Phylogeny, classification and taxonomy of European dragonflies and damselflies (Odonata): a review

K.-D. B. Dijkstra & V. J. Kalkman

REVIEW

Phylogeny, classification and taxonomy of European dragonflies and damselflies (Odonata): a review

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Abstract Although Europe is the cradle of dragonfly systematics and despite great progress in the last 2 decades, many issues in naming its species and understanding their evolutionary history remain unresolved. Given the public interest, conservation importance and scientific relevance of Odonata, it is time that remaining questions on the species' status, names and affinities are settled. We review the extensive but fragmentary literature on the phylogeny, classification and taxonomy of European Odonata, providing summary phylogenies for well-studied groups and an ecological, biogeographic and evolutionary context where possible. Priorities for further taxonomic, phylogenetic and biogeographic research are listed and discussed. We predict that within a decade the phylogeny of all European species will be known.

Introduction

Europe is the cradle of dragonfly systematics. Linnaeus (1758) named the first species, Charpentier (1840) provided the first continental synthesis of an odonate fauna, and Selys

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with his countless contributions laid the very fundament of odonatology. More than 700 of the currently nearly 5,700 recognised species bear his names, a figure followed only distantly by another European, Lieftinck, with just over 500 species. Despite the head start, many issues in naming European dragonflies and understanding their history remain unresolved. Only after 170 years a thorough Ukrainian morphologist noticed that "*Brachythemis leucosticta*" as found north of the Mediterranean Sea was not what Burmeister (1839) named as such from South Africa. Over 240 years after the first dragonfly was named, it still proved possible for an inquisitive Bulgarian to discover a completely unique form, possibly even a genus, in the continent's extreme southeastern corner. Also large but indecisive fractions of users have preferred 'dissident' combinations of genus and species names: over a third use *Anaciaeschna* for *Aeshna isoceles*, almost a quarter *Chalcolestes* for *Lestes viridis* and nearly a fifth *Stylurus* for *Gomphus flavipes* (Zoological Records 1980-2004). These are just some examples of the slow maturation of European odonatology. On the other hand, interest for Odonata in Europe has never been greater: thousands now spend their summer days observing dragonflies, the 16 species listed in the European Union's Habitat Directive make them the primary invertebrates in freshwater conservation, and dragonflies are also often used as model organisms in scientific research. The recent advancements in our knowledge of odonate phylogeny are therefore of interest to many, and it is time that remaining questions on the species' status, names and affinities are settled. We therefore review the taxonomy and especially phylogeny and classification of European Odonata, summarising the large number of papers published in the last 2 decades. As old approaches reach their limitations, new methods came to fruition: what vein counts and spot shapes never resolved, base pair sequences possibly will (Trueman 2007). More than anyone, Mike May has shown

how to embrace novelty by knowing history. Therefore this European review is dedicated to that amiable American.

What do we consider a species?

Linnaean nomenclature aims for two conflicting things: (1) to offer stable labels for taxa and (2) to provide information about relationships of these taxa in a nested classification. Consequently, often to the dismay of users, new insights into relationships may lead to names changing. When defining a species, most apply a biological concept: a species is a group of populations whose members can produce viable offspring in nature. However, in most cases such detailed knowledge is unavailable, forcing taxonomists to apply more practical (usually morphological, but increasingly genetic) criteria to define species. Where populations appear different, but it is uncertain whether they constitute a distinct species, the subspecies category is often applied. Most lower-level taxonomic problems with European Odonata concern either (1) whether a subspecies is so distinct that recognising it as full species is more appropriate or (2) whether subspecies are distinct enough to be named at all. Criteria that may be applied are: (1) distinctness, i.e. both species and subspecies differ genetically from their nearest relatives without much gradual variation in-between, (2) distribution, i.e. subspecies of the same species cannot breed at the same location, and (3) appropriateness, i.e. is it more preferable to recognise a full species rather than a subspecies? The latter criterion is largely practical, because the presence of overlap is easier to prove than its absence, and because the characters distinguishing subspecies tend to be closer to ordinary individual variation, good species are easier to recognise than good subspecies. Nonetheless, past taxonomists often named variations (e.g. of size or paleness under environmental influence), thus swamping well-defined taxa with poorly defined ones. The paradox is that recognising a lower rank (subspecies) actually requires more scrutiny: (1) phenotypic expression must be ruled out to explain differences, (2) geographic analysis is needed to rule out gradual variation, (3) the possibility of recognising the taxon as a full species must be considered and (4) the previous three criteria must be considered also for the nominotypic subspecies, which is created automatically by the introduction of a subspecies.

What do we consider a genus?

Once a species' distinctness is confirmed, the question arises to which genus it belongs. Unlike with species, there is no biological definition for genera, families or any other higher taxonomic category. Their use can solely be governed by stability (names and classifications should change as little as possible) and monophyly (name should reflect the shared and exclusive ancestry of the species included, see below). Thus any change in name combinations should be preceded by (1) phylogenetic analysis, to preclude creation of non-monophyletic groups and (2) consideration of the solution that leads to least change, considering splits with additional care. Because genera are practical tools rather than biological entities, supplementary subjective arguments may be considered, such as numbers of species included. By unravelling evolutionary histories, phylogenetic studies aid to classify species into natural groups. Informative characters for phylogenetic reconstructions are generally either morphological or molecular. While venation was used as the main guide to define families and genera in the past, recent work has shown that such features may not identify groups of close relatives reliably, as similar characters, such as the reduction of certain veins, have evolved multiple times (e.g. Carle et al. 2008; Dijkstra and Vick 2006; Fleck 2004; Fleck et al. 2008a; Pilgrim and 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 of genitalia and larvae, may help overcome this problem (e.g. Fleck et al. 2008a; Pessacq 2008; Rehn 2003; von Ellenrieder 2002), as will genetic studies (e.g. Bybee et al. 2008; Dumont et al. 2009). Generally when molecular and morphological evidence is in agreement, often in synchrony with geographical or ecological patterns, relationships are resolved most convincingly.

Review of European Odonata

For ease of reference, discussed European genera (and higher taxa) are bold where discussed in detail.

There is general agreement that extant Odonata, **Zygoptera** and Anisoptera are all monophyletic groups (Bechly 1996; Bybee et al. 2008; Carle et al. 2008; Davis et al. 2011; Dumont et al. 2009; Hasegawa and Kasuya 2006; Rehn 2003; Saux et al. 2003). There is consensus that **Lestidae** and some smaller families (together representing just 7.5 % of global damselfly diversity) are the sister group of all other damselflies (Fig. 1; Bybee et al. 2008; Carle et al. 2008; Davis et al. 2011; Dumont et al. 2009). These 'lestomorphs' share distinctive features of the head and secondary genitalia (Rehn 2003), and consist of three small families (Hemiphlebiidae, Perilestidae, Synlestidae) with largely relictual distributions concentrated in Central America, southern Africa, southeastern Asia and Australia, inhabiting mostly montane or forested streams, as well as the very successful cosmopolitan Lestidae (about 150 species) that mainly occupies open, stagnant and often temporary waters. Although further relationships within Zygoptera are not well resolved,
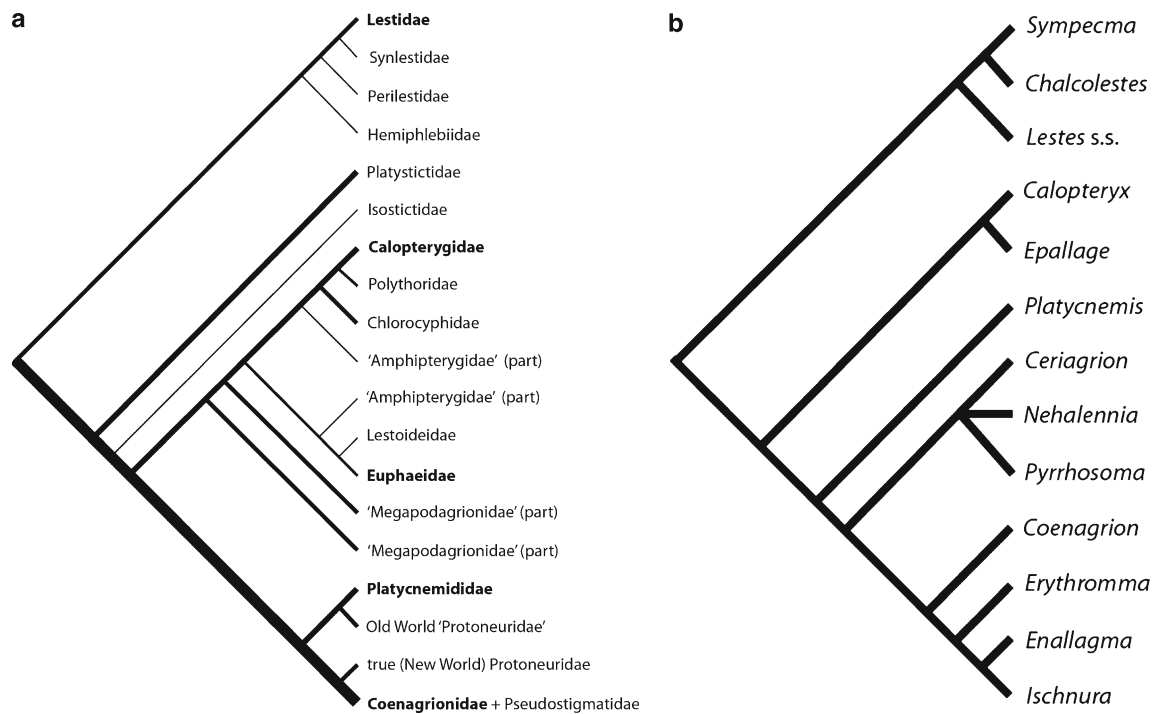
Fig. 1 Inferred phylogeny of global families (**a**, line thickness is indicative of species diversity, European taxa in *bold* font) and European genera of Zygoptera (**b**), based on Bybee et al. (2008), Carle et al. (2008), Dumont et al. (2009) and other sources cited in the text. These trees only show groups' relative positions, but provide no estimate of their relatedness (i.e. shorter branch lengths do not indicate more recent shared ancestry)

evidence suggests that excluding lestomorphs and the relictual families Platystictidae (tropical Asia to New Guinea and Central and northern South America) and Isostictidae (mainly Australia and New Guinea) damselflies break up into two large groups, but understanding within these two groups is sketchy at present. One group includes Coenagrionidae and two similar families of small damselflies, Platycnemididae and Protoneuridae, of which the latter is certainly polyphyletic. Together this clade, Coenagrionoidea, comprises 57 % of all zygopteran species. The other group incorporates everything else including such exotic and spectacular families as Calopterygidae, Euphaeidae, and the Palaeotropical Chlorocyphidae and Neotropical Polythoridae. For example *Calopteryx* and *Epallage*, both robust with mesh-like unstalked wings, may seem very close in a European perspective. Within the continent they are probably indeed each other's nearest relatives, but many tropical families may stand between them.

