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1. Phylogeny and biogeography of the Platystictidae (Odonata)

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1. **Introduction**

2. **Methods**

3. **Results**

4. **Discussion**

Appendices

1. Introduction

1.1. Introduction to the Platystictidae

Forest damselflies (Odonata, Zygoptera, Platystictidae) are restricted to Central and the northern part of South America (subfamily Palaemnematinae), and tropical Southeast Asia (subfamilies Platystictinae and Sinostictinae) (Fig. 1). With 213 valid species, the family is species-rich, but remarkably homogeneous in general appearance (Figs 2 and 3). Based on morphological characters the monophyly of the Platystictidae is undisputed (Bechly 1996, Rehn 2003).

The larvae typically live between plant debris in small streams or seepages in deep shade; the imagos are found hanging on branches or from the tips of leaves or twigs in such sites. Both larvae and imagos are inconspicuous in coloration and behaviour. The forest-dwelling platystictids have poor flying capacity, and their low dispersal power is reflected in the small distributional ranges of most species.

Despite their homogeneity in habitus, platystictids are remarkably variable in structural details of their anal appendages, secondary genitalia and pronotum. Also, details in coloration show distinct interspecific variation. One or two species from southeastern China and northern Vietnam, defined by morphological

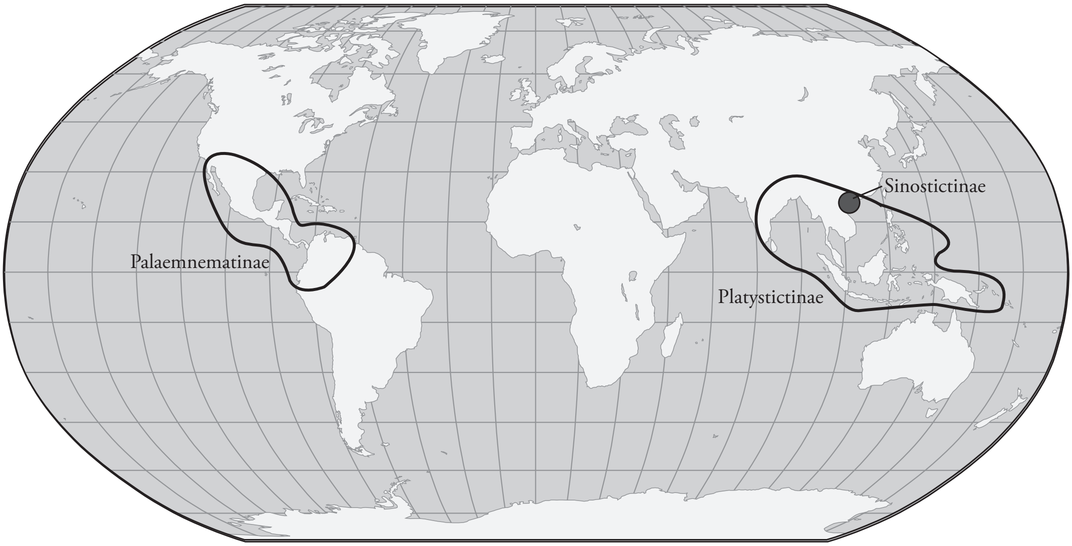

Figure 1. Global distribution of Platystictidae. The subfamily Platystictinae is confined to southeast Asia, and the subfamily Palaemnematinae to Central and northern South America. The Sinostictinae are only known from southeastern China.

characters, have markedly different colour forms (Wilson & Reels 2003, van Tol 2008).

The family is an almost ideal and *a priori* choice for the biogeographer. As stated by Platnick (1991), 'in biogeography we can always prefer to initiate our studies with those taxa that are maximally endemic – those which include the largest number of species, with the smallest ranges, in the area of interest'. This condition is perfectly fulfilled in Platystictidae for biogeographical patterns in southeast Asia. The occurrence of a subfamily of the Platystictidae endemic to the New World reveals a pattern that presumably goes back to the Late Cretaceous (van Tol & Müller 2003).

Our knowledge of the fauna of China, the Philippines and Indonesia has significantly increased by extensive fieldwork during the last fifteen years. The material that became available added to the information on the distribution of previously described species, and also provided the basis for descriptions of many new species (e.g., Matsuki & Saito 1996, Theischinger & Richards 2005, van Tol 2000-2008, Wilson 1997, Wilson & Reels 2001, 2003, Wilson & Xu 2007). Nevertheless, our insight in the phylogenetic relationships, and the historical biogeography, has remained superficial.

In the present paper we aim to understand the phylogenetic position of the Platystictidae in the Odonata, and to reconstruct the phylogeny and historical biogeography of this family. Our study is mainly based on an analysis of the morphological characters, but an analysis of a restricted taxon sample to study the relationships based on molecular characters is included in this paper as well. The reconstruction of historical biogeography of the Platystictidae, based on a reconstruction of the phylogeny, focuses on the species of southeast Asia.

Present knowledge of the phylogeny of the Zygoptera (damselflies), and the biogeography and geological history of southeast Asia is summarized in the next paragraphs.

1.2 **Relationships of families of Zygoptera**

Monophyly of the Odonata, and its suborders. – Both the monophyly of the Odonata and that of the Zygoptera is based on morphological characters (e.g., Bechly

Figures 2-3. General appearance of Platystictidae. – 2, *Protosticta linnaei* van Tol. Vietnam, Chu Yang Sin National Park. 3, *Protosticta satoi* Asahina (dark form). Vietnam, Tam Dao. Photographs by J. van Tol.

1996, Rehn 2003). The remark by Hasegawa & Kasuya (2006: 55), viz., that the analysis of Bechly revealed the paraphyletic nature of the Zygoptera, is incorrect (cf. Bechly 1996: 263). The monophyly of the Zygoptera was established by Rehn (2003: 193) (see Fig. 4) based on six synapomorphies of morphological characters, although the interpretation of many characters was hampered since they could not be studied in the (fossil) outgroup taxa. The monophyly of the suborder Anisoptera is also strongly supported by many apomorphies, but this clade does not appear as the sister group of the Zygoptera in all analyses, especially so if fossils are taken into account (e.g., Bechly 1996). For instance, a molecular analysis (16S and 28S) of a restricted taxon sample of the Odonata, using a mayfly (Ephemeroptera) as outgroup, revealed a paraphyletic nature of the Zygoptera (Hasegawa & Kasuya 2003). In the same analysis, the Anisoptera appeared as a monophyletic sister group of *Epiophlebia* Calvert, 1903b, a genus traditionally assigned to the Anisozygoptera. The sister group of the Anisoptera + Anisozygoptera appeared inconsistent between various applied analytical methods. Recently, Bybee *et al.* (2008) presented a reconstruction of the phylogeny of the Odonata based on morphological and molecular characters. This study included specimens assigned to 109 genera representing 30 families out of 34 families presently recognized. Apart from the morphological characters as used by Rehn (2003), six genes were studied: 12S rDNA, 16S rDNA, and COII from the mitochondrion, and Histone 3, 18S rDNA and 28S rDNA from the nucleus. In this study, the Zygoptera were recovered as a sister group of the Epiprocta [= Anisoptera + 'Anisozygoptera'] + Tarsophlebiidae [fossils only].

Phylogeny of the Zygoptera families based on morphological studies. – The first attempts to reconstruct the phylogeny of the order Odonata were published by Tillyard (1917, 1928), Tillyard & Fraser (1938, 1939, 1940), Fraser (1957), and Kennedy (1919, 1920). These phylogenies and classifications were primarily based on wing venation characters, or the secondary genitalia of the males. Kennedy (1920) distinguished 16 'subfamilies', comparable to families in recent classifications. He considered the position of the Platystictidae as doubtful, and ranked it close to the Megapodagrionidae or the Pseudostigmatidae.

The phylogenetic relationships of the Odonata were also illustrated by Fraser's (1957: frontispiece). There is no general agreement on the interpretation of this figure, but we conclude that the family Platystictidae is meant to be the sister group of the (Protoneuridae (Coenagrionidae + Platycnemididae)).

Carle (1982), Trueman (1996) and Bechly (1996) published the first studies using cladistic methods on a dataset of morphological characters. Bechly's study included a new classification including all fossil groups, which is summarized in Rehn (2003, fig. 8). Rehn (2003) further extended this dataset, and based his results on explicit cladistic methodology (Fig. 4). Several other studies published since 2003 provided reconstructions of the phylogenetic relationships of higher taxa within the odonates, such as Gassmann (2005) of the subfamily Calicnemiinae (Platycnemididae).

Rehn's (2003) study confirmed the monophyly of the Zygoptera. The genus *Philoganga* Kirby, 1890 (Lestoideidae) appeared as the sister taxon to all other Zygoptera. The Calopterygoidea (= Caloptera) and the rest of the Zygoptera are sister groups in this tree, but the Calopterygoidea did not include the Amphipterygidae (e.g. *Amphipteryx* Selys, 1853 and *Devadatta* Kirby, 1890). Amphipterygidae are usually included in the Calopterygoidea (*e.g.*, Davies & Tobin 1984). The position of the Platystictidae in Rehn's trees changed according to the algorithms applied. Based on a NONA analysis with all characters equally weighted (Rehn 2003: fig. 4) (Fig. 4), the Platystictidae are the sister group of the genus *Lestoidea* Tillyard, 1913. In the consensus tree of a parsimony analysis with all characters treated as unordered, the position of the Platystictidae is hardly resolved against the other non-calopterygoid Zygoptera. Finally, in the consensus tree of a parsimony analysis with implied weighting (Rehn 2003, fig. 6), the Platystictidae are the sister group of a clade including the Coenagrionidae, Pseudostigmatidae, Platycnemididae, Protoneuridae, Lestoideidae and Isostictidae.

In conclusion, the phylogeny of the Zygoptera and the position of the Platystictidae within the Zygoptera based on morphological characters, remains poorly understood, also at the level of families and subfamilies. The origin of this problem is the relatively small number of characters, and the complicated interpretation of character states due to convergence or character reversal, which are themselves caused by a relatively low character change during at least hundred million years. This is illustrated by the fact that most superfamilies had already developed before the Cretaceous (135 Ma) (Rasnitsyn & Pritykina 2002).

Phylogeny reconstruction of the Zygoptera families based on molecular studies.– The most comprehensive analysis of the phylogeny of the Odonata based on a complete dataset, including molecular characters, has recently been published by Bybee *et al.* (2008) (summary in Fig. 5). Previous publications on the phylogenetic relationships of odonates using molecular data mainly included Anisoptera, such as Ware *et al.* (2007). Zygoptera had only been studied for small subsamples. Up to now, most attention has been paid to the Calopterygidae (Dumont *et al.* 2005, 2007), the genus *Calopteryx* Leach, 1815 (Misof *et al.*, 2000; Weekers *et al.*, 2001), and some genera of the Coenagrionidae, e.g. *Megalagrion* McLachlan, 1883 (Jordan *et al.*, 2003), *Erythromma* Charpentier, 1840 and *Cercion* Navás, 1907 (Weekers & Dumont 2004). The study of Hasegawa & Kasuya (2006) is based on a phylogenetically more diverse taxon sampling, although only 32 odonate taxa were included in the analysis. In conclusion, anisopteran families have received far more attention than zygopteran families, although extant Zygoptera are much more diverse than extant Anisoptera.

The reconstruction of Bybee *et al.* (2008) is based on thirty families and 109 genera of odonates. The morphological dataset is the same as Rehn (2003), but the molecular data are largely new. The Platystictidae are represented with *Palaemnema melanostigma* (Hagen in Selys)[1] and *Protosticta sanguinostigma* Fraser. Apart from the monophyly of the Zygoptera, as mentioned above, the analysis of the molecular characters

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[1] Authorities of species names of all Platystictidae, and of other species used for phylogenetic analysis, are given in Appendix 1 of this chapter (p. 60-65).

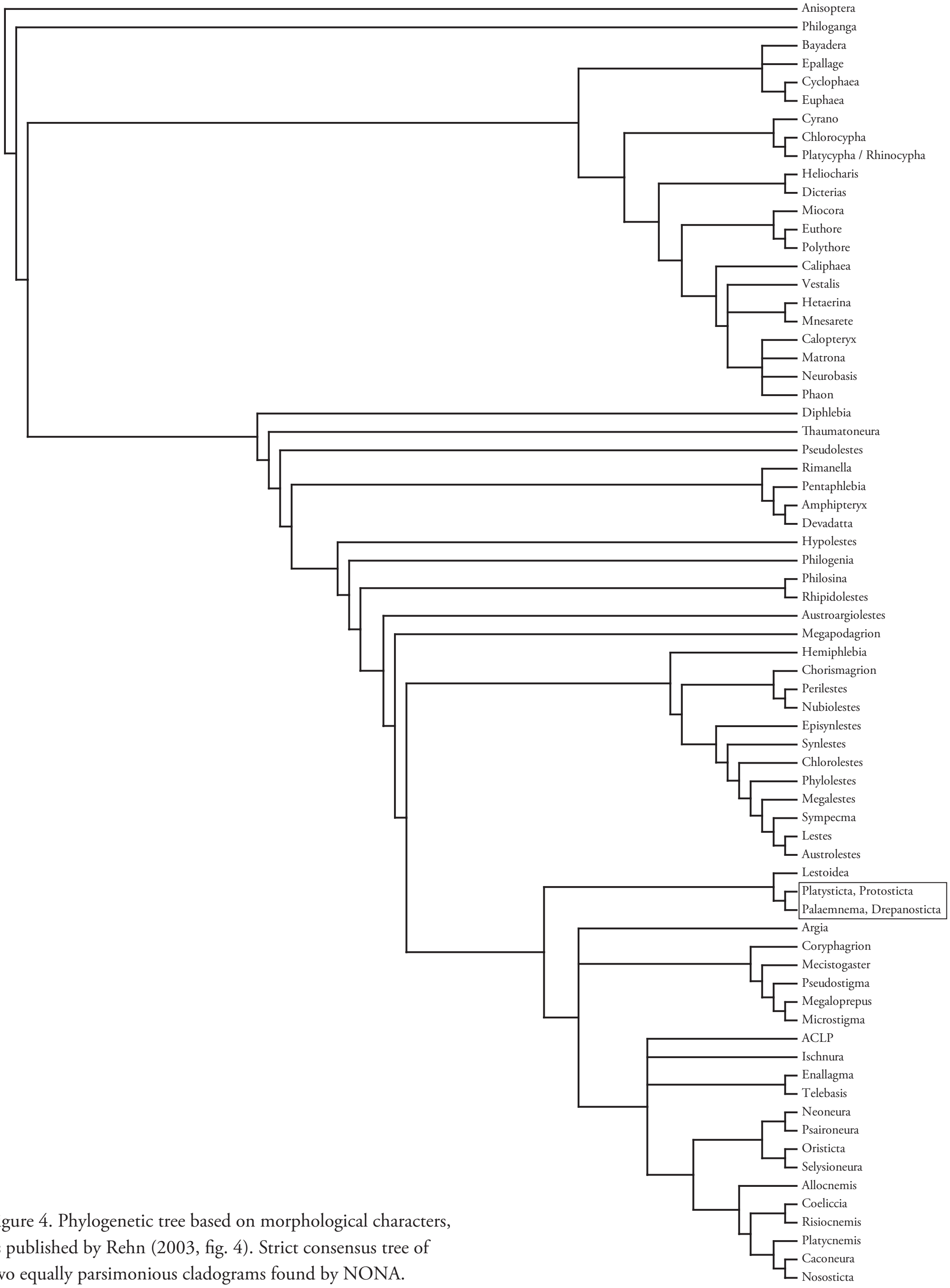

Figure 4. Phylogenetic tree based on morphological characters, as published by Rehn (2003, fig. 4). Strict consensus tree of two equally parsimonious cladograms found by NONA.

