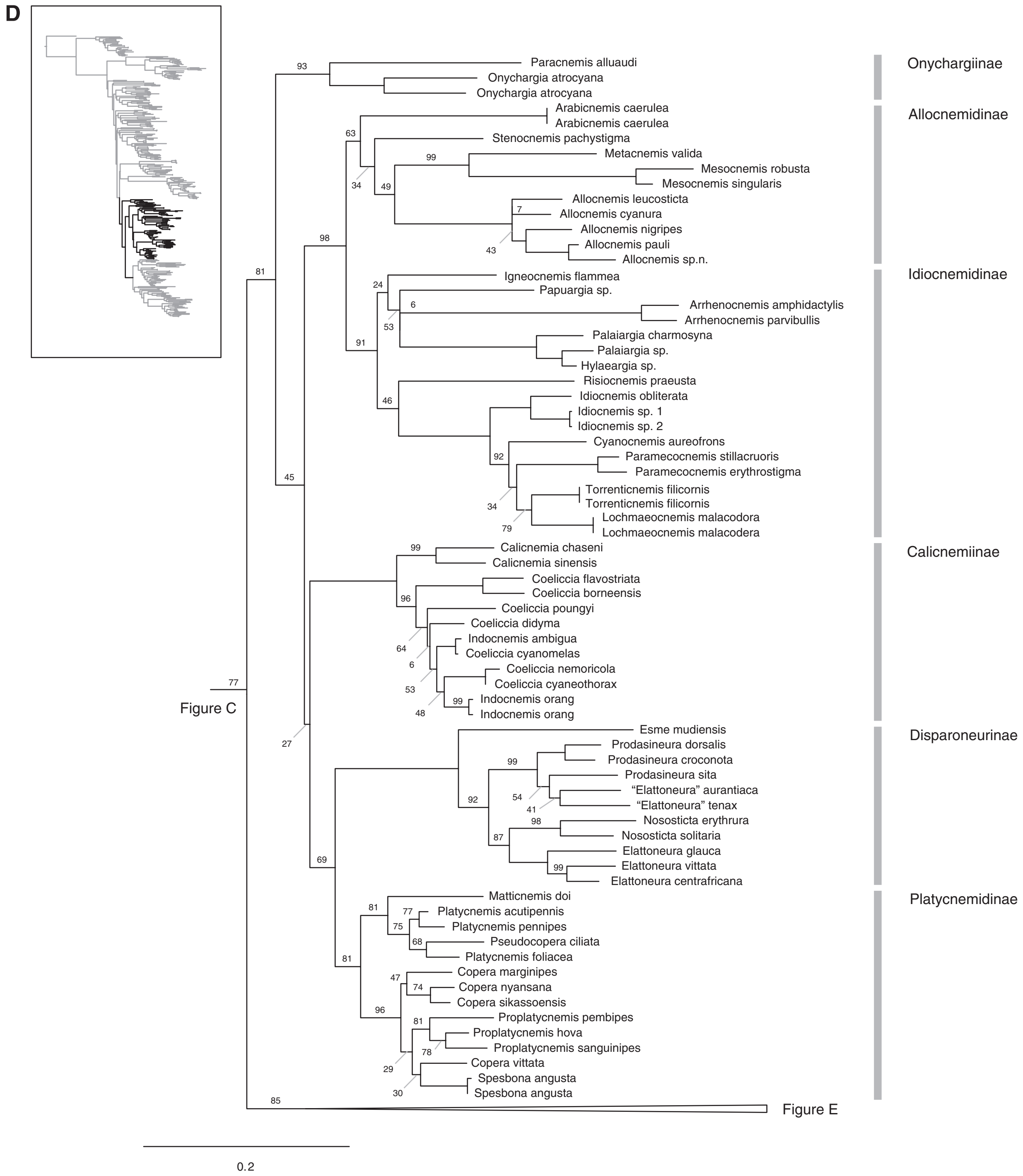

Fig. 3. Continued.

one of about 100 platycnemidid species occurring east of Huxley's Line. The studied New Guinean genera with crenulated wingtip margins (*Cyanocnemis*, *Idiocnemis*, *Lochmaeocnemis*, *Paramecocnemis*, *Torrenticnemis*) form a well-supported monophyletic subgroup. Based on this and other morphology, *Rhyacocnemis* from New Guinea and *Lieftinckia* and *Salomocnemis* from the Solomon Islands belong here too (Gassmann, 2005). This subfamily, to be called Idiocnemidinae **subfam.n.**, also includes New Guinean genera with absent or reduced wingtip crenulation: *Arrhenocnemis* was placed previously in Megapodagrionidae but shown to belong here by Gassmann (2005) and Orr & Kalkman (2010). *Palaiargia* and

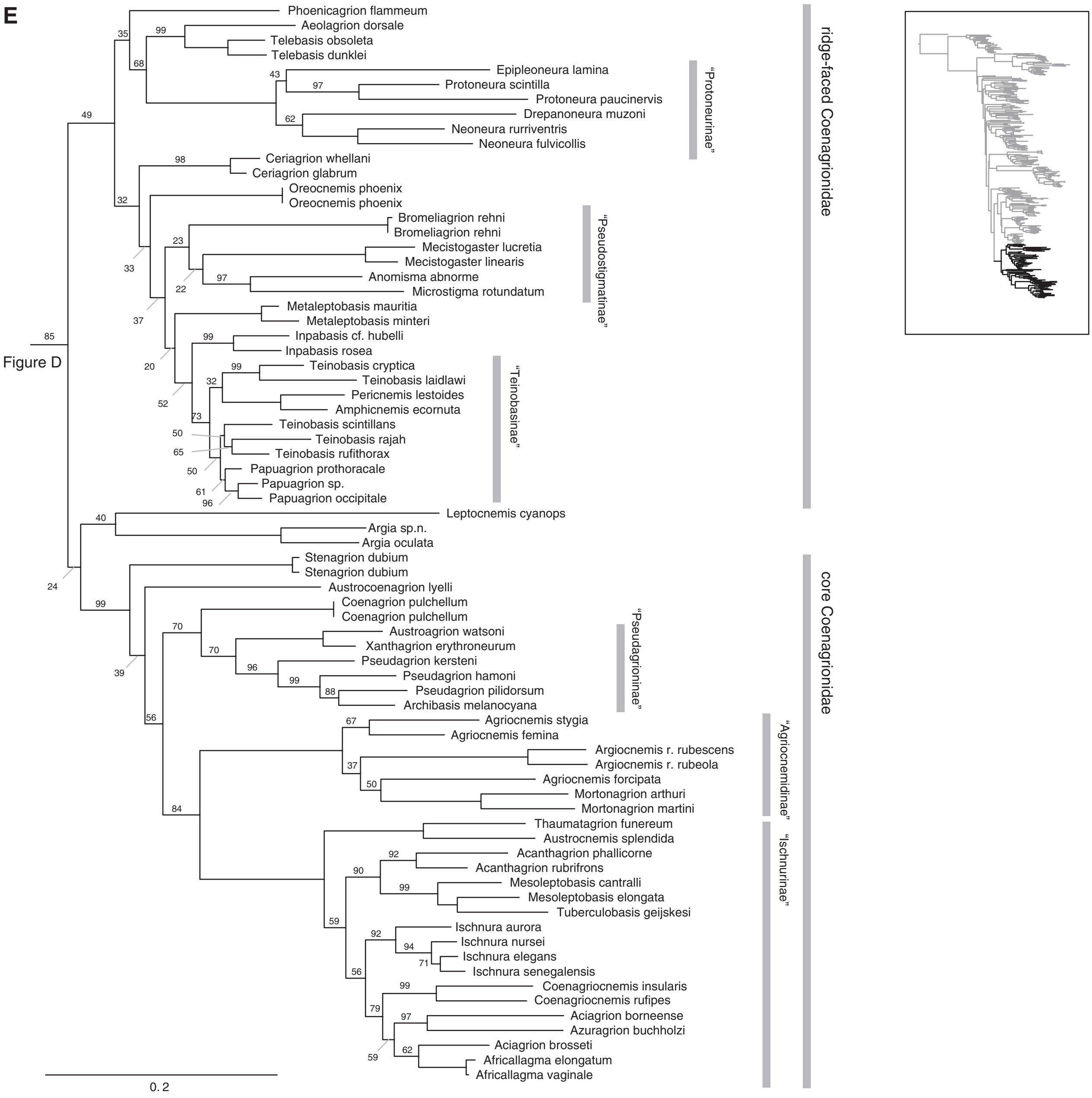

Fig. 3. Continued.

Papuargia (as well as presumably *Archboldargia*) were considered previously as 'argiine' Coenagrionidae, based on their venation and lacking the lateral expansion of the head (Lieftinck, 1949). *Hylaeargia* was found to fall within *Palaiargia* although the male appendages are rather different; better taxon sampling is needed before a decision can be made on its status. The Philippine genus *Risiocnemis* was recovered here consistently. The positions of the morphologically well-defined subgenera (cf. Gassmann & Hämäläinen, 2002) varied by analysis, but they were never recovered as sister groups and this warrants recognizing *Igneocnemis* as a genus (Table S4). The gills of *Hylaeargia*, *Lieftinckia* and *Palaiargia* larvae form a unique three-dimensional ruff (Lieftinck, 1957; Corbet, 1999). Whether this is an apomorphy of Idiocnemidinae is unclear, as no other larvae have been described.

Calicnemiinae is limited to the Oriental genera *Calicnemia*, *Coeliccia* and *Indocnemis* in our analyses, which together have about 85 species. Within the family, these genera are notable for possessing distinct elongate pale spots on the posterior border of the postocular lobes (Gassmann, 2005). *Indocnemis* makes *Coeliccia* paraphyletic. That genus probably requires further subdivision and more species may be placed in

Indocnemis, so synonymizing it now would be confusing. Moreover, the sister group of remaining *Coeliccia*, Dow's (2010) *borneensis* group from Borneo, shares some characters with *Coeliccia lieftincki* Laidlaw from Java and *Coeliccia* species from the Philippine islands Mindoro, Mindanao and Palawan. The Philippine species are especially close to the Palawan genus *Asthenocnemis*, 16S data groups *Coeliccia dinoceras* from Mindanao firmly with the *borneensis* group. *Asthenocnemis* may make *Coeliccia* paraphyletic and major generic reclassification of the subfamily is needed.

Disparoneurinae includes distinct African, Asian and Papua-Australian clades (representing over 25, 45 and 55 species, respectively) that together form the largest platycnemidid radiation. This includes all platycnemidids with a largely or entirely reduced anal vein, except some *Allocnemis*, and typically rather short and high male appendages. The Papua-Australian clade conforms to the genus *Nososticta*, but species currently assigned to *Elattoneura* and *Prodasineura* are mixed in both the African and Asian clades. The slightly less reduced anal vein that supposedly separates *Elattoneura* from *Prodasineura* is obviously not reliable. Nonetheless, most species can be assigned to the correct continent by their combination of coloration (e.g. blue is frequent in Asia, but absent in Africa), venation (complete reduction anal vein only in Asia) and paraproct shape, the distal border of which is rather vertical in Africa, but tends to slope in Asia (Dijkstra, 2007). As the type-species of *Elattoneura* is African and that of *Prodasineura* is Asian, all African species should be placed in *Elattoneura* (Table S4). The situation in Asia is more complicated, as the species now placed in *Elattoneura* may not be closely related to the type of *Prodasineura* and the entire group requires revision. The Arabian *Arabineura* and Indian *Disparoneura* presumably belong to this clade too, as both have appendages nearest *Prodasineura*. Ten 'caconeurine' species are endemic to southern India, but although morphologically very distinctive as a group, the four genera (*Caconeura*, *Esme*, *Melanoneura*, *Phylloneura*) are almost identical. We retrieved *Esme* as the sister group of all other Disparoneurinae sampled, but Dumont *et al.* (2010) retrieved *Caconeura* within *Prodasineura*. The latter study had a narrow taxon-sampling, and while Bybee *et al.* (2008) confirmed that *Phylloneura* is disparoneurine, they only had *Nososticta* to compare. As with the Allocnemidinae and Idiocnemidinae, the African *Elattoneura* and Papua-Australian *Nososticta* were retrieved mostly as sister groups of each other, rather than of the Oriental *Prodasineura*, a pattern worthy of closer investigation and supported by the generally vertical profile of their paraprocts.

