



<http://dx.doi.org/10.11646/zootaxa.3703.1.9>

<http://zoobank.org/urn:lsid:zoobank.org:pub:9F5D2E03-6ABE-4425-9713-99888C0C8690>

The classification and diversity of dragonflies and damselflies (Odonata)*

KLAAS-DOUWE B. DIJKSTRA¹, GÜNTER BECHLY², SETH M. BYBEE³, RORY A. DOW¹, HENRI J. DUMONT⁴, GÜNTHER FLECK⁵, ROSSER W. GARRISON⁶, MATTI HÄMÄLÄINEN¹, VINCENT J. KALKMAN¹, HARUKI KARUBE⁷, MICHAEL L. MAY⁸, ALBERT G. ORR⁹, DENNIS R. PAULSON¹⁰, ANDREW C. REHN¹¹, GÜNTHER THEISCHINGER¹², JOHN W.H. TRUEMAN¹³, JAN VAN TOL¹, NATALIA VON ELLENRIEDER⁶ & JESSICA WARE¹⁴

¹Naturalis Biodiversity Centre, PO Box 9517, NL-2300 RA Leiden, The Netherlands. E-mail: dijkstra@naturalis.nl; dow@naturalis.nl; matti.hamalainen@helsinki.fi; kalkman@naturalis.nl; tol@naturalis.nl

²Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany. E-mail: guenter.bechly@smns-bw.de

³Department of Biology, Brigham Young University, 401 WIDB, Provo, UT. 84602 USA. E-mail: seth.bybee@gmail.com

⁴Department of Biology, Ghent University, Ledeganckstraat 35, B-9000 Ghent, Belgium. E-mail: henri.dumont@ugent.be

⁵France. E-mail: fleckgunther@gmail.com

⁶Plant Pest Diagnostics Branch, California Department of Food & Agriculture, 3294 Meadowview Road, Sacramento, CA 95832-1448, USA. E-mail: rosser.garrison@cdfa.ca.gov; natalia.ellenrieder@gmail.com

⁷Kanagawa Prefectural Museum of Natural History, 499 Iryuda, Odawara, Kanagawa, 250-0031 Japan.

E-mail: paruki@nh.kanagawa-museum.jp

⁸Department of Entomology, Rutgers University, Blake Hall, 93 Lipman Drive, New Brunswick, New Jersey 08901, USA.

E-mail: may@aesop.rutgers.edu

⁹Griffith School of the Environment, Griffith University, Nathan Q 4111, Australia. E-mail: agorr@bigpond.com

¹⁰Slater Museum of Natural History, University of Puget Sound, Tacoma, Washington 98416, USA.

E-mail: dennispaulson@comcast.net

¹¹4856 9th Avenue, Sacramento, California, 95820, USA. E-mail: arehn@sbcglobal.net

¹²Water Science, Office of Environment and Heritage, NSW Department of Premier and Cabinet, PO Box 29, Lidcombe NSW 1825, Australia. E-mail: gunther.theischinger@environment.nsw.gov.au

¹³Division of Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra ACT 0200, Australia. E-mail: john.trueman@anu.edu.au

¹⁴Room 206 Boyden Hall, 195 University Avenue, Rutgers University, Newark, NJ, 07102, USA.

E-mail: jware42@andromeda.rutgers.edu

* In: Zhang, Z.-Q. (Ed.) Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013). *Zootaxa*, 3703, 1–82.

Abstract

An updated classification and numbers of described genera and species (until 2010) are provided up to family level. We argue for conserving the family-group names Chlorocyphidae, Euphaeidae and Dictyodidae, as well as retaining Epiophlebiidae in the suborder Anisozygoptera. Pseudostigmatidae and New World Protoneuridae are sunk in Coenagrionidae and Old World Protoneuridae in Platycnemididae. The families Amphipterygidae and Megapodagrionidae as traditionally recognized are not monophyletic, as may be the superfamily Calopterygoidea. The proposal to separate Chlorogomphidae, Cordulegastriidae and Neopetaliidae from Libelluloidea in their own superfamily Cordulegastroidea is adopted. Macromiidae, Libellulidae and Synthemistidae and a restricted Corduliidae are accepted as families, but many genera of Libelluloidea are retained as *incertae sedis* at present. 5952 extant species in 652 genera have been described up to 2010. These are placed here in 30 families; recent proposals to separate additional families from Amphipterygidae and Megapodagrionidae have not yet been incorporated.

Introduction

This publication presents a classification of extant suborders, superfamilies and families of Odonata, based on the principles of taxonomic stability (usage should change as little as possible) and monophyly of extant groups, ordered preferably by placing smaller sister-groups first (see Dijkstra & Kalkman 2012). Family-group names and authorities follow Bechly (1996; 2003), i.e. assuming that Selys's legions are not available (see Bechly 1999; Trueman 1999). Exceptions are three names that should be assigned to Kennedy (1920), three that are conserved because of prevailing usage, and the preferred spelling Yakobson over Jacobsen. Subfamilies are omitted as these generally are still unresolved. Novel (often rankless) terms like Lestomorpha, Caloptera, Epiprocta, Aeshnomorpha and Cavilabiata are avoided as these, in our opinion, have only a vernacular application.