revealed (see Fig. 5) (a) a sister group relationship of the superfamily Lestoidea (= Lestidae, Perilestidae, Synlestidae, and Chorismagrionidae), with the rest of the Zygoptera, (b) a sister group relationship of the Platystictidae with all other Zygoptera except Lestoidea as defined above. Thus, these results differ considerably from those obtained by Rehn (2003) and Hasegawa & Kasuya (2006).
The position of the family Platystictidae among the other Odonata may have important impact on the topology of the relationships within the Platystictidae. Therefore, we have also analysed our own molecular dataset to reveal the relationships of the zygopteran families (see paragraph 3.1).

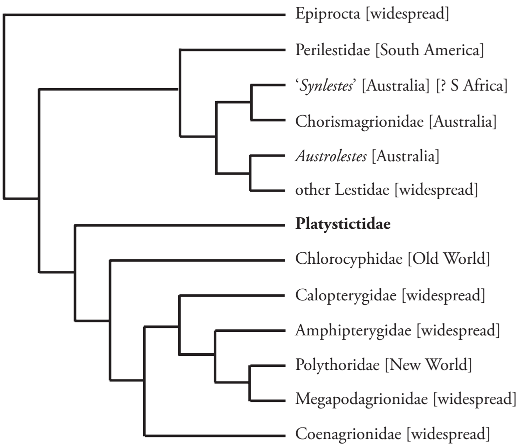

Figure 5. Simplified version of Hypothesis I of phylogenetic relationships of Odonata by Bybee et al. (2008: fig. 6 and 2). African Synlestinae were not studied.

1.3 Classification

Classification of the Platystictidae. – Present classifications (e.g. Tsuda 2000, van Tol 2007a, Wilson 1997) distinguish three subfamilies in the Platystictidae, viz. Palaemnematinae, Platystictinae and Sinostictinae. The Palaemnematinae, with only the genus *Palaemnema* Selys, 1860, are restricted to the New World, while the Platystictinae are distributed from India and Sri Lanka in the west, up to the Papuan region. The recently recognized Sinostictinae are confined to southeastern China, especially Hong Kong and Hainan (Wilson 1997; K.D.P. Wilson and G.T. Reels, personal communication). The phylogenetic relationships of these groups are poorly understood. Traditionally, three genera are recognized in the Oriental Platystictinae, viz. *Platysticta* Selys, 1860, *Protosticta* Selys, 1885 and *Drepanosticta* Laidlaw, 1917. Several authors have expressed their doubts whether the present genus definitions based on wing venational characters, reflect phylogenetic relationships. Lieftinck (1933: 285), describing *Protosticta feronia* and *Drepanosticta dupophila* already stated 'Indeed, I am inclined to think that *feronia*, although immediately distinguished from *dupophila* by the generic character found in the anal wing veins, is closely related to that species, for I can hardly imagine that so striking a similarity can be brought forward by convergence only'. More recently, Orr (2003: 69-72) more or less dropped the recognition of *Protosticta* and *Drepanosticta* for the Bornean species, and preferred to distinguish three or four 'forms' of platystictids including members of both genera. Generally, however, most authors refrained from changing or updating the formal classification. Wilson (1997) and van Tol (2005) erected new genera for considerably different species that could not properly be placed in one of the three recognized genera of southeast Asia. Wilson (1997) erected the genus *Sinosticta* and the new subfamily Sinostictinae to accommodate that genus, mainly since *Sinosticta* has several characters in the wing venation in common with the genus *Palaemnema* Selys, while the anal appendages are unlike any other species of Platystictidae.

1.4 Species diversity and distribution of Platystictidae

Palaemnematinae (Central and South America). – Although the first species of Platystictidae, *Libellula paulina* was described as early as 1773 (Drury 1773), the special character of this group was first recognised by Selys[2] (1860), when he erected the subgenus

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[2] The name of E. de Selys Longchamps is usually abbreviated as 'Selys' in odonatological literature, as was the custom of the author himself.

Palaemnema Selys in the new genus *Platysticta* to receive *L. paulina* from Honduras and Mexico, and described *P. angelina* (Guatemala) and *P. melanostigma* from Puerto Cabello (Venezuela) as new to science. Knowledge of the species of the strictly New World *Palaemnema* increased significantly by publications of Ris (1918) with three species, Calvert (1903, 1931) (one and 14 species, respectively), Kennedy (1938) (three species) and Donnelly (1992) (six species). Presently, 42 species of *Palaemnema* are known. The highest diversity is found in Central America, while also a few species inhabit the northwestern part of South America (e.g., Belle 2002, De Marmels 1989, 1990). One Mexican species just reaches the southernmost part of the USA (Hoekstra & Garrison 1999).

Platystictinae and Sinostictinae (southeast Asia). – Selys (1860) also described the first six species of Platystictidae from southeast Asia, all placed in the subgenus *Platysticta*. Five species originated from Ceylon (Sri Lanka), including *P. maculata*, designated as type species of *Platysticta* by Kirby (1890). The other species from Ceylon, placed by Selys (1860) in the *P. hilaris* group, are presently assigned to *Drepanosticta* Laidlaw. The only species from outside Ceylon described in Selys' (1860) paper, *Platysticta quadrata*, presently *Drepanosticta quadrata*, was collected by Wallace in Singapore. Nine more species of Platystictidae from southeast Asia were described during the 19th century, remarkably all from islands and none from the mainland: one more species from Ceylon, two from Sulawesi, three from the Philippines, and one each from Borneo, Java and New Guinea. The genus *Protosticta* was erected by Selys (1885) to accommodate *Platysticta simplicinervis* Selys from Celebes (Sulawesi). Publications, mainly by Fraser (e.g. 1933a, b), Kimmins (1936) and Lieftinck (e.g., 1932, 1933, 1934, 1938, 1939, 1949, 1965) based on field work in India, Burma, the Malay archipelago and New Guinea extended our understanding of the diversity of this family. Van Tol (2005) described the diversity of this family in the Philippines, adding 21 species new to science, and also revised the material from Sulawesi and the Moluccas (van Tol 2000, 2007b-c). Thus, the largest subfamily Platystictinae is widespread in the mainland of southeast Asia, from Sri Lanka (Ceylon) (Kirby 1894, Fraser 1933a, Lieftinck 1955, 1971) via India (Laidlaw 1917, Fraser 1933b), Thailand (Asahina 1984, Hämäläinen & Pinratana 1999), southern China (Wilson 1997 [including the subfamily Sinostictinae], Wilson & Reels 2001, 2003, Wilson & Xu 2007), Laos , Myanmar (Burma), Vietnam (Asahina, 1984, 1997b, van Tol 2008), into the Malay peninsula (Lieftinck 1965), the Philippines (Hämäläinen & Müller 1997, Lieftinck 1961, van Tol 2004, 2005) and Indonesia (Lieftinck 1954, van Tol 2000, 2007b, c). Relatively few species are known from the Papuan region (New Guinea, Solomon, d'Entrecasteaux and Bismarck islands) (e.g., Lieftinck 1938, 1949, and unpublished data the National Museum of Natural History Naturalis at Leiden [RMNH]). One species is known from oceanic Palau (Lieftinck 1962).

Presently (October 2008), the number of valid species of Platystictinae and Sinostictinae in southeast Asia is: *Drepanosticta* Laidlaw, 123 species; *Platysticta* Selys, two species; *Protosticta* Selys, 40 species; *Sinosticta* Wilson three species; *Sulcosticta* van Tol, three species.

1.5 **Biogeography and palaeogeography**

Van Tol & Gassmann (2007) (Chapter 2) have extensively reviewed the historical biogeography of freshwater biotas of southeast Asia in relation to palaeogeography. We discuss here results of studies reconstructing the biogeography based on phylogenies of a wide variety of plants and animals. The historical biogeography of rain forest plant families is particularly relevant for the Platystictidae, since these damselflies are virtually restricted to the rain forest habitat.

Areas of endemism. – 'An area of endemism can be defined by the congruent distributional limits of two or more species' (Platnick 1991). The Platystictidae, with small distributional ranges in most areas, can define areas of endemism, indeed usually based on the distributions of two or more species. Mainly due to restricted taxon sampling to reconstruct platystictid phylogeny, many 'areas of endemism' in our study are based here on just one species, especially in the analysis based on molecular characters. Several of the areas of endemism distinguished here, as well as in many other studies, are extensive (*e.g.,* 'New Guinea'). Platnick (1991) argues that the time has come to change the focus from such large territories to smaller, natural areas, since many of the larger areas are geographically and not biologically defined. Indeed, most species of Platystictidae have much more restricted ranges within the areas mentioned in the present paper (see, for instance, van Tol 2000, 2005). We envisage that a reconstruction of the phylogenetic relationships based on a dataset of more species of Zygoptera, on more (molecular) characters, and on increased knowledge of the distributional ranges, will significantly improve our understanding of the historical biogeography of aquatic biotas.

Taxon–area relationships. – Reliable reconstructions of the phylogeny are a prerequisite for an analysis of the historical biogeography of monophyletic groups, as well as for reconstructions of the historical relationships of areas.

Up to now, construction of generalized area cladograms of southeast Asia, including the Malay archipelago, based on vicariance patterns have proved to be unsuccessful (e.g., Schuh & Stonedahl 1986, Turner *et al.* 2001). It is still uncertain to what extent this is due to incompletely resolved or false phylogeny reconstructions, or to constraints of the methodology applied. The major constraints of the construction of a generalized area cladogram, and how these constraints influence the construction of a generalized area cladogram in the region under discussion, is discussed below.

Most formal methods for the reconstruction of area relationships up to now are based on vicariance patterns. Recently, however, some methods were developed that take dispersal into account. Sanmartín & Ronquist (2004) discussed the relevance of geological area cladograms in 'event-based models' (Page 1995, Ronquist 1997, 1998) in biogeography, such as dispersal–vicariance analysis (Ronquist 1997), or parsimony-based tree fitting methods as used in studying host-parasite systems (Ronquist 1998, 2002). Such models may reveal dispersal events when fitting phylogenies on a geological area cladogram. Tree-fitting methods distinguish between four different events, viz. vicariance, duplication, dispersal and extinction. For a dispersal analysis, Sanmartín & Ronquist used this method, for instance, by comparing organism phylogenies with geological area cladograms, such as the 'southern Gondwana pattern' [(Africa (New Zealand (S South America + Australia)))] as a model. Dispersal is then defined as the events remaining after geologically predicted events (vicariance) have been removed. Unfortunately, the optimal area cladograms as based on different groups, e.g. 'animals' and 'insects, excluding Eucnemidae)' (Sanmartín & Ronquist 2004: fig 7) are so different, that they hardly contribute to our understanding of the hierarchical relationships of areas in a biogeographical context. Observed incongruencies between the optimal area cladogram and the area cladogram of a particular group, may thus be attributed to either dispersal, or an incorrect 'optimal area cladogram'. We agree with Sanmartín & Ronquist (2004) that, although their 'results clarify some points concerning Southern Hemisphere biogeography, many questions remain to be answered', since this method asks for detailed knowledge of phylogeny and distribution patterns.

Palaeogeography of Gondwana. – The present distribution of the Platystictidae in southeast Asia and Central America, and the presumably old age of the families of the Odonata (Rasnitsyn & Pritykina 2002), suggest that the geological history and palaeogeography of the Late Mesozoicum and Early Cenozoicum is relevant to understand the historical biogeography of the family. Van Tol & Müller (2003) dated the division of the Palaemnematinae and Platystictinae as early as the Late Cretaceous in a tropical climate period of the northern hemisphere. However, also during the Late Paleocene and Early Eocene, exchange of tropical biotas between Laurasia and the northern part of the New World was common (Morley 2000). This will be further discussed below.