Over 80 species, occurring in all continents except Antarctica, have been placed in **Lestes**. While the genus is obviously heterogeneous — Pinhey (1980) for example recognised seven subgenera in Africa alone — no attempts to unravel this diversity have been made. Of the European species placed in *Lestes*, *L. parvidens* and *L. viridis* differ notably from the other five by their larger, sleeker and greener (no pruinosity) appearance, as well as by their habit of laying eggs in living wood. Kennedy (1920) created

Chalcolestes for *L. viridis* based on small differences in venation and the penis, and Lohmann (1993a) noted that the larval prementum lacked the distinctive stalked shape found in *Lestes*. Although based on limited taxon-sampling, Dumont et al. (2009) and Gyulavári et al. (2011) found that *Chalcolestes* shared a more recent common ancestor with *Sympecma* and the Asian genus *Indolestes* than with *L. sponsa*, the type species of *Lestes* (Fig. 2). Thus retaining *Chalcolestes* within *Lestes* makes *Lestes* paraphyletic and we therefore recommend recognising it as a genus. Furthermore, *C. parvidens* was for a long time considered to be a subspecies of *C. viridis*. While Dell'Anna et al. (1996) found that mixed populations of both taxa in Italy were differentiated in seasonal and daily activity, it was only recently demonstrated that the two overlap widely across southeastern Europe (Olias et al. 2007). Although specimens with intermediate characters presumed to be hybrids have been found across a wide area (Olias et al. 2007), Gyulavári et al. (2011) found no shared haplotypes and therefore these two taxa, being easily distinguished and overlapping widely, are best treated as species. The five true European *Lestes* fall into a northern (*L. dryas*, *L. sponsa*) and southern clade (*L. barbarus*, *L. macrostigma*, *L. virens*), but probably the nearest relatives of many species are North American or northeast Asian (Fig. 2). A global phylogeny of *Lestes* (sensu lato) is needed to resolve that and will probably lead to the tropical groups being split off as separate
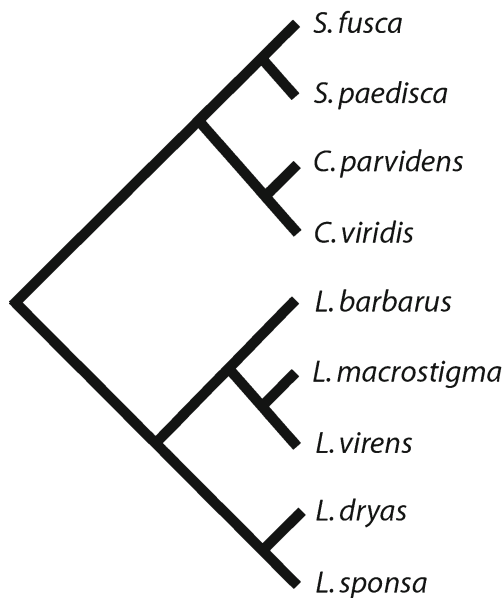
Fig. 2 Phylogeny of European Lestidae, based on molecular data (Dumont et al. 2009; Gyulavári et al. 2011), *S. paedisca* is placed by default, being the only other European *Sympecma* species. *C.* (*Chalcolestes*), *L.* (*Lestes*) and *S.* (*Sympecma*) are abbreviations of genera

genera. Another unresolved debate concerns the subspecies of *L. virens*, as summarised by Jödicke (1997). Being a widespread and variable taxon this issue seems minor, were it not that Samraoui et al. (2003) found two genetically and seasonally segregated (and thus reproductively isolated) populations in Algeria. They recognised one as the new species *L. numidicus* and the other as 'true' *L. virens*. However, the genetic identity of topotypical *L. virens* (southern Portugal) is unknown, as is the geographic extent of phenological variation within the complex. Northern climates do not allow temporally separated generations, but variation may be gradual within the Mediterranean basin: *L. numidicus* could be much more widespread and possibly evenly synonymous with 'true' *L. virens*, as defined by its type, or might represent an extreme condition rather than a good species (see Jödicke 2003). While many tropical odonates survive unfavourable periods as adult, ***Sympecma*** is the only temperate genus with a similar strategy, overwintering on often remarkably exposed perches. The three closely similar species occur together in Central Asia, but while *S. gobica* is restricted to that region, *S. fusca* extends to North Africa and *S. paedisca* to The Netherlands and Japan.

The phylogeny of **Calopterygidae** is better resolved than any other in the order (Dumont et al. 2005, 2007). Males of most species have distinct wing pigmentation, which plays a role in often elaborate agonistic and courtship behaviours. All species are confined to running water. The family's greatest diversity is found in eastern Asia. Probably the genus ***Calopteryx*** originated there, with dispersal to North America leading to a monophyletic radiation of five species,

and westwards across the Palaearctic to an unresolved complex of about 20 species (Misof et al. 2000; Dumont et al. 2007). Several eastern species probably do not belong in *Calopteryx* and are either more closely related to the Asian genera *Matrona* or *Atrocalopteryx*, or belong to still unnamed genera. All Western Palaearctic species appear closely related, and the limits between them are hazy, in part due to the large number of subspecies described and the meagre morphological differences between them, most notably in the *splendens* complex. Various studies indicate that this complexity stems from the isolation of populations in habitat refuges during glaciations and their subsequent expansion and large-scale hybridisation, and that similarities in the shape of the wing and its markings do not necessarily reflect close relationships and cannot help define the taxa more clearly (Misof et al. 2000; Weekers et al. 2001; Dumont et al. 2005; Sadeghi et al. 2010). Unfortunately each study applied a different molecular approach, using one mitochondrial marker (Misof et al. 2000), two nuclear markers (Weekers et al. 2001), three additional nuclear ones (Dumont et al. 2005) or AFLP 'fingerprinting' (Sadeghi et al. 2010), on differing selections of taxa. The results have a generally low genetic and geographic resolution, as well as limited congruency. For example, the very distinctive *C. haemorrhoidalis* is the sister-taxon of *C. virgo* in the first two studies, falls within the *splendens* complex in the analysis of Dumont et al. (2005), and was not studied by Sadeghi et al. (2010) at all. As a result, the complex is still largely unresolved, and in its nature may even be impossible to disentangle. Most 'subspecies' of *C. splendens* (e.g. *ancilla*, *balcanica*, *caprai*, *cartvelica*, *faivrei*, *intermedia*, *mingrelica*, *taurica*, *tschaldirica*) are probably hybrid populations from at least three ancestral gene pools in western Asia and one in the western Mediterranean, which should not be defined as subspecies, let alone as species. Currently only *C. exul* from North Africa and *C. xanthostoma* from Iberia and adjacent France are commonly treated as distinct from *C. splendens*, the first because it is conveniently completely separate in range and appearance, the second because it overlaps rather than intergrades with *C. splendens* in France and is genetically rather distinct there (Weekers et al. 2001). Other potentially valid species in the complex are *C. waterstoni* on the southeastern fringe of the Black Sea and *C. orientalis* on the southern fringe of the Caspian Sea, while other seemingly distinctive taxa, like *C. syriaca* and *C. hyalina* in the Near East, have simply not been studied genetically at all (Sadeghi et al. 2010).

Together with Chlorogomphidae, the **Euphaeidae** is the only odonate family largely endemic to the Oriental region (Kalkman et al. 2008). With their rather large size, sturdy build and numerous antenodal cross-veins the approximately 70 species resemble Calopterygidae, although they lack metallic colours. Euphaeid larvae are easily recognised by their sack-like caudal gills and unique finger-like lateral

abdominal gills, a character that supports the family's monophyly. Many species have coloured wings, which presumably have a function in courtship or territorial behaviour, but no species have been studied in detail. All species breed in running water, most of them in forest. The only *Epallage* species ranges from southeastern Europe to Pakistan. The nearest Euphaeidae occur in the Himalayas of western India and do not overlap with *Epallage*. The genus *Bayadera* might be its nearest relative (personal communication M. Hämäläinen), but the almost unstalked wings, robustness and appendage shape make *E. fatime* unique enough to merit its own genus. Also, *Epallage* usually holds its wings outstretched (shared with *B. melanopteryx*) when perched, rather than closed or half open, and is the only euphaeid with completely densely pruinose males, which is probably an adaptation to exposed habitats (personal communication M. Hämäläinen and H. Zhang).

Platycnemididae is entirely confined to the Old World. The highest diversity is in tropical Africa, southeastern Asia, and New Guinea. Together with the Asian *Copera*, **Platycnemis** forms a monophyletic group of about 35 species with characteristic feather-like tibiae. The group comprises two radiations. In tropical Asia (including the type species of *Copera*), Africa and Madagascar the larvae have unique frilled lamellae. Males can have white, yellow, orange, red, blue or black tibiae. The other group always has white tibiae and lamellae with smooth borders. Its origin appears to lie in eastern Asia (Indonesia to Japan) from which the monophyletic *pennipes* group of six species are derived: three occurring in Europe, two in the Near East and one in northwestern Africa. The Afrotropical species are still placed in *Platycnemis*, but are more closely related to *Copera*, and thus the genus must be restricted to its Palaearctic representatives: aside from six aforementioned species, four are present in the east (personal communication K.-D.B. Dijkstra and F. Stokvis).