In the past, wing venation was used as the main guide for classifying Odonata, but as similar characters evolved multiple times, this often does not reliably indicate close relationships (e.g. Carle *et al.* 2008; Dijkstra & Vick 2006; Fleck *et al.* 2008a; Pilgrim & von Dohlen 2008; Ware *et al.* 2007). Moreover, as any potential outgroup of winged insects lacks wings, wing-based phylogenies and classifications (e.g. Bechly 1996; 2003; Trueman 1996) rely on prior assumptions about wing evolution, and must thus be treated with caution (Trueman 2007). Studies incorporating other morphological features, such as those of genitalia and larvae, may help overcome this (e.g. Fleck *et al.* 2008a; Pessacq 2008; Rehn 2003; von Ellenrieder 2002), as increasingly are genetic studies (e.g. Bybee *et al.* 2008; Dumont *et al.* 2010). Recent phylogenetic progress in Anisoptera (Blanke *et al.* 2013) and Zygoptera (Dijkstra *et al.* 2013) could not be fully integrated in the present paper. We exclude fossil taxa, since they lack most morphological and all genetic information, and can therefore not be classified with the same criteria as extant taxa. Once the phylogeny of extant Odonata is settled this may provide a framework to classify fossils (Trueman 2007).

Information on the number of genera and species per family is derived from the Global Species Database Odonata prepared for the Catalogue of Life (van Tol 2005), updated by the compiler to 2010. 5952 extant species of Odonata have been described (30 families, 652 genera), of which 2941 belong to the suborder Zygoptera (18 families, 308 genera; but see notes 11 and 20), 3011 to the Anisoptera (11 families, 344 genera), and two in one genus to the Anisozygoptera (but see note 29). It is estimated that between 1000 and 1500 species still await description (Kalkman *et al.* 2008). If true, the actual number of extant species will lie between 7000 and 7500. Since 1970 nearly 40 species have been described annually and with an undiminished rate of description an estimated 95% of all species will be described by 2030. About 250 species were described between 2006 to 2010, nearly all from tropical regions, with the highest contributions from the Neotropical (43%), Oriental (28%) and Australasian regions (19%, nearly all from New Guinea and Wallacea). Three-fifths belonged to just three families, Coenagrionidae (85 species), Libellulidae (37), and Platystictidae (27). In 2011 and 2012 approximately 90 new species and 10 genera were described and, as a number of species were also synonymized, the total is estimated to be close to 6000 species.

Classification

Order **Odonata** Fabricius, 1793 (3 suborders, 10 superfamilies, 30 families) ¹

Suborder **Zygoptera** Selys, 1854 (4 superfamilies, 18 families) ²

-
1. Modern odonates are considered monophyletic, consisting of three suborders. Zygoptera is placed first because it has about 70 fewer species than its sister-group. Anisoptera plus Anisozygoptera is now larger by a factor of only 1.02 and as the number of undiscovered species may be higher in Zygoptera, the total number may as well. Even if that is the case, we would favour retaining the traditional sequence of the suborders.
 2. It is generally agreed that Zygoptera is monophyletic (Bechly 1996; 2003; Bybee *et al.* 2008; Carle *et al.* 2008; Dumont *et al.* 2010; Rehn 2003). See superfamilies for the phylogenetic reasoning for their order.

- Superfamily **Lestoidea** Calvert, 1901 (4 families)³
- Family **Hemiphlebiidae** Kennedy, 1920 (1 genus, 1 species)⁴
- Family **Perilestidae** Kennedy, 1920 (2 genera, 19 species)⁵
- Family **Synlestidae** Tillyard, 1917 (9 genera, 39 species)^{6 7}
- Family **Lestidae** Calvert, 1901 (9 genera, 151 species)⁸
- Superfamily **Platystictoidea** Kennedy, 1920 (1 family)
- Family **Platystictidae** Kennedy, 1920 (6 genera, 224 species)⁹
- Superfamily **Calopterygoidea** Selys, 1850 (10 families)¹⁰
- Family **Amphipterygidae** Tillyard, 1917 (4 genera, 14 species)¹¹
- Family **Calopterygidae** Selys, 1850 (21 genera, 185 species)¹²