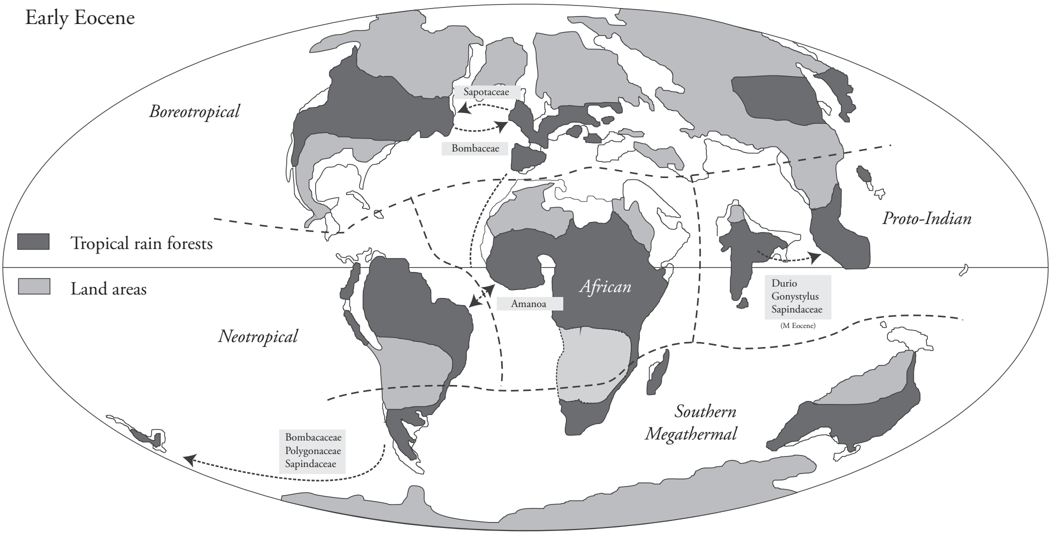

Figure 6. Distribution of closed-canopy tropical rain forests during the Late Paleocene / Early Eocene thermal maximum. Redrawn after Morley (2000, fig. 13.3), names of plant genera and families omitted. Arrows indicate 'noteworthy dispersals of megathermal plants relating to the thermal maximum, and Middle Eocene dispersals into SE Asia relating to the collision of the Indian and Asian plates, as suggested by the palynological record'.

Land connections and climate of the Old en New World since the Early Cretaceous. – Up to about 130 Ma (million years ago) South America, Africa and India were connected as the supercontinent Gondwana. India became isolated from Africa at about that time, but remained very close to the mainland of Africa, and only separated from Madagascar about 88 Ma. Exchange of biotas between India and Madagascar or Africa presumably even continued up to the end of the Cretaceous (65 Ma) (Ashton & Gunatilleke 1987: 256). Morley (2000: 94-95) stated that up to that time 'many plant taxa were able to disperse from Africa, via Madagascar and its associated islands to India'. India with Sri Lanka drifted towards the mainland of southern Asia and collided between 65 and 56 Ma, although according to McLoughlin (2001) about 43 Ma. The vegetation of India consisted of ancient, gondwanic elements, mainly gymnosperms and pteridophytes, of pantropical, megathermal, angiosperm elements, and of endemic elements that evolved during the drift of India through various climate zones (Ashton & Gunatilleke 1987, Morley 2000: 95-96). India was warm and wet during the Eocene. After India's contact with southern Asia, the flora of India moved into the mainland. However, not many Asian elements moved into the Indian subcontinent, presumably due to a changing climate in India. Elements of Tertiary floras related to African taxa survived on Sri Lanka (Ashton & Gunatilleke, 1987), while they got extinct in India. Also for several groups of animals, such as ranid frogs *Lankanectes* Dubois & Ohler, 2001, agamid lizards *Ceratophora* Gray, 1835 and land snails, Sri Lanka is a 'significant reservoir of ancient lineages' (Bossuyt *et al*. 2004, 2005).

Australia separated from Gondwana at about 85 Ma. South America and Africa were connected up to about 90 Ma (all connections severed between 95-80 Ma) (Hallam 1994), but direct dispersal routes between both continents have probably existed up to the end of the Cretaceous, presumably via Antarctica (see Goldblatt 1993). Various studies, summarized by Morley (2000), Wen (1999), Donoghue *et al*. (2001), and Davis *et al*. (2002a, b), revealed close Eocene relationships between the floras of these continents, indicating alternative dispersal routes, *e.g.*, via Europe. However, Africa became more and more isolated due to a changing climate, while it was also still widely separated from Eurasia by the Tethyan Ocean, and only moved slowly northward during the Eocene and Miocene towards its present position.

During the Early Paleocene, multistratal tropical rain forests developed in the so-called Boreotropical zone, presumably in relation to the extinction of the large herbivorous dinosaurs by the end of the Cretaceous, and the subsequent evolution of fruit and seed eating and dispersing mammals. The aridification of Africa, beginning in the late Palaeogene, was due to uplift of the continent, and possibly also the closing of the northern extension of the Tethys, the Turgai Straits. Especially during the Eocene (50 Ma) the northern hemisphere was tropical and considered suitable for migrations via the 'North Atlantic Land Bridge' sensu Tiffney (1985a, b). This 'land bridge' formed a connection from northern North America to northern Europe during the Early Eocene (54-49 Ma). The plant family Sapotaceae de Jussieu, 1789, and the plant genera *Alangium* Lamarck, 1783 and *Platycarya* Siebold & Succarini, 1789 have dispersed from Europe to America via this land bridge, while the plant family Bombaceae Kunth, 1822 used the bridge in opposite direction (Fig. 6). According to Lang *et al.* (2007), the plant genus *Castanea* P. Miller, 1754 evolved in eastern Asia during the Early Eocene, and dispersed in western direction via Europe to North America during the Late Eocene.

Other biotas may have used a migration route from Asia via Beringia, the so-called 'Bering Land Bridge', but the climate was probably too cool at the high latitude of this route to support tropical species (Morley, 2000). On the other hand, for the genus *Castanea* we consider dispersal via the Bering Land Bridge a realistic scenario (*contra* Lang *et al.*, 2007). The genus may have evolved in eastern Asia, dispersed into North America, and then to Europe; this scenario is just as parsimonious as a dispersal route *via* Europe into North America, as proposed by Lang *et al.* (2007), and better accommodates ecological data.

The role of the North Atlantic Land Bridge was discussed in several recent studies. Davis *et al.* (2002a, b) reconstructed a dispersal from South America to Africa of the plant genus *Acridocarpus* Guillemin, Perrottet & A. Richard (Malpighiaceae de Jussieu, 1789) via this land bridge at c. 55 Ma, while the vicariance event of the African and Asian taxa was estimated to be c. 50 Ma, and the dispersal from Africa into Madagascar c. 35 Ma. Sanmartín *et al.* (2001) investigated patterns of dispersal and vicariance in the Holarctic. They extensively discussed the role of the North Atlantic Land Bridge, and other palaeogeographical data, to understand present biogeographical patterns. Although they studied mostly temperate taxa, tropical groups of plants and animals were included as well, mainly in their discussion of the eastern North America – Asia disjunction. It appeared that 'the trans-Atlantic route was the most important pathway for the spread of boreotropical elements', with Eastern Nearctic – Eastern Palaearctic disjunctions usually dating back to the Early Tertiary. There is no agreement on the predominant direction of the dispersal over the land bridge, with different results for plants and animals. Eastern Asia is usually considered the centre of origin of the boreotropical flora, and plants have usually dispersed towards the New World. Sanmartín *et al.* (2001), however, found no significant difference in dispersal direction of faunas of the Nearctic and Palaearctic regions.

Cenozoic palaeogeography of southeast Asia. – The biotas of southeast Asia and the west Pacific have evolved in an extremely complicated setting. The last decades, reconstructions of the tectonic history of this region have become available. e.g. Kroenke (1996), Hall (1998, 2002), Metcalfe (2001), and Hill & Hall (2003). Van Tol & Gassmann (2007) present a recent summary of these studies in a zoogeographical context. Polhemus & Polhemus (1998) put more emphasis on

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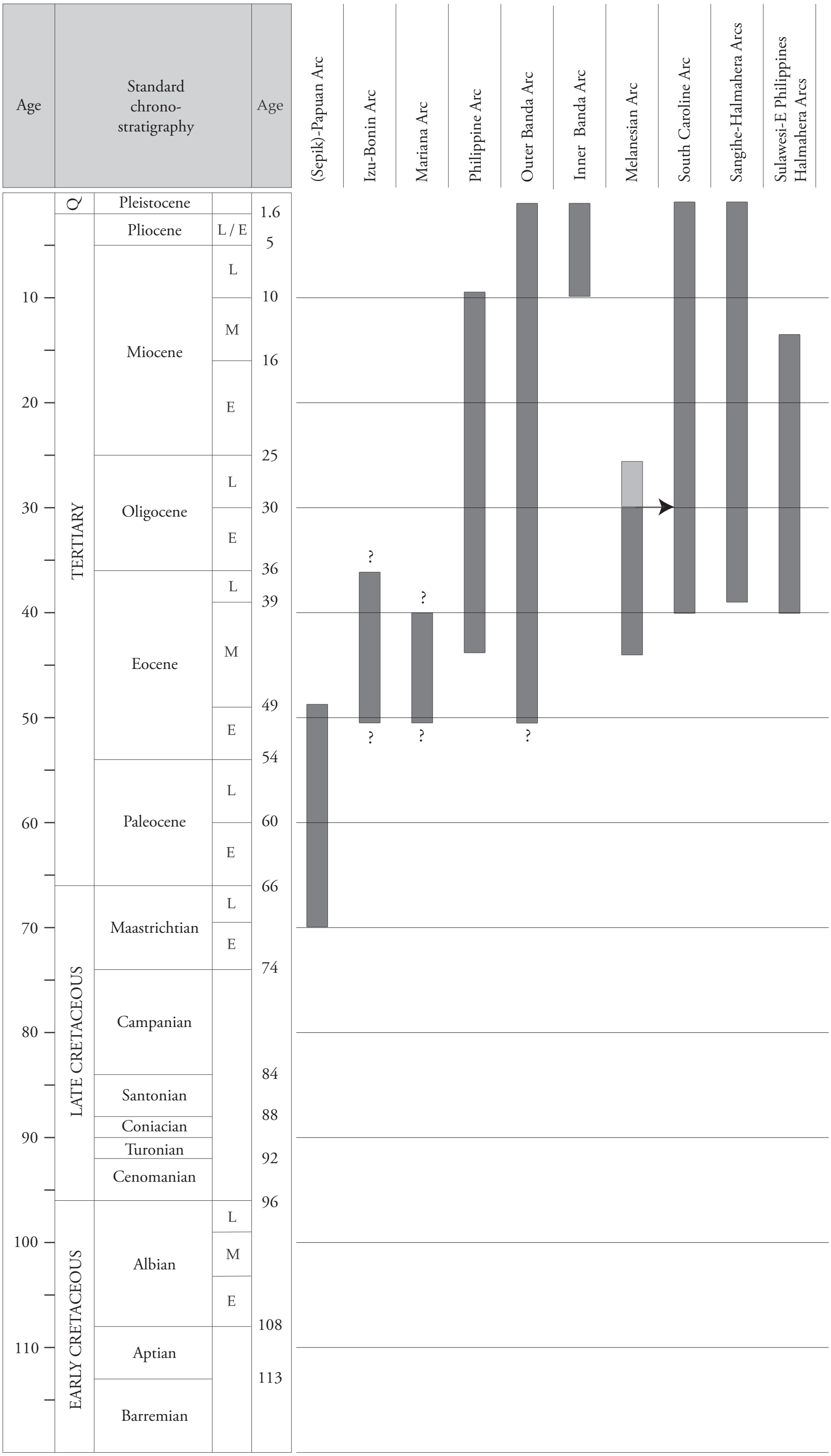
Right

Figure 7. The history of island arcs of southeast Asia and the western Pacific.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EARLY CRETACEOUS
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
L / E
L
M
E
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the west Pacific region. Since island arcs must have played an important role as dispersal routes into the western Pacific, we provide a concise summary of the history of these arcs based on published sources (Fig. 7).

Vicariance and dispersal. – Many of the islands of the Philippines, parts of Sulawesi, and the northern fragments of New Guinea were formed along the contact zone of the rotating Pacific or Philippine Plates and their adjoining plates since the Cretaceous. Very few islands have been in contact with the mainland of southeast Asia, so that we presume that dispersal from Asia or Australia into the archipelago played the dominant role in the evolution of the composition of the island biotas. Since most palaeo-islands were arranged in islands arcs, most dispersal events may have occurred between islands of the island arcs, rather than from the mainland towards to islands.

Some dispersive elements, such as birds or bats, and even some species of larger insects, *e.g.*, some Libellulidae among the odonates, may reach isolated islands from time to time. However, for many other organisms the chance of successful dispersal to and settlement on such isolated places must be considered very low. Platystictidae are insects of which little success in dispersal can be expected: their flying capabilities and population densities are low, and most species are extreme habitat specialists. It is difficult to understand that such organisms can successfully cross hundreds of kilometers, or even just a few kilometers, over open water. Even if they have succeeded to cross such a barrier, *e.g.*, during a cyclone, the survival rate of specimens that reached new territories must be low, and the chance that they meet a conspecific seems to be immeasurably low indeed. Nevertheless, it is certain that even some extremely unlikely places have been populated by damselflies, such as the islands of Hawaii by a species of *Pseudagrion* Selys, 1876 (Coenagrionidae) as the founder of the group of *Megalagrion* MacLachlan species now confined to that group of islands (Polhemus & Asquith 1996). The occurrence of a species of *Drepanosticta* on Palau, presently *ca*. 800 km east of Mindanao, presumably the nearest founder population, is another enigma. While we should accept dispersal as an uncommon, but realistic, scenario for settling of Platystictidae on some islands, the present distribution patterns of Platystictidae are the result of a complex set of causes, including settlement of the damselfly population in the longer or shorter past, speciation events by vicariance, local extinction, and the displacement of the islands during the geological history.

2. Methods

2.1. Material

Our phylogeny reconstruction of the Platystictidae is based on a morphological study of *c.* 30% of extant Platystictidae. Our taxon sampling is determined by availability of specimens, diversity of external morphological characters, and geographical provenance. The molecular dataset for the Platystictidae is more limited. Fresh material of many important taxa for our analysis was not available, such as specimens of *Sinosticta*, *Platysticta,* and specimens of *Drepanosticta* and *Protosticta* from Luzon, most parts of Indonesia, and Papua New Guinea. However, our dataset of non-platystictid Zygoptera is much more extensive than previously available for most other studies (Appendix 1). Names in this paper follow van Tol (2007a). Sources of identifications are mentioned in Appendix 1.

Morphology. – Specimens of all species studied for the reconstruction of the phylogeny are kept in the RMNH Leiden. Some taxa were made available for our studies by others (see acknowledgements), and donated to the Leiden Museum. Our study is based on an analysis of 53 species of Platystictidae; *Lestes temporalis* Selys, 1883 was used as outgroup.