The subfamily Platycnemidinae as previously known, defined by feather-like tibiae (expanded, coloured) in males, is a monophyletic assemblage of nearly 40 species, including the family's only notable Malagasy and Palaearctic radiations. It consists of two well-supported clades, both of which contain species presently classified in *Platycnemis* and *Copera*. The clade with the generotypic *Copera marginipes* (Rambur), which we recognize as the tribe Coperini **trib.n.**, has a unique larval character (gills with frilled borders) and adult males often have barred eyes, colourful legs (white, yellow, orange, red, blue) and an internal tooth on the cerci. Aside from the true Oriental *Copera* species, it includes all Afrotropical species until now placed in *Platycnemis*. The name *Proplatycnemis* is available for the Malagasy species (Table S4), which have a distinctive genital ligula shape; *Proplatycnemis pembipes* (Dijkstra *et al.*) from the Tanzanian island Pemba belongs here (Dijkstra *et al.*, 2007). The continental African species group with the morphologically similar true *Copera*, and are best transferred accordingly (Table S4). The South African genus *Spesbona* is the sister group of *Proplatycnemis*; its sole species *Spesbona angusta* (Selys) was previously placed in *Metacnemis* but is distantly related to the type of the genus, *M. valida* (Dijkstra, 2013). The species' markings, genital ligula and appendages are close to those of *Proplatycnemis*. Its tibiae, however, are black and not widened, which prevented an earlier association with its true relatives. This and the bulging postocular lobes, pointed pterostigmata and deep blue colour are unique within the subfamily (Dijkstra, 2013). The tribe Platycnemidini has smooth-bordered gills and males always have white legs and no cercal tooth. It consists of the Palaearctic *Platycnemis* species (including the generotype) and the black-and-white species placed formerly in *Copera*, which extend from Japan to Java. The genus *Platycnemis* should be limited to the Palaearctic species, and for its probable sister group of 'false' *Copera* species the name *Pseudocopera* is available (Table S4). The recently described *Matticnemis doi* (Hämäläinen) is the sister group of these two genera (Hämäläinen, 2012; Dijkstra, 2013).

Family Coenagrionidae

Encompassing almost 1300 species, remaining Coenagrionoidea represents the greatest damselfly radiation. Earlier subdivisions are generally unsupported by morphology (O'Grady & May, 2003), but molecular studies are revealing some notable groups. We sampled 45 of 115 genera and, and with data published for another 17, these groups are becoming increasingly well supported. As detailed in the following, two major groups can be distinguished, both of which are cosmopolitan and contain over 600 species, but only the group including *Coenagrion* is unquestionably monophyletic. This group is generally defined by well-developed postocular spots and dominates in the Holarctic and Palaeotropics, representing over 80% of species diversity in the Palaearctic and Afrotropics and just 30% (ischnurines only) in the Neotropics. The remainder rarely possesses postocular spots, but is characterized by a ridged frons in most species, although the large genus *Argia* is the notable exception for both characters. This half is richest in the Neotropics with 70% of species, including Pseudostigmatidae and true Protoneuridae. It also has a notable Palaeotropical presence, e.g. teinobasines and *Ceriagrion*, representing over 40% of species in the Oriental, Australian and Pacific regions.

We treat all this diversity within a massively expanded Coenagrionidae. Such an inclusive approach serves stability, although given the size of this group (about 30% larger than any other odonate family), applying the family rank to more manageable units might seem appropriate when better phylogenetic support is obtained. The oldest name available for the non-core genera is Pseudostigmatidae Kirby 1890, applied for over 120 years to just a score of peculiar species. It seems counterintuitive to apply that name to about 30 times as many generally 'ordinary' damselflies. Given its long history in a polyphyletic sense, using Protoneuridae Yakobson & Bianchi 1905 for almost 500 species never known by that name may also cause confusion. Both 'families' as currently known are apophyletic groups (i.e. their distinctness resulted in an exaggerated taxonomic rank; see O'Grady & May, 2003), defined by the extreme expansion and reduction of their venation, respectively. Although taxonomic names are governed by rules, they are applied by consensus. We expect these names will continue to signify only these damselflies for most users, even if only in a colloquial sense, as they have for over a century. The family-group name Teinobasidae Tillyard 1917 has been applied for most of the former Coenagrionidae in the ridge-faced group (De Marmels, 2007), yet is sufficiently unfamiliar to most users to be neutral. *Teinobasis* and other 'Teinobasinae' are characterized by all features defining the group. We believe that if the monophyly of the whole group is resolved and a name for it is required, this one would be carried best by the odonatological community. Prioritizing it would, however, require a ruling of the International Commission on Zoological Nomenclature. The data suggest that Agriocnemidinae, Ischnurinae and Pseudagrioninae constitute distinct groups within core Coenagrionidae, as may Argiinae, Protoneurinae, Pseudostigmatinae and Teinobasinae among the remainder. Thus a taxonomic solution in which most familiar names can be conserved as subfamilies is conceivable and therefore perhaps preferable. However, sampling and support are still insufficient for a comprehensive subdivision and thus, for now, we apply these names only in a vernacular sense.

Core Coenagrionidae

The monophyly of this group representing over 650 species is well supported in our and all previous molecular analyses (Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010). Three well-supported clades conforming to previously named subfamilies are recovered within it, which together appear to contain almost nine-tenths of the species. The largest clade represents just over half and conforms to the cosmopolitan Ischnurinae, including all genera that possess a vulvar spine in the female, although it is occasionally absent: *Acanthagrion*, *Aciagrion*, *Africallagma*, *Austrocnemis*, *Azuragrion*, *Coenagriocnemis*, *Dolonagrion* (based on 28S only), *Ischnura*, *Mesoleptobasis* (with *Tuberculobasis* within it) and *Xiphiagrion* (16S only). The formerly 'platycnemidid' *Thaumatagrion* is closely related to *Austrocnemis*, also a dark-bronzy long-legged Papua-Australian genus, which is supported by its spiny genital ligula (Gassmann, 2005). Hovmöller (2006) previously investigated the group's monophyly, adding *Amphiallagma*, *Cyanallagma*, *Homeoura* and *Oxyagrion*, while *Amphiagrion*, *Enallagma*, *Hesperagrion* and *Proischnura* belong here as well (Carle *et al.*, 2008; Dumont *et al.*, 2010), all possessing the vulvar spine. Based on this character and/or similarity to other ischnurines, the genera *Acanthallagma*, *Andinagrion*, *Argentagrion*, *Austroallagma*, *Denticulobasis* (denticulate vulvar plate is assumed homologous), *Enacantha*, *Leptobasis*, *Leucobasis*, *Mesamphiagrion*, *Millotagrion*, *Oreagrion*, *Oreiallagma*, *Oxyallagma*, *Pinheyagrion*, *Protallagma*, *Tigriagrion* and *Zoniagrion* can be added. *Amorphostigma* Fraser, *Boninagrion* Asahina, *Rhodischnura* Laidlaw and probably *Pacificagrion* must be subsumed into *Ischnura* (O'Grady & May, 2003; Hovmöller, 2006; Karube *et al.*, 2012). *Anisagrion*, *Apanisagrion* and *Calvertagrion* lack the vulvar spine, but form a largely Central American, probably monophyletic, group with the spined *Hesperagrion* (De Marmels, 2002a).

The clade incorporating *Agriocnemis*, *Argiocnemis* and *Mortonagrion* conforms to the Palaeotropical Agriocnemidinae of about 55 species. The first appears paraphyletic, but all three genera require redefinition (Dow, 2011). It is the only coenagrionid subfamily supported by the morphological analysis of O'Grady & May (2003), the arculus being shifted considerably distal to the second antenodal cross-vein. The clade of *Archibasis*, *Austroagrion*, *Pseudagrion* and *Xanthagrion* conforms to the mostly Palaeotropical Pseudagrioninae, including almost 200 species. The Asian *Pseudagrion* species sampled was closer to the Asian *Archibasis* than to the two African species studied. As the type of *Pseudagrion* is African, this indicates that the Asian taxa may have to be reclassified. Earlier results suggest that the Palaearctic *Erythromma* and Oriental *Paracercion* and *Stenagrion* are related (Carle *et al.*, 2008; Dumont *et al.*, 2010), as may be the Antipodean *Caliagrion* and *Xanthocnemis*, but we found no clear relationship for *Stenagrion*. Also the Australian *Austrocoenagrion* and Holarctic *Coenagrion* were not recovered with any specific subgroup, although their genetic distinctiveness confirms their separation as genera (Dijkstra & Kalkman, 2012). Jordan *et al.* (2003) could not resolve the origin of the Hawaiian *Megalagrion* radiation; Dumont *et al.* (2010) recovered it between agriocnemidines and ischnurines.

An apomorphy of all genera discussed earlier is the usual presence of well-developed postocular spots (cf. De Marmels, 1984). Although variable in their extent and development, the spots are typically positioned centrally on the postocular lobes and enclosed by dark coloration. In *Austrocnemis*, *Thaumatagrion*, most *Amphiagrion* and occasional species of other genera (e.g. *Erythromma*), the head is so dark to have obliterated them, while in *Andinagrion* and *Oxyallagma*, the head and thorax are uniformly reddish, and in *Tigriagrion* the spots are partially obliterated by a dark pattern. Postocular spots are absent in 89% of the remaining coenagrionoid genera, discussed later. Where markings occur, these usually differ in their shape and position, e.g. a pale occipital bar may expand laterally and/or posteriorly onto the postocular lobes. None of the core Coenagrionidae members have an angularly ridged frons, which is present in 75% of remaining genera. Although extremely plastic, the male appendages of core Coenagrionidae often show typical features, with notably swollen paraproct bases and terminally branched cerci, both branches often being hooked and bearing a soft pad between them. The distal segment of the genital ligula often has a well-developed pair of median lobes. The discussed characters suggest that *Himalagrion* and *Neoerythromma* are core Coenagrionidae too.

Remaining Coenagrionidae

The relationships of the remaining genera are much less resolved than for the core Coenagrionidae. Generally we retrieved them as the monophyletic sister group of core Coenagrionidae, but with weak support and different groups (sometimes combined) excluded in certain analyses: *Argia* and *Leptocnemis* in ML 28S + 16S, *Argia* and Protoneuridae in BI 28S + 16S + COI, and *Argia* only in ML 28S + 16S + COI, probably because COI was unavailable for *Leptocnemis*. *Argia* and *Leptocnemis* together were the sister group of all other Coenagrionidae in BI 28S + 16S. Carle *et al.* (2008) retrieved them as monophyletic, including *Argia* and the protoneurid *Neoneura*, although their taxon sampling was limited and excluded *Leptocnemis*. Separate ML 28S + 16S of a wider coenagrionid sampling (outgroup: *Platycnemis*) recovered all non-core genera together, except for *Leptocnemis*, which was the sister group of all other Coenagrionidae. Although the entire group may yet prove to be monophyletic, further analysis is needed, especially of the monotypic genus *Leptocnemis* from the Seychelles and the American genus *Argia*. The latter is the only remaining genus of Argiinae, now that all Old World 'argiines' (*Mesocnemis*, *Onychargia*, *Palaiargia* and relatives) have been confirmed as Platycnemididae. It is probably the largest odonate genus, with at least 130 species, and differs from most taxa discussed in the following (but is similar to core coenagrionids) in having a rounded frons and prominent postocular spots (Garrison *et al.*, 2010). *Leptocnemis* was regarded as platycnemidid but lacks features of that family, possessing a spiny genital ligula (Gassmann, 2005). It also has a rounded frons and peculiar postocular spots shifted towards the vertex.

As in core Coenagrionidae, three notable clades are apparent in the remaining assemblage, although we estimate that together these represent less than half of over 600 species involved. All investigated genera of true Protoneuridae form a well-supported clade (*Amazoneura* based on 28S only, *Drepanoneura*, *Epipleoneura*, *Neoneura*, *Protoneura*, *Psaironeura*) in all analyses. Its position varied, being recovered with reasonable support with *Aeolagrion* and *Telebasis* within the complex of remaining genera in BI/ML 28S + 16S, but forming the sister group of all those genera in ML 28S + 16S + COI or falling outside the complex together with *Argia* in BI 28S + 16S + COI with only moderate support. However, as discussed in the following, 'protoneurid' morphology is very consistent with non-core Coenagrionidae and its position well inside that family is certain.