-
3. A monophyletic group that includes Lestidae and three smaller families is the sister-group of all other Zygoptera (Bybee *et al.* 2008; Carle *et al.* 2008; Davis *et al.* 2011; Dumont *et al.* 2010). This is treated as a superfamily, called either Lestoidea (e.g. Carle *et al.* 2008) or Lestinoidea (e.g. Bybee *et al.* 2008; Rehn 2003) to avoid confusion with the unrelated genus *Lestoidea* Tillyard, 1913. Grammatically the former is correct, while the latter implies there is also a family Lestiniidae (etc.); the principle of homonymy does not apply where names belong to different groups (family- and genus- respectively). Moreover, if the principle would be applied, the genus name would be the junior homonym. Thus Lestoidea is used and, while inconvenient, its meaning should be obvious from context. Family order is phylogenetic (Bybee *et al.* 2008; Dumont *et al.* 2010).
 4. The monotypic Hemiphlebiidae is the sister-group of all remaining Lestoidea (Davis *et al.* 2011; Dumont *et al.* 2010; Rehn 2003).
 5. The monophyly of this small and fairly homogeneous family was supported by morphological analyses (Bechly 1996; 2003; Rehn 2003), but not by some permutations of molecular analyses (Bybee *et al.* 2008). The latter excluded the geographically disparate *Nubiolestes*, for which Bechly (1996) established the subfamily Nubiolestinae. Genetic data and morphology indicate it belongs to Synlestidae (Dijkstra *et al.* 2013; May *et al.* unpubl.). Bybee *et al.* (2008) doubted their own recovery of this family as paraphyletic, suggesting data limitations of sequenced genes as one possible explanation.
 6. Synlestidae may not be monophyletic: the monotypic Chorismagrionidae Tillyard & Fraser, 1938 is probably included (Bybee *et al.* 2008; Dumont *et al.* 2010), but the placement of *Megalestes* (= Megalestidae Tillyard & Fraser, 1938) and other similar genera vary among analyses (Bechly 1996; 2003; Dumont *et al.* 2010; Rehn 2003). New molecular evidence suggests the family includes *Nubiolestes* (note 5) and the geographically disparate genus *Phylolestes* (May *et al.* unpubl.).
 7. The name Chlorolestidae Fraser, 1951 is frequently used (23% preference in Google search), but predated by Synlestidae.
 8. Lestidae appears to be monophyletic (Bybee *et al.* 2008; Dumont *et al.* 2010; Rehn 2003).
 9. The family Platystictidae is monophyletic and the sister-group of all Zygoptera excluding Lestoidea (Bybee *et al.* 2008; Davis *et al.* 2011; Dumont *et al.* 2010; van Tol *et al.* 2009). Thus it falls well outside Coenagrionoidea and requires a superfamily Platystictoidea of its own.
 10. The superfamily name Calopterygoidea has been used for a very diverse assemblage of mostly densely-veined damselflies. With the superfamilies Lestoidea, Platystictoidea and Coenagrionoidea reasonably well defined (notes 3, 9, 24), the remaining families are left together without much support for their monophyly, although Bybee *et al.* (2008) found support for it in some analyses, as did Carle *et al.* (2008) if Isostictidae is included. Because of the ‘amphipterygid’ and ‘megapodagrionid’ problems (notes 11, 20), relationships between the families are unresolved, and therefore it is most convenient to group all these families together for the time being. Calopterygoidea may prove paraphyletic, requiring the creation of further superfamilies. Families are listed alphabetically.
 11. Based on larvae, Novelo-Gutiérrez (1995) restricted Amphipterygidae to the small and geographically disjunct genera *Amphipteryx* and *Devadatta* (together forming subfamily Amphipteryginae), and *Pentaplebia* and *Rimanella* (forming Rimanellinae Davies & Tobin, 1984 = Pentaplebiinae Novelo-Gutiérrez, 1995). Rehn’s (2003) morphological phylogenetic reconstruction confirmed this classification, but molecular analysis shows the group is probably polyphyletic (Bybee *et al.* 2008; Dumont *et al.* 2010), although the important position of *Amphipteryx* was untested. Recent molecular analysis indicates that each genus is probably best regarded a family of its own (Dijkstra *et al.* 2013).
 12. Calopterygidae appears monophyletic (Bybee *et al.* 2008; Dumont *et al.* 2010; Rehn 2003), although Caliphaecidae Fraser, 1929 and especially Hetaerinidae Tillyard & Fraser, 1939 are sometimes considered as separate families. The former falls within Calopterygidae, while the latter is the sister-group of all remaining Calopterygidae (Dijkstra *et al.* 2013; Dumont *et al.* 2005; 2010). However, with Calopterygidae *sensu lato* monophyletic as a whole, taxonomic stability is served by treating *Hetaerina* and its close relatives as a subfamily.

- Family **Chlorocyphidae** Cowley, 1937 (19 genera, 144 species)^{13 14}
 Family **Dicteriadiidae** Montgomery, 1959 (2 genera, 2 species)^{15 16}
 Family **Euphaeidae** Yakobson & Bianchi, 1905 (12 genera, 68 species)^{17 18}
 Family **Lestoideidae** Munz, 1919 (2 genera, 9 species)¹⁹
 Family **Megapodagrionidae** Calvert, 1913 (42 genera, 296 species)²⁰
 Family **Philogangidae** Kennedy, 1920 (1 genus, 4 species)²¹
 Family **Polythoridae** Munz, 1919 (7 genera, 59 species)²²
 Family **Pseudolestidae** Fraser, 1957 (1 genus, 1 species)²³
 Superfamily **Coenagrionoidea** Kirby, 1890 (3 families)²⁴
 Family **Isostictidae** Fraser, 1955 (12 genera, 46 species)²⁵