Molecular studies. – We examined 51 samples, and added data of four more taxa as studied by Hasegawa & Kasuya (2006). Appendix 1 describes details of each sample, viz. family, genus, species name, sample number, locality data, collecting year, collector, and the person responsible for identification, and molecular analysis. Apart from collections made by J. van Tol, we received valuable material from colleagues in the

Leiden Museum and others (see acknowledgements). The senior author collected specimens in Vietnam, Borneo and the Philippines. At the time of the analysis, most specimens were less than five years old, and kept on 95-98% ethylalcohol.

We used 28S rDNA (nuclear genome) and 16S rDNA (mitochondrial genome) for the phylogenetic analysis. Nuclear DNA is known to have slower substitution rates than mitochondrial DNA, so that both datasets may reveal additional patterns. According to Hasegawa & Kasuya (2006), there is some controversy whether the total evidence approach based on molecular data, should be preferred above the separate analysis. If both sets are congruent, the results will be reinforced. There are, however, examples that nuclear DNA and mitochondrial DNA do not show the same phylogenetic signal, as a result of hybridization events. Although the effect of hybridization in the past may be obscured by, *e.g.*, accumulation of changes, Hasegawa & Kasuya consider combined analysis not the first choice. The higher evolvement rate of the mitochondrial genome may also result in more convergences. As one may expect in old lineages, Misof *et al.* (2000) reported decay of phylogenetic signal of the mitochondrial DNA in odonates. In conclusion, according to Hasegawa & Kasuya (2006), a combined analysis is only advisable if the results of separate analyses do not show major incongruences.

In general, we do not agree with this statement. The reconstruction of phylogenies is based on changes of character states in characters of which the value in analyses is not *a priori* known. *A posteriori* analysis of character changes over the preferred tree is one of the aims of phylogenetic analysis. The only way to reveal homoplasies is to use as many relevant characters as possible for the analysis. Hasegawa & Kasuya's statement in the most extreme form would mean that the analysis of just one character would be sufficient to reconstruct phylogenies. However, we agree that incongruent signal of mitochondrial and nuclear DNA should be properly evaluated to reveal presumable causes.

2.2. **Morphological methods**

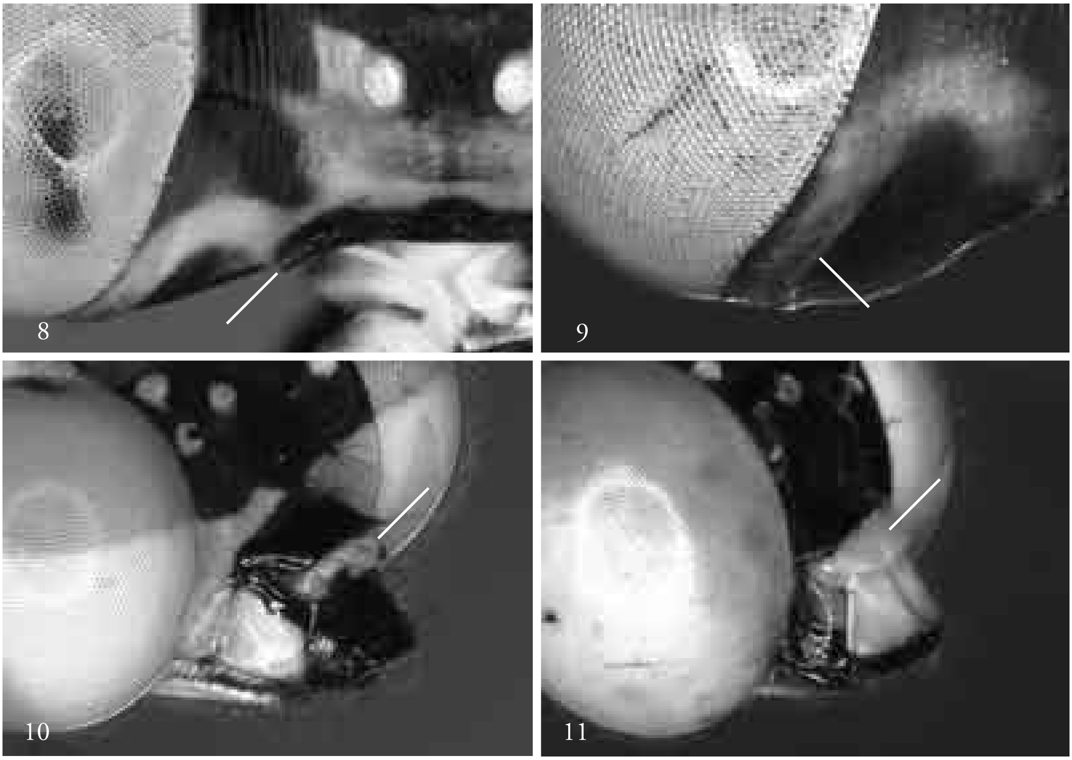
The characters chosen for our phylogenetic analysis were partly derived from previous analyses as published in systematic papers (Calvert 1931; Rehn 2003), supplemented with characters not studied systematically before, including the ligula of the male. The datamatrix is presented in Appendix 2, with the coding of the respective character states for the specimens studied. All specimens were examined by the senior author using a variety of stereomicroscopes, but mainly a Leica MZ16A with magnification up to 110×. Only males were used for our study, primarily since reliably identified females of many species were not available. Unfortunately, also larvae are very scarce in collections.

Since we inferred the monophyly of the Platystictidae from various sources, including Rehn (2003) and Bybee *et al.* (2008), and the results of the analysis of our own molecular dataset, we refrained from using a large dataset of non-platystictid Zygoptera for our morphological analysis. Bybee *et al.* (2008) reconstructed a sister group relationship of the superfamily Lestoidea with all other Zygoptera. This topology was confirmed by our own study (see Fig. 47). Thus, only *Lestes temporalis* Selys, 1883 was added as a non-platystictid Zygoptera species to our dataset, since this species was also used in our molecular study.

Morphological characters used for phylogeny reconstruction. – We discuss here the characters used in the analysis. Some character states are illustrated in the present paper, or references are given to previously published illustrations.

Character states were coded 'ordered' in those characters where a trait in development could be defended. An examples is character M01, with an extremity from 'absent' via 'small' to 'angulate' (or in opposite direction).

M01 Head: lateral extremities of transverse occipital carina. – (0) absent, (1) small, (2) angulate. Most Platystictidae have a distinct transverse occipital carina, which may have more or less distinct lateral extremities (Fig. 8). No



Figures 8-11. Characters of Platystictidae; stripes indicate character. – 8, Hind margin of head, *Protosticta grandis* Asahina. Note the transverse occipital carina, which is angulate in this species, but is inconspicuous or absent in many other species of Platystictidae. – 9, Hind margin of head, *Protosticta grandis* Asahina. Parorbital carina. – 10, *Coeliccia* sp. n. Vietnam (Platycnemididae). Like most Zygoptera, Platycnemididae have a rectangular clypeus. – 11, Head, oblique view, *Drepanosticta lestoides* Brauer. Character 1 of Rehn (2003). The shape of the clypeus is flattened, with anteclypeus tilted back and not distinct from dorsal facing post-clypeus.

difference was made between 'absent' and 'non-applicable', since the transverse occipital carina can be very indistinct and not separable from 'not present'. Ordered.

M02 Head: parorbital carina. – (0) absent, (b) present. Seems to be a unique apomorphy of all Platystictidae (Fig. 9).

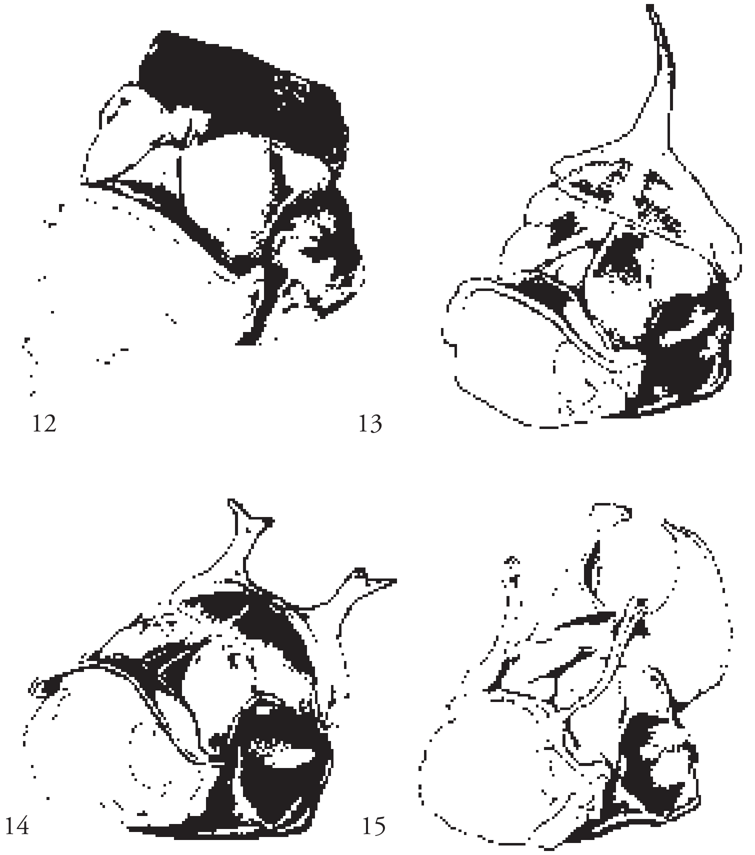
M03 Shape of clypeus. – (0) rectangular (ante- and postclypeus forming distinct faces) (e.g., *Coeliccia* Kirby, 1890, Fig. 10), (1) flattened (anteclypeus tilted back) (e.g., *Drepanosticta lestoides* (Brauer), Fig. 11).

M04 Prothorax anterior margin: (0) simple (Fig. 14), (1) partly widened, (2) with processes (Fig. 15).

M05 Prothorax: median lobes with protuberances. – (0) absent, (1) present. Most distinctly developed in *Protosticta simplicinervis* from Sulawesi, type species of *Protosticta*.

M06 Prothorax: posterior margin of posterior lobe. – (0) simple, i.e. without processes (e.g., *Drepanosticta lestoides*, Fig. 12), (1) single median process (e.g., *Drepanosticta ceratophora* Lieftinck, Fig. 13), (2) paired process, triangular (3) paired process, round and straight, (4) Paired process, short and curved, (5) paired process, straight with knob or fork (e.g., *Drepanosticta lymetta* Cowley, Fig. 14), (6) paired process, shields (e.g., *Drepanosticta*

Figures 12-15. Characters of Platystictidae (continued). Pronotum in oblique view. – 12, *Drepanosticta lestoides* Brauer (Mindanao); both anterior and posterior lobe of pronotum simple, without any processes. – 13, *Drepanosticta ceratophora* Lieftinck; anterior lobe simple, posterior lobe with one median process. – 14, *Drepanosticta lymetta* Cowley (Mindanao); anterior lobe simple, posterior lobe with a forked pair of processes. – 15, *Drepanosticta moorei* van Tol & Müller (Luzon); both anterior and posterior lobe of pronotum provided with paired processes. All illustrations from van Tol (2005): figs 58, 55, 41 and 28, respectively.



moorei van Tol & Müller, Fig. 15). Very significant variation of this structure, especially in the genus *Drepanosticta*. Evolutionary traits of this character uncertain. Unordered.

M07 Prothorax: posterior lobe with lateral appendage. – (0) absent, (1) present, short, (2) Present, at least two times as long as wide (e.g. *Drepanosticta paruatia*; van Tol 2005, fig. 71).

M08 Synthorax: antehumeral stripe. – (0) absent, (1) present.

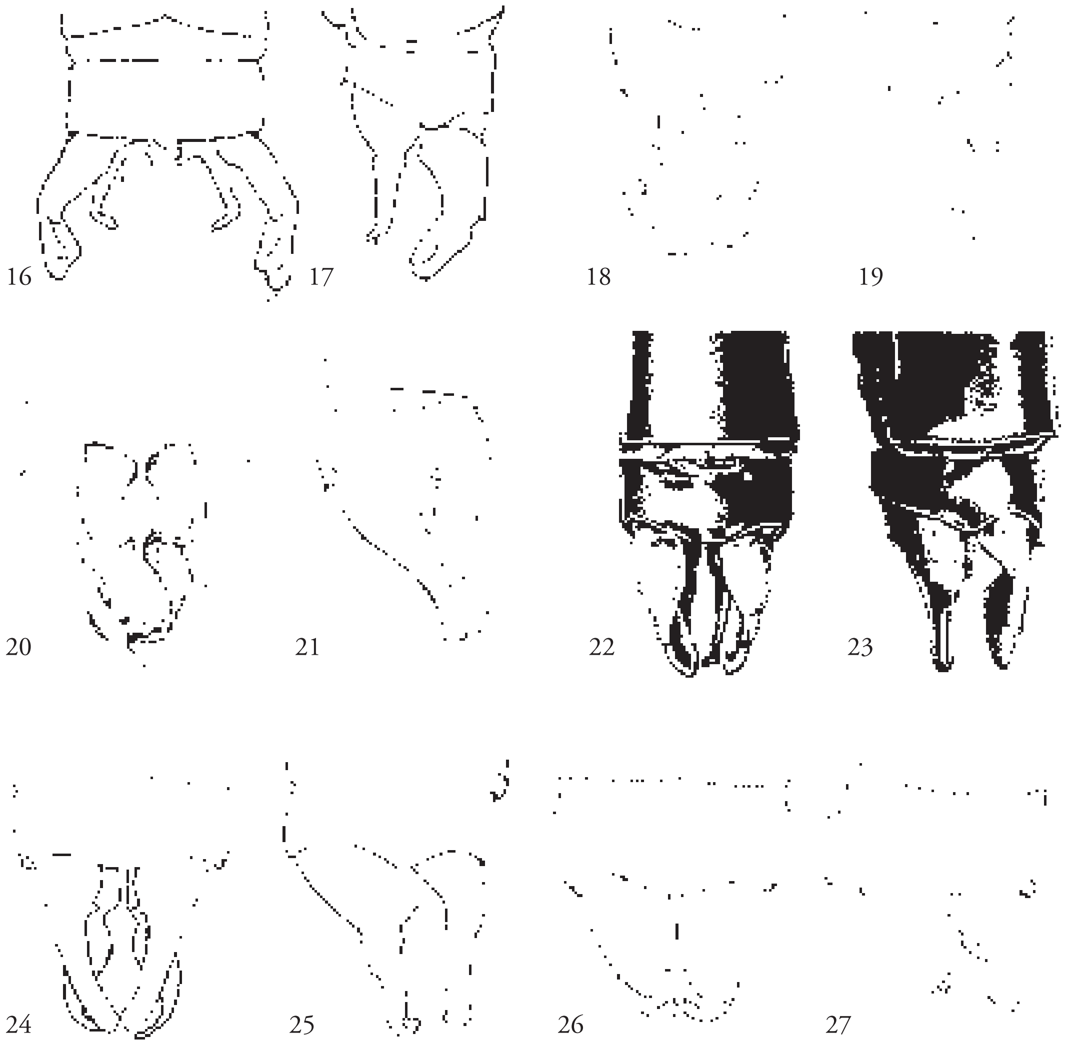
M09 Synthorax: colour venter. – (0) pale, (1) black, (2) variegate, (3) bicolorous. In most species the synthorax is pale. Coded as ‘bicolorous’ if distinctly different in anterior and posterior part, otherwise coded as ‘variegate’, e.g. for longitudinal dark stripes. Unordered.