Earlier molecular studies focused exclusively on the charismatic but small 'family' Pseudostigmatidae (Groeneveld *et al.*, 2007; Ingley *et al.*, 2012). Adults are substantially larger than other damselflies, have highly modified venation and pterostigmata (from which their name derives), a genital ligula with distal segment modified to form a very long single flagellum, feed mostly on orb-weaving spiders and their prey, and breed in phytotelmata. We found only moderate support for the group's monophyly. It was represented by *Anomisma*, *Mecistogaster* and *Microstigma*, but also includes *Megaloprepus*, *Pseudostigma* and possibly the eastern African *Coryphagrion*, which would be the only non-Neotropical representative and lacks the flagellum. Our study and earlier molecular work suggest that the smaller-bodied American genera *Bromeliagrion*, *Diceratobasis* and *Leptagrion* are close or should be included too (Groeneveld *et al.*, 2007; Carle *et al.*, 2008; Ingley *et al.*, 2012). The latter genera lack modified wings, although they are still comparatively large-bodied and also breed in phytotelmata. This reproductive habitat is not unique to the group, however, also occurring occasionally in the third well-supported clade, represented in our dataset by the (principally) Malesian genera *Amphicnemis*, *Papuagrion*, *Pericnemis* and *Teinobasis*. De Marmels (2007) considered these four genera as Teinobasinae (subfamily of Coenagrionidae) with a cercal spur, an articulated ventral process at the appendage base that is typically directed posteriorly.

De Marmels (2007) also treated *Bromeliagrion*, *Chromagrion*, *Melanesobasis*, *Nehalennia*, *Plagulibasis*, *Pyrrhosoma* and *Tepuibasis* as Teinobasinae with a cercal spur, to which *Aceratobasis* and *Diceratobasis* can be added (Garrison *et al.*, 2010). Such a structure is not found in any core Coenagrionidae, but a potentially homologous (but seldom articulated) basal process occurs in about half the remaining genera, including the 'pseudostigmatid' *Microstigma* (near which the spurred *Bromeliagrion* and *Diceratobasis* have been recovered) and many 'protoneurids', e.g. *Epipleoneura*, *Forcepsioneura*, *Idioneura*, *Microneura*, *Neoneura*, *Peristicta*, *Phasmoneura*, *Protoneura* and *Psaironeura*. Given its plasticity, we doubt this structure (also when articulated) defines a monophyletic group and hence no strict delimitation of the subgroup nearest *Teinobasis* can presently be made. We suspect it is an Indo-Pacific complex, including also *Melanesobasis* and *Plagulibasis*, which have a cercal spur, and *Nesobasis* and *Vanuatubasis*, which do not, but it is apparent from the paraphyly of *Teinobasis* and the recent separation of *Luzonobasis*, *Pandanobasis* and *Sangabasis* from Philippine *Amphicnemis* (Villanueva, 2012) that generic revision is needed. The precise positions of genera listed by De Marmels (2007) as Teinobasinae lacking the spur (*Aeolagrion*, *Ceriagrion*, *Inpabasis*, *Metaleptobasis*, *Phoenicagrion* and *Telebasis*; only *Hylaeonympha*, *Leptagrion* and *Minagrion* were unavailable for our study) varied by analysis, but were always recovered near the 'protoneurid', 'pseudostigmatid' and 'teinobasine' clades (cf. Bybee *et al.*, 2008; Carle *et al.*, 2008; Dumont *et al.*, 2010), as was the monotypic genus *Oreocnemis* from Mt Mulanje in Malawi. Although described in Platycnemididae, the last lacks all features associated with that family and possesses a spiny genital ligula. Carle *et al.* (2008) and Dumont *et al.* (2010) retrieved *Chromagrion*, *Nehalennia* and *Pyrrhosoma* here as well (cf. De Marmels, 2007).

Aside from the general lack of postocular spots and the frequently present cercal spur, 83% of the non-core coenagrionid genera for which there is molecular evidence possess an angularly ridged frons. Other ridge-faced coenagrionids are *Aceratobasis*, *Angelagrion*, *Antiagrion*, *Leptagrion*, *Melanesobasis* and *Minagrion*. The ridge is variably present in species of *Tepuibasis*, as in the sampled genus *Phoenicagrion*. Of the Protoneuridae not sampled only *Junix*, *Phasmoneura* and *Proneura* lack the ridge, although *Amazoneura* and some *Protoneura* species also lack it. Another potentially informative character is the female's deeply or entirely divided 10th tergite (O'Grady & May, 2003; Garrison *et al.*, 2010) in *Aeolagrion*, *Amphicnemis*, *Antiagrion*, *Argia*, *Ceriagrion*, *Chromagrion*, *Hylaeonympha*, *Leptocnemis*, *Minagrion*, *Nehalennia*, *Papuagrion*, *Pyrrhosoma*, *Teinobasis* and *Telebasis*, although it sometimes occurs in the core coenagrionid *Pseudagrion*. Extensive metallic coloration in genera as disparate as *Amphicnemis*, *Epipleoneura* and *Nehalennia*, as well as a prominently modified epiproct, also appears to occur in this group but not in core Coenagrionidae. Although *Schistolobos* and *Telagrion* have a rounded frons and somewhat spot-like postocular markings, their appendages and setose genital ligula suggest a relationship to *Aceratobasis*. The metallic coloration and genital ligula of *Tukanobasis* imply it also belongs near the ridge-faced genera despite a rounded frons. The mysterious monotypic genera *Argiagrion* Selys and *Moroagrion* Needham & Gyger also have features of the group, but have been found to be synonyms of *Leptagrion* and *Pyrrhosoma*, respectively (Dijkstra & Kalkman, 2013).

Superfamily 'Calopterygoidea'

With the superfamilies Lestoidea, Platystictoidea and Coenagrionoidea reasonably defined, the position of the remaining 27% of damselfly diversity (almost 800 species) is left uncertain. Thus far, the superfamily name 'Calopterygoidea' and the more colloquial 'Caloptera' have been used for about three-fifths of this diverse assemblage. Rehn (2003) limited it to the most densely veined families Calopterygidae, Chlorocyphidae, Dicteriadidae, Euphaeidae and Polythoridae, whereas Bechly (1996) included Amphipterygidae and the genera *Diphlebia*, *Philoganga*, *Pseudolestes* and *Thaumatoneura* as well. This leaves only the genus *Lestoidea* (not to be confused with the unrelated superfamily) and heterogeneous Megapodagrionidae 'in limbo'. There is no convincing evidence for the combined monophyly of all (or any combination) of these groups, although Bybee *et al.* (2008) found weak support in some analyses, as did Carle *et al.* (2008) if Isostictidae was included, although that was also unstable. 'Calopterygoidea', by almost any definition, may ultimately prove paraphyletic, requiring the creation of further superfamilies. In the following sections we discuss all well-supported groups within this complex.

Family Calopterygidae

With almost a quarter of the species, Calopterygidae is the largest and most widespread family in the complex. Despite their distinctive appearance, good morphological apomorphies are unclear, although they probably exist in the shape of the larval prementum and antennae. Our results are broadly congruent with those of Dumont *et al.* (2005, 2007, 2010) based on a different set of (exclusively nuclear) markers. The strictly American Hetaerininae (including *Mnesarete* and presumably *Bryoplathanon* and *Ormenophlebia*; see Garrison *et al.*, 2010), with about a third of the species, is confirmed as the sister group of the remaining Calopterygidae. Dumont *et al.* (2010) prefer to treat this group as a family, but as Calopterygidae is monophyletic (cf. Rehn, 2003; Bybee *et al.*, 2008) stability is served by retaining the present ranks and separating the distinct clades within Calopteryginae as tribes. The distinctness of ranks is subjective: classifying all lineages as one family best communicates their common ancestry. Three tribes are largely Oriental: Vestalini (*Vestalaria*, *Vestalis*), Calopterygini (*Atrocalopteryx*, *Matrona*, *Matronoides*, *Neurobasis*, with only *Calopteryx* extending across the Holarctic) and Mnaisini (*Archineura*, *Echo*, *Mnais*, *Psolodesmus*). Dumont *et al.* (2010) recovered the last clade but retained the genera in Calopterygini. However, Vestalini variably form the sister group of Calopterygini s.s. or Mnaisini in our and Dumont's analyses, and Mnaisini can thus best be separated. Saphoini is strictly Afrotropical (*Phaon*, *Sapho*, *Umma*). The distinctive Oriental genera *Caliphaea* and *Noguchiphaea* each represents a monogeneric tribe, as does the only South American calopterygine, *Iridictyon* (Dumont *et al.*, 2010).

Family Chlorocyphidae

The more than 140 Palaeotropical species are unique by the adult's expanded eyes and clypeus, short abdomen, and the larva's spike-like paraprocts and reduced epiproct (Bechly, 1996). Our results confirm their monophyly (cf. Rehn, 2003; Bybee *et al.*, 2008; Dumont *et al.*, 2010) and show reasonable congruence with Bechly's (1996) classification. Subfamilies could be recognized, but because two of the available names (Disparocyphinae and Libellagininae) are older than the family name in prevailing use, we refrain from applying them formally until the nomenclatory conundrum is resolved (see Dijkstra *et al.*, 2013). Four Afrotropical genera form the monophyletic 'Chlorocyphinae'. The analyses indicate that '*C*.' *centripunctata* Gambles, which also shares details of markings and extended paraprocts with *A. lacuselephantum* (Karsch), should be transferred to *Africocypha* (Table S4). *Stenocypha* is the sister group of the remaining African genera and formerly made up the *gracilis* group of *Chlorocypha*, making that genus paraphyletic (Dijkstra, 2013). Only BI/ML 28S and ML 28S + 16S suggest that the clear-winged Africans are the sister group of the entire Asian radiation, in which marked wings predominate. Two consistently well-supported clades include *Rhinocypha* species and would constitute Bechly's (1996) 'Rhinocyphinae', but their combined monophyly was not recovered. One clade is predominantly continental and also includes *Aristocypha* and *Heliocypha* (often treated as subgenera of *Rhinocypha*) and all species with a brightly coloured mid-dorsal wedge on the thorax and/or wing markings with clear fields within the dark pattern. The second clade is largely insular and includes the type species of *Rhinocypha*, *Rhinoneura* and *Sundacypha*. Major generic revision is required, including the probably related genera *Calocypha*, *Heterocypha* and *Paracypha*. 'Libellagininae' is well supported and its main constituent genus *Libellago* also consists of two clades differing in wing markings: those with dark tips (including *Sclerocypha* and presumably *Melanocypha* and *Watuwila*) and those without, including *Pachycypha*. Wing markings are thus unexpectedly informative about relationships within the group: the clear-winged genera *Cyrano* (Philippines) and *Indocypha* (south Asia), and the Sulawesi *Disparocypha*, with its narrow wings and a distally broadened pterostigmata, stand apart from the major Asian radiations in all analyses, probably representing monogeneric subfamilies.

Families Euphaeidae and Lestoideidae

All analyses recovered the Asian family Euphaeidae of almost 70 species as monophyletic with good support (cf. Rehn, 2003; Bybee *et al.*, 2008; Dumont *et al.*, 2010), and identified *Diphlebia* plus *Lestoidea* as its sister group (cf. Bybee *et al.*, 2008; Carle *et al.*, 2008). The most notable apomorphy of Euphaeidae is that the larvae possess lateral gills on the eighth abdominal segment as well as on the six preceding segments (Bechly, 1996). The close relation of the superficially dissimilar Australian genera *Diphlebia* and *Lestoidea* was suggested by Novelo-Gutiérrez (1995), based on their similar larvae and venation ground plan, although no shared apomorphies are known: the genera differ only in venation density, *Lestoidea* lacking numerous cross-veins and most of the anal vein. As family-group names are available, each of these distinctive genera could also be treated as a family. However, as genus- and family-group names that refer to the same group of species seem rather redundant, and distinctiveness is subjective, classifying these lineages together in the family Lestoideidae to communicate their common ancestry is preferred.

Family Polythoridae

Our limited sampling shows this Neotropical family to be monophyletic (cf. Rehn, 2003; Bybee *et al.*, 2008; Dumont *et al.*, 2010). The almost 60 species share several notable larval characters, such as lateral gills on the second to seventh abdominal segments, dorsal abdominal spines or knobs (shared with *Teinopodagrion* in Megapodagrionidae) and swollen gills with angular or finger-like projections (Garrison *et al.*, 2010). The apical projection of the genital ligula is also distinctive. The family has been considered close to the Euphaeidae, because the larvae share lateral abdominal gills (e.g. Bechly, 1996), but no support has been found in any molecular studies.