-
13. The distinctive family Chlorocyphidae is clearly monophyletic (Bybee *et al.* 2008; Dumont *et al.* 2010; Rehn 2003).
 14. Widely known as Chlorocyphidae (almost 99% preference in Google search), although that name is predated by Libellaginidae Yakobson & Bianchi, 1905. An application to the ICZN for the suppression of this name will be prepared by some of the present authors.
 15. A tiny but distinctive family, molecular data and larvae indicate Dicteriadiidae fall within the calopterygoid complex (Dumont *et al.* 2010; Fleck *et al.* 2008b; 2012).
 16. Three family-group names are in use and while Heliocharitidae Tillyard & Fraser, 1939 is the oldest (5% preference in Google search), Dicteriadiidae (85%) and Dicteriastidae (10%) are preferred. An application to the ICZN for the preservation of Dicteriadiidae will be prepared by some of the present authors.
 17. The distinctive family Euphaeidae appears to be monophyletic (Bybee *et al.* 2008; Dumont *et al.* 2010; Rehn 2003).
 18. Bechly (1999) argues that the older name Epallagidae Needham, 1903 should be applied, although Euphaeidae dominates in usage by almost 85% (Google search). An application to the ICZN for the suppression of the older name will be prepared by some of the present authors.
 19. Novelo-Gutiérrez (1995) recognized the shared characters of the superficially dissimilar genera *Diphlebia* and *Lestoidea*, placing them in Diphlebiidae Heymer, 1975, which is predated by Lestoideidae Munz (van Tol 1995). Molecular evidence confirms this placement (Bybee *et al.* 2008; Carle *et al.* 2008; Dijkstra *et al.* 2013). As family-group names are available, each of these rather distinct genera could also be treated as a family. However, genus- and family-group names that refer to the same group of species are redundant, while distinctness is subjective: classifying these lineages under a single name communicates their common ancestry.
 20. The heterogeneity of Megapodagrionidae has long been recognized, as is apparent from the many family-group names available (e.g. Philosinidae Kennedy, 1925; Hypolestidae Tillyard & Fraser, 1938; Thaumatonneuridae Tillyard & Fraser, 1938; Argiolestidae Fraser, 1957; Heteragrionidae Rácenis, 1959; Philogeniidae Rácenis, 1959). Molecular and morphological data indicate the group is not monophyletic and contains at least six independent lineages (Bybee *et al.* 2008; Dumont *et al.* 2010; Kalkman *et al.* 2010; Rehn 2003; van Tol *et al.* 2009). Recent molecular analyses suggest that all aforementioned families should be reinstated and up to eight additional families may require description (Dijkstra *et al.* 2013; Kalkman & Theischinger 2013).
 21. Novelo-Gutiérrez (1995) removed *Philoganga* from Amphipterygidae, assuming it was close to *Diphlebia*. That, however, is not supported by the phylogenetic evidence published (Bybee *et al.* 2008; Dijkstra *et al.* 2013; Rehn 2003). It is best to place this distinctive genus in its own family Philogangidae.
 22. The distinctive family Polythoridae appears to be monophyletic (Bybee *et al.* 2008; Rehn 2003).
 23. The distinct morphology of *Pseudolestes mirabilis* warrants considering it a monotypic family and not part of the polyphyletic Megapodagrionidae, where it has often been placed, or Amphipterygidae, with which it shares larval features (Yu & Bu 2011). This is confirmed by molecular analysis (Dijkstra *et al.* 2013).
 24. A monophyletic group including Coenagrionidae, Protoneuridae, Platycnemididae and Pseudostigmatidae as traditionally known, is well supported (Bybee *et al.* 2008; Carle *et al.* 2008; Dijkstra *et al.* 2013). Isostictidae is either the sister-group of this assemblage (Bybee *et al.* 2008) or part of the calopterygoid complex (Carle *et al.* 2008). We believe that until further evidence is available, the best solution is to retain them in Coenagrionoidea, placing them before the remaining families. The family classification and order of those families, however, have been unsettled by the discovery of the polyphyly of Protoneuridae Yakobson & Bianchi, 1905 *sensu lato*, and paraphyly of Platycnemididae and Coenagrionidae *sensu stricto* (notes 26–27).
 25. Molecular evidence suggests Isostictidae is monophyletic (Bybee *et al.* 2008; Carle *et al.* 2008; Dijkstra *et al.* 2013).

Family **Platycnemididae** Yakobson & Bianchi, 1905 (40 genera, 404 species)²⁶

Family **Coenagrionidae** Kirby, 1890 (114 genera, 1267 species)²⁷

Suborder **Anisozygoptera** Handlirsch, 1906 (1 superfamily, 1 family)²⁸

Superfamily **Epiophlebioidea** Muttkowski, 1910 (1 family)