M10 Synthorax: metepisternum. – (0) dark, (1) short pale anterior stripe, (2) short pale posterior stripe, (3) long pale stripe, (4) fully pale.

M11 Synthorax base colour. – (0) brownish black or black (e.g., *Protosticta satoi* Asahina, Fig. 3), (1) pale brown, (2) metallic green. Only code 0-1 apply to Platystictidae, code 2 was used for the outgroup *Lestes temporalis*.

M12 Wings: number of antenodal crossveins (Fig. 28). – (0) two, (1) more than two.

M13 Wings. – Cux (also known as pcv [post-cubital cross-vein] sensu Fraser (1957), or as CuP- sensu Bechly 1996). – (0) absent (Fig. 32), (1) present (e.g., Fig. 28). This additional cross-vein in the cubital space is present in all species

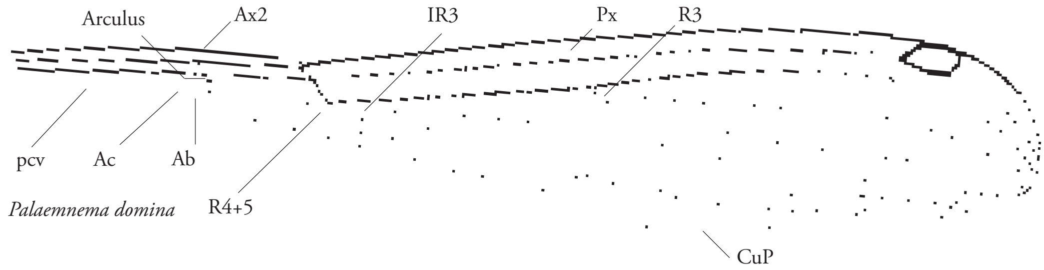


Figures 16-27. Anal appendages of male Platystictidae. – 16-17, *Palaemnema melanostigma* Hagen, dorsal and left lateral view (from Calvert 1931, figs. 57a, b). – 18-19, *Protosticta feronia* Lieftinck, dorsal and right lateral view (from Lieftinck 1965, fig. 1). – 20-21, *Protosticta geijskesi* van Tol, dorsal and left lateral view (modified after van Tol 2000, figs. 17-18). – 22-23, *Drepanosticta krios* van Tol, dorsal and left lateral view (from van Tol 2005: figs. 11-12). – 24-25, *Drepanosticta rudicula* van Tol, dorsal and left lateral view (from van Tol 2007c, figs. 17, 18). – 26-27, *Sinosticta ogatai* (Matsuki & Saito), dorsal and left lateral view (original).

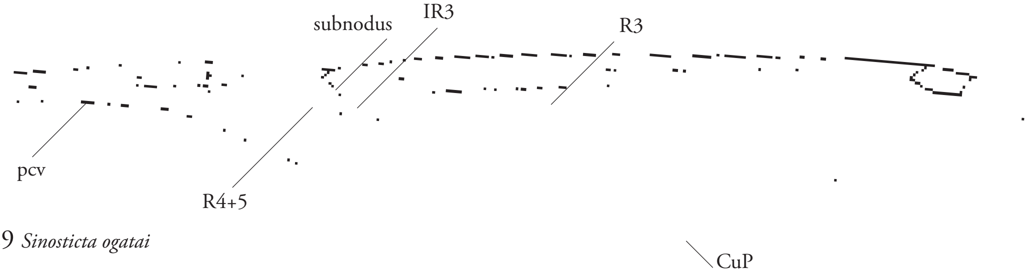
assigned to the Platystictidae. In rare cases there is more than pcv, but in the aberrant *Sinosticta ogatai* three or even four of these cross-veins may be present (Fig. 29).

M14 Number of postnodal cross-veins (fore wing) (Fig. 28). – (0) 10-12, (1) 13-15, (2) 16-18. (3) 19-21, (4) 22-24, (5) 25-27, (6) more than 27, (7) less than 10. Ordered.

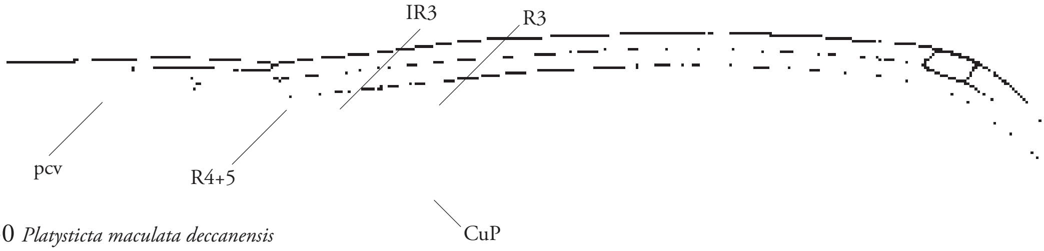
M15 Number of postnodal cross-veins (hind wing) (Fig. 28). – (0) 10-12, (1) 13-15, (2) 16-18. (3) 19-21, (4) 22-24, (5) 25-27, (6) more than 27, (7) less than 10. Ordered.



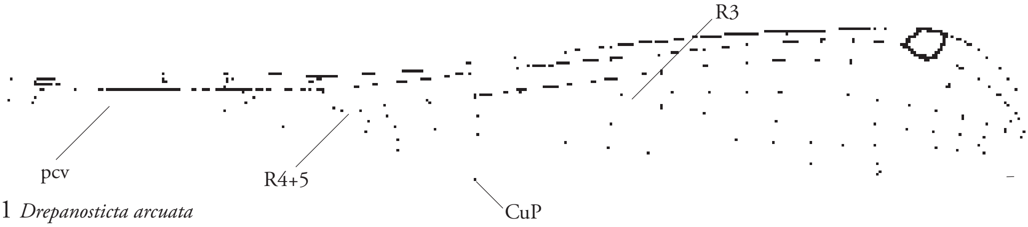
28 *Palaemnema domina*



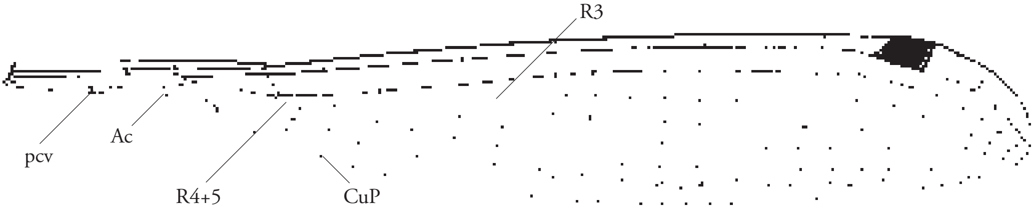
29 *Sinosticta ogatai*



30 *Platysticta maculata deccanensis*



31 *Drepanosticta arcuata*



32 *Protosticta simplicinervis*

Figures 28-32. Wings of various genera of Platystictidae. Relevant characters of wing venation indicated. – 28, *Palaemnema domina* Calvert, hind wing. – 29, *Sinosticta ogatai* (Matsuki & Saito), hind wing. – 30, *Platysticta maculata deccanensis* Laidlaw, fore wing. – 31, *Drepanosticta arcuata* Lieftinck, hind wing. – 32, *Protosticta simplicinervis* (Selys), hind wing.

M16 Position R4+5 in relation to nodus (hind wing). – (0) proximal (e.g., *Sinosticta ogatai*, Fig. 29), (1), at, (2) distal (e.g., *Drepanosticta arcuata* Lieftinck, Fig. 31). Variation was not taken into account. Ordered.

M17 IR3. – (0) far proximal to subnodus (Fig. 29), (1) at subnodus, (2) distal to subnodus (Fig. 31).

M18 Position Arculus in relation to Ax2. – (0) proximal, (1) at (Fig. 29), (2) distal (Fig. 31). Coding was used very strict: code (1) means that Arculus is situated at most the width of a vein from Ax2. Ordered.

M19 Arculus. – (0) stalked, (1) sessile / divided.

M20 Ab vein. – (0) absent (e.g., *Protosticta simplicinervis*, Fig. 32), (1) present (e.g., *Drepanosticta arcuata*, Fig. 31). The absence of the Ab vein is considered a diagnostic character of the genus *Protosticta*.

M21 Y-vein (Ac plus Ab). – (0) absent, (1) sessile (e.g., *Drepanosticta arcuata*, Fig. 31), (2) stalked (e.g., *Palaemnema domina* Calvert, 1903a, Fig. 28), (3) divided. This character partly overlaps with the previous character, but is coded separately since an Ab vein is also present in the outgroup. For *Lestes* this character was coded 'absent', like in *Protosticta* (but Ab vein coded as 'present' in *Lestes*). Intraspecific variation was not coded.

M22 Wing: distal side of quadrangle of fore wing. – (0) rectangular, (1) oblique, (2) sharp.

M23 CuP meeting hind margin of fore wing. – (0) proximal to origin of R3 (e.g., *Drepanosticta arcuata*, Fig. 31), (1) at origin of R3, (2) distal to origin of R3 (e.g., *Sinosticta ogatai*, Fig. 29). Ordered.

M24 CuP meeting hind margin of hind wing. – (0) proximal to origin of R3, (1) at origin of R3, (2) distal to origin of R3. Ordered.

M25 Terminal part of wing. – (0) hyaline, (1) opaque.

M26 Abdomen: dorsal denticle on superior appendage. – (0) absent (e.g., *Drepanosticta rudicula* van Tol, Fig. 25), (1) discernable (e.g., *Drepanosticta krios* van Tol, Figs 22-23), (2) long and conspicuous.

M27 Abdomen: ventral denticle on superior appendage. – (0) absent, (1) discernable, (2) long and conspicuous.

M28 Superior appendage with distal half. – (0) rounded or somewhat flattened, (1) extremely flat and large.

M29 Appendix inferior with tip. – (0) rounded, (1) sharp, (2) boxing glove, (3) long bifid, (4) short bifid, (5) bent apicad, (6) reduced, (7) cup-shaped.

M30 Inferior appendage with basal tooth. – (0) absent (e.g., *Drepanosticta rudicula*, Fig. 24), (1) present (e.g., *Palaemnema melanostigma*, Fig. 16).

M31 Inferior appendage with terminal tuft of setae. – (0) absent, (1) present.

M32 Sub-terminal tooth of inferior appendage. – (0) absent (Fig. 24), (1) small, (2) large (Fig. 20).

M33 Ligula, cleft between branches. – (0) triangular, sharp (e.g., *Palaemnema angelina*, Fig. 34), (1) rounded (e.g., *Protosticta lepteca*, Fig. 40), (2) squarish (e.g., *Drepanosticta clavata*, Fig. 42), (3) convex (e.g., *Protosticta geijskesi*, Fig. 38), (4) wide and straight (e.g., *Drepanosticta dorcadion* (Fig. 43).

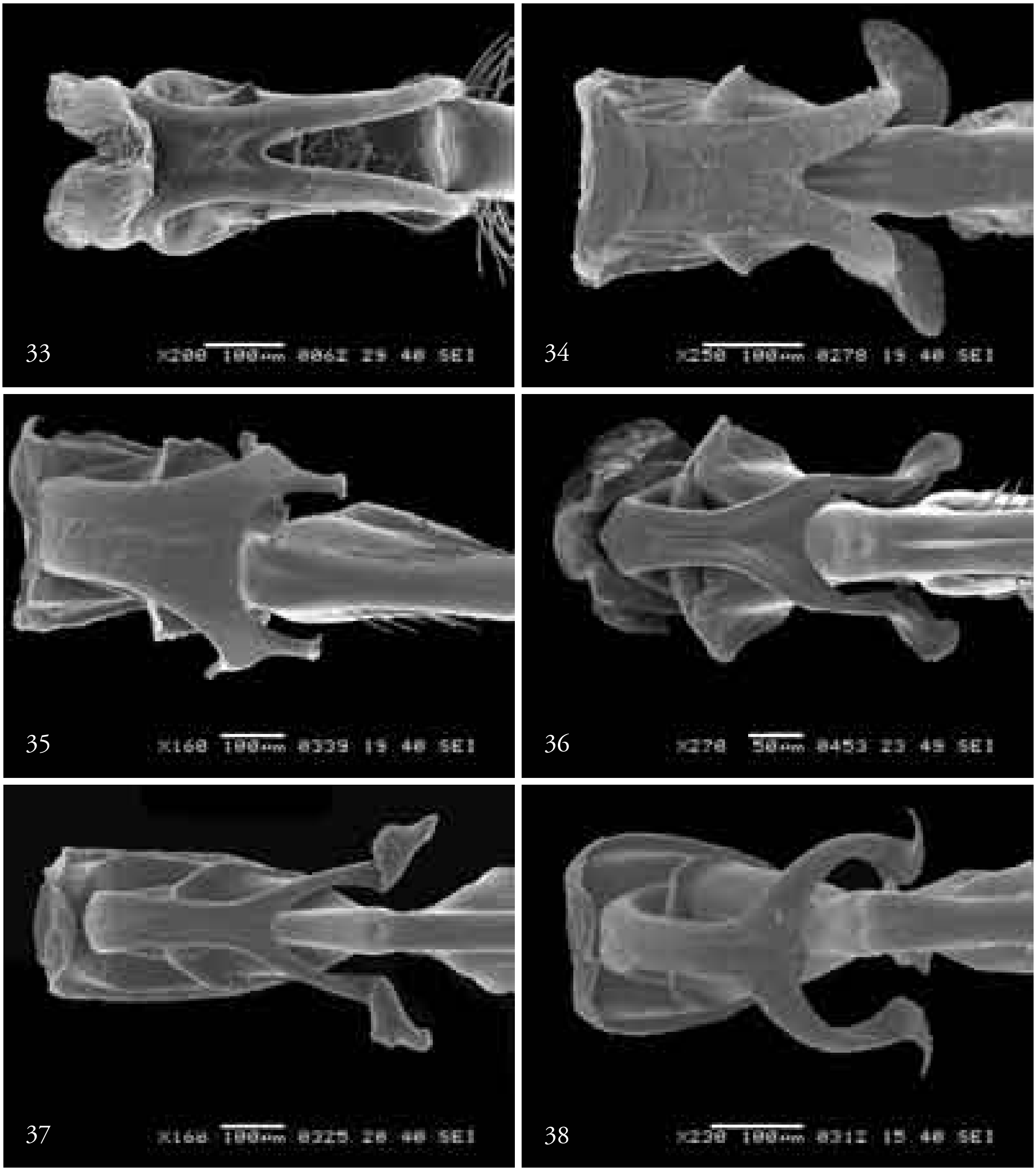
M34 Ligula, last segment medially. – (0) straight or concave, (1) convex.