Totalling almost 1,100 species, **Coenagrionidae** is the largest family of damselflies, forming a major part of the odonate fauna in all continents. With Lestidae it is the only damselfly family of which many species inhabit standing waters. Many species have strong dispersal powers and comparatively large distributions. They are often the only damselflies on oceanic islands, which sometimes led to notable radiations, such as the 23 *Megalagrion* species in Hawaii. Historically the family has been divided into subfamilies, but most of these are not supported by morphology (O'Grady and May 2003), although Hovmöller (2006) presented genetic support for Ischnurinae, which are characterised by a vulvar spine. Although molecular studies were so far based on limited selections of species, they indicate that Coenagrionidae consists of two major clades, one including *Ceriagrion*, *Nehalennia* and *Pyrrhosoma*, and the other the remaining European genera (Fig. 1). Many genera in the first group, including *Ceriagrion*, possess a marked transverse ridge between the antennae, while all in the second group have a rounded frons. Remarkably, the family Pseudostigmatidae, the famous giant damselflies of tropical America, appears to fall within the ridge faces, as do probably all American members of what is now known as the family Protoneuridae (Bybee et al. 2008; Carle et al. 2008; Dumont et al. 2009; Pessacq 2008).

About 50 *Ceriagrion* species occur in the warm parts of Africa and Asia with one species just reaching northern Australia. Like our *C. tenellum* and *C. georgifreyi*, most species are red, but they can also be (partly) shades of blue, green and yellow. Generally, however, dark markings are absent. Thus the two European species are not only unusual by their temperate distribution, although they favour warm microhabitats, but also by their dark bronzy thorax (Kalkman 2005). The only similar species is *C. sinensis*, which is known from a handful of mountainous sites in southeastern China (Asahina 1967; personal communication H. Zhang). These sites also have a temperate climate and *C. sinensis* is likely to be the nearest relative of the European species. Kennedy (1920) proposed the genus *Palaeobasis* for *C. tenellum* and De Marmels (2007) stated that it "does not fit smoothly in the Old World *Ceriagrion*, but, instead, shares some characters with the New World *Telebasis*". The only evidence provided, however, is that some *Telebasis* also have a bronzy-black thorax. Dumont et al. (2009) placed *C. tenellum* as sister group of all other *Ceriagrion* sampled, but did not include *Telebasis*. Although the Palaearctic *Ceriagrion* may thus not be closely related to the large Palaeotropical radiation, the name *Palaeobasis* does not need to be revived as long as there is no evidence that *Ceriagrion* as a whole is poly- or paraphyletic.

Five of the six **Nehalennia** species are American, while *N. speciosa* is found from Europe to Japan. All species are very small and possess a distinctively spiny abdomen tip, but while the four temperate species are largely metallic green, two tropical American ones are black (Paulson 2009). They inhabit standing waters, often with dense sedges and grasses. Unlike other European coenagrionids, the wings are not held on the side of the abdomen at rest, but above it. The nearest relative of this distinctive genus is among the ridge-faced coenagrionids like *Ceriagrion*, but its precise relationships are unclear; the Nearctic bog species *N. gracilis* is the sister species of *N. speciosa* (De Marmels 1984). It presumably is a relatively recent American arrival in the Palaearctic, and shows almost no genetic diversity across its huge and extremely fragmented range (Bernard and Schmitt 2010; Bernard et al. 2011; Suvorov 2011). Such poverty may be explained by the colonisation of large parts of the Palaearctic from a single refugium, most likely in the Asian Far East, since the end of the last Ice Age, only 10,000 years ago (Bernard et al. 2011).

Two species of **Pyrrhosoma** are completely (*P. elisabethae*) or largely confined to Europe (*P. nymphula*) and two

are poorly known endemics of China. All are rather robust red damselflies marked with black and yellow, which lack postocular spots (Kalkman and Lopau 2006; Yu et al. 2008). The blue-and-black *Chromagrion conditum*, the single species of a North American genus, has larval and adult characters resembling *Pyrrhosoma* (including the absence of postocular spots and the shape of the secondary genitalia and appendages) and is probably its sister genus (De Marmels 2002; O'Grady and May 2003). It is also a fairly robust spring species, which shares its habit of sitting on leaves with slightly open wings.

Coenagrion has around 40 species in the Palaearctic and 3 more in the Nearctic. Based on its distribution, it seems almost certain that the southeastern Australian *C. lyelli* should be placed in *Austrocoenagrion* (Kennedy 1920). Dumont et al. (2009) and Carle et al. (2008) place *Coenagrion* as the sister group of most genera with a rounded frons (Fig. 1). Nineteen species are found in the Western Palaearctic, 14 of which are in Europe. Several authors (Battin 1993; Lohmann 1992a, 1993b; Schmidt 1929) suggested species groups based on general resemblance, which is supported quite well by a molecular phylogeny of 13 species (Dumont et al. 2009). The northern European species fall into the *hylas* (*hylas*, *johanssoni*) and *lunulatum* groups (*lunulatum*, *hastulatum*, *ecornutum*). Despite its aberrant appendages, the unassigned *C. armatum*, as well as the presumably related *C. glaciale* (Lohmann 1992a), is probably close to the latter. The North American *C. interrogatum* and *C. resolutum* seem close to the *hylas* group; *C. angulatum* to the *lunulatum* group (Dumont et al. 2009; Westfall and May 2000). All these species inhabit standing, often boggy, waters and include the most boreal of all damselflies. The southern European species may be divided into the *scitulum* (*scitulum*, *caerulescens*, probably *mercuriale*) and *puella* groups (*intermedium*, *puella*, *pulchellum*, *ornatum*), which both include many species of flowing waters. While the former group is centred in the western Mediterranean, the latter is most diverse to the east, with several additional (but extremely similar) species in southwestern Asia. Thus far, *C. mercuriale* is the only European species for which the impact of habitat fragmentation on genetic diversity has been studied. Especially in small populations isolation has clearly resulted in genetic impoverishment: the variability on the particularly isolated Welsh island of Anglesey is even among the lowest reported for insects (Watts et al. 2006).

The red-eyed *Erythromma* species *E. najas* and *E. viridulum* resemble each other strongly, but *E. lindenii* was until recently placed in *Cercion*. Heidemann and Seidenbusch (1993) first postulated that it should be included in *Erythromma*, based on larval characters. This was not accepted until Weekers and Dumont (2004) provided molecular support. Several characters of the adults agree with these findings, including the shape of the appendages, the configuration of blue markings and the male's habit to perch on vegetation far from banks. Also *E. lindenii*, like the two red-eyed species, lacks the dark dorsum of the eye that is present in other European coenagrionids (Dijkstra 2006; Dijkstra and Lewington 2006). The Palaeotropical genus *Pseudagrion* and the Oriental *Paracercion* may be the nearest relatives of *Erythromma* (Bybee et al. 2008; Carle et al. 2008; Dumont et al. 2009). A study on the northwards expansion of *E. viridulum* in England during the past 30 years showed that populations become genetically less diverse towards the limit of its distribution, presumably caused by the founder effect of repeated colonisations (Watts et al. 2010).

While 40 *Enallagma* species occur in the New World (mostly North America), only four inhabit the Old World. May (2002) transferred numerous African (and a few Asian) species to six different genera without considering their relationship to the large and closely similar Palaeotropical genus *Aciagrion*. Thus, while their removal from *Enallagma* is justified, their final taxonomic fates are still unsettled. Morphological and genetic studies revealed that *Enallagma* consists of two subgenera (Fig. 3; Brown et al. 2000; May 2002; Turgeon and McPeek 2002; Turgeon et al. 2005). *Chromatallagma* includes 17 species with a mostly southern Nearctic distribution. The species are often colourful (red, orange, yellow, green) and radiated largely before the Quaternary. The diversity of *Enallagma* (sensu stricto) is much younger and has a more northern Holarctic distribution. Males of nearly all species are blue with a black pattern, resembling the European *E. cyathigerum*. The subgenus includes two explosive North American radiations. A third radiation originates from the colonisation of northern Eurasia, resulting in the four Palaearctic taxa (*cyathigerum*, *risi*, *deserti*, *circulatum*) that are variably considered as species or as subspecies of *E. cyathigerum* (Kosterin and Zaika 2010; Stoks et al. 2005). The past 250,000 years have seen elevated rates of speciation in North America, promoted by the Quaternary glaciations: the expansion of ice sheets split populations up, while their retreat made huge amounts of new habitat available (Turgeon et al. 2005). Interestingly, during the same period the Eurasian clade showed almost no speciation. The male appendages and larval morphology and behaviour of the Palaearctic *E. cyathigerum* are nearly identical to those of the Nearctic *E. annexum* and *E. vernale*, as are those of the Palaearctic *E. circulatum*, *E. risi* and *E. deserti* to the Nearctic *E. boreale*, although these similar species are not closely related. This remarkable case of parallel evolution is thought to be driven by similar selection pressures in both areas, mainly in response to predation (Stoks et al. 2005).