Family **Epiophlebiidae** Muttkowski, 1910 (1 genus, 2 species)²⁹

Suborder **Anisoptera** Selys, 1854 (5 superfamilies, 11 families)³⁰

Superfamily **Aeshnoidea** Leach, 1815 (2 families)³¹

Family **Austropetaliidae** Carle & Louton, 1994 (4 genera, 11 species)³²

-
26. Old World ‘protoneurids’ are not closely related to the true New World Protoneuridae (Pessacq 2008), possibly being the sister-group of Platycnemididae (Bybee *et al.* 2008; Dumont *et al.* 2010; van Tol *et al.* 2009), but falling within that family in more extensive analyses (Carle *et al.* 2008; Dijkstra *et al.* 2013; Rehn 2003). We prefer to merge these morphologically similar groups, as combined they are monophyletic and separating them establishes a family name that would probably soon disappear again. Molecular evidence for the transfer of a few genera from Coenagrionidae and vice versa is incorporated in the diversity figures (Dijkstra *et al.* 2013).
27. While earlier subdivisions of Coenagrionidae are not supported by morphology (O’Grady & May 2003), molecular studies indicate that the family consists of two major groups. The first includes large genera like *Agriocnemis*, *Coenagrion* and *Pseudagrion*, and ‘ischnurine’ genera characterized by a vulvar spine, such as *Enallagma* and *Ischnura* (see also Hovmöller 2006). The second, of which many genera possess an angulate frons, incorporates Protoneuridae *sensu stricto*, Pseudostigmatidae Kirby, 1890, Teinobasinae Tillyard, 1917 (see De Marmels 2007), and possibly other genera such as *Argia* (Bybee *et al.* 2008; Carle *et al.* 2008; Dijkstra *et al.* 2013; Dumont *et al.* 2010). Coryphagrionidae Pinhey, 1962 was recovered with Pseudostigmatidae (Bechly 1996; Clausnitzer & Lindeboom 2002; Groeneveld *et al.* 2007; Ingley *et al.* 2012; Rehn 2003). Each of the two groups may contain over 600 species. If they are supported by more extensive investigations, each could be treated as a family. As they are likely to be sister-groups, each could also be considered a subfamily, retaining a massive Coenagrionidae as the order’s largest family, as is done here.
28. *Epiophlebia* is accepted as the extant sister-group of ‘true’ Anisoptera (Bechly 1996; 2003; Bybee *et al.* 2008; Davis *et al.* 2011; Fleck *et al.* 2008b; Rehn 2003). The genus has traditionally been placed in the suborder Anisozygoptera, although the initial usage of that name was for fossil taxa. Because that assemblage is considered paraphyletic, the suborder is often rejected (e.g. Davis *et al.* 2011) and all extant non-zygopteran odonates are combined in an alternative suborder Epiprocta Lohmann, 1996 (= Epiproctophora Bechly, 1996). Alternatively, Anisoptera could be expanded to include *Epiophlebia* (Dumont *et al.* 2010) or all ‘anisozygopterans’ (Trueman 2007). As higher level names are not governed by the ICZN we prefer a solution that retains Anisoptera and Anisozygoptera as well-understood and widely preferred terms predating Epiprocta by 142 and 90 years. Moreover, we believe that each of the three fundamentally different types of male secondary genitalia found in Odonata deserve separate and equivalent taxonomic status. Therefore we leave *Epiophlebia* in Anisozygoptera and accept the consequence that, while the suborder is monophyletic so far as extant species are concerned, it may be paraphyletic when fossil taxa are included. Alternatively, Epiophlebioptera Bechly, 1996 (introduced as infra-order) can be accepted as a suborder. However, this only replaces a familiar name for the extant species, while leaving fossil Anisozygoptera paraphyletic as before, except that now it is so by the inclusion of Anisoptera as well as Epiophlebioptera. If the fossil group is paraphyletic, we anticipate its subdivision with further revision, ultimately restricting Anisozygoptera to the extant species and its nearest fossil relatives.
29. A third and fourth species of *Epiophlebia* were described recently from China based on limited evidence (Carle 2012; Li *et al.* 2012), especially in the light of negligible genetic variation found in three of the species (Büsse *et al.* 2012).
30. There is general agreement that Anisoptera is monophyletic (Bechly 1996; 2003; Bybee *et al.* 2008; Carle *et al.* 2008; Davis *et al.* 2011; Fleck *et al.* 2008b; Rehn 2003). Although the major groupings are resolved, three well-defined monophyletic groups (Aeshnoidea, Gomphoidea and Petaluroidea, sometimes combined into larger clades) rotate as the sister-group of remaining anisopterans in the various published trees. This makes the order of the first three superfamilies difficult: we follow the most comprehensive analysis of odonate phylogeny (Bybee *et al.* 2008) in placing Aeshnoidea sister to the remainder of Anisoptera (followed by Petaluroidea, Gomphoidea and the remaining groups), although extensive recent morphological analysis places Gomphoidea there (Blanke *et al.* 2013).
31. The monophyly of Aeshnidae, Austropetaliidae and their combination in Aeshnoidea is well supported (Bybee *et al.* 2008; Carle *et al.* 2008; Davis *et al.* 2011; Fleck *et al.* 2008b), with only Fleck *et al.* (2008b) and Fleck (2011) presenting support for an even larger monophyletic group including Petaluridae as well. We propose to exclude the latter from the superfamily, as did Fleck (2011).
32. Bechly (1996) separated *Archipetalia* in Archipetaliidae, but while a detailed phylogenetic analysis of Austropetaliidae is wanting, the whole appears monophyletic and splitting is thus unwarranted.

- Family **Aeshnidae** Leach, 1815 (51 genera, 456 species)³³
 Superfamily **Petaluroidea** Needham, 1903 (1 family)
 Family **Petaluridae** Needham, 1903 (5 genera, 10 species)³⁴
 Superfamily **Gomphoidea** Rambur, 1842 (1 family)
 Family **Gomphidae** Rambur, 1842 (87 genera, 980 species)³⁵
 Superfamily **Cordulegastroidea** Hagen, 1875 (3 families)³⁶
 Family **Chlorogomphidae** Needham, 1903 (3 genera, 47 species)³⁷
 Family **Cordulegastridae** Hagen, 1875 (3 genera, 46 species)³⁸
 Family **Neopetaliidae** Tillyard & Fraser, 1940 (1 genus, 1 species)³⁹