Family Megapodagrionidae

The greatest systematic challenge in Zygoptera is classifying the over 300 species currently or formerly associated with Amphipterygidae and Megapodagrionidae. Their heterogeneity has long been recognized, as is apparent from the fact that many family-group names reinstated below are over half a century old. Previous studies showed that so-called 'megapods' are not monophyletic, containing at least five or six lineages that are richest in tropical America, Madagascar, South-east Asia, New Guinea and Australia (Rehn, 2003; Bybee *et al.*, 2008; van Tol *et al.*, 2009; Dumont *et al.*, 2010; Kalkman *et al.*, 2010). Until now, however, no comparative phylogenetic data were available for the majority of genera. We obtained molecular data for 92% of the 51 genera involved, most of which are morphologically well defined (e.g. Garrison *et al.*, 2010; Kalkman & Theischinger, 2013), and the results indicate that Megapodagrionidae includes between eight and 15 distinct (potentially family-level) clades and Amphipterygidae includes four. No 16S data were available for the family's type genus, the monotypic Amazonian *Megapodagrion*. In BI/ML 28S it was the sister group of the Andean *Teinopodagrion*, represented by two species with complete sequences in our dataset. These two genera, together with the southern Brazilian *Allopodagrion*, were already recognized to be a monophyletic group by De Marmels (2001). In comparison to other formerly 'megapod' genera, both the adults and larvae have very long legs. The latter have long triquetral paraprocts and long antennae with an elongated first segment (De Marmels, 2001; Kalkman *et al.*, 2010; Neiss *et al.*, 2011; Fleck *et al.*, 2012). Fleck *et al.* (2012) noted a close resemblance between *Allopodagrion*, *Megapodagrion* and *Teinopodagrion* larvae and those of Calopterygidae and Dicteriadidae, but our dataset provides no support for a relationship with these groups. *Megapodagrion* and *Teinopodagrion* were not recovered close to any other 'megapods', and as they possess distinct morphology, Megapodagrionidae should be restricted to just these three genera.

Family Argiolestidae

Over 100 'megapod' species form a well-supported clade confined to the Old World tropics in all analyses. Separated as the family Argiolestidae, it comprises two subfamilies divided by Huxley's Line (Kalkman & Theischinger, 2013). This group includes all 'megapod' genera entirely lacking spines on the shaft of the genital ligula (Kalkman *et al.*, 2010) except for *Amanipodagrion* and *Protolestes*, which do not seem to be closely related (see later). They differ from all other Zygoptera by the larval gills forming a horizontal fan (Kalkman *et al.*, 2010). The only other damselflies described as having such gills are the Madagascan *Protolestes* and South American *Dimeragrion*. Our analyses implied these are not related to Argiolestidae, which is supported by other details of the larval gills and adult morphology (Tennessen, 2010; Pérez-Gutiérrez & Montes-Fontalvo, 2011; Kalkman & Theischinger, 2013). Another apomorphy is a central ridge of tubercles on the male cerci, which is present in all genera and absent only secondarily in a few species. It seems absent from all other Zygoptera, although *Heteragrion*, *Oxystigma* and *Heteropodagrion* possess something similar. The subfamily Argiolestinae makes up almost three-quarters of the family's species diversity, restricted largely to Australia, New Guinea and New Caledonia, with some isolated species in Sulawesi and the Philippines. Podolestinae includes *Podolestes* in South-east Asia, *Allolestes* in the Seychelles, *Nesolestes* in Madagascar and the Comores, and *Neurolestes* in Central Africa.

Family Philosinidae

The Oriental *Philosina* and *Rhinagrion* are similar in morphology both in the adult stage, sharing the general shape of the genital ligula with notably long and dense setae on its shaft, and in the larval stage, with the larval paraprocts forming a unique tube around the epiproct (Kalkman & Villanueva, 2011; Zhang *et al.*, 2011). Their sister group relationship is highly supported in all analyses and together they are recognized as Philosinidae, encompassing only 12 known species, but no near relatives were identified.

Family Thaumatoneuridae

The Central American *Paraphlebia* and *Thaumatoneura* were recovered consistently as sister genera, sharing details of genital ligula, venation and larval morphology. They are also the only 'megapod' genera with dimorphic males in some species, the wings being either distinctly marked or completely clear (Garrison *et al.*, 2010). All analyses except BI/ML 28S retrieved these two combined with the Asian genera *Agriomorpha*, *Bornargiolestes*, *Burmargiolestes* and *Rhipidolestes* as monophyletic, with *Bornargiolestes* as the Americans' sister group, but while support was good in BI/ML 28S + 16S it was poor in BI/ML 28S + 16S + COI. The Oriental genera are similar in general morphology, but no apomorphies are known for them or for this possible subtropical group as a whole. They include some of the few 'megapods' with distinct wing markings or that perch with closed wings. *Agriomorpha* and *Paraphlebia* share very hairy larval gills and all genera have notably dense venation towards the wing margins, but all these tendencies require further study. We combine the two American genera into the family Thaumatoneuridae, but leave the rest as *incertae sedis*. *Burmargiolestes xinglongensis* Wilson & Reels is nearer to *Agriomorpha* than to the other *Burmargiolestes* and is transferred to that genus (Table S4).

Remaining Neotropical 'megapods' and family Dicteriadidae

The status of the remaining Neotropical 'megapods' is only partly resolved, but we retrieved three notable groups. Firstly, a well-supported relationship was found between *Philogenia* (35 species) and the small Ecuadorian genus *Archaeopodagrion* in all analyses. These genera are rather distinct morphologically, but share the presence of very long coiled flagella on the genital ligula. Secondly, the large genus *Heteragrion* (over 50 species) and smaller *Oxystigma* were recovered together with high support in all analyses. These genera resemble each other closely in the shape of the male appendages, genital ligula and markings. A probable apomorphy is the inflated larval gills, which bear rows of strongly curved spines (Geijskes, 1943; De Marmels, 2004). Thirdly, the localized *Dimeragrion* (Guiana Shield) and *Heteropodagrion* (northern Andes) were sister groups in MP 28S + 16S and BI/ML 28S + 16S + COI. Based on their closed wings at rest (except *Dimeragrion*), angulate frons (found also in *Heteragrion*) and especially the adult female's uniquely divided eighth tergite (Garrison *et al.*, 2010), we assume the monotypic Colombian *Mesagrion* belongs here too.

Heliocharis and *Hypolestes* were recovered as sister groups with moderate support in all analyses except BI/ML 28S/28S + 16S. *Heliocharis* forms the Amazonian family Dicteriadidae with the also monotypic *Dicterias*, while *Hypolestes* is endemic with three species to the Greater Antilles. Dicteriadid adults are peculiar among Zygoptera for their anteriorly widened postclypeus, drawn-out palpal hooks and almost bare legs. *Hypolestes* differs considerably from other 'megapods' by venation, genital ligula and appendages, but the two groups bear no obvious morphological resemblance, making this result rather inexplicable (Garrison *et al.*, 2010). The Venezuelan *Sciotropis* shares the presence of several basal cross-veins with Polythoridae, but not with other 'megapod' genera except for the occasional *Dimeragrion* (N. von Ellenrieder, *in litt*.), and a general similarity of the male appendages and genital ligula can be seen (cf. Garrison *et al.*, 2010). However, this genus was resolved as the sister group of Polythoridae, with negligible support only in MP 28S + 16S (COI unavailable).

Although some of these groups grouped together in some analyses – sometimes also with other Neotropical taxa such as *Rimanella* and Polythoridae – good support for further relationships was not found. Therefore the complex taxonomy cannot be resolved definitively at present, also because the oldest name available (Hypolestidae) is connected to one of the more disparate taxa. However, considering the results and keeping nomenclatorial stability in mind, we tentatively propose to divide this group. Such a solution at least progresses from the previous situation, in which most genera were included in a clearly polyphyletic Megapodagrionidae. Dicteriadidae should be retained for *Dicterias* and *Heliocharis*, while the family-group name Philogeniidae is available for *Archaeopodagrion* and *Philogenia*, Heteragrionidae for *Heteragrion* and *Oxystigma*, and Hypolestidae for *Hypolestes*. While *Dimeragrion*, *Heteropodagrion* and

Mesagrion may form another group, no name is available and these genera are considered *incertae sedis*, as is *Sciotropis*.

Families Philogangidae, Pseudolestidae and the 'amphipterygid' complex

Novelo-Gutiérrez (1995) removed the Papua-Australian *Diphlebia* and Oriental *Philoganga* from Amphipterygidae, restricting the family to four small and geographically disjunct genera with larvae possessing gill tufts: *Amphipteryx* in Central America and *Devadatta* in South-east Asia forming the subfamily Amphipteryginae, and *Pentaphlebia* in central Africa and *Rimanella* in northern South America constituting Rimanellinae. Rehn's (2003) morphological analysis confirmed this classification, but molecular studies recovered the group as polyphyletic (Bybee *et al.*, 2008; Dumont *et al.*, 2010). The larva of *Pseudolestes mirabilis* Kirby from the Chinese island Hainan also possess tufts (Yu & Bu, 2011a), but with sufficiently distinct morphology to consider Pseudolestidae a monotypic family. As discussed earlier, the affinities of *Diphlebia* are with the genus *Lestoidea* and Euphaeidae, whereas no support for relationships of *Amphipteryx*, *Devadatta*, *Philoganga*, *Pentaphlebia*, *Pseudolestes* and *Rimanella* with each other or with any damselfly genera could be found. Although the molecular evidence cannot disprove the relationship, the morphological grounds to retain any except *Amphipteryx* in Amphipterygidae are weak. For example, *Pseudolestes* has gill tufts but was never placed in that family, while *Philoganga* and *Diphlebia* do not have gill tufts but were long considered amphipterygids. Other larval features, especially of the paraprocts and epiproct, differ strongly between the genera. While the genera were grouped for possessing numerous postnodal cross-veins that are not aligned with adjacent veins, they differ in number and alignment of the antenodal cross-veins, the position of the radial sectors and the shape of the quadrangles, but all these characters are probably homoplasious (Rehn, 2003). As each genus has distinctive adult and larval morphology (see Appendix 2) and family-group names are available (except for Devadattidae **fam.n.**), all can be considered best as monogeneric families. Even if any of these genera were sister groups, the phylogenetic and geographic distance between them is great and recognizing them as highly localized families seems the most convenient and stable solution.

Remaining Palaeotropical 'megapods'

After the reclassification of most 'megapod' genera, six from tropical Asia, Madagascar and Africa remain unassigned. The Chinese *Priscagrion* and *Sinocnemis* are recovered as sister groups in all analyses with reasonable support. Based on morphology, both De Marmels (2002b) and Yu & Bu (2011b) suggested *Priscagrion* was close to Argiolestidae, but molecular data indicate this is unlikely. *Sinocnemis* has a more simplified venation, but these characters are highly homoplasious. The two genera appear similar, most strikingly in the shape of the genital ligula and the modification of its internal fold. This is long and tapering in at least one *Sinocnemis* species and even drawn out and filament-like in one *Priscagrion* species (Yu & Bu, 2011b). The similar appearance of *Sinocnemis* to the sympatric genus *Mesopodagrion* was noted by Kalkman (2008), but their very different genital ligulae and our molecular data imply there is no close relationship. Both *Mesopodagrion* species have the terminal rim of the 10th tergite distinctively extended between the cerci (Yu & Bu, 2009), although something similar occurs in the coenagrionid genus *Inpabasis*.

No close relatives could be identified for the monotypic *Amanipodagrion* from the East Usambara Mountains in Tanzania, or for *Protolestes* and *Tatocnemis* from Madagascar. Each possesses a combination of adult characters that fits none of the recognized groups. *Amanipodagrion* has a hanging resting posture and banded wings, creating a superficial resemblance to the unrelated *Chlorolestes*, and lacks spines on the genital ligula shaft. *Tatocnemis* has crenulated wingtips, shared with idiocnemidine Platycnemididae, but is not close otherwise. *Protolestes* has a broadened head recalling many Platycnemididae, but supposedly has fan-like larval gills found otherwise only in Argiolestidae and possibly *Dimeragrion* (Kalkman *et al.*, 2010). None of these genera appears to have close relatives and future work is likely to show that they constitute five separate families, assuming a close relation between *Priscagrion* and *Sinocnemis*. Study of the unknown and poorly known (*Tatocnemis* and *Protolestes*) larvae is likely to confirm these groups' isolated positions. Pending further study these genera are regarded as *incertae sedis*.