The nearly 70 species of *Ischnura* are found on all continents except Antarctica. Most species inhabit standing or slow-flowing waters, and especially in the temperate region they are often among the most common and widespread odonates. Males of most species possess a bicoloured pterostigma, while females often occur in genetically discrete colour forms
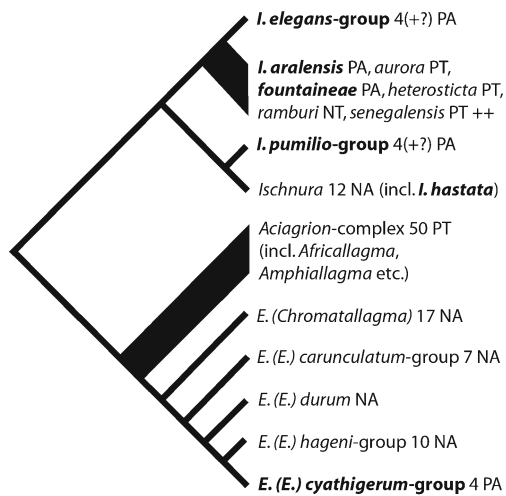
Fig. 3 Inferred phylogeny of *Ischnura* (*I.*), *Enallagma* (*E.*) and associated genera based on preliminary genetic data (Chippindale et al. 1999; Turgeon et al. 2005; Hovmöller 2006; Dumont et al. 2009). Unresolved potentially paraphyletic groups are indicated with broad lines, and known numbers of species in each group are given. The taxa occur in the Nearctic (*NA*), Neotropics (*NT*), Palaearctic (*PA* and *bold* font) or Palaeotropics (*PT*). Sampling is very incomplete in *Ischnura* and the presented hypothesis is therefore tentative. The relationships of numerous (especially Neotropical) ischnurines are unknown, although Hovmöller (2006) found his selection to form the sister group of the assemblage presented here

that also vary with age. Although published molecular phylogenies have poor taxon sampling, *Ischnura* breaks up into several groups (Fig. 3; Chippindale et al. 1999; Hovmöller 2006; Dumont et al. 2009). The Eurasian *pumilio* group is closest to a Nearctic radiation that includes *I. hastata*, of which the world's only parthenogenetic odonate populations occur in the Azores. Besides *I. pumilio*, the group includes the Asian *I. asiatica*, *I. intermedia* and *I. forcipata* (Dumont and Borisov 1995). Some of the most widespread tropical damselflies are found among the remaining species, such as *I. senegalensis* from Africa and Asia, *I. heterosticta* from Australia, *I. aurora* in Australasia and the Pacific, and *I. ramburi* from the Americas. The Western Palaearctic *elegans* group originates from this warm-adapted diversification. It represents a presumably recent radiation centred on the western Mediterranean basin, with *I. elegans* mostly north of the Pyrenees, *I. graellsii* roughly south of it to the Atlas, *I. saharensis* south of that, and *I. genei* on the Tyrrhenian islands. The species are very closely related and almost completely separated geographically. However, where they meet — *I. elegans* and *I. genei* on small islands between Corsica and the Italian mainland, and *I. graellsii* and *I. saharensis* on the Sahara's northern fringe — they mingle without interbreeding. The notable exception is in Spain, where *I. elegans* penetrates deep into *I. graellsii* territory. While they appear and behave as distinct species, female *I. graellsii* frequently mate with *I. elegans* males, resulting in fertile hybrid offspring. However, female *I. elegans* do not mate with male *I. graellsii*, probably due to mechanical

constraints. Hybrid females are capable of mating with hybrid or *I. elegans* males, but rarely mate with *I. graellsii*. This unidirectional hybridisation favours *I. elegans*, which has been expanding in the Iberian Peninsula at the cost of *I. graellsii* (Monetti et al. 2002; Sánchez-Guillén et al. 2011). The marginally European species *I. aralensis* (southern Urals) and *I. fountaineae* (Pantellaria) are closely related to the *elegans* group, but their exact positions are unresolved.

The dragonflies that share a functional, unreduced ovipositor with Zygoptera are generally considered the sister group(s) of all other **Anisoptera** (Fig. 4). Aside from the large and widespread family **Aeshnidae**, this is found in the tiny relictual families Austropetaliidae (temperate South America and Australia) and Petaluridae (North America, Japan, Chile, Australia and New Zealand). It remains unresolved whether they form a monophyletic group (Fleck et al. 2008b; Fleck 2011) or not (Bybee et al. 2008; Davis et al. 2011). von Ellenrieder (2002, 2003) provided a phylogeny based on the morphology of all existing aeshnid genera (2002) and the species assigned to *Aeshna* (2003), but no extensive molecular work on the family has been published to date. Nonetheless, both morphology and genetics support that the two crepuscular stream-loving genera *Boyeria* and *Caliaeschna* are more closely related to each other than to the European standing-water aeshnids *Aeshna*, *Anax* and *Brachytron* (Fig. 4).

Von Ellenrieder (2002) did not identify any genera related closely to **Boyeria** and the species within the genus itself are heterogeneous in appearance, although all are crepuscular stream dwellers. Two closely similar species are restricted to eastern North America, and three rather different species to eastern Asia. The Western Palaearctic species are also very distinctive in appearance: *B. irene* is confined to southwestern Europe and northwestern Africa. The isolated *B. cretensis* on Crete was only recognised as a distinct species 141 years after its discovery (Peters 1991). Its range is completely surrounded by that of the only **Caliaeschna** species, *C. microstigma*, which replaces *Boyeria* on streams from southeastern Europe to Iran. It is closely related to the genus *Cephalaeschna* (von Ellenrieder 2002), which occurs from Afghanistan to China and Taiwan. Further study may well show that *C. microstigma* is a western representative of *Cephalaeschna* and is better subsumed in that genus, although it lacks the latter's characteristic inflated frons. **Brachytron** *pratense* is the only species of a genus confined largely to Europe, though occurring throughout most of it. The three or four species of *Aeschnophlebia* from eastern Asia and the single *Nasiaeschna* and *Epiaeschna* species from eastern North America are morphologically and ecologically similar, occurring in temperate marshlands, often early in the season. The similarity of their distributions with those of the three groups in *Boyeria* is notable: both are probably examples of Holarctic groups that became isolated
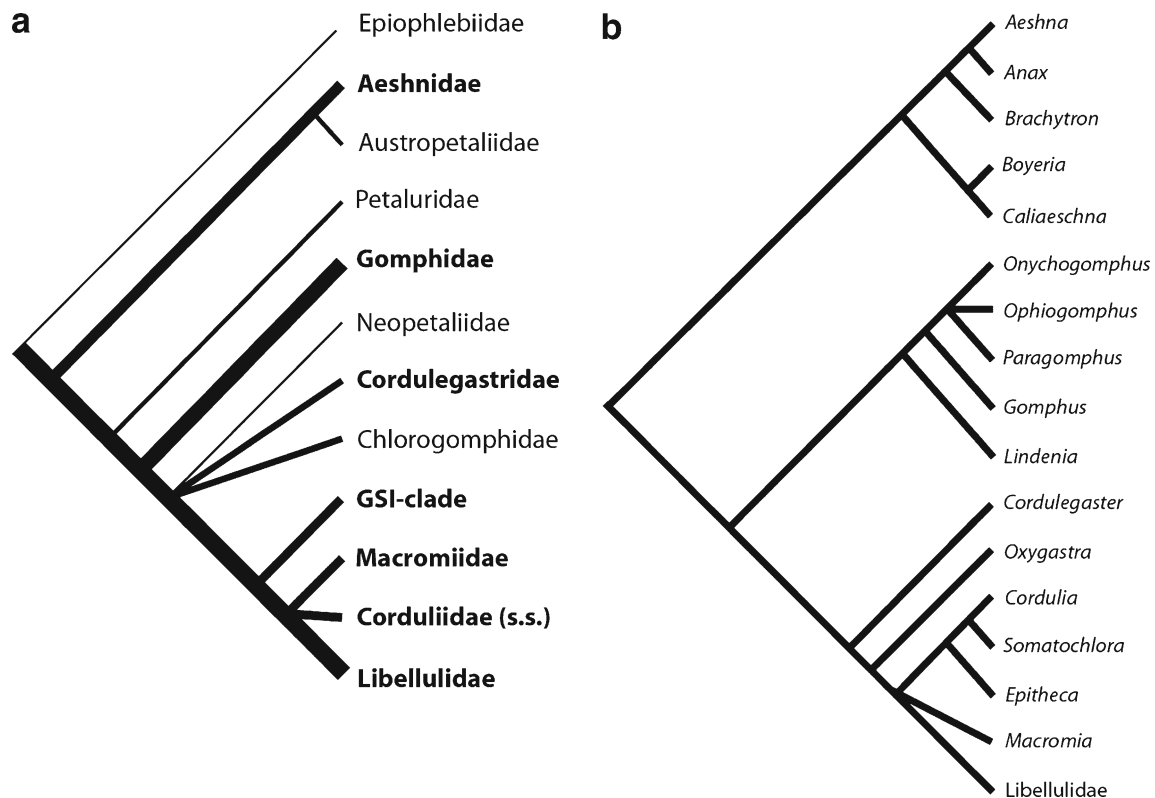
Fig. 4 Inferred phylogeny of global families (**a**; line thickness is indicative of species diversity; European taxa in *bold* font) and European genera of Anisoptera (**b**; see Fig. 6 for details of Libellulidae), based principally on Bybee et al. (2008), as well as Fleck et al. (2008b), Ware et al. (2007) and other sources cited in the text. These trees only show groups' relative positions, but provide no estimate of their relatedness (i.e. shorter branch lengths do not indicate more recent shared ancestry)

in areas of suitable habitat during Pleistocene glaciations. Von Ellenrieder (2002) and Peters and Theischinger (2007) confirm their close relationship, as well as with *Tetracanthagyna*, a genus of tropical Asian forest streams that includes some of the largest dragonflies.

While the two genera are closely related, some species now placed in *Aeshna* are nearer to *Anax* than others, because *Aeshna* has functioned as a receptacle for over 80 superficially similar species. Von Ellenrieder (2003) provided the most detailed analysis to date (Fig. 5). Eight more northerly European species belong to a purely Holarctic radiation that includes the type species *A. grandis* and can thus be regarded as the 'true' *Aeshna*. They fall into two clades, of which one is represented only by *A. cyanea* in Europe, which indeed differs quite markedly by appendages, coloration and even ecology from its European congeners. Until the early 1990s, a paraphyletic assemblage of over 50 species sister to *Anax* and *Anaciaeschna* was also referred to as "*Aeshna*", but most of these four to eight lineages have since been made into genera: Watson (1992) created *Adversaeschna* and De Marmels (1994) *Andaeshna*, while von Ellenrieder (2003) revived *Rhionaeschna*, and Peters and Theischinger (2011) split off *Pinheyschna* and *Zosteraeschna*. The massive subtraction of species has cost

"*Aeshna*" almost two thirds of its diversity, and now only three aberrant Palaearctic species and the Central American *A. williamsoniana* remain 'in limbo'. The latter shares features with *Zosteraeschna*, as well as with *A. affinis* and *A. mixta*, while *A. isoceles* is nearer *Andaeshna* than *Anaciaeschna*, in which it has frequently been placed (von Ellenrieder 2003). Judging from their distinct biogeography and ecology we expect that the European species will also be moved into two new genera and a molecular phylogeny supporting the breakup of "*Aeshna*" is highly anticipated. Such an analysis must also incorporate the diverse cosmopolitan genus *Anax*. Peters (2000) argued that sinking the genus *Hemianax* (for *A. ephippiger* and its Australian sister-species *A. papuensis*) avoids making *Anax* paraphyletic. His inclusive approach seems sensible given the morphological, ecological and geographical diversity of *Anax*; knowing the phylogenetic positions of peculiar stream-dwelling species like the Asian *A. immaculifrons* and African *A. speratus* (*Anax* predominantly favours warm and stagnant water) would be especially enlightening in this regard. The entire clade including *Anax*, *Anaciaeschna* and the aberrant "*Aeshna*" species has a more southern distribution than true *Aeshna*.