-
33. A morphological analysis of all existing genera found little support for most recognized subfamilies of Aeshnidae (von Ellenrieder 2002). Some of these are occasionally treated as families, for example by Bechly (1996; 2003) and Peters & Theischinger (2007), e.g. Allopetaiidae Cockerell, 1913; Brachytronidae Cockerell, 1913; Gynacanthidae Cockerell, 1913; Telephlebiidae Cockerell, 1913; Gomphaeschnidae Tillyard & Fraser, 1940; Caliaeschnidae Bechly, 1996. No extensive molecular work has been published to date.
34. The well supported monophyletic family Petaluridae (Bybee *et al.* 2008; Fleck *et al.* 2008b) is best separated in a superfamily of its own, Petaluroidea (see Fleck 2011; note 30, 31).
35. The monophyly of the family Gomphidae is well supported (Bybee *et al.* 2008; Dumont *et al.* 2010; Fleck *et al.* 2008b; Rehn 2003). The first two authors favoured its recognition at superfamily level, which we follow. Carle (1986) recognised eight subfamilies, of which Lindeniidae Yakobson & Bianchi, 1905 is occasionally treated as a family (e.g. Davis *et al.* 2011). However, with no extensive molecular phylogenetic reconstruction available, the validity of any classification remains untested. Moreover, for the sake of stability, it seems best to express any supported subdivision at the subfamily level at most.
36. While the monophyly of the ‘higher’ libelluloids (*sensu* Ware *et al.* 2007) is strongly supported (note 40) both the inclusion of the three ‘lower’ families in Libelluloidea and their relationships to each other and the ‘higher’ families are poorly resolved (e.g. Blanke *et al.* 2013; Dumont *et al.* 2010; Fleck *et al.* 2008b). Fleck (2011) defined Cordulegastroidea to include Cordulegastridae and Neopetaliidae, but left the position of Chlorogomphidae undecided, although not ruling out the possibility that they may form the sister-group of the former pair. Indeed, some analyses suggest they form a monophyletic group, but sampling has been very limited (Bybee *et al.* 2008; Carle *et al.* 2008; Davis *et al.* 2011). We propose to restrict the superfamily Libelluloidea to Libellulidae and its nearest relatives, and classify Chlorogomphidae in Cordulegastroidea, although there is a chance the latter is paraphyletic. As Chlorogomphidae is morphologically more diverse than the other two families, only an extensive molecular study can settle the matter. The family order is alphabetic.
37. Until recently Chlorogomphidae was included in Cordulegastridae but it is morphologically distinct (Carle 1995; Fleck 2011) and in some analyses comes out closer to Neopetaliidae (e.g. Carle *et al.* 2008; Fleck *et al.* 2008b), ‘higher’ libelluloids (e.g. Bechly & Ueda 2002; Blanke *et al.* 2013; Davis *et al.* 2011; Ware *et al.* 2007) or as sister-group to Cordulegastroidea and Libelluloidea combined (e.g. one scenario in Fleck 2011).
38. The homogeneous family Cordulegastridae is very likely monophyletic (Lohmann 1992).
39. Neopetaliidae is monotypic since all genera except *Neopetalia* were transferred to the distantly related Austropetaliidae (Carle & Louton 1994).

Superfamily **Libelluloidea** Leach, 1815 (4 families)⁴⁰

Family **Synthemistidae** Tillyard, 1911 (9 genera, 46 species)⁴¹

Family **Macromiidae** Needham, 1903 (4 genera, 125 species)⁴²

Family **Corduliidae** Selys, 1850 (20 genera, 154 species)⁴³

Family **Libellulidae** Leach, 1815 (142 genera, 1037 species)⁴⁴

Genera *incertae sedis* (19 genera, 98 species)⁴⁵

-
40. The monophyly of Libelluloidea (Libellulidae plus Corduliidae *sensu lato*) is strongly supported (Bybee *et al.* 2008; Davis *et al.* 2011; Dumont *et al.* 2010; Fleck *et al.* 2008b; Ware *et al.* 2007). However, the paraphyletic nature of traditional ‘corduliids’ has long been recognized, as is apparent from the many family-group names available. Ware *et al.* (2007) retrieved four clades, which find support in the other studies listed as well. We recognize three of these as families, although relationships within and among them are largely unresolved, and leave a large number of genera *incertae sedis* (note 45). We follow the supertree of Davis *et al.* (2011) in placing Synthemistidae as the sister-group of remaining Libelluloidea, and Corduliidae *sensu stricto* as the sister-group of Libellulidae. This also seems most in agreement with morphology (Bechly 1996; 2003).
41. Ware *et al.* (2007) found similar support for their so-called GSI-clade as for the families Macromiidae, Corduliidae *sensu stricto* and Libellulidae. This is completely incongruent with the morphological analysis of Bechly (1996; 2003), who placed the constituent genera in seven families. Ware *et al.* (2007) recovered four of these as polyphyletic: Synthemistidae represented by *Choristhemis*, *Eusynthemis*, *Synthemiosis* and *Synthemis* (*Archaeosynthemis*, *Austrosynthemis*, *Palaeosynthemis*, *Parasynthemis* and *Tonyosynthemis* not sampled); Gomphomacromiidae Tillyard & Fraser, 1940 by *Archaeophya* and *Gomphomacromia*; Austrocorduliidae Bechly, 1996 by *Austrocordulia*, *Austrophya*, *Lathrocordulia*, *Micromidia* and *Syncordulia* (*Apocordulia* and *Lauromacromia* not sampled); Oxygastridae Bechly, 1996 by *Hesperocordulia* and *Oxygastra* (*Neocordulia* not sampled). The genera *Idionyx* and *Macromidia* of Idionychidae Tillyard & Fraser, 1940 were sister-groups with low support, while only *Cordulephya* was sampled of Cordulephyidae Tillyard, 1917 (*Neophya* not). Pseudocorduliidae Lohmann, 1996 was sampled but is monotypic. The genera *Idomacromia* and *Nesocordulia* of Idomacromiidae Tillyard & Fraser, 1940 were not sampled. Bechly’s “eurypalpid” (Synthemistidae, Gomphomacromiidae and Pseudocorduliidae) and “trichopalpid” groups (remaining families) were also not recovered. While this result calls the validity of these families into question, the inconsistency (even for the morphologically and geographically compact Synthemistidae) also raises concerns about the suitability of the available molecular data to resolve the presumably deep splits. As the recovered monophyly may be artificial, we consider all GSI-genera as *incertae sedis* (note 45). However, Synthemistidae is the oldest available name in the complex and will thus eventually be retained in some form or other. As it is counterproductive to temporarily cancel this name, we apply it here for the traditional combination of genera (Bechly 1996; 2003).
42. May (1997) showed that *Macromia*, *Phyllomacromia*, *Didymops* and *Epophthalmia* form a monophyletic group based on morphology, which is supported by the molecular analysis of Ware *et al.* (2007).
43. In its restricted sense, Corduliidae consist of mostly Holarctic genera, a few Neotropical groups and the predominantly Australasian group around *Hemicordulia*, which Bechly (1996) separated as Hemicorduliidae. The latter, however, makes the family paraphyletic (Ware *et al.* 2007). Genera included by Ware *et al.* (2007) were *Aeschnosoma*, *Cordulia*, *Epithecina*, *Helocordulia*, *Hemicordulia*, *Neurocordulia*, *Pentathemis*, *Procordulia*, *Rialla*, *Somatochlora*, to which *Antipodochlora*, *Cordulisantonia*, *Dorocordulia*, *Guadalca*, *Heteronaias*, *Libellulosoma*, *Metaphya*, *Navicordulia*, *Paracordulia* and *Williamsonia* can be added based on morphology (Bechly 1996; 2003; Fleck 2012).
44. The monophyly of Libellulidae is strongly supported (Bybee *et al.* 2008; Dumont *et al.* 2010; Fleck *et al.* 2008b; Ware *et al.* 2007). Although a few clusters of related genera have been identified, no overall divisions are apparent (Fleck *et al.* 2008a; Ware *et al.* 2007; 2008; Pilgrim & von Dohlen 2007). Of many named subfamilies, only Urothemistidae Lieftinck, 1954 (= Macrodiplactidae Fraser, 1957) is sometimes recognized as a family (e.g. Bechly 1996; 2003). While it may be monophyletic, it does not stand apart from Libellulidae as a whole (Ware *et al.* 2007; Fleck *et al.* 2008b; Pilgrim & von Dohlen 2008).
45. The genera *Apocordulia*, *Archaeophya*, *Austrocordulia*, *Austrophya*, *Cordulephya*, *Gomphomacromia*, *Hesperocordulia*, *Idionyx*, *Idomacromia*, *Lathrocordulia*, *Lauromacromia*, *Macromidia*, *Micromidia*, *Neocordulia*, *Neophya*, *Nesocordulia*, *Oxygastra*, *Pseudocordulia* and *Syncordulia* are considered *incertae sedis*. The only alternative would be to treat the main libelluloid clades retrieved by Ware *et al.* (2007) equally and unite these genera associated with GSI-clade under the oldest available name (Synthemistidae), but we are hesitant to apply a name associated with a strictly Papua-Australian group to such a diverse and dispersed assemblage without more evidence (note 41).