M35 Ligula: shape of tip of branch. – (0) sharp, (1) spoon-shaped, (2) hook-shaped/bifid.

M36 Length of horns of ligula. – (0) less than half of segment (e.g., *Platysticta deccanensis*, Fig. 35), (1) half to twice length of segment (e.g., *Protosticta simplicinervis*, Fig. 37), (2) more than twice length of segment (e.g., *Sinosticta*, Fig. 33).

M37 Segment at base of horns.. – (0) widened, (1) straight, (2) constricted.

M38 Ligula, shape of horns. – (0) Long, tip curved upwards (e.g., *Protosticta geijskesi*, Fig. 38), (1) long, tip as bird's head, (e.g., *Drepanosticta clavata*, Fig. 42) (2) short, curved upwards, (3)



Figures 33-38. Ligula of male Platystictidae in ventral view. – 33, *Sinosticta ogatai* (Matsuki & Saito) (JvT 26582). – 34, *Palaemnema angelina* (Selys) (JvT 27934). – 35, *Platysticta maculata deccanensis* Laidlaw (JvT 19349). – 36, *Sulcosticta striata* van Tol (JvT 19224). – 37, *Protosticta simplicinervis* (Selys) (JvT 02044). – 38, *Protosticta geijskesi* van Tol (JvT 11878).

ending in disc (e.g., *Drepanosticta dorcadion*, Fig. 43), (4) ending in threadlike structure, (5) ending in short bifid structure (e.g., *Platysticta deccanensis*, Fig. 35), (6) sharp, curved downwards.

The file was analysed using PAUP 4.0b10 with the heuristic search algorithm, using TBR (Swofford 2003). Trees were constructed with TreeView (Page 1996).

2.3. **Molecular methods**

DNA extraction. – All samples which were successfully used for the analysis, had been stored in 96 to 98% ethylalcohol. DNA was extracted using tissue from a thoracic leg or part of the muscles in the thorax, using the Qiagen DNeasy Tissue Kit (Qiagen, Hilden, Germany). The manufacturer's protocol for animal tissue was followed, except that lysis was done overnight.

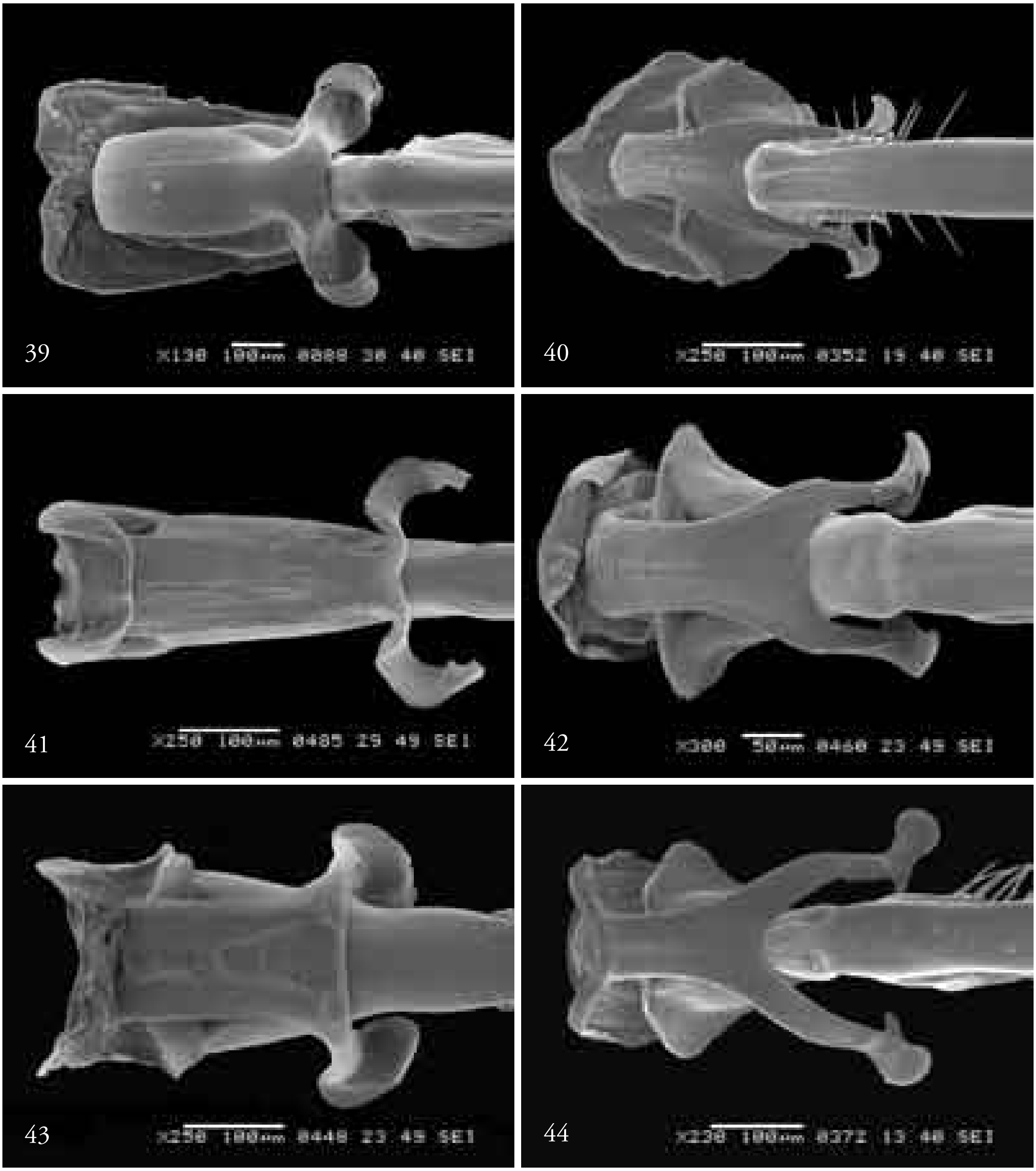
Amplification and sequencing. – The DNA thus obtained was used for direct amplification by PCR of partial 16S and 28S rDNA sequences. The following primers were used for PCR and sequencing reactions: 16S: LR-J-12887 (5' - CCG GTC TGA ACT CAG ATC ACG T-3') and LR-N-13398 (5' – CGC CTG TTT AAC AAA AAC AT 3') (Hasegawa & Kasuya, 2006); 28S: ODO28SF HAT (5' – TTG AGC TTG ACT CTA GTC TGG CAC – 3'), and ODO28SR HAT (5' – CGC CAC AAG CCA GTT ATC C -3'). The 28S primers were specifically designed for this study from previously published sequences available from GenBank by selecting conservative sequences adjoining variable regions. We thus amplified 504-513 bp of 16S and 534-559 bp of 28S markers using the reaction profiles specified in Table 1.

The cleaned PCR products (Wizard PCR Preps DNA Purification System, Promega, Madison, Wisconsin, USA) were sent to a commercial sequencing facility (Macrogen Inc., Korea, http://www.macrogen.com), where sequencing reactions were carried out using supplied primers, and where the sequence products were run.

Phylogenetic analyses. – Sequences were inspected and edited in Sequencer 4.1.4 (GeneCodes, Madison, Wisconsin, USA), and aligned using Clustral W multiple alignment, under default parameters, as implemented in BioEdit (Hall 1999). This resulted in alignments of 483 and 545 bp in length for 16S and 28S, respectively. The 16S alignment contained an ambiguous site of 50 bp, which appeared to be unalignable, and was therefore deleted from the datamatrix. Based on a comparison with a complete mitochondrial sequence of *Drosophila melanogaster* Meigen, 1830 in Genbank (accession number NC_001709), the deleted site appeared to consist of bp 13094 to 13144. In contrast to 16S, the 28S datamatrix was relatively straightforward, with only some ambiguities around gaps, which were edited manually, and finally used for the analysis as presented in this paper. Eventually, both datasets were combined into a single dataset, which was transferred into a Nexus-block to be used in PAUP. It appeared that out of 1028 characters, 712 were constant, 72 were variable but parsimony-uninformative, while 244 characters were parsimony informative.

Table 1
Markers, primers and protocols used for PCR amplification.

16S		^{0}C	t (min)
Forward: LR-J-12887 5'-CCG GTC TGA ACT CAG ATC ACG T-3'	Initial denaturation	94	60
Reverse: LR-N-13398 5'-CGC-CTG TTT AAC AAA AAC AT-3'	40 cycles of: Denaturation	94	30
28S	Annealing	50	30
Forward: ODO28SF HAT 5'-TTG AGC TTG ACT CTA GTC TGG CAC-3'	Extension	72	30
Reverse: ODO28SR HAT 5'-CGC CAC AAG CCA GTT ATC C-3'	Final extension	72	120



Figures 39-44. Ligula of male Platystictidae in ventral view (continued). – 39, *Protosticta grandis* Asahina (JvT 28490). – 40, *Protosticta lepteca* van Tol (JvT 18210). – 41, *Drepanosticta arcuata* Lieftinck (JvT 19484). – 42, *Drepanosticta clavata* Lieftinck (JvT 23449). – 43, *Drepanosticta dorcadion* Lieftinck (JvT 19540). – 44, *Drepanosticta flavomaculata* van Tol (JvT 18913).

We performed full heuristic searches under Maximum Parsimony (MP) with 10,000 bootstrap replicates and Maximum Likelihood in PAUP* 4.10b . Maximum parsimony and bootstrap trees were generated using tree-bisection-reconnection (TBR) branch swapping, random addition sequence (100 repetitions) and equally weighted unordered characters. Bayesian analyses were carried out in MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; http://mrbayes.csit.fsu.edu). The Akaike Information

Criterion (AIC) as implemented in Modeltest (Posada & Crandall, 1998; http://darwin.uvigo.es/software/modeltest.html) and MrModelTest 2.2 (Nylander, 2004; http://www.abc.se/~nylander/) served as a basis to select the General Time Reversible model with gamma distribution and invariant sites (GTR+I+G) as the most likely models of DNA evolution for implementation in ML and Bayesian analyses respectively. Parameters were fixed in ML analyses. However, in Bayesian analyses base frequency parameters were estimated under the assumption of a Dirichlet distribution. In PAUP* only a single model for base substitutions can be implemented, and parameters were, therefore, calculated for combined sequences of 16S and 28S. For our Bayesian analysis the GTR+I+G evolutionary model was selected for the 16S and 28S dataset. Consequently we did not partition our dataset, but subjected the evolutionary model on the combined dataset. Two separate runs of six Markov Chain Monte Carlo (MCMC) chains were run simultanuously for 4,000,000 generations and trees were sampled every 50 generations, resulting in 80,000 trees. By default, 25% of these trees were discarded as burnin, and the remaining trees were used to construct a 50% majority consensus tree in PAUP* 4.10b. *Epiophlebia superstes* (Selys, 1889) was used as outgroup to root the trees from all analyses.

We have added the data of some species as published by Hasegawa & Kasuya (2006) as available in GenBank, viz. *Epiophlebia superstes*, *Sympetrum depressiusculum* (Selys, 1841) [published as *S. frequens* Selys, 1841)], *S. eroticum* (Selys, 1883), and *Lestes temporalis* Selys [published as *L. japonicus* Selys]. These taxa were selected based on the results of the phylogenetic reconstruction of the Odonata of Bybee *et al.* (2008). *Epiophlebia superstes* represents the sister group of all extant Anisoptera, represented in this analysis by the two species of *Sympetrum* Newman, 1833. The group of Anisoptera + Epiophlebiidae is known as Epiprocta. The Epiprocta plus the extinct *Tarsophlebia* Hagen, 1866 are the sister group of the Zygoptera. According to Bybee *et al.* (2008), a clade including the lestoid families (Lestidae, Synlestidae, Perilestidae etc) is the sister group of all other Zygoptera. The next branching is shows the family Platystictidae versus all other Zygoptera. We consider our taxon sample, including *Epiophlebia*, Anisoptera, Lestidae and a significant number of species of the Zygoptera families Platystictidae, Megapogagrionidae, Platycnemididae, Protoneuridae and Coenagrionidae, as sufficiently large for a well-founded reconstruction of the evolution of the Platystictidae.