Gomphidae is the third largest odonate family after Libellulidae and Coenagrionidae, but while one in three
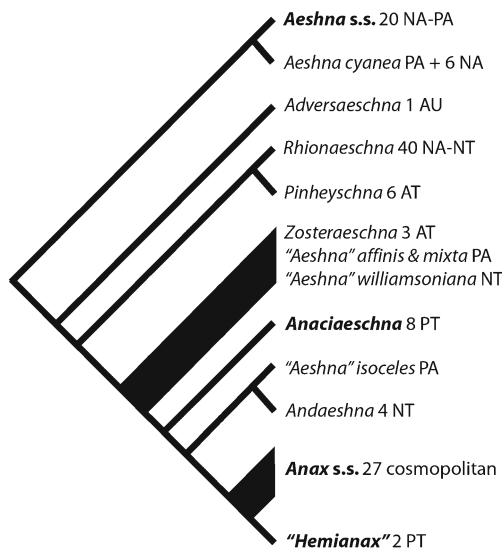
Fig. 5 Phylogeny of *Aeshna*, *Anax* and associated genera based on morphology (after von Ellenrieder 2002, 2003). Only *bold* genera were recognised before the 1990s, the remainder of species being retained in *Aeshna* (sensu lato). Unresolved paraphyletic groups are indicated with *broad lines*, and approximate numbers of species in each group are given. The taxa occur in the Afrotropics (*AT*), Australia (*AU*), Nearctic (*NA*), Neotropics (*NT*), Palaearctic (*PA*) or Palaeotropics (*PT*)

anisopteran species is a gomphid, in Europe only one in seven is. Nearly all gomphids prefer running water and their larvae show diverse adaptations for living in different substrates. Carle (1986) recognised eight subfamilies, of which Lindeniinae (*Lindenia*), Gomphinae (*Gomphus*) and Onychogomphinae (*Onychogomphus*, *Ophiogomphus* and *Paragomphus*) occur in Europe. With no extensive molecular phylogeny available, the validity of this classification remains untested, although published data are congruent with it for the European genera (Fig. 4). Moreover, many gomphid genera are poorly defined, and of all European odonate genera, the three most in need of global revision are gomphid: *Gomphus*, *Onychogomphus* and *Paragomphus*. The first two are almost certainly polyphyletic, with many non-European species likely to be placed in different genera in the near future.

The monotypic genus ***Lindenia*** appears to be unique among Gomphidae in three ways. Firstly, *L. tetraphylla* may develop pruinosity with age. Secondly, it has distinct melanism, which might also be (partly) age-related, although in some populations tenerals are already completely black, suggesting it is determined by environmental conditions. Finally, it has clear migratory tendencies, although this has never been observed in Europe (Schneider 1981). In Europe, *L. tetraphylla* is the only gomphid mainly inhabiting lakes, and it seems well adapted to the ephemeral conditions that prevail in its range from the Mediterranean shores to Pakistan and southern Arabia (Schorr et al. 1998). Its nearest relative must be among the other lindeniine genera, which are all tropical

and share the distinctive shape of the larva. Perhaps the Palaeotropical *Ictinogomphus*, which also favour standing and sluggish waters, is the most likely candidate, although *Lindenia* is unusual in having greatly developed foliations on the seventh abdominal segment rather than on the eighth.

Almost 40 Nearctic, 10 Western Palaearctic and nearly 20 Eastern Palaearctic species have been placed in ***Gomphus***. The genus *Gomphus* has been used as a receptacle for 'difficult' gomphines and is likely to be poly- or paraphyletic. Several subgenera have been in use in North America, but a revision of the group is needed to evaluate their validity: according to Carle (1986) *Gomphus* forms a group with the North American *Arigomphus* and *Dromogomphus,* the Chinese *Gastrogomphus* and the North American and East Asian genus *Stylurus*. While molecular data seem to support the North American (sub-) genera, the problem is that the phylogenetic position of the type species of *Gomphus* (the European *G. vulgatissimus*) has not been determined (personal communication E. Pilgrim). Furthermore, Schmidt (1987, 2001) argued that the Eurasian *Gomphus flavipes* belongs in *Stylurus*. This is supported by characters in both adults (slender posterior hamules) and larvae (drawn-out abdomen, absence of tibial hooks). While it seems wiser to retain *flavipes* in *Gomphus* until a proper study of the gomphines is conducted, it does not seem part of what appears to be a tight Western Palaearctic *Gomphus* radiation. Beside the five remaining European species, this includes localised species in North Africa (*G. lucasii*) and the Near East (*G. davidi*, *G. kinzelbachi*). Detailed morphological and especially genetic research in their potential area of overlap in the southern Balkan must reveal whether *G. schneiderii* should remain separated from *G. vulgatissimus*.

Species currently placed in ***Onychogomphus*** are found in the Afrotropics (12), Western Palaearctic (7) and Eastern Palaearctic and Oriental region (over 40). *Onychogomphus* is almost certainly polyphyletic and probably all tropical species should be removed to other genera. Together with four southwest Asian species, the European *O. forcipatus* (the genus's type) and *O. uncatus* form the 'core *Onychogomphus*', which favour running waters with stretches of stones or gravel. Boudot et al. (1990) demonstrated that, if sufficient numbers of specimens are studied from each location, three subspecies of *O. f. forcipatus* can be identified based on the appendages. With *O. lefebvrii* from the Near East, these subspecies probably form a monophyletic group, each taxon with a discrete and non-overlapping range. While only *O. lefebvrii* is generally separated as a species, genetic work may well show that all taxa should be treated equally, either as subspecies or species. The West-Mediterranean *O. costae*, which has notably pale coloration, very distinct appendages and a peculiar tuft of white hair below the abdominal club, is probably not

closely related to the other Western Palaearctic species. It inhabits rather dry regions, possibly favouring ephemeral conditions, and may represent an unnamed genus as well.

While twenty species of **Ophiogomphus** are found in the Nearctic, only four occur in the Palaearctic. In addition to this, a few poorly known Oriental species and the slightly better known 'Ophiogomphus' sinicus are placed in this genus, although probably none of these belong there (e.g. Wilson and Xu 2009). True Ophiogomphus share a similar general appearance, being robust with a green thorax and bold yellow middorsal abdominal spots. The nearest relative of the European O. cecilia seems to be the Eastern Palaearctic O. obscurus, which has been regarded as a subspecies or synonym of it. However, Asahina's (1979) characters are clearly expressed and both species overlap in southern Siberia, having even been found at one site together (Kosterin and Zaika 2010). Probably they form a monophyletic group with the central and eastern Asian O. reductus and O. spinicornis, originating from a single dispersal event from North America.

Paragomphus is a large Palaeotropical genus with about 30 species in Africa and adjacent Eurasia and an additional 16 in Asia. Males typically have prominent foliations on the eighth and ninth abdominal segment and long hooked cerci. Many Afrotropical species are poorly known, with variation in markings and slight differences in appendages complicating their taxonomy (Dijkstra 2003a). Although most species breed in running water, P. genei favours standing and even temporary water. Consequently it is the most numerous and wide-ranging gomphid in Africa and the only one to reach Europe. The genus is very close to the six Afrotropical species in Crenigomphus, with intermediate characters in some species (Suhling and Marais 2010). If it is found that Crenigomphus makes Paragomphus paraphyletic, the former name has precedence.

Females of **Cordulegastridae** have a prolonged spike-like subgenital plate, a character unique within Odonata. Until recently the Asian Chlorogomphidae were included in this family but they are now generally regarded as a separate family based on differences in venation and the absence of the prolonged subgenital plate, although a proper phylogenetic analysis is lacking (Bybee et al. 2008; Dumont et al. 2009; Kalkman et al. 2008). Generally three cordulegastrid genera are recognised (but see below), of which Anotogaster and Neallogaster are largely confined to the Eastern Palaearctic and the northern Oriental region. Of the about 25 Holarctic species of **Cordulegaster**, 10 are found in the Nearctic and 9 in the Western Palaearctic, with 7 occurring in Europe. The Palaearctic species are split into two groups based on small differences in markings, venation and appendages. Moreover, while the bidentata group is mainly found at seepages and the upper courses of streams, the boltonii group mostly occupies lower stream reaches. Lohmann's (1992b) proposal to restrict Cordulegaster to

the boltonii group and place the bidentata group in Thecagaster and Sonjagaster has found almost no support, nor has the division of the much more diverse Nearctic fauna into six genera (Garrison et al. 2006; Needham et al. 2000; Paulson 2009). Many European species were recognised relatively recently: the Italian C. trinacriae, Balkan C. heros and Greek C. helladica were described within the last 40 years (Lohmann 1993c; Theischinger 1979; Waterston 1976). The species' markings often vary regionally, which has led to the description of many subspecies, most notably in C. boltonii (e.g. Boudot and Jacquemin 1995). However, while molecular data find good support for all the Western Palaearctic species, none of the subspecies are genetically well defined (personal communication S. Ferreira).