Cited references

- Bechly, G. (1996) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der phylogentischen Systematik und des Grundplanes der Odonata. *Petalura (Special Volume)*, 2, 1–402.
- Bechly, G. (1999) Epallagidae versus Euphaeidae revisited. *International Journal of Odonatology*, 2, 137–139.
<http://dx.doi.org/10.1080/13887890.1999.9748124>
- Bechly, G. (2003) Phylogenetic systematics of Odonata. In: Schorr, M. & Lindeboom, M. (eds): *Dragonfly Research, Volume 1*. Zerf-Tübingen (CD-ROM).
- Bechly, G. & Ueda, K. (2002) The first fossil record and first New World record for the dragonfly clade Chlorogomphida (Insecta: Odonata: Anisoptera: Araripechlorogomphidae n. fam.) from the Crato Limestone (Lower Cretaceous, Brazil). *Stuttgarter Beiträge zur Naturkunde Serie B*, 328, 1–11.
- 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.
<http://dx.doi.org/10.1111/syen.12012>
- Büsse, S., von Grumbkow, P., Hummel, S., Shah, D.N., Tachamo Shah, R.D., Li, J., Zhang, X., Yoshizawa, K., Wedmann, S. & Hörnschemeyer, T. (2012) Phylogeographic analysis elucidates the influence of the ice ages on the disjunct distribution of relict dragonflies in Asia. *PLoS One*, 7, e38132.
<http://dx.doi.org/10.1371/journal.pone.0038132>
- 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.
<http://dx.doi.org/10.1111/j.1096-0031.2007.00191.x>
- Carle, F.L. (1986) The classification, phylogeny and biogeography of the Gomphidae (Anisoptera). I. Classification. *Odonatologica*, 15, 275–326.
- Carle, F.L. (1995) Evolution, taxonomy, and biogeography of ancient Gondwanian libelluloides, with comments on anisopteroid evolution and phylogenetic systematics (Anisoptera: Libelluloidea). *Odonatologica*, 24, 383–424.
- Carle, F.L. (2012) A new *Epiophlebia* (Odonata: Epiophlebioidea) from China with a review of epiophlebian taxonomy, life history, and biogeography. *Arthropod Systematics & Phylogeny*, 70, 75–83.
- 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.
- Carle, F.L. & Louton, J.A. (1994) The larva of *Neopetalia punctata* and establishment of Austropetaliidae fam. nov. (Odonata). *Proceedings of the Entomological Society of Washington*, 96, 147–155.
- Clausnitzer, V. & Lindeboom, M. (2002) Natural history and description of the dendrolimnetic larvae of *Coryphagrion grandis* (Odonata). *International Journal of Odonatology*, 5, 29–44.
<http://dx.doi.org/10.1080/13887890.2002.9748175>
- 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.
<http://dx.doi.org/10.1186/1471-2148-11-252>
- 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. & Kalkman, V.J. (2012) Phylogeny, taxonomy and classification of European dragonflies and damselflies (Odonata): a review. *Organisms Diversity & Evolution*, 12, 209–227.
<http://dx.doi.org/10.1007/s13127-012-0080-8>
- Dijkstra, K.-D.B., Kalkman, V.J., Dow, R.A., Stokvis, F.R., & van Tol, J. (2013) Redefining the damselfly families: the first comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology*
<http://onlinelibrary.wiley.com/doi/10.1111/syen.12035/pdf>
- 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.
<http://dx.doi.org/10.1080/13887890.2006.9748263>
- 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.
<http://dx.doi.org/10.1080/10635150590949869>
- Dumont, H.J., Vierstraete, A. & Vanfleteren, J.R. (2010) A molecular phylogeny of the Odonata (Insecta). *Systematic Entomology*, 35, 6–18.