3. Results

3.1 Monophyly of the Platystictidae

The phylogenetic relationships of the Zygoptera were first studied based on a molecular character set of the 16S and 28S rDNA genes. The selection of the samples was focused on the research question of the monophyly of the Platystictidae. Other taxa from a wider variety of odonate families were added as far as this was feasible within the framework of this study (see methods). We examined representatives of the families Libellulidae, Epiophlebiidae, Lestoideidae Megapodagrionidae, Protoneuridae, Platycnemididae, Coenagrionidae and Platystictidae. The Calopterygoidea or Caloptera (Amphipterygidae, Calopterygidae, Chlorocyphidae, Euphaeidae) were not included in this study; also, no representative of the southeast Asian non-Caloptera family Isostictidae was available.

Analysis of 16S. – The analysis using heuristics search (1000 replicates, TBR, addition sequence random) of the character set of the mitochondrial 16S rDNA resulted in six most parsimonious trees (tree length 879, consistency index = 0.3811, retention index =0.6839, rescaled consistency index=0.2606).
Out of 483 characters, 272 were constant, 38 parsimony-uninformative, and 173 parsimony-informative. The 50% majority rule consensus tree (Fig. 45) revealed (a) the monophyly of the presently recognized Zygoptera families Platystictidae, Platycnemididae and Protoneuridae, (b) the sister group relationship of the subfamilies Platystictinae (southeast Asia) and Palaemnematinae (America) of the Platystictidae, as well as the sister group

relationship of the Platycnemidinae and Calicnemiinae of the family Platycnemididae. The monophyly of the Megapodagrionidae is not confirmed by the present analysis. The sister group of the Platystictidae in the present taxon set is *Sinocnemis yangbingi* Wilson & Zhou, 2000, a species described in the Platycnemididae, but recently recognized as a member of the Megapodagrionidae (Kalkman 2008).

Analysis of 28S. – We have tried to perform a parsimony analysis on this dataset, but it was stopped (several times) after the first replicate had run for more than four hours. We conclude that the dataset does not include structure to for an analysis based on parsimony.

16S and 28S combined analysis. – A heuristic search with PAUP of the combined dataset of 16S and 28S (100 random-addition-sequence replications), resulted in 37 most parsimonious trees, length 1262 (consistency index excluding uninformative characters = 0.3475; retention index = 0.6841; rescaled consistency index = 0.2678) (see Fig. 46, strict consensus). Following the reconstruction of the phylogeny of the Odonata by Bybee *et al.* (2008), which is partly based on morphological characters as presented by Rehn (2003) plus a new molecular data set of six genes, our trees were rooted with *Epiophlebia superstes* (Epiophlebiidae).

In the parsimony analysis, the Zygoptera are monophyletic. The superfamily Lestoidea (represented by *Lestes temporalis*) is the sister group of all other Zygoptera. The Platystictidae, Platycnemididae and Protoneuridae are all monophyletic clades. The Platycnemididae and Protoneuridae are sister groups. The Coenagrionidae [represented by *Ischnura elegans* (vander Linden, 1820)] appear as the sister group of all Zygoptera, except Lestoidea. All other species, presently mainly assigned to the Megapodagrionidae, are scattered through the cladogram and do not form a monophyletic group. The two subfamilies of the Platycnemididae, *viz.*, Platycnemidinae (*Platycnemis* Burmeister, 1839 and *Copera* Kirby, 1890) and Calicnemiinae (all other species), are monophyletic, and sister groups. The topology of the tree within the family Platystictidae will be discussed below.

The Bayesian analysis of this dataset revealed a somewhat different topology in tree based on the 50% majority rule consensus tree, although most monophyletic groups and their sister group relationships, as discussed above, are also represented in this tree (Fig. 47). However, the family Platystictidae appears in a basal trichotomy with *Sinocnemis yangbingi* Wilson & Zhou and all other Zygoptera except the Lestoidea. The two presently recognized subfamilies of the Platycnemididae are not fully supported by this analysis, since *Risiocnemis* Cowley, 1934, traditionally in the Calicnemiinae, appears in a poorly supported trichotomy with the rest of the Calicnemiinae and the Platycnemidinae.

The traditional Megapodagrionidae are again widespread in this tree. The position of *Ischnura elegans* (Vander Linden), as sister group to *Agriomorpha fusca* May, is poorly supported and asks for further study of the position of the Coenagrionidae in the tree.

Within the framework of this paper, the most relevant result of these analyses based on molecular characters is the confirmation of the monophyly of the Platystictidae.

3.2 Phylogeny of Platystictidae (molecular characters)

We will further discuss the results of the combined analysis of 16S and 28S only, and consider the trees of the parsimony analysis (Fig. 46) and the Bayesian analysis (Fig. 47).

Within the Platystictidae, the basal subdivision of the Platystictidae in the subfamilies Platystictinae and Palaemnematinae, already defined by Selys (1860) based on morphological characters, is corroborated by the molecular study. Both classical subfamilies are well-supported clades and sister groups. The presently recognized genera are, however, not distinctly represented in the tree (but see discussion below), although taxon sampling is too limited to draw final conclusions.

The Platystictinae are divided into two clades. One clade represents three ‘typical’ Philippine species

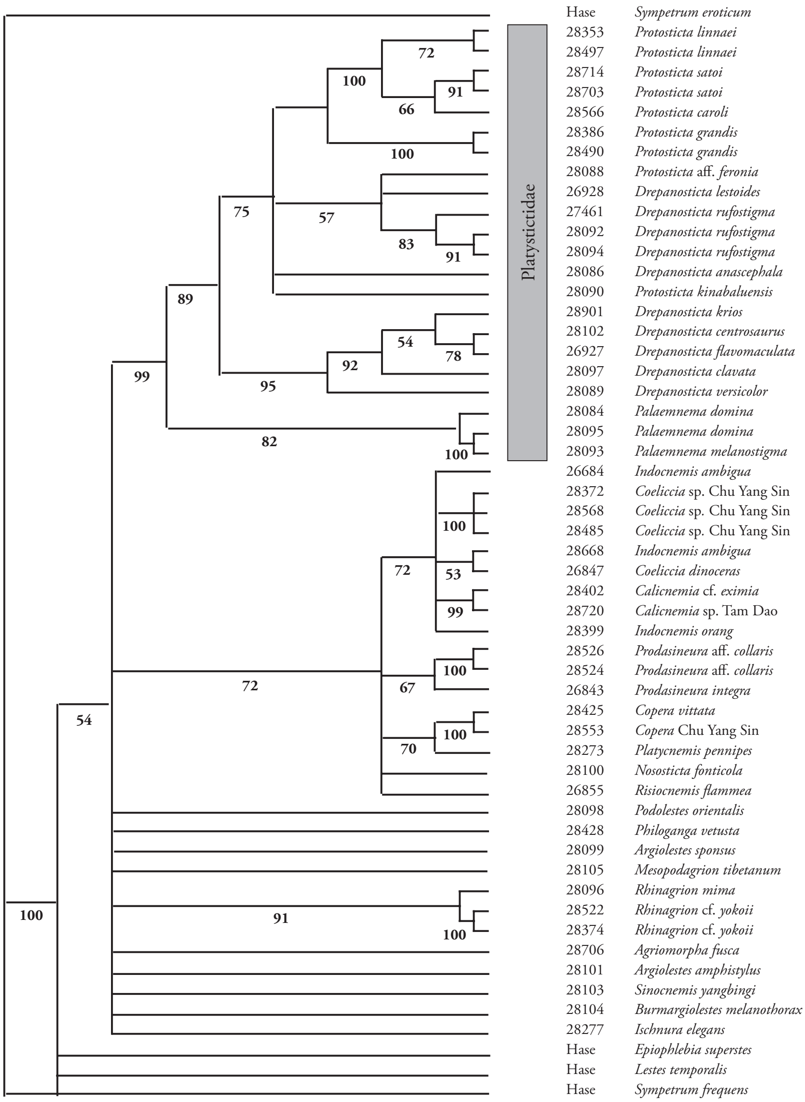


Figure 45. Bootstrap 50% majority-rule consensus tree based on 16S rDNA.

of *Drepanosticta* available for this molecular study, viz. *D. flavomaculata* van Tol, *D. centrosaurus* van Tol and *D. krios* van Tol, plus *D. clavata* (NW New Guinea) and *D. versicolor* of Borneo. The position of *D. clavata* in this clade, as sister species of *D. krios*, is weakly supported in the Bayesian analysis. In the strict parsimony analysis *D. clavata* is the sister group of all species from Mindanao included in our analysis. Based on the results of the morphological analysis, where these species also cluster, this clade is named the 'East Malesian clade'. The sister taxon of this clade is *D. versicolor* (Borneo), which is not a member of the 'East Malesian clade' of the morphological analysis.

The 'West-Malesian clade' in the molecular analysis is an assemblage of species presently assigned to *Drepanosticta* or *Protosticta*. Three specimens of *D. rufostigma* from various parts of Borneo form a monophyletic group with *Drepanosticta lestoides* (Philippines) and '*Protosticta*' aff. *feronia* (Borneo) (see also Lieftinck's remark on this taxon, referred

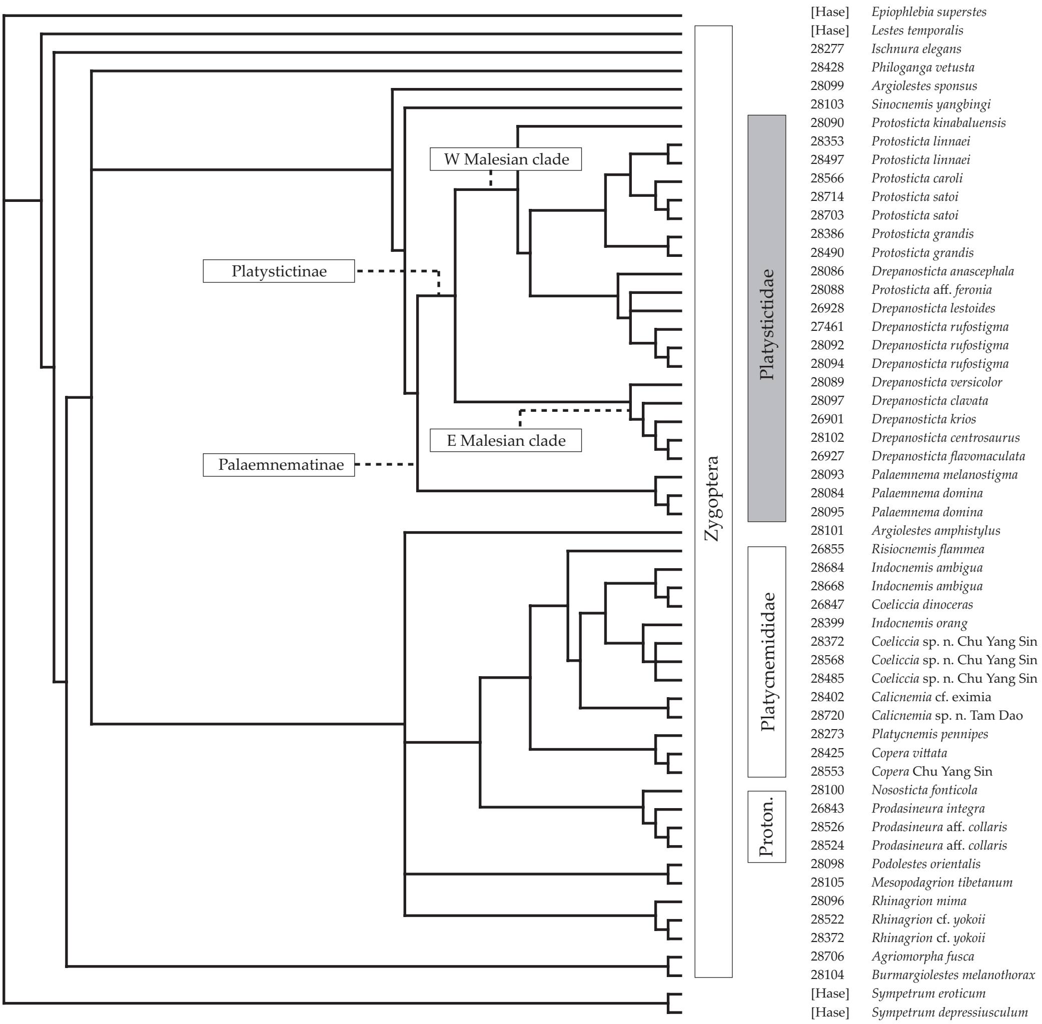


Figure 46. Strict consensus tree of 37 most parsimonious trees of a heuristic search of the 16S28S rDNA data. 'Hase' refers to data from Hasegawa & Kasuya (2006). 'Proton' = Protoneuridae.

to above, 1.3). Both species also share some notable morphological characters, but *feronia* is assigned to the genus *Protosticta* based on the absence of the Ab vein. The sister group of the clade of *D. rufostigma*, *D. lestoides* and *'P.' feronia* plus *Drepanosticta anascephala* Fraser, 1933 (mainland of southeast Asia) consists of the 'genuine' *Protosticta* species of our sample.

The sister group of the clade of *Protosticta* plus 'West Malesian' *Drepanosticta* is *Protosticta kinabaluensis*, a species confined to northern Borneo (Mt. Kinabalu).

3.3. **Phylogeny of the Platystictidae (morphological characters)**

Introduction. – We analysed a dataset of morphological characters (see 2.2) of 53 species of Platystictidae, representing the morphological and the geographical variation of this family, plus *Lestes temporalis*. Attention was paid to include species from all parts of southeast Asia, with special emphasis on island endemics.