Rather like the coenagrionoid dominance in Zygoptera, the 'higher' **Libelluloidea** (sensu Ware et al. 2007) amount to about half (48 % to be precise) of all species diversity in Anisoptera, only gomphids approaching their dominance. The main family, Libellulidae, with over 1,000 species, is monophyletic (Bybee et al. 2008; Ware et al. 2007). The remaining 400 libelluloid species have long been grouped into Corduliidae, and while their precise positions relative to libellulids remain unclear, these 'corduliid' groups are certainly not monophyletic as a whole, falling apart into Corduliidae (sensu stricto), Macromiidae and the GSI-clade (Figs. 4, 6). The latter refers to the 'corduliid' subfamilies Gomphomacromiinae, Synthemistinae and Idionychinae, which make up the main body of this group (Ware et al. 2007). This clade contains many often poorly known genera, which are predominantly found in seepages or streams, often within small or relictual distributions. Future study may subdivide the clade into several small families. The only European GSI genus is **Oxygastra**, whose most striking feature is the dorsal crest on the terminal abdominal segment. The Neotropical Neocordulia and Madagascan Nesocordulia possess somewhat similar structures, but these genera were not sampled by Ware et al. (2007). Whether such a distant relationship is proven or not, it appears that Oxygastra represents the phylogenetically most isolated odonate in Europe and possibly its oldest relict. The only species, O. curtisii, survives in running water in southwestern Europe and Morocco.

Based on morphology, May (1997) showed that Macromia together with the African Phyllomacromia, North American Didymops and Asian Epophthalmia forms a monophyletic group. The molecular phylogeny of Ware et al. (2007) confirmed that the group is best treated as the family **Macromiidae**. While Epophthalmia and some species of the other genera breed in lakes, most species are exclusive to running waters. The genus **Macromia** has a curious distribution: over 70 species are found in the (sub-) tropical parts of Asia to northern Australia and 7 in North America. Two species occur in the Palaearctic: M. amphigena in Siberia and M. splendens in southwestern Europe, separated from its
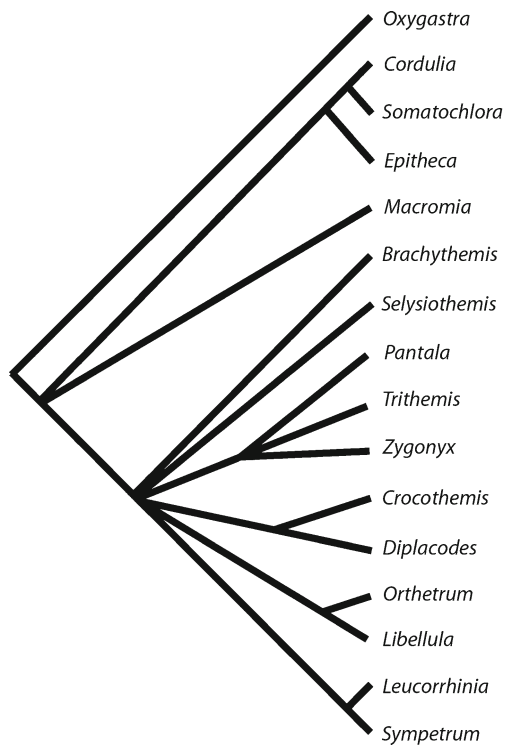
Fig. 6 Inferred phylogeny of European 'higher' Libelluloidea, based on Ware et al. (2007), Pilgrim and von Dohlen (2008) and Fleck et al. (2008a, b). These trees only show groups' relative positions, but provide no estimate of their relatedness (i.e. shorter branch lengths do not indicate more recent shared ancestry)

nearest possible relative by over 5,500 km. Based on their Holarctic distribution, the European species might be expected to be closest to the Siberian or North American species. However, although based on limited taxon sampling, both Dumont et al. (2009) and Fleck et al. (2008b) suggest that *M. amphigena* and North American taxa are closer to each other than to *M. splendens* and that the latter is closer to tropical Asian species.

Corduliidae (sensu stricto) are well represented in temperate regions of the Northern Hemisphere, but have a marginal presence in the tropics and south, generally being montane (e.g. Oriental *Procordulia*), peripheral (*Rialla* in Chile) and insular in occurrence (most notably *Hemicordulia* in Australia and the Indo-Pacific). While most species of the GSI clade and the Macromiidae are limited to running water, Corduliidae (s.s.) predominantly occur in standing waters.

Epitheca females possess a large and bilobed vulvar scale, which is used to hold an egg mass that unfolds as a gelatinous strand in water. Two Palaearctic species (*E. marginata* in eastern Asia and *E. bimaculata* from Europe to Japan) belong to the subgenus *Epitheca*, while the Nearctic species have been placed in *Epicordulia* (one species) and *Tetragoneuria* (nine). These subgenera are sometimes treated as genera. The molecular phylogeny by Fleck et al. (2008b) suggests that each subgenus is monophyletic, with

Epitheca (sensu stricto) as the sister group of all American species. However, the genus as a whole also appears monophyletic, making any decision about the level at which these taxa should be recognised subjective. As the differences are modest and stability should be served, it seems best to retain all species within *Epitheca* and recognise *Epicordulia* and *Tetragoneuria* only as subgenera (Garrison et al. 2006).

Somatochlora is represented by 26 species in North America and about 20 in the Palaearctic and adjacent parts of the Oriental region. The European species can be divided into two groups: the *metallica* group has mostly bright metallic adults and larvae with mid-dorsal abdominal spines, while *arctica* group adults are duller black overall and the notably hairy larvae lack such spines. The latter group's species inhabit small standing waters in cold environments and have boreo-alpine (*S. alpestris*, *S. arctica*) or even arctic (*S. sahlbergi*) distributions. The *metallica* group (*S. flavomaculata*, *S. meridionalis*, *S. metallica*) extends further south and favours warmer habitats, although it does tend to more shading, current or elevation towards the south. *S. meridionalis* largely replaces *S. metallica* in southeastern Europe: where they co-occur *S. metallica* is limited to elevated lakes and bogs, while *S. meridionalis* is found in lowland streams. This situation recalls that in *Chalcolestes viridis* and *C. parvidens*, and while ecological differences are greater, their morphology is almost identical. A geographic genetic study as performed in *Chalcolestes* is needed to unravel the history of this couple. Further work must also determine the position of the European groups within the much greater eastern Asian and (especially) American diversity. Marinov and Seidenbusch (2007) erected the genus *Corduliochlora* for *S. borisi* based on several adult characters, of which the broadly notched male epiproct and the short deeply split vulvar scale are most notable. The larvae, however, match those of the *metallica* group (Fleck et al. 2007). The highly anticipated results of genetic analysis will hopefully resolve the issue, as well as identify the closest relatives of *Somatochlora*. While *Cordulia* may be nearest, the North American *Dorocordulia* and *Helocordulia* and temperate South American *Rialla* also seem close (Bybee et al. 2008; Ware et al. 2007). **Cordulia** has a unique deeply bifid epiproct with a pair of dorso-apical teeth. Jödicke et al. (2004) found no evidence of gene flow among the North American *C. shurtleffii*, Western Palaearctic *C. aenea* and its Eastern Palaearctic subspecies *amurensis*, and thus recognised them as three distinct species. However, no differences in morphology, behaviour or ecology are known, and thus whether and where *C. aenea* and *C. amurensis* meet and if they merge or coexist is unknown as well. Kosterin and Zaika (2010) argued that the lack of gene flow does not mean that speciation has occurred and therefore regarded the taxonomical decision to consider the taxa as a good species premature.

Although the phylogeny of **Libellulidae** has been studied more than any other in Anisoptera (Fleck et al. 2008a; Ware et al. 2007; Pilgrim and von Dohlen 2007), the results are still rather inconclusive. The libellulid radiation is very large and probably occurred explosively, which limits the resolving power of studied genes and requires dense taxon sampling to be representative. Although a few clusters of related genera have been identified, no overall divisions are apparent. In Europe only four genera are dominant in species and individual numbers: *Libellula* and *Orthetrum* are part of the largely tropical 'libelluline' diversification; *Sympetrum* and *Leucorrhinia* belong to the mostly Holarctic 'sympetrine' clade (see below). Aside from these, seven heat-loving genera occur regularly in Europe, each until recently with only a single representative. Published phylogenies are especially inconclusive about the relationships of these 'exotic singletons', which are discussed first below.

The **Brachythemis** species that occurs in southern Iberia, Sardinia and Sicily was long known as *B. leucosticta*, which extends to South Africa and Madagascar. However, Dijkstra and Matushkina (2009) showed that that species only occurs south of the Sahara. There it overlaps broadly with *B. impartita*, which differs mainly in the male abdominal structure and venation coloration. It is this species that extends around the Sahara to the Mediterranean. The genus is otherwise small, with two more African species, one in the Near and Middle East, and one in the Oriental region, although the East Asian *Deielia phaon* probably falls within *Brachythemis* too (Pilgrim and von Dohlen 2008). *Brachythemis* belongs to a predominantly crepuscular group that includes the well-known tropical genera *Tholymis* and *Zyxomma* (Dijkstra 2003b; Pilgrim and von Dohlen 2008; Ware et al. 2007). Species of *Brachythemis* itself are also especially active at dusk.

Selysiothemis belongs to a distinct group including the heat-loving *Aethriamanta*, *Macrodiplax* and *Urothemis*, which are sometimes separated as the subfamily (or even family) Urothemistinae (= Macrodiplactinae). While their monophyly is supported by preliminary molecular results (e.g. Ware et al. 2007; Fleck et al. 2008b; Pilgrim and von Dohlen 2008), they do not stand apart from Libellulidae as a whole. Their venation is very open, the secondary genitalia simple in structure, and the vulvar scale strongly bilobed. Although the genus has only a single species, *S. nigra* is very close to *Macrodiplax* morphologically and ecologically. Both *Macrodiplax* species are tolerant to brackish water and found mainly in coastal pools, the blackish *M. balteata* from the Caribbean Sea to the Gulf of California and in the desert between them, the red *M. cora* around the Indian Ocean and western Pacific. *S. nigra* breeds in (often ephemeral) ponds and lakes in arid and coastal regions around the Mediterranean Sea, and from northern Africa to central Asia.