Outlook

Altogether, our phylogenetic reconstruction is largely congruent with the traditional classification of Zygoptera. Nonetheless, we reinstate, raise and create 11 damselfly families, bringing the total to 27, with at least another seven likely to be separated in the near future. While this seems radical, most changes are in smaller groups and the family affiliation of only one in five damselfly species changes. Also, we believe the revised classification will prove to be stable: further splits are considered more likely than the remerging of groups. Furthermore, we have refrained from subjectively recognizing 'distinctive' families (e.g. Diphlebiidae, Disparoneuridae, Hetaerinidae, Sinostictidae) for which there was no phylogenetic imperative. Most of the 'new' names have existed for over half a century, constituting taxonomic 'hunches' for which no decisive evidence was available (or accepted) at the time of introduction.

Consensus for the suggested reclassification must be found, as attained for the better-known Anisoptera (Dijkstra *et al.*, 2013), but we feel separating well-supported groups is more consistent than retaining unsupported groups for tradition's sake. All 11 (re-)instated families come from only two former families composed mostly of geographically isolated groups. These families were 'waste baskets' for equally unusual taxa, which persisted in stable but isolated areas, with no or only very distant relatives surviving elsewhere. Although better support for relationships between families may be obtained with more sequence data and morphological evidence (especially of larvae and genitalia), our expectations are modest, as the most challenging groups are so isolated phylogenetically, and morphologically so simplified, that comparable groups may not be identifiable with the available methods.

Finally, two general observations about the phylogeny and taxonomy of damselflies must be made. First, almost all larger genera for which multiple species were sampled (e.g. *Drepanosticta*, *Libellago*, *Rhinocypha*, *Coeliccia*, *Agriocnemis*, *Pseudagrion*, *Teinobasis*) are not monophyletic and thus extensive revision of the suborder must take place. Secondly, many identified clades lack strong morphological apomorphies, and this also applies to many long-established families, such as Calopterygidae, Euphaeidae and Platycnemididae, even prior to molecular investigations. Characters of venation, in particular, show little congruence with our molecular results. The most poignant example is Protoneuridae, characterized by the absence or reduction of the anal vein. The family dissolves completely and in its broadest historic definition is seen to include six clades from five families: all Platystictidae, *Lestoidea* in Lestoideidae, all Isostictidae, most *Allocnemis* species and all Disparoneurinae in Platycnemididae, and true 'Protoneurinae' in Coenagrionidae. This result challenges the current taxonomy for fossil Odonata which is based almost entirely on venation, and stresses the importance of a review of fossil data in the light of molecular results.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12035

Table S1. Primer combinations used for amplification of 28S, 16S and COI.

Table S2. List of analysed samples.

Table S3. Support in analyses for proposed classification of Zygoptera.

Table S4. Summary of proposed taxonomic changes, including new combinations.

Acknowledgements

Our thanks go first and foremost to those who supplied crucial samples from all over the world or provided valuable comments: Christine Apodaca, Matjaž Bedjanič, Evan Bowen-Jones, Seth Bybee, Viola Clausnitzer, Jürg De Marmels, Henri Dumont, Tim Faasen, Rosser Garrison, Dirk Gassmann, Justin Gerlach, Enrique González-Soriano, Andre Günther, Matti Hämäläinen, John Kaize, Haruki Karube, Walter Kebing, Milen Marinov, Mike May, Nyegang Megan, Nicolas Mézière, Kees Mostert, C.M. Nazareno, Yong Foo Ng, Mike Parr, Dan Polhemus, Bert Orr, Graham Reels, Andy Rehn, Bob Reimer, Steve Richards, Richard Rowe, Wolfgang Schneider, Kai Schütte, John Simaika, Andy Skinner, Harry Smit, John Smit, Luke Southwell, Stephen Stone, Warwick Tarboton, Jan Taylor, Ken Tennessen, Günther Theischinger, John Trueman, Reagan Villanueva, Gert Veurink, Jessica Ware, Marcel Wasscher, Natalia von Ellenrieder, Wen-Chi Yeh and Haomiao Zhang. Yvonne van Nierop helped in the collection at Naturalis. Kevin Beentjes, Camiel Doorenweerd, Ullasa Kodandaramaiah and Rutger Vos advised on analyses.

References

Ballare, E.F. & Ware, J.L. (2011) Dragons fly, biologists classify: an overview of molecular odonate studies, and our evolutionary understanding of dragonfly and damselfly (Insecta: Odonata) behavior. *International Journal of Odonatology*, **14**, 137–147.

Bechly, G. (1996) Morphologische untersuchungen am Flügelgeäder der rezenten libellen und deren stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer berücksichtigung der phylogenetischen systematik und des grundplanes der Odonata. *Petalura*, Special Volume, **2**, 1–402.

Blanke, A., Greve, C., Mokso, R., Beckman, F. & Misof, B. (2013) An updated phylogeny of Anisoptera including formal convergence analysis of morphological characters. *Systematic Entomology*, **38**, 474–490.

Bybee, S.M., Ogden, T.H., Branham, M.A. & Whiting, M.F. (2008) Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. *Cladistics*, **24**, 477–514.

Carle, F.L., Kjer, K.M. & May, M.L. (2008) Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). *Arthropod Systematics & Phylogeny*, **66**, 37–44.

Corbet, P.S. (1999) *Dragonflies, Behavior and Ecology of Odonata*. Harley Books, Colchester.

Davis, R.B., Nicholson, D.B., Saunders, E.L.R. & Mayhew, P.J. (2011) Fossil gaps inferred from phylogenies alter the apparent nature of diversification in dragonflies and their relatives. *BMC Evolutionary Biology*, **11**, 252–261.

De Marmels, J. (1984) The genus *Nehalennia* Selys, its species and their phylogenetic relationships (Zygoptera: Coenagrionidae). *Odonatologica*, **13**, 501–527.

De Marmels, J.C. (2001) *Revision of* Megapodagrion *Selys, 1886 (Insecta, Odonata: Megapodagrionidae)*. Dissertation, Universität Zürich, Zürich.

De Marmels, J. (2002a) A study of *Chromagrion* Needham, 1903, *Hesperagrion* Calvert, 1902, and *Zoniagrion* Kennedy, 1917: three monotypic North American damselfly genera with uncertain generic relationships (Zygoptera: Coenagrionidae). *Odonatologica*, **31**, 139–150.

De Marmels, J. (2002b) Phylogenetic relationships of *Priscagrion* Zhou & Wilson, 2001, with a description of *Teinopodagrion croizati* spec. nov. from Ecuador (Zygoptera: Megapodagrionidae). *Odonatologica*, **31**, 389–394.

De Marmels, J. (2004) *Heteragrion makiritare* sp. nov., with descriptions of hitherto unknown females and larvae of other species from Venezuela (Odonata: Megapodagrionidae, Lestidae). *International Journal of Odonatology*, **7**, 439–458.

De Marmels, J. (2007) *Tepuibasis* gen. nov. from the Pantepui region of Venezuela, with descriptions of four new species, and with biogeographic, phylogenetic and taxonomic considerations on the Teinobasinae (Zygoptera: Coenagrionidae). *Odonatologica*, **36**, 117–146.

Dijkstra, K.-D.B. (2007) The name-bearing types of Odonata held in the Natural History Museum of Zimbabwe, with systematic notes on Afrotropical taxa. Part 2: zygoptera and descriptions of new species. *International Journal of Odonatology*, **10**, 137–170.

Dijkstra, K.-D.B. (2013) Three new genera of damselflies (Odonata: Chlorocyphidae, Platycnemididae). *International Journal of Odonatology*, **16**, in press.

Dijkstra, K.-D.B. & Kalkman, V.J. (2012) Phylogeny, taxonomy and classification of European dragonflies and damselflies (Odonata): a review. *Organisms, Diversity and Evolution*, **12**, 209–227.

Dijkstra, K.-D.B. & Kalkman, V.J. (2013) The ‘African’ genus *Argiagrion* is a Brazilian *Leptagrion* species and the ‘Philippine’ *Moroagrion* a European *Pyrrhosoma* (Odonata: Coenagrionidae). *International Journal of Odonatology*, **16**, 189–191.

Dijkstra, K.-D.B. & Vick, G.S. (2006) Inflation by venation and the bankruptcy of traditional genera: the case of *Neodythemis* and *Micromacromia*, with keys to the continental African species and the description of two new *Neodythemis* species from the Albertine Rift (Odonata: Libellulidae). *International Journal of Odonatology*, **9**, 51–70.

Dijkstra, K.-D.B., Clausnitzer, V. & Martens, A. (2007) Tropical African *Platycnemis* damselflies (Odonata: Platycnemididae) and the biogeographical significance of a new species from Pemba Island, Tanzania. *Systematics and Biodiversity*, **5**, 187–198.

Dijkstra, K.-D.B., Bechly, G., Bybee, S.M. *et al.* (2013) The classification and diversity of dragonflies and damselflies (Odonata), *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness*, (ed. by Z.-Q. Zhang). *Zootaxa* in press.

Dow, R.A. (2010) Revision of the genus *Coeliccia* (Zygoptera: Platycnemididae) in Borneo. Part I: the *borneensis*-group of species. *Zoologische Mededelingen Leiden*, **84**, 117–157.

Dow, R.A. (2011) *Mortonagrion indraneil* spec. nov. from Borneo, and a redescription of *M. arthuri* Fraser (Odonata: Zygoptera: Coenagrionidae). *Zootaxa*, **3093**, 35–46.

Dow, R.A. & Orr, A.G. (2012) *Telosticta*, a new damselfly genus from Borneo and Palawan (Odonata: Zygoptera: Platystictidae). *The Raffles Bulletin of Zoology*, **60**, 365–401.

Drummond, A.J., Ashton, B., Buxton, S. *et al.* (2011) Geneious v5.4 [WWW document]. URL http://www.geneious.com.

Dumont, H.J., Vanfleteren, J.R., De Jonckheere, J.F. & Weekers, P.H.H. (2005) Phylogenetic relationships, divergence time estimation, and global biogeographic patterns of calopterygoid damselflies (Odonata, Zygoptera) inferred from ribosomal DNA sequences. *Systematic Biology*, **54**, 347–362.

Dumont, H.J., Vierstraete, A. & Van Fleteren, J.R. (2007) A revised molecular phylogeny of the Calopteryginae (Zygoptera: Calopterygidae). *Odonatologica*, **36**, 365–372.

Dumont, H.J., Vierstraete, A. & Vanfleteren, J.R. (2010) A molecular phylogeny of the Odonata (Insecta). *Systematic Entomology*, **35**, 6–18.

Fleck, G., Brenk, M. & Misof, B. (2008a) Larval and molecular characters help to solve phylogenetic puzzles in the highly diverse dragonfly family Libellulidae (Insecta: Odonata: Anisoptera): the Tetrathemistinae are a polyphyletic group. *Organisms, Diversity and Evolution*, **8**, 1–16.

Fleck, G., Ullrich, B., Brenk, M., Wallnisch, C., Orland, M., Bleidissel, S. & Misof, B. (2008b) A phylogeny of anisopterous dragonflies (Insecta, Odonata) using mtRNA genes and mixed nucleotide/doublet models. *Journal of Zoological Systematics and Evolutionary Research*, **46**, 310–322.

Fleck, G., Neiss, U.G. & Hamada, N. (2012) The larva of *Dicterias* Selys, 1853 (Odonata: Heliocharitidae [= Dicteriadidae]), and taxonomic and phylogenetic notes on Heliocharitidae. *Zootaxa*, **3164**, 32–40.

Fraser, F.C. (1957) *A Reclassification of the Order Odonata*. Royal Zoological Society of New South Wales, Syndey.

Garrison, R.W., von Ellenrieder, N. & Louton, J.A. (2010) *Damselfly Genera of the New World: An Illustrated and Annotated Key to the Zygoptera*. The Johns Hopkins University Press, Baltimore, Maryland.

Gassmann, D. (2005) The phylogeny of Southeast Asian and Indo-Pacific Calicnemiinae (Odonata: Platycnemididae). *Bonner Zoologische Beiträge*, **53**, 37–80.

Gassmann, D. & Hämäläinen, M. (2002) A revision of the Philippine subgenus *Risiocnemis* (*Igneocnemis*) Hämäläinen (Odonata: Platycnemididae). *Tijdschrift voor Entomologie*, **145**, 213–266.

Geijskes, D.C. (1943) Notes on Odonata of Surinam. IV. Nine new or little known Zygopterous nymphs from the inland waters. *Annals of the Entomological Society of America*, **36**, 165–184.

Goloboff, P., Farris, J. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

Groeneveld, L.F., Clausnitzer, V. & Hadrys, H. (2007) Convergent evolution of gigantism in damselflies of Africa and South America? Evidence from nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution*, **42**, 339–346.

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, New York, New York.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, **41**, 95–98.