- <http://dx.doi.org/10.1111/j.1365-3113.2009.00489.x>
- Fleck, G. (2011) Phylogenetic affinities of Petaluridae and basal Anisoptera families (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, 4, 83–104.
- Fleck, G. (2012) Preliminary notes on the genus *Aeschnosoma* Selys, 1870 (Odonata: Anisoptera: Corduliidae s.s.). *Annales de la Société Entomologique de France*, 48, 225–228.
<http://dx.doi.org/10.1080/00379271.2012.10697766>
- 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 & Evolution*, 8, 1–16.
<http://dx.doi.org/10.1016/j.ode.2006.08.003>
- 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.
<http://dx.doi.org/10.1111/j.1439-0469.2008.00474.x>
- Fleck, G., Neiss, U.G. & Hamada, N. (2012) The larva of *Dieterias* Selys, 1853 (Odonata: Heliocharitidae [= Dieteriidae]), and taxonomic and phylogenetic notes on Heliocharitidae. *Zootaxa* 3164, 32–40.
- 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 & Evolution*, 42, 339–346.
<http://dx.doi.org/10.1016/j.ympev.2006.05.040>
- 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.
- Ingle, 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.
<http://dx.doi.org/10.1111/j.1463-6409.2012.00555.x>
- 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.
<http://dx.doi.org/10.1080/13887890.2010.9748366>
- Kalkman, V.J. & Theischinger, G. (2013) Generic revision of Argiolestidae (Odonata), with four new genera. *International Journal of Odonatology*, 16, 1–52.
<http://dx.doi.org/10.1080/13887890.2012.749450>
- 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.
<http://dx.doi.org/10.1007/s10750-007-9029-x>
- Kennedy, C.H. (1920) The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *Ohio Journal of Science*, 21, 83–88.
- Lohmann, H. (1992) Revision der Cordulegastridae. 1. Entwurf einer neuen Klassifizierung der Familie (Odonata: Anisoptera). *Opuscula Zoologica Fluminensia*, 96, 1–18.
- Li, J., Nel, A., Zhang, X., Fleck, G., Gao, M., Lin, L. & Zhou, J. (2012) A third species of the relict family Epiophlebiidae discovered in China (Odonata: Epiproctophora). *Systematic Entomology*, 37, 408–412.
<http://dx.doi.org/10.1111/j.1365-3113.2011.00610.x>
- May, M.L. (1997) Reconsideration of the status of the genera *Phyllomacromia* and *Macromia* (Anisoptera: Corduliidae). *Odonatologica*, 26, 405–414.
- Novelo-Gutiérrez, R. (1995) The larva of *Amphipteryx* and a reclassification of Amphipterygidae *sensu lato*, based upon the larvae (Zygoptera). *Odonatologica*, 24, 73–87.
- 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.
<http://dx.doi.org/10.1080/0022293021000007453>
- Pessacq, P. (2008) Phylogeny of Neotropical Protoneuridae (Odonata: Zygoptera) and a preliminary study of their relationship with related families. *Systematic Entomology*, 33, 511–528.
<http://dx.doi.org/10.1111/j.1365-3113.2007.00414.x>
- Peters, G. & Theischinger, G. (2007) Die gondwanischen Aeshniden Australiens (Odonata: Telephlebiidae und Brachytronidae) *Denisia*, 20, 517–574.
- 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.
<http://dx.doi.org/10.1111/j.1365-3113.2007.00401.x>
- Rehn, A.C. (2003) Phylogenetic analysis of higher-level relationships of Odonata. *Systematic Entomology*, 28, 181–239.
<http://dx.doi.org/10.1046/j.1365-3113.2003.00210.x>

- Trueman, J.W.H. (1996) A preliminary cladistic analysis of Odonate wing venation. *Odonatologica*, 25, 59–72.
- Trueman, J.W.H. (1999) The family-group names based on Selys' Légions. *International Journal of Odonatology*, 2, 141–144.
<http://dx.doi.org/10.1080/13887890.1999.9748125>
- Trueman, J.W.H. (2007) A brief history of the classification and nomenclature of Odonata. *Zootaxa*, 1668, 381–394.
- van Tol, J. (1995) Family-group names based on *Amphipteryx*, *Diphlebia*, *Philoganga*, *Lestoidea*, *Rimanella* and *Pentaplebia* (Zygoptera). *Odonatologica*, 24, 245–248.
- van Tol, J. (2005) *Global Species Database Odonata*. <http://www.odonata.info> (5 August 2005)
- 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, 3–70.
- von Ellenrieder, N. (2002) A phylogenetic analysis of the extant Aeshnidae (Odonata: Anisoptera). *Systematic Entomology (London)*, 27, 437–467.
<http://dx.doi.org/10.1046/j.1365-3113.2002.00190.x>
- 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 & Evolution*, 45, 289–310.
<http://dx.doi.org/10.1016/j.ympev.2007.05.027>
- Yu, X. & Bu, W. (2011) A description of the remarkable larva of *Pseudolestes mirabilis* Kirby (Odonata: Pseudolestidae). *International Journal of Odonatology*, 14, 105–110.
<http://dx.doi.org/10.1080/13887890.2011.592486>