Crocothemis and *Diplacodes* belong to a large tropical radiation that includes *Erythrodiplax* with almost 60 species in the Americas and *Neurothemis* with 13 in Australasia. The taxonomic boundaries within this radiation require further study and genera may change in the near future (Pilgrim and von Dohlen 2008). Currently *Crocothemis* and *Diplacodes* are both small Palaeotropical genera with very widespread species: *Diplacodes* has five each in the African and Australasian tropics, while *Crocothemis* is principally African (five species) with single species confined to Madagascar, Asia and Australia. The species that reached Europe, *D. lefebvrii* and *C. erythraea*, are both the most widespread African representative of their genus, being found together at almost any open stagnant habitat in the continent.

There is some support that *Pantala*, *Trithemis* and *Zygonyx* and some other predominantly tropical genera are quite closely related (Ware et al. 2007; Pilgrim and von Dohlen 2008; Dumont et al. 2009; Fleck et al. 2008b). These superficially dissimilar genera share features such as a reduced pronotal hindlobe, narrowing forewing discoidal field and a large-hooked hamule. *Zygonyx* contains over 20 species in the African and Asian tropics, which are peculiar for patrolling in flight over fast-flowing waters, especially rapids and waterfalls. Over half the species occur south of the Sahara and here also the greatest morphological diversity is found. The most widespread species is *Z. torridus*, which is even capable of finding suitable habitat in deserts. Not surprisingly, it was that species that colonised India, Mauritius and southern Europe. *Pantala* *flavescens* is also a patrolling libellulid, but adapted to ephemeral pools. No dragonfly develops faster and wanders further than it does, annually crossing the ocean between India and Africa (Anderson 2009). This capacity made it the most widespread (and possibly most abundant) of all odonates. The genus's second species, *P. hymenaea*, is confined to the Americas. As are probably the previous genera, *Trithemis* is a recent arrival to Europe. The first records of *T. annulata*, from Spain, are in the late 1970s. Three decades later, *T. kirbyi* also entered Europe there. A third African species, *T. arteriosa*, may soon follow suit, although it is still comparatively localized in North Africa and Turkey. The largest anisopteran genus in Africa, with over 40 species, *Trithemis* dominates dragonfly communities across the continent, from cool permanent streams to warm temporary pools, from desert to rainforest, and from lowlands to highlands. Damm et al. (2010) inferred their ecological evolution using a molecular phylogeny of over four-fifths of the species. This analysis suggests an origin between 6 and 9 million years ago in open stagnant habitats, coinciding with savanna expansion: while drying disadvantaged many aquatic species, it favoured those adapted to exposed and temporary conditions. Indeed, *T. kirbyi*, which is sister species to the radiation of all other *Trithemis* species, is best adapted to

live in desert environments. The main radiation may have coincided with a wetter period between 5 and 3.5 million years ago: possibly forest expansion separated populations in open areas, giving rise to many lineages in little time. As open habitats began to coalesce again after this period, the species adapted to temporary conditions expanded into largely overlapping ranges. These include *T. annulata* and *T. arteriosa*, two of Africa's most widespread dragonflies, which are currently expanding northwards in the Western Palaearctic. At least five more dispersals to Eurasia or Madagascar occurred, demonstrating Africa's variable environment as a cradle for adaptable species. However, with such potential for gene flow, the adaptable lineages barely radiated further. Most species diversity in Africa originated from three ecologically constrained lineages, in lowland streams, highland streams and swampy habitats respectively: none of these reached beyond the Afrotropics.

Libellula *quadrimaculata* was the first dragonfly to be named, featured first in Linnaeus's *Systema Naturae*. While, being the type species of the first-named genus, it can never be named differently, it has been argued that the two other European species classified in *Libellula* are too distinct to be placed in the same genus, and should be called *Ladona fulva* and *Platetrum depressum* (or *Plathemis depressa*) instead. Artiss et al. (2001) sequenced two parts of the mitochondrial genome, sampling most *Libellula* species. Their omission of *L. melli* from China and *L. pontica* from the Near East

cannot affect the analysis much, because these are very close to *L. depressa* and *L. fulva* respectively. Carle and Kjer (2002) analysed 242 morphological characters. The two resulting phylogenies are remarkably similar, placing confidence in the position of taxa for which genetic data were unavailable (Fig. 7). *Libellula* (sensu stricto) is a largely Nearctic assemblage with the Holarctic *L. quadrimaculata* and its two close relatives (eastern Asian *L. angelina* and North American *L. semifasciata*) form the subgenus *Libellula*, which is the sister group of an American radiation of 20 species placed in three or four subgenera. The remaining taxa fall outside this assemblage, with *L. depressa* and *L. fulva* close to the American *Ladona* species. While the morphological phylogeny places the American *Plathemis* with *L. depressa*, the molecular data suggest that a representative of the largely Neotropical genus *Orthemis* is nearer *Libellula* (s.s.) and *Ladona* than to *Plathemis*. The work by Ware et al. (2007) and Fleck et al. (2008b) suggests that further tropical genera are inserted within *Libellula* (sensu lato) and it actually represents three or more independent incursions of tropical libellulids into the temperate zone. Although further analysis of related genera is needed to resolve the matter, it seems likely that *L. depressa* and *L. fulva* should be reclassified in the near future, probably in *Ladona*.

Orthetrum includes about 60 species, of which one half is tropical African and the other extends across Eurasia to Australia. Although some species, including seven known
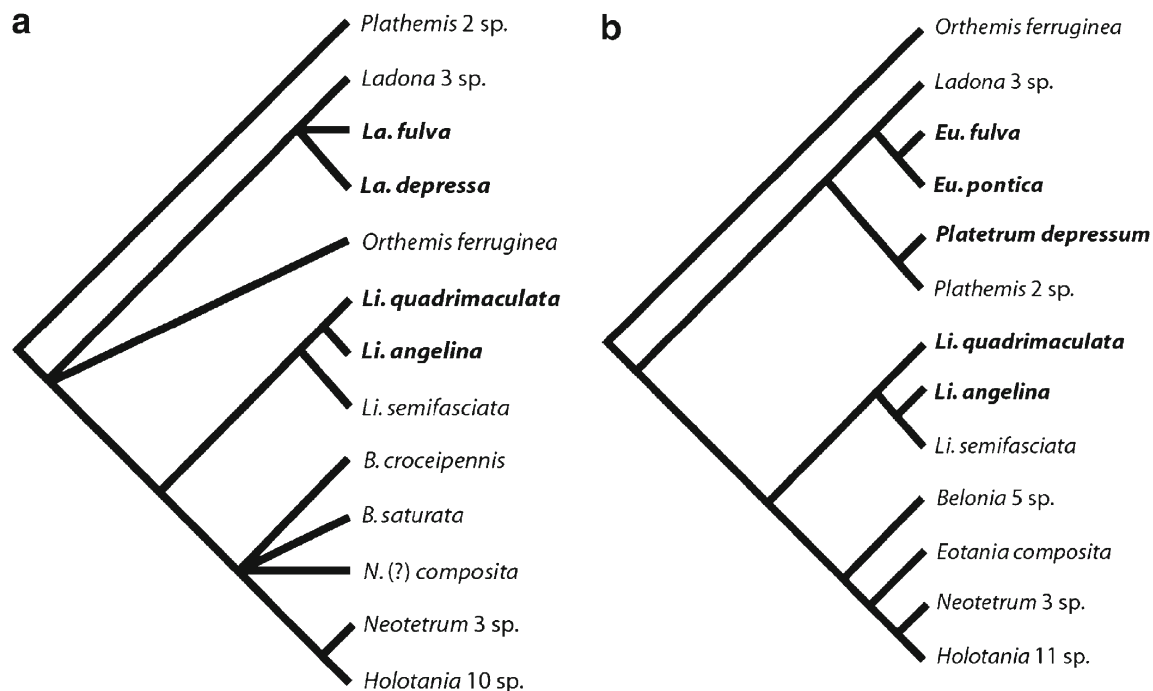
Fig. 7 Phylogeny of *Libellula* (sensu lato), based on molecular data (**a**, after Artiss et al. 2001; Kambhampati and Charlton 1999) and morphology (**b**, after Carle and Kjer 2002). *B.* (*Belonia*), *Eu.* (*Eurothemis*), *La.* (*Ladona*), *Li.* (*Libellula* sensu stricto) and *N.* (*Neotetrum*) are abbreviations of genera and subgenera as proposed by stated authors; their interpretation is discussed in the text. Monophyletic groups of North American species are indicated with a (sub-) genus name and number of species. *Bold* taxa occur in the Eurasia; the others are American

in Europe, extend into the Palaearctic, even these prefer warmer habitats and regions. The genus is rather heterogeneous across its wide range, although the many similar African species suggest a recent explosive radiation as in *Trithemis* (see above): *O. chrysostigma* is common throughout the continent and one of the species best adapted to arid conditions. Its establishment in Europe is therefore in parallel with similarly adaptive Africans as *P. genei*, *B. impartita*, *C. erythraea*, *T. kirbyi* and *Z. torridus*. *O. brunneum*, *O. coerulescens* and *O. nitidinerve* may be part of this radiation; some still refer to Mediterranean populations of *O. coerulescens* as *O. anceps*, but Mauersberger (1994) demonstrated that Iberia, Sicily and large parts of southeastern Europe are inhabited by intermediate forms, rendering them synonymous. The closely related and very distinctive *O. albistylum* and *O. cancellatum* are likely to have Asian roots. The genus is notably diverse in appearance in the Oriental region, including red, boldly patterned and wing-marked species. Finally, *O. trinacria* forms a distinct group with *O. sabina* and *O. serapia*, with notably slender abdomens, a peculiar hamule structure, aggressive behaviour (often taking dragonflies as prey) and a strong colonising potential. The African *O. trinacria* extends to Madagascar, Mesopotamia and Europe, while *O. sabina* is tropical Asia's most abundant dragonfly, penetrating to northern Africa and Turkey, and possibly into Europe soon as well. In the Pacific it partly gives way to *O. serapia*, but the geographic limits between these recently separated species are poorly known. Unfortunately no phylogenetic analysis is yet available: Ware et al. (2007) and Pilgrim and von Dohlen (2008) found some support for the monophyly of *Orthetrum*, but the inclusion of the Asian species *Lyriothemis pachygastra* and *Potamarcha congener* suggests some unresolved complexity.