Hämäläinen, M. (2012) *Platycnemis doi* sp. nov. from Huu Lien nature reserve in northern Vietnam (Odonata: Platycnemididae). *International Journal of Odonatology*, **15**, 223–228.

Hasegawa, E. & Kasuya, E. (2006) Phylogenetic analysis of the insect order Odonata using 28S and 16S rDNA sequences: a comparison between data sets with different evolutionary rates. *Entomological Science*, **9**, 55–66.

Hovmöller, R. (2006) *Monophyly of Ischnurinae (Odonata: Zygoptera, Coenagrionidae) established from COII and 16S sequences*. In: R. Hovmöller, *Molecular phylogenetics and taxonomic issues in dragonfly systematics (Insecta: Odonata)*. PhD Thesis, Stockholm University, Stockholm.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Ingley, S.J., Bybee, S.M., Tennessen, K.J., Whiting, M.F. & Branham, M.A. (2012) Life on the fly: phylogenetics and evolution of the helicopter damselflies (Odonata, Pseudostigmatidae). *Zoologica Scripta*, **41**, 637–650.

Jordan, S., Simon, C. & Polhemus, D. (2003) Molecular systematics and adaptive radiation of Hawaii’s endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology*, **52**, 89–109.

Kalkman, V.J. (2008) Taxonomy, behaviour, and habitat of *Mesopodagrion* and *Sinocnemis*. Notes on Old World Megapodagrionidae 3. (Odonata). *International Journal of Odonatology*, **11**, 185–193.

Kalkman, V.J. & Orr, A.G. (2012) The Australian monsoon tropics as a barrier for exchange of dragonflies (Insecta: Odonata) between New Guinea and Australia. *Hydrobiologia*, **693**, 55–70.

Kalkman, V.J. & Theischinger, G. (2013) Generic revision of Argiolestidae (Odonata), with four new genera. *International Journal of Odonatology*, **16**, 1–52.

Kalkman, V.J. & Villanueva, R.J.T. (2011) A synopsis of the genus *Rhinagrion* with description of two new species from the Philippines (Odonata: Megapodagrionidae). *International Journal of Odonatology*, **14**, 11–31.

Kalkman, V.J., Clausnitzer, V., Dijkstra, K.-D.B., Orr, A.G., Paulson, D.R. & van Tol, J. (2008) Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia*, **595**, 351–363.

Kalkman, V.J., Choong, C.Y., Orr, A.G. & Schütte, K. (2010) Remarks on the taxonomy of Megapodagrionidae with emphasis on the larval gills (Odonata). *International Journal of Odonatology*, **13**, 119–135.

Karube, H., Futahashi, R., Sasamoto, A. & Kawashima, I. (2012) Taxonomic revision of Japanese odonate species based on nuclear and mitochondrial gene genealogies and morphological comparison with allied species. Part I. *Tombo*, **54**, 75–106.

Katoh, K., Asimenos, G. & Toh, H. (2009) Multiple alignment of DNA sequences with MAFFT. *Methods in Molecular Biology,* **537**, 39–64.

Lieftinck, M.A. (1949) The dragonflies (Odonata) of New Guinea and neighbouring islands. Part VII. Results of the Third Archbold expedition 1938–1939 and of the Le Roux expedition 1939 to Netherlands New Guinea (II. Zygoptera). *Nova Guinea (N.S.)*, **5**, 1–271.

Lieftinck, M.A. (1957) Notes on some argiine dragonflies (Odonata) with special reference to the genus *Palaiargia* Förster, and with descriptions of new species and larval forms. *Nova Guinea (N.S.)*, **8**, 41–80.

Neiss, U.G., Fiorentni, G.L. & De Marmels, J. (2011) The larva of *Allopodagrion brachyurum* De Marmels, 2001 (Odonata: Zygoptera: Megapodagrionidae) from Southern Brazil. *Zootaxa*, **2836**, 44–50.

Novelo-Gutiérrez, R. (1995) The larva of *Amphipteryx* and a reclassification of Amphipterygidae sensu lato, based upon the larvae (Zygoptera). *Odonatologica*, **24**, 73–87.

Nylander, J.A.A. (2004) *Mr Modeltest v2*. Program distributed by the author, Evolutionary Biology Centre, Uppsala University, Uppsala.

Orr, A.G. & Kalkman, V.J. (2010) *Arrhenocnemis parvibullis* sp. nov. (Odonata: Platycnemididae), a new calicnemiine damselfly from Papua New Guinea, with a description of the female of *A. amphidactylis* Lieftinck, 1949. *The Australian Entomologist*, **37**, 137–146.

O'Grady, E.W. & May, M.L. (2003) A phylogenetic reassessment of the subfamilies of Coenagrionidae (Odonata: Zygoptera). *Journal of Natural History*, **37**, 2807–2834.

Pérez-Gutiérrez, L.A. & Montes-Fontalvo, J.M. (2011) Rediscovery of *Mesagrion leucorrhinum* (Zygoptera: Megapodagrionidae): a "formal" description of female and ultimate stadium of larva with notes on habits. *International Journal of Odonatology*, **14**, 91–100.

Pessacq, P. (2008) Phylogeny of Neotropical Protoneuridae (Odonata: Zygoptera) and a preliminary study of their relationship with related families. *Systematic Entomology*, **33**, 511–528.

Pilgrim, E.M. & von Dohlen, C.D. (2008) Phylogeny of the Sympetrinae (Odonata: Libellulidae): further evidence of the homoplasious nature of wing venation. *Systematic Entomology*, **3**, 159–174.

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: the barcode of life data system (www.barcodinglife.org). *Molecular Ecology Notes*, **7**, 55–364.

Rozen, S. & Skaletsky, H.J. (2000) Primer3 on the WWW for general users and for biologist programmers. *Bioinformatics Methods and Protocols: Methods in Molecular Biology* (ed. by S. Krawetz and S. Misener), pp. 365–386. Humana Press, Totowa, New Jersey.

Rehn, A.C. (2003) Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology*, **28**, 181–239.

Silsby, J. (2001) *Dragonflies of the World*. CSIRO Publishing, Collingwood.

Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology*, **75**, 758–771.

Tennessen, K.J. (2010) The madicolous nymph of *Heteropodagrion sanguinipes* Selys (Odonata: Megapodagrionidae). *Zootaxa*, **2531**, 29–38.

van Tol, J., Reijnen, B.T. & Thomassen, H.A. (2009) *Phylogeny and biogeography of the Platystictidae (Odonata)*. In: van Tol, J., *Phylogeny and biogeography of the Platystictidae (Odonata)*. PhD Thesis, Leiden University, Leiden, pp. 3–70.

Trueman, J.W.H. (1996) A preliminary cladistic analysis of Odonate wing venation. *Odonatologica*, **25**, 59–72.

Trueman, J.W.H. (2007) A brief history of the classification and nomenclature of Odonata. *Zootaxa*, **1668**, 381–394.

Villanueva, R.J.T. (2012) Review of the Philippine taxa formerly assigned to the genus *Amphicnemis* Selys. Part I: overview and descriptions of three new genera (Odonata: Coenagrionidae). *Zoologische Mededelingen*, **86**, 79–604.

Ware, J., May, M. & Kjer, K. (2007) Phylogeny of the higher Libelluloidea (Anisoptera: Odonata): an exploration of the most speciose superfamily of dragonflies. *Molecular Phylogenetics and Evolution*, **45**, 9–310.

Wilson, K.D.P. (1997) The Platystictidae of Hong Kong and Guangdong, with descriptions of a new genus and two new species (Zygoptera). *Odonatologica*, **26**, 53–63.

Yu, X. & Bu, W.J. (2009) A revision of *Mesopodagrion* McLachlan, 1896 (Odonata: Zygoptera: Megapodagrionidae). *Zootaxa*, **2202**, 59–68.

Yu, X. & Bu, W.J. (2011a) A description of the remarkable larva of *Pseudolestes mirabilis* Kirby (Odonata: Pseudolestidae). *International Journal of Odonatology*, **14**, 105–110.

Yu, X. & Bu, W.J. (2011b) A preliminary phylogenetic study of Megapodagrionidae with focus on the Chinese genera *Sinocnemis* Wilson & Zhou and *Priscagrion* Zhou & Wilson (Odonata: Zygoptera). *Hydrobiologia*, **665**, 195–203.

Zhang, H., Kalkman, V.J. & Tonga, X. (2011) A synopsis of the genus *Philosina* with descriptions of the larvae of *P. alba* and *P. buchi* (Odonata: Megapodagrionidae). *International Journal of Odonatology*, **14**, 55–68.

Accepted 1 July 2013

Appendix 1: Classification of the suborder Zygoptera

The proposed classification follows Dijkstra *et al.* (2013). Superfamilies and families are provided for all genera, subfamilies and tribes for selected ones (see text). For convenience, groups of (presumably) related genera within Coenagrionidae also are indicated (see text). The order of superfamilies and families is phylogenetic (smallest sister group first), while that of lower ranks and 'calopterygoid' families is alphabetical. Sampled genera are indicated with an asterisk. Three widely accepted family names are outdated by older names, although these have, at most, 15% of usage (Google search): Libellaginidae Yakobson & Bianchi, 1905 and Disparocyphidae Munz, 1919 for Chlorocyphidae, Heliocharitidae Tillyard

& Fraser, 1939 for Dicteriadidae, and Epallagidae Needham, 1903 for Euphaeidae. An application to the International Commission on Zoological Nomenclature for the suppression of the older names will be prepared (Dijkstra *et al.*, 2013). Because of this problem, groups within Chlorocyphidae are listed informally.

Superfamily Lestoidea Calvert, 1901

- Family Hemiphlebiidae Kennedy, 1920 (*Hemiphlebia* Selys, 1869)
- Family Perilestidae Kennedy, 1920 (**Perilestes* Hagen, 1862, **Perissolestes* Kennedy, 1941)
- Family Synlestidae Tillyard, 1917 (**Chlorolestes* Selys, 1862, *Chorismagrion* Morton, 1914, **Ecchlorolestes* Barnard, 1937, **Episynlestes* Kennedy, 1920, **Megalestes* Selys, 1862, **Nubiolestes* Fraser, 1945, *Phylolestes* Christiansen, 1948, *Sinolestes* Needham 1930, **Synlestes* Selys, 1868)
- Family Lestidae Calvert, 1901 (*Archilestes* Selys, 1862, **Austrolestes* Tillyard, 1913, *Chalcolestes* Kennedy, 1920, **Indolestes* Fraser, 1922, **Lestes* Leach, 1815, **Orolestes* McLachlan, 1895, *Platylestes* Selys, 1862, *Sinhalestes* Fraser, 1951, **Sympecma* Burmeister, 1839)

Superfamily Platystictoidea Kennedy, 1920

- Family Platystictidae Kennedy, 1920
  - Subfamily Palaemnematinae Tillyard & Fraser, 1938 (**Palaemnema* Selys, 1860)
  - Subfamily Platystictinae Kennedy, 1920 (**Ceylonosticta* Fraser, 1931, **Platysticta* Selys, 1860)
  - Subfamily Protostictinae **subfam.n**. (**Drepanosticta* Laidlaw, 1917, **Protosticta* Selys, 1885, *Sulcosticta* van Tol, 2005, **Telosticta* Dow & Orr, 2012)
  - Subfamily Sinostictinae Wilson, 1997 (**Sinosticta* Wilson, 1997)

Superfamily 'Calopterygoidea' Selys, 1850

- Family Amphipterygidae Tillyard, 1917 (**Amphipteryx* Selys, 1853)
- Family Argiolestidae Fraser, 1957
  - Subfamily Argiolestinae Fraser, 1957 (**Archiargiolestes* Kennedy, 1925, **Argiolestes* Selys, 1862, **Austroargiolestes* Kennedy, 1925, **Caledargiolestes* Kennedy, 1925, **Caledopteryx* Kennedy, 1925, **Celebargiolestes* Kennedy, 1925, *Eoargiolestes* Kalkman & Theischinger, 2013, **Griseargiolestes* Theischinger, 1998, **Luzonargiolestes* Kalkman & Theischinger, 2013, **Metagrion* Calvert, 1913, **Miniargiolestes* Theischinger, 1998, **Podopteryx* Selys, 1871, **Pyrrhargiolestes* Kalkman & Theischinger, 2013, *Solomonargiolestes* Kalkman & Theischinger, 2013, **Trineuragrion* Ris, 1915, **Wahnesia* Förster, 1900)
  - Subfamily Podolestinae Kalkman & Theischinger, 2013 (**Allolestes* Selys, 1869, **Nesolestes* Selys, 1891, **Neurolestes* Selys, 1882, **Podolestes* Selys, 1862)