"Sympetrinae" was once considered one of the largest libellulid subfamilies, including (among others) the tropical radiation of *Crocothemis* and related genera (see above). However, only *Celithemis*, *Leucorrhinia* and *Sympetrum* are closely related (Ware et al. 2007; Pilgrim and von Dohlen 2008; Fleck et al. 2008b). With about 70 species combined, they form the only truly Holarctic libellulid radiation, as all others are rooted distinctly in the tropics. Indeed, in Europe they represent two-thirds of libellulid species north of the Alps. While *Leucorrhinia* and *Sympetrum* occur throughout the Holarctic (with a few species in the adjacent tropics), *Celithemis*, whose species recall *Leucorrhinia* with strongly patterned wings, is purely Nearctic. **Leucorrhinia** is the only larger European genus for which a complete global molecular phylogeny is published (Fig. 8; Hovmöller and Johansson 2004). A group of pruinose species, including the pair *L. albifrons* and *L. caudalis* plus the American *L. frigida*, is sister to the remaining species. The latter separates into an American group of six species and a group with all remaining Palaearctic
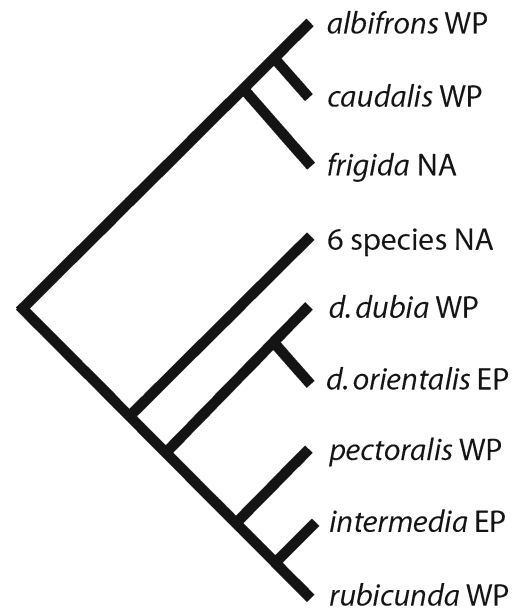
Fig. 8 Phylogeny of *Leucorrhinia* (one monophyletic North American group not given in detail), based on Hovmöller and Johansson (2004). The taxa occur in the Eastern Palaearctic (*EP*), Nearctic (*NA*) or Western Palaearctic (*WP*)

species. It has long been debated whether the latter includes three or five species, depending on whether the Far Eastern populations are considered as subspecies of *L. dubia* and *L. rubicunda*, or as the distinct species. Kosterin and Zaika (2010) pointed out that differences in the adult coloration and larval spines of *L. orientalis* were variable and probably environmentally related, opting to consider it a subspecies *L. dubia*, while *L. intermedia* differed specifically from *L. rubicunda* in the shape of the vulvar scale. The fourth species, *L. pectoralis*, is nearest to the pair *L. intermedia* and *L. rubicunda*.

Pilgrim (2006, 2012) presented a phylogeny based on morphological and (nuclear and mitochondrial) genetic data of about two-thirds of the over 50 **Sympetrum** species (Fig. 9). Including the Hawaiian endemic *S. blackburni* (formerly in its own genus *Nesogonia*), and excluding two tropical African species transferred to *Trithetrum* (Dijkstra and Pilgrim 2007), *Sympetrum* is monophyletic. However, all species that occur in the tropics, including many that extend into warm temperate areas and *S. blackburni*, which seems to originate from long-distance dispersal from the Americas, fall outside the main monophyletic radiation of the genus, confined to temperate habitats in North America, Eurasia and northern Africa. This suggests that the origin of the genus may lie with well-dispersing species from the tropics (Pilgrim suggested South America) establishing themselves in the temperate zone. Most species that have been suggested to form the subgenus (or distinct genus) *Tarnetrum*, including *S. fonscolombii*, belong to these warmth-loving 'outsiders'. However, because *Tarnetrum* as proposed is not monophyletic
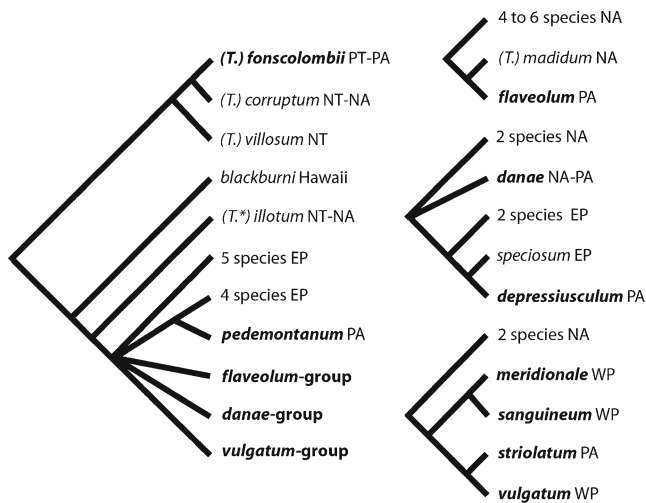
Fig. 9 Phylogeny of *Sympetrum*, based on Pilgrim (2006, 2012) and Pilgrim and von Dohlen (2008). Norwegian *S. nigrescens* and Himalayan *S. commixtum* are included with *S. striolatum* following Pilgrim and von Dohlen (2007); Japanese *S. frequens* with *S. depressiusculum* following Sawabe et al. (2004). Monophyletic non-European groups not given in detail; three larger groups are detailed on *right*. The taxa occur in the Eastern Palaearctic and adjacent Oriental Region (*EP*), Nearctic (*NA*), Neotropics (*NT*), entire Palaearctic (*PA*), Palaeotropics (*PT*) or Western Palaearctic (*WP*). *Bold* species occur in Europe; species classified in subgenus *Tarnetrum* (* type species) are indicated

and its type species is not closely related to any of the other species, it is inappropriate to recognise it. Interestingly, *S. corruptum*, the American sister species of *S. fonscolombii*, is similar both in appearance and ecology, being strongly migratory. The large temperate radiation of *Sympetrum* consists of five genetically well-separated groups, each with at least five species. The relationships between these groups are not apparent from the data, suggesting they originated simultaneously and rather suddenly. All five groups are represented in eastern Asia, but only four in western Eurasia and three in North America. This suggests a lot of dispersal of *Sympetrum* across the Northern Hemisphere, and a possible origin of this diversity in eastern Asia. *S. danae*, *S. depressiusculum*, *S. flaveolum* and *S. pedemontanum* each range across to Japan (*S. danae* even to North America) but have no close relatives in Europe, while the remaining European species (probably including *S. sinaiticum*) seem to form a distinctly west-Eurasian radiation of very closely related species. Pilgrim and von Dohlen (2007) compared (presumed) *S. nigrescens* from Norway and Ireland with *S. striolatum* from The Netherlands, Turkey and Japan, and found no genetic or morphological evidence to consider them as distinct species. Parkes et al. (2009) sampled from the south (*striolatum*) to the north (*nigrescens*) of Great Britain and also found the latter merely to represent a dark variation of the former. Neither study included *S. nigrifemur* from the Canaries and Madeira, but probably that taxon should also be subsumed in *S. striolatum*. The subspecies *ibericum* of *S. vulgatum* occurs isolated from *S. v. vulgatum* in the mountains

of northwestern Spain and adjacent France: molecular study may clarify the status of this poorly known taxon.

Conclusion

As the taxonomy of European Odonata began over 250 years ago and involves less than 140 species, it is remarkable that so many uncertainties still remain. Nonetheless good progress has been made, especially in the past decade, and it seems likely that within another 10 years the phylogeny of all European species will be known. European odonatologists have probably thought that the taxonomy of their species was nearing its conclusion throughout the past century, but now the methods for phylogenetic reconstruction based on morphology have matured, while molecular methods provide an independent tool to test them. Indeed, Trueman (2007) also predicted that by 2017 and at most 2027 all major global issues in dragonfly classification and nomenclature will have been resolved. Taking the checklist provided by Dijkstra and Lewington (2006) as a reference, sufficient evidence is published to recognise *Chalcolestes* and rename European populations of *Brachythemis leucosticta* as *B. impartita*. *Macromia* and *Oxygastra* can be removed from *Corduliidae*, but while *Macromiidae* is available for the former, the family name for the latter remains to be determined. There is no evidence to separate *Sympetrum fonscolombii* in *Tarnetrum*, or to treat *S. nigrescens* (and probably *S. nigrifemur*) as distinct from *S. striolatum*. From a nomenclatory perspective, the following seem to be the foremost phylogenetic challenges remaining, in order of importance:

1. *Aeshna* and *Anax*; generic identity of *A. affinis*, *A. isoceles*, *A. mixta* and *A. ephippiger*.
2. *Libellula*; generic identity of *L. depressa* and *L. fulva* in relation to *Ladona*.
3. *Gomphus* (sensu lato); generic identity of *G. flavipes* in relation to *Stylurus*, status of *G. schneiderii* in relation to *G. vulgatissimus*.
4. *Onychogomphus*; generic identity of *O. costae*, specific identity of taxa related to *O. forcipatus*.
5. *Somatochlora*; validity of *Corduliochlora* for *S. borisi*, status of *S. meridionalis* in relation to *S. metallica*.
6. *Lestes*; specific identity of *L. virens* taxa in relation to *L. numidicus*.
7. *Sympetrum*; separation of *S. nigrifemur* and *S. striolatum*, identity of *S. vulgatum ibericum*.
8. *Caliaeschna*; generic identity of *C. microstigma* in relation to *Cephalaeschna*.

To reconstruct the glacial isolation and postglacial colonisation of Holarctic dragonflies, global phylogenies of *Lestes*, *Coenagrion*, *Aeshna*, *Gomphus*, *Cordulegaster*, *Somatochlora* and *Orthetrum* would be most useful.

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