Family Calopterygidae Selys, 1850

- Subfamily Calopteryginae Selys, 1850
  - Tribe Caliphaeini Fraser, 1929 (**Caliphaea* Hagen, 1859)
  - Tribe Calopterygini Selys, 1850 (*Atrocalopteryx* Dumont *et al.*, 2005, **Calopteryx* Leach, 1815, **Matrona* Selys, 1853, *Matronoides* Foerster, 1897, **Neurobasis* Selys, 1853)
  - Tribe Iridictyonini Dumont *et al.*, 2005 (*Iridictyon* Needham & Fisher, 1940)
  - Tribe Mnaisini Ishida, 1996 (**Archineura* Kirby, 1894, **Echo* Selys, 1853, **Mnais* Selys, 1853, *Psolodesmus* McLachlan, 1870)
  - Tribe Noguchiphaeini Dumont *et al.*, 2005 (*Noguchiphaea* Asahina, 1976)
  - Tribe Saphoini Dumont *et al.*, 2005 (**Phaon* Selys, 1853, **Sapho* Selys, 1853, **Umma* Kirby, 1890)
  - Tribe Vestalini Needham, 1903 (*Vestalaria* May, 1935, **Vestalis* Selys, 1853)
- Subfamily Hetaerininae Tillyard & Fraser, 1939 (*Bryoplathanon* Garrison, 2006, **Hetaerina* Hagen, 1853, **Mnesarete* Cowley, 1934, *Ormenophlebia* Garrison, 2006)

Family Chlorocyphidae Cowley, 1937

- 'Chlorocyphinae' (**Africocypha* Pinhey, 1961, **Chlorocypha* Fraser, 1928, **Platycypha* Fraser, 1949, **Stenocypha* Dijkstra, 2013)
- 'Disparocyphinae' (**Disparocypha* Ris, 1916)
- 'Libellagininae' (**Libellago* Selys, 1840, *Melanocypha* Fraser, 1949, **Pachycypha* Lieftinck, 1950, **Sclerocypha* Fraser, 1949, *Watuwila* van Tol, 1998)
- 'Rhinocyphinae' (**Aristocypha* Laidlaw, 1950, *Calocypha* Fraser, 1928, **Heliocypha* Fraser, 1949, *Heterocypha* Laidlaw, 1950, *Paracypha* Fraser, 1949, **Rhinocypha* Rambur, 1842, **Rhinoneura* Laidlaw, 1915, **Sundacypha* Laidlaw, 1950)
- Incertae sedis (**Cyrano* Needham & Gyger, 1939, **Indocypha* Fraser, 1949)

Family Devadattidae **fam.n**. (**Devadatta* Kirby, 1890)
Family Dicteriadidae Montgomery, 1959 (*Dicterias* Selys, 1853, **Heliocharis* Selys, 1853)

Family Euphaeidae Yakobson & Bianchi, 1905 (**Anisopleura* Selys, 1853, *Bayadera* Selys, 1853, **Cryptophaea* Hämäläinen, 2002, *Cyclophaea* Ris, 1930, **Dysphaea* Selys, 1853, *Epallage* Charpentier, 1840, **Euphaea* Selys, 1840, *Heterophaea* Cowley, 1934, *Schmidtiphaea* Asahina, 1978)

Family Heteragrionidae Rácenis, 1959 (**Heteragrion* Selys, 1862, **Oxystigma* Selys, 1862)

Family Hypolestidae Fraser, 1938 (**Hypolestes* Gundlach, 1888)

Family Lestoideidae Munz, 1919

Subfamily Diphlebiinae Heymer, 1975 (**Diphlebia* Selys, 1869)

Subfamily Lestoideinae Munz, 1919 (**Lestoidea* Tillyard, 1913)

Family Megapodagrionidae Calvert, 1913 (*Allopodagrion* Förster, 1910, **Megapodagrion* Selys, 1885, **Teinopodagrion* De Marmels, 2001)

Family Pentaphlebiidae Novelo-Gutiérrez, 1995 (**Pentaphlebia* Förster, 1909)

Family Philogangidae Kennedy, 1920 (**Philoganga* Kirby, 1890)

Family Philogeniidae Rácenis, 1959 (**Archaeopodagrion* Kennedy, 1939, **Philogenia* Selys, 1862)

Family Philosinidae Kennedy, 1925 (**Philosina* Ris, 1917, **Rhinagrion* Calvert, 1913)

Family Polythoridae Munz, 1919 (**Chalcopteryx* Selys, 1853, *Chalcothore* De Marmels, 1985, *Cora* Selys, 1853, *Euthore* Selys, 1869, *Miocora* Calvert, 1917, **Polythore* Calvert, 1917, *Stenocora* Kennedy, 1940)

Family Pseudolestidae Fraser, 1957 (**Pseudolestes* Kirby, 1900)

Family Rimanellidae Davies & Tobin, 1984 (**Rimanella* Needham, 1934)

Family Thaumatoneuridae Fraser, 1938 (**Paraphlebia* Selys, 1861, **Thaumatoneura* McLachlan, 1897)

Incertae sedis group 1: **Agriomorpha* May, 1933, **Bornargiolestes* Kimmins, 1936, **Burmargiolestes* Kennedy, 1925, **Rhipidolestes* Ris, 1912; group 2: **Amanipodagrion* Pinhey, 1962; group 3: **Dimeragrion* Calvert, 1913, **Heteropodagrion* Selys, 1885, *Mesagrion* Selys, 1885; group 4: **Mesopodagrion* McLachlan, 1897; group 5: **Priscagrion* Zhou & Wilson, 2001, **Sinocnemis* Wilson & Zhou, 2000; group 6: **Protolestes* Förster, 1897; group 7 (= 'Tatocnemidinae Rácenis, 1959'): **Tatocnemis* Kirby, 1889; group 8: **Sciotropis* Rácenis, 1959

Superfamily Coenagrionoidea Kirby, 1890

Family Isostictidae Fraser, 1955 (*Austrosticta* Tillyard, 1908, *Cnemisticta* Donnelly, 1993, *Eurysticta* Watson, 1969, **Isosticta* Selys, 1885, *Labidiosticta* Watson, 1991, *Lithosticta* Watson, 1991, **Neosticta* Tillyard, 1913, *Oristicta* Tillyard, 1913, *Rhadinosticta* Watson, 1991, **Selysioneura* Förster, 1900, **Tanymecosticta* Lieftinck, 1935, *Titanosticta* Donnelly, 1993)

Family Platycnemididae Yakobson & Bianchi, 1905

Subfamily Allocnemidinae **subfam.n.** (**Allocnemis* Selys, 1863, **Arabicnemis* Waterston, 1984, **Mesocnemis* Karsch, 1891, **Metacnemis* Hagen, 1863, **Stenocnemis* Karsch, 1899)

Subfamily Calicnemiinae Fraser, 1957 (*Asthenocnemis* Lieftinck, 1949, **Calicnemia* Strand, 1928, **Coeliccia* Kirby, 1890, **Indocnemis* Laidlaw, 1917)

Subfamily Disparoneurinae Fraser, 1957 (*Arabineura* Schneider & Dumont, 1995, *Caconeura* Kirby, 1890, *Disparoneura* Selys, 1860, **Elattoneura* Cowley, 1935, **Esme* Fraser, 1922, *Melanoneura* Fraser, 1922, **Nososticta* Hagen, 1860, *Phylloneura* Fraser, 1922, **Prodasineura* Cowley, 1934)

Subfamily Idiocnemidinae **subfam.n.** (*Archboldargia* Lieftinck, 1949, **Arrhenocnemis* Lieftinck, 1933, **Cyanocnemis* Lieftinck, 1949, **Hylaeargia* Lieftinck, 1949, **Idiocnemis* Selys, 1878, **Igneocnemis* Hämäläinen, 1991, *Lieftinckia* Kimmins, 1957, **Lochmaeocnemis* Lieftinck, 1949, **Palaiargia* Förster, 1903, **Papuargia* Lieftinck, 1938, **Paramecocnemis* Lieftinck, 1932, *Rhyacocnemis* Lieftinck, 1956, **Risiocnemis* Cowley, 1934, *Salomocnemis* Lieftinck, 1987, **Torrenticnemis* Lieftinck, 1949)

Subfamily Onychargiinae **subfam.n.** (**Onychargia* Selys, 1865, **Paracnemis* Martin, 1902)

Subfamily Platycnemidinae Yakobson & Bianchi, 1905

Tribe Coperini **trib.n.** (**Copera* Kirby, 1890, **Proplatycnemis* Kennedy, 1920, **Spesbona* Dijkstra, 2013)

Tribe Platycnemidini Yakobson & Bianchi, 1905 (**Matticnemis* Dijkstra, 2013, **Platycnemis* Burmeister, 1839, **Pseudocopera* Fraser, 1922)

Family Coenagrionidae Kirby, 1890

Core Coenagrionidae [genera associated with *Agriocnemis* ('Agriocnemidinae Fraser, 1957'): **Agriocnemis* Selys, 1877, **Argiocnemis* Selys, 1877, **Mortonagrion* Fraser, 1920; genera associated with *Ischnura* ('Ischnurinae Fraser, 1957'): **Acanthagrion* Selys, 1976, *Acanthallagma* Williamson & Williamson, 1924, **Aciagrion* Selys, 1891, **Africallagma* Kennedy, 1920, *Amphiagrion* Selys, 1876, *Amphiallagma* Kennedy, 1920, *Andinagrion* Bulla, 1973, *Anisagrion* Selys, 1876, *Apanisagrion*

Kennedy, 1920, *Argentagrion* Fraser, 1948, *Austroallagma* Lieftinck, 1953, **Austrocnemis* Tillyard, 1913, **Azuragrion* May, 2002, *Calvertagrion* St Quentin, 1960, **Coenagriocnemis* Fraser, 1949, *Cyanallagma* Kennedy, 1920, *Denticulobasis* Machado, 2009, **Dolonagrion* Garrison & von Ellenrieder, 2008, *Enacantha* Donnelly & Alayo, 1966, *Enallagma* Charpentier, 1840, *Hesperagrion* Calvert, 1902, *Homeoura* Kennedy, 1920, **Ischnura* Charpentier, 1840, *Leptobasis* Selys, 1877, *Leucobasis* Rácenis, 1959, *Mesamphiagrion* Kennedy, 1920, **Mesoleptobasis* Sjöstedt, 1918, *Millotagrion* Fraser, 1953, *Oreagrion* Ris, 1913, *Oreiallagma* von Ellenrieder & Garrison, 2008, *Oxyagrion* Selys, 1876, *Oxyallagma* Kennedy, 1920, *Pacificagrion* Fraser, 1926, *Pinheyagrion* May, 2002, *Proischnura* Kennedy, 1920, *Protallagma* Kennedy, 1920, **Thaumatagrion* Lieftinck, 1932, *Tigriagrion* Calvert, 1909, **Tuberculobasis* Machado, 2009, **Xiphiagrion* Selys, 1876, *Zoniagrion* Kennedy, 1917; genera associated with *Pseudagrion* ('Pseudagrioninae Tillyard, 1917'): **Archibasis* Kirby, 1890, **Austroagrion* Tillyard, 1913, *Caliagrion* Tillyard, 1913, *Erythromma* Charpentier, 1840, *Paracercion* Weekers & Dumont, 2004, **Pseudagrion* Selys, 1876, **Xanthagrion* Selys, 1876, *Xanthocnemis* Tillyard, 1913; remaining genera: **Austrocoenagrion* Kennedy, 1920, **Coenagrion* Kirby, 1890, *Himalagrion* Fraser, 1920, *Megalagrion* McLachlan, 1883, *Neoerythromma* Kennedy, 1920, **Stenagrion* Laidlaw, 1915]

Ridge-faced complex [genera associated with *Protoneura* ('Protoneurinae Yakobson & Bianchi, 1905'): **Amazoneura* Machado, 2004, **Drepanoneura* von Ellenrieder & Garrison, 2008, **Epipleoneura* Williamson, 1915, *Epipotoneura* Williamson, 1915, *Forcepsioneura* Lencioni, 1999, *Idioneura* Selys, 1860, *Junix* Rácenis, 1968, *Lamproneura* De Marmels, 2003, *Microneura* Hagen, 1886, **Neoneura* Selys, 1860, *Peristicta* Hagen, 1860, *Phasmoneura* Williamson, 1916, *Proneura* Selys, 1889, **Protoneura* Selys, 1857, **Psaironeura* Williamson, 1915, *Roppaneura* Santos, 1966; genera associated with *Pseudostigma* ('Pseudostigmatinae Kirby, 1890'): **Anomisma* McLachlan, 1877, **Bromeliagrion* De Marmels, 2005, *Coryphagrion* Morton, 1924, *Diceratobasis* Kennedy, 1920, *Leptagrion* Selys, 1876, **Mecistogaster* Rambur, 1842, *Megaloprepus* Rambur, 1842, **Microstigma* Rambur, 1842, *Pseudostigma* Selys, 1860; genera associated with *Teinobasis* ('Teinobasinae Tillyard, 1917'): **Amphicnemis* Selys, 1863, *Luzonobasis* Villanueva, 2012, *Melanesobasis* Donnelly, 1984, *Nesobasis* Selys, 1891, *Pandanobasis* Villanueva, 2012, **Papuagrion* Ris, 1913, **Pericnemis* Selys, 1863, *Plagulibasis* Lieftinck, 1949, *Sangabasis* Villanueva, 2012, **Teinobasis* Kirby, 1890, *Vanuatubasis* Ober & Staniczek, 2009; remaining genera: *Aceratobasis* Kennedy, 1920, **Aeolagrion* Williamson, 1917, *Angelagrion* Lencioni, 2008, *Antiagrion* Ris, 1904, **Ceriagrion* Selys, 1876, *Chromagrion* Needham, 1903, *Hylaeonympha* Rácenis, 1968, **Inpabasis* Santos, 1961, **Metaleptobasis* Calvert, 1907, *Minagrion* Dos Santos, 1965, *Nehalennia* Selys, 1850, **Oreocnemis* Pinhey, 1971, **Phoenicagrion* von Ellenrieder, 2008, *Pyrrhosoma* Charpentier, 1840, *Schistolobos* von Ellenrieder & Garrison, 2008, *Telagrion* Selys, 1876, **Telebasis* Selys, 1865, *Tepuibasis* De Marmels, 2007, *Tukanobasis* Machado, 2009]

Undetermined [**Argia* Rambur, 1842 (= 'Argiinae Tillyard, 1917'), **Leptocnemis* Selys, 1886]

Appendix 2: Diagnoses of new and revised family-group names

Allocnemidinae **subfam.n.** (type genus: *Allocnemis* Selys, 1863 by present designation) – small damselflies separated within range (Africa and Arabia) from other genera with two antenodal cross-veins (Ax), no spines on shaft of genital ligula, long leg spines, rounded frons and no postocular spots by combination of arculus clearly proximal to Ax2, which often converges posteriorly with Ax1; cubital cross-vein distal to origin of anal vein by about three times its length (by about its length in *Stenocnemis*); often more than three cells between quadrilateral and subnode (two in *Arabicnemis* and *Stenocnemis*). *Allocnemis* differs from similar genera in range by combination of R4 originating closer to subnode than IR3 (Tillyard & Fraser terminology); cubital cross-vein at origin of anal vein; wings often stained yellow. Male cerci in all genera are triangular (broad base and pointed tip) and usually with ventral process near base; paraprocts simple, often rather pointed or elongate.

Amphipterygidae (type genus: *Amphipteryx* Selys, 1853) – large damselflies with seven to eight Ax, two to three in subcostal space; arculus near Ax3; quadrangle without cross-veins; IR3 (Tillyard & Fraser terminology) originating at level of quadrangle, much closer to arculus than to nodus. Wings clear and closed at rest. Thorax and abdomen black with blue pattern on thorax and tip of abdomen but without metallic shine. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts roundish in cross-section but not balloon-shaped, broadest at approximately one-fifth of their base from where they gradually taper to a single point, as well as two filamentous gills tufts located beneath them.

Argiolestidae (type genus: *Argiolestes* Selys, 1862) – medium-sized to large damselflies with two (rarely three) Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear and held open at rest. Most species largely brown to black, often with blue, orange or red pattern on face, thorax, legs and/or tip of abdomen. Shaft of genital ligula without setae. Larvae with epiproct and paraprocts broad and flat, lying in a horizontal plane.

Coperini **trib.n**. (type genus: *Copera* Kirby, 1890 by present designation) – small damselflies featuring typical characters of subfamily Platycnemidinae, characterized by feather-like tibiae, which are dilated and bright white, yellow, orange, red or blue, and used in display; only entirely black and not widened in *Spesbona angusta* (Selys). Differs from tribe Platycnemidini by: caudal lamellae of larvae with frilled border (unique character among Odonata); inner side of the male cerci with a tooth- or branch-like process, but tiny in *C. sikassoensis* (Martin) and *C. vittata* (Selys), and reduced completely in *C. marginipes* (Rambur); male tibiae often not white.

Devadattidae **fam.n**. (type genus: *Devadatta* Kirby, 1890 by present designation) – large damselflies with seven to 12 Ax, four to five in subcostal space; arculus between Ax4 and Ax6; quadrangle with two to three cross-veins; IR3 originating at level of quadrangle, much closer to arculus than to nodus. Wings clear except for brown spot at the tips; closed at rest. Thorax and abdomen dull, without metallic shine or bright colours. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts sturdy and pyramidal, widest subbasally and terminating in single (paraprocts) or triple (epiproct) points, as well as two filamentous gills tufts located beneath them.

Heteragrionidae (type genus: *Heteragrion* Selys, 1862) – medium-sized to large damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear and held open at rest. Body of many species marked with bright orange or red. Genital ligula with setae on shaft and distal segment with paired laterally directed apical flagella. Larvae with epiproct and paraprocts inflated and triangular in cross-section, bearing a filament at tip; basal part with dorsal rib carrying a row of strongly curved spines.

Hypolestidae (type genus: *Hypolestes* Gundlach, 1888) – medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating somewhat distal to quadrangle, much closer to arculus than to nodus. Wings clear and held open at rest. Body dark brown or black with pale yellow pattern; mature males with extensive light grey pruinosity on head, thorax and ninth and 10th abdominal segments. Genital ligula with setae on shaft and distal segment with paired lateral and apical flagella. Larvae with epiproct and paraprocts inflated, constricted in the middle and ending in a long and sharply pointed filament.

Idiocnemidinae **subfam.n**. (type genus: *Idiocnemis* Selys, 1878 by present designation) – small to medium-sized damselflies with two Ax; the arculus at Ax2; pterostigma with costal side subequal to distal side; anal vein terminates in distal half of wing; shaft of genital ligula without spines; spines on legs long. Margins of wing tips crenulated (not in *Archboldargia*, *Hylaeargia*, *Palaiargia*, *Papuargia*, and weakly developed in *Rhyacocnemis*; similar character state acquired independently, but weakly developed, in *Tatocnemis*). Larvae with epiproct and paraprocts forming a unique three-dimensional ruff (described only for *Hylaeargia*, *Lieftinckia* and *Palaiargia*).

Megapodagrionidae (type genus: *Megapodagrion* Selys, 1885) – small to medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear and held open at rest. Shaft of genital ligula with setae. First antennal segment in both larvae and adults long, usually similar to slender second segment; legs also very long, with hind femur reaching anterior margin of third abdominal segment or beyond. Larvae with paraprocts long and thickened, each with a median outer ridge along their length, and foliaceous, wider and shorter epiproct

Onychargiinae **subfam.n**. (type genus: *Onychargia* Selys, 1865 by present designation) – small damselflies with two Ax; arculus at Ax2; pterostigma with costal side subequal to its distal side; anal vein terminates in distal half of wing; shaft of genital ligula without spines; spines on legs long. Head not laterally expanded, frons not angulate, dorsum black and lacking postocular spots but often with a pale line running from eye to eye across the lateral ocelli (sometimes partly broken). Margins of wing tips not crenulated. Male cerci distinctly shorter than 10th abdominal segment and subequal to paraprocts.

Pentaphlebiidae (type genus: *Pentaphlebia* Förster, 1909) – large damselflies with four to six Ax, two in subcostal space; arculus close to Ax2; quadrangle without cross-veins; IR3 originating at level of quadrangle, much closer to arculus than to nodus. Wings clear to smoky with darkened falcate tips and very long pterostigmata; closed at rest. Adult male is rather dark and plain, with reddish to black thorax and abdomen. Shaft of genital ligula with setae. Second antennal segment distinctly elongated, thin in adults and swollen in larvae. Larvae with blade-like paraprocts, expanded laterally near base and shorter than abdomen, short trifid epiproct, as well as two filamentous gills tufts located beneath them.

Philogangidae (type genus: *Philoganga* Kirby, 1890) – very large damselflies with 11–13 Ax, 14–17 in subcostal space; arculus close to Ax2; quadrangle without cross-veins; IR3 originating distal to quadrangle, closer to arculus than to nodus. Wings clear with long pterostigmata; held open at rest. Thorax and abdomen black, boldly marked with yellow or orange. Shaft of genital ligula without or with a few setae. Larvae with epiproct and paraprocts similar, inflated at base and tapering to finely pointed tips, without filamentous gills tufts.

Philogeniidae (type genus: *Philogenia* Selys, 1862) – medium-sized to large damselflies with 2 Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear or with brownish tips; held open at rest. Body dark brown to black with yellow, blue or green pattern and blue pruinosity on dorsum of abdomen in males. Genital ligula with setae on shaft; distal segment with paired long and slender spiral-shaped apical flagella. Larvae with epiproct and paraprocts inflated, constricted in the middle and ending in a filament.

Philosinidae (type genus: *Philosina* Ris, 1917) – medium-sized to large damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear (except for diffuse dark spot at tips in *Philosina buchi* Ris) and held open at rest. Head, thorax and abdomen in most species with bold pattern of yellow, orange, red or blue; partly covered with pruinosity in *Philosina*; dorsum of tip of abdomen weakly sclerotized in males allowing them to expand their abdomen. Shaft of genital ligula with dense long setae. Larvae with paraprocts thick and undulating, longer than thinner and foliaceous epiproct; in life the paraprocts form a tube folded around the epiproct.

Protostictinae **subfam.n**. (type genus: *Protosticta* Selys, 1885 by present designation) – small to moderately large damselflies, with venation characteristic of family, i.e. node at about one-quarter of wing length from base, and a cross-vein in the postcubital space closer to wing base than to the level of the proximal Ax. Distinctive combination of characters: IR3 arising distal to subnode (typically at level of subnode in other genera of family); CuP vein meeting hind margin of forewing at level of R3, or even proximal to it; anal bridge vein present ('*Drepanosticta*') or absent ('*Protosticta*'); R4 + 5 at or distal to subnode (as in Platystictinae s.s.). Male appendages very diverse in form; genital ligula with squarish cleft (rather than triangular as in *Sinosticta* and *Palaemnema*) and long horns (short in *Platysticta*).

Pseudolestidae (type genus: *Pseudolestes* Kirby, 1900) – medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings held open at rest, forewing clear; hind wing shorter than forewing, broadened in apical half and slightly falcate at tip, dark with bright orange patches (male) or clear with a broad iridescent subapical black band (female). Adult male has blue face and a black body with yellow lines on thorax. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts inflated and sack-like, each as broad as the abdomen itself and ending a short nipple-like filament, as well as two filamentous gills tufts located beneath them.

Rimanellidae (type genus: *Rimanella* Needham, 1934) – large damselflies with two Ax; arculus at Ax2; quadrangle without cross-veins; IR3 originating somewhat distal to quadrangle, much closer to arculus than to nodus. Wings clear with long pterostigmata; closed at rest. Adult male is colourful with blue pattern on head, yellowish green thorax with dark stripes and red to reddish brown abdomen. Sternum of 10th abdominal segment in both sexes forms a concave semicircular plate, delimited by lateral carinae from tergum. Shaft of genital ligula with setae. Larvae with whip-like paraprocts that are jointed near base and longer than abdomen, short trifid epiproct, as well as two filamentous gills tufts located beneath them.

Thaumatoneuridae (type genus: *Thaumatoneura* McLachlan, 1897) – medium-sized to large damselflies with two to four Ax (only two in subcostal space) and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings broad, with numerous intercalated veins in posterior portion and one to two accessory cross-veins distal to the cubital cross-vein, posterior to quadrangle. Several species with dimorphic males, i.e. wings either clear or with broad black band; wings closed at rest. Shaft of genital ligula with setae; distal segment with pair of broad lateral lobes. Larvae with epiproct and paraprocts inflated, strongly constricted in middle and ending in a filament, both inflated base and filament covered with stout stiff setae.