The datamatrix (Appendix 2) of 38 morphological characters was analysed with PAUP using heuristic

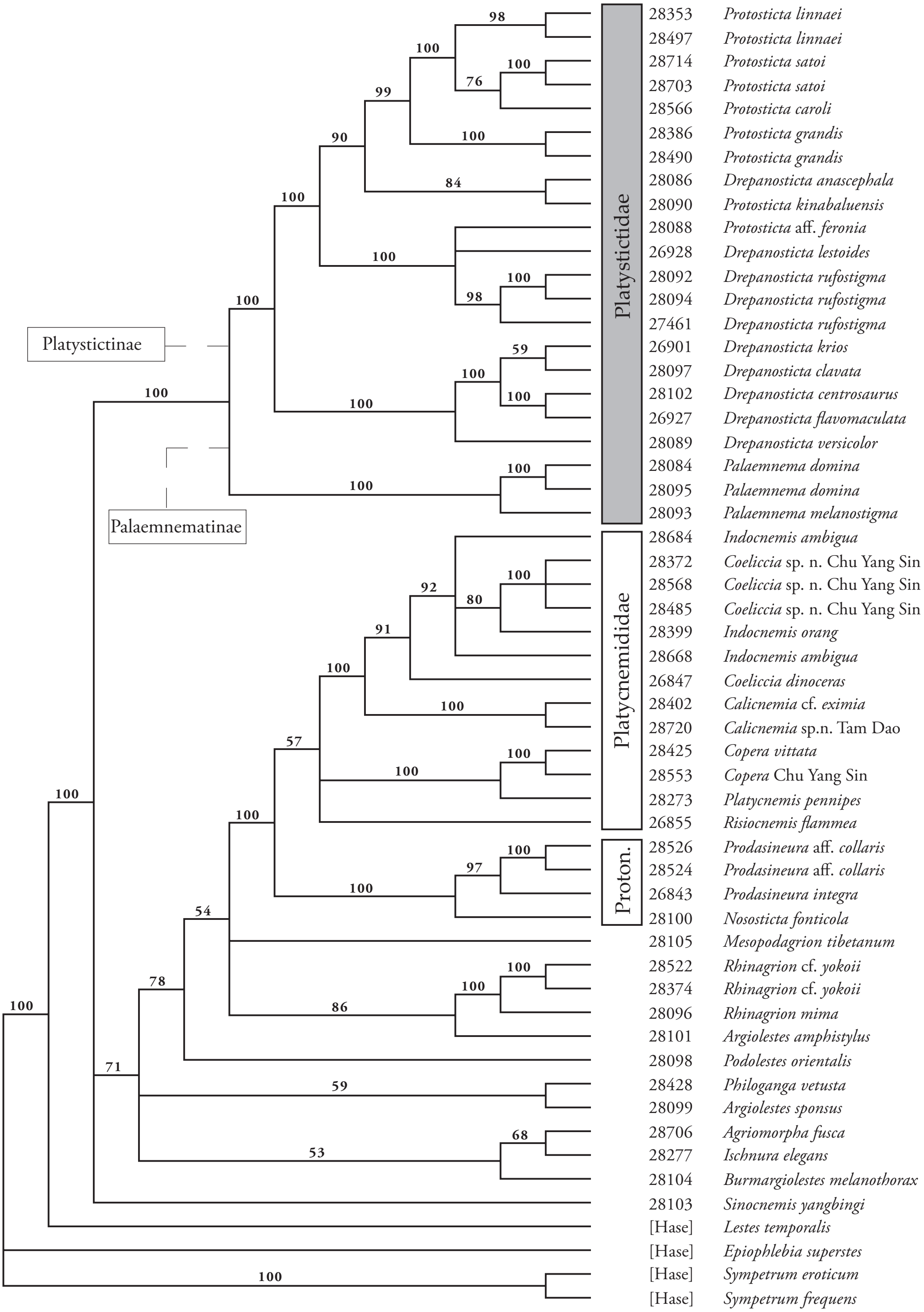


Fig. 47. Majority rule consensus tree of Bayesian analysis of 16S and 28S rDNA data of 54 taxa. Numbers of branchs refer to percentage of trees which supported the clade. 'Hase' refers to data from Hasegawa & Kasuya (2006). 'Proton' = Protoneuridae.

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search with TBR branch-swapping. Seven characters were coded as 'ordered'.

The parsimony analysis with addition sequence of taxa specified as 'addseq=random' and hundred replicates, resulted in ten most parsimonious trees, each with tree length 308, consistency index = 0.2597, retention index 0.5624, and rescaled consistency index = 0.1461. The trees only differed in the group with *Protosticta caroli*, *P. satoi*, *P. linnaei* and *P. foersteri.* Sixty percent of the trees supported the sister group relationship *P. linnaei* and *P. satoi*, and this clade formed a (100% supported) trichotomy with the other species just mentioned. Although the analysis revealed only a limited number of trees, and a highly resolved strict consensus tree, a preliminary bootstrap analysis (results not presented) showed that support for most branches is low.

Consensus tree. – Since we found a limited number of trees only, which also proved to be highly congruent, we restrict the discussion to the strict consensus tree (Fig. 48, see also Fig. 55).

With *Lestes temporalis* as designated outgroup, *Sinosticta ogatai* (Sinostictinae) is the most basal clade in the cladogram[3]. It is the sister group of all other Platystictidae. The latter clade has two well-supported branches, of which one includes nearly all species presently assigned to the Platystictinae. The other branch includes (a) the genus *Palaemnema*, (b) the genus *Platysticta* and (c) some *Drepanosticta* species from New Guinea. Remarkably, a species of *Platysticta* (*deccanensis*) is the sister taxon of two species of *Drepanosticta* from New Guinea [*D. conica* (Martin) and *D. dorcadion* Lieftinck], while *Platysticta apicalis* is the sister taxon of *Palaemnema melanostigma*, the only species of the Palaemnematinae included in this analysis. This suggests that the subfamily Palaemnematinae as presently defined (with only *Palaemnema* included) is paraphyletic.

The sister group of the '*Platysticta –Palaemnema*'-clade is very speciose. In this clade, the first branching consists of one species of the genus *Drepanosticta* from Sri Lanka, *D. nietneri* (Fraser). This species is the sister group of the rest of the Platystictinae. The latter clade consists of two large groups, which we call the 'East Malesian clade' ('6' in Fig. 55), including the species of the Moluccas and the rest of the species from New Guinea. The sister group is called the 'West Malesian clade' ('5' in Fig. 55), and is widespread on the mainland, the Greater Sunda islands, and Sulawesi; it includes all species presently assigned to *Protosticta.*

The basal branching of the 'West Malesian clade' consists of *Drepanosticta carmichaeli* (Laidlaw) from Nepal and the rest of the species assigned to *Drepanosticta*. *D. moorei* from Luzon ('7' in Fig. 55) is the next branch, which represents an early dispersal towards the northern Philippines. The other branch includes two sister groups, which both dispersed from the mainland into the Greater Sunda Islands. One branch ('7a' in Fig. 55) is especially speciose in Borneo, from where it presumably reached the southern Philippines. The other clade ('7b' in Fig. 55) includes all species presently assigned to the genus *Protosticta*, and is strongly represented in the mainland, Borneo and Sulawesi. It also includes *Sulcosticta striata* van Tol from Luzon, as a sister taxon of *Protosticta hearsayi* Fraser of the mainland. Although this confirms the distinct nature of this taxon within the fauna of the Philippines, it is also an indication that the genus *Sulcosticta* may have a evolved more recently than previously presumed (van Tol 2005).

The 'East Malesian clade' has no extant representatives on the mainland. Apparently, the origin of this clade must be sought in a dispersal event from the mainland into the southern Indonesian archipelago (Java, or Sulawesi). There is a basal branch with *Drepanosticta* species from Sulawesi and the South Moluccas. The other branch includes a group of species occurring in the Philippines, the northern Moluccas and New Guinea. Sister-group relationships between species

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[3] *Note added in proof.* We have recently been able to study 16S and 28S rDNA of an undescribed species of *Sinosticta* from Hainan (donated by G. Reels, Hong Kong, molecular laboratory work by F. Stokvis, Naturalis Leiden). These data were added to the dataset as described in 3.2. In preliminary analyses using NJ and parsimony, *Sinosticta* appeared as the sister group of all other Platystictidae included in the dataset, confirming our conclusions based on the morphological dataset.

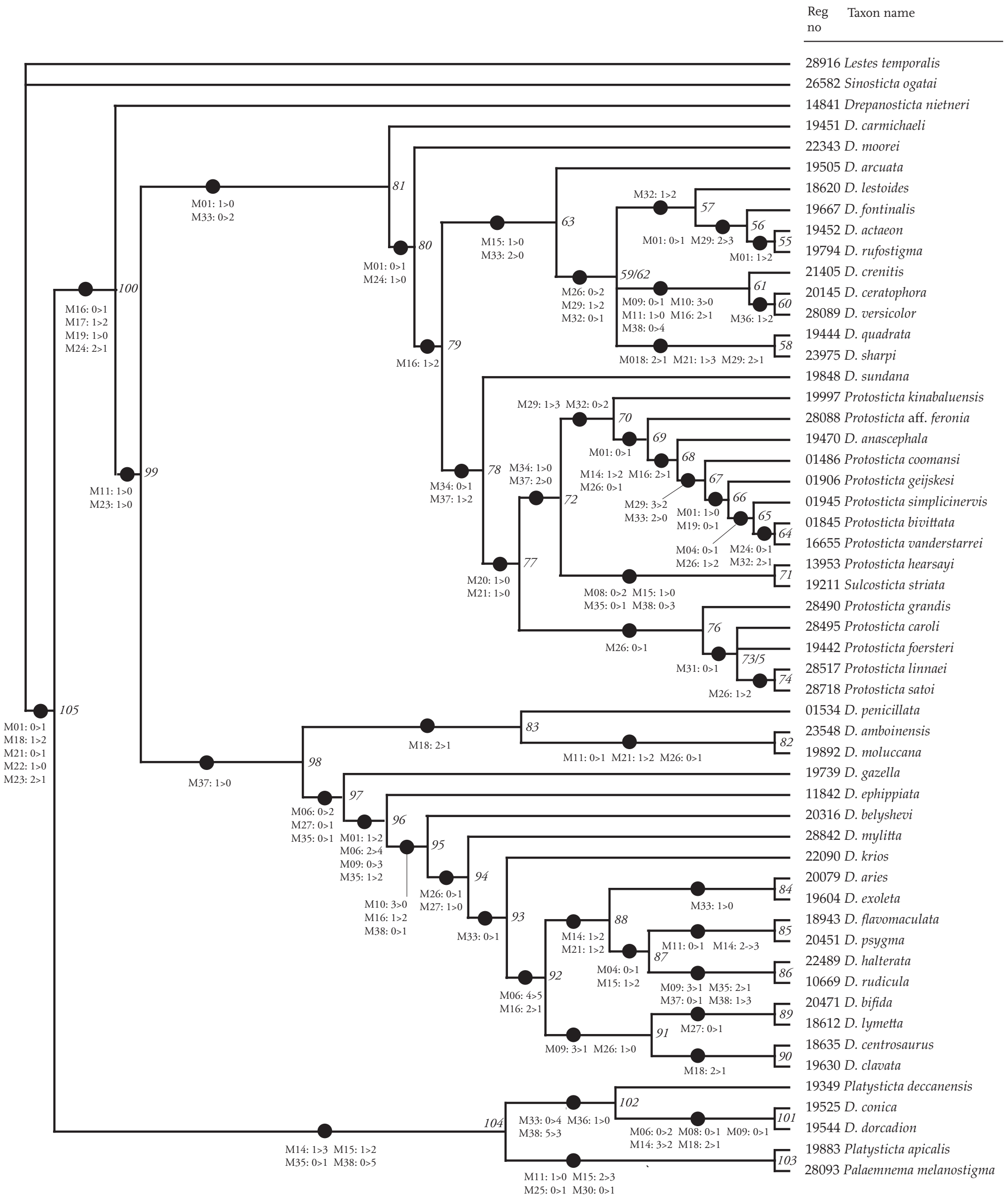


Figure 48. Strict consensus tree of ten most parsimious trees of 53 species of Platystictidae plus one Lestidae (*Lestes temporalis*) (morphological dataset). Character changes of morphological characters (except for terminal taxa). Numbers of nodes in italics. See Appendix 3 for complete change list.

from the Philippines and the northern Moluccas or New Guinea frequently occur in this clade, indicating a general vicariant or dispersal event.

Comparison of trees based on molecular and morphological characters. – The topology of the consensus tree based on morphological agrees to a large extent with the relevant part of the reconstruction based on molecular characters. The basal position of *Palaemnema* is confirmed, although *Sinosticta* from SE China (only available for molecular studies after finishing our analyses) is the more basal clade based on morphological characters. Based on our molecular analysis, the Palaemnematinae and the Platystictinae are sister groups, but this may be an artefact since no representative of the genus *Platysticta*, nor one of the New Guinean species *Drepanosticta conica* or *D. dorcadion* were available. Lieftinck (1949: 59) placed his new species *D. lepyricollis* and *D. dorcadion* in a small group, characterized by the presence of pale-coloured antehumeral spots or stripes on the dorsum, and by clearly defined, variously shaped, somewhat angulate pale marks on the sides of the thorax. Unfortunately, Lieftinck did not study the highly characteristic ligula of these species (Fig. 43), which resemble the same structure in *Platysticta* and *Palaemnema* in various ways (Figs 34-35). Also the coloration of the thorax of the species of this clade is characteristic.

The 'West Malesian clade' and the 'East Malesian clade' are represented in both analyses based on morphological and molecular characters, respectively. However, the position of *Drepanosticta versicolor* from Borneo is significantly different in both results. In the molecular analysis, it is the sister taxon of the species of the 'East Malesian clade', while it clusters with a Bornean clade with *D. crenitis* and *D. ceratophora* in the morphological study.

The topology of various species of *Protosticta* from Vietnam, e.g. *P. linnaei*, *P. satoi* and *P. caroli*, is also somewhat different.

In the morphological analysis, as well as in the molecular analysis, *Drepanosticta anascephala* clusters among *Protosticta*. '*Protosticta*' aff. *feronia* clusters among the other *Protosticta* species, while it superficially resembles some species of *Drepanosticta*. In both analyses, *Drepanosticta clavata* from New Guinea clusters among a group of closely related species from Mindanao, although the sister species of both analyses is different, viz. *D. centrosaurus* in the morphological, and *D. krios* in the molecular analysis.

3.4 Morphological character evolution

We have examined the morphological character evolution of the Platystictidae plotted on the tree based on molecular characters. Some characters that play an important role in defining monophyletic groups in the strict consensus tree based on morphological characters, are discussed.

Head. – The lateral extremities of the transverse occipital carina (Character M01, Fig. 49) are absent in the outgroup and in the Sinostictinae. This character defines (absent to small) the Palaemnematinae + Platystictinae. These extremities are again absent in most species of the 'West Malesian clade' (present in *D. carmichaeli*), but in some clades they are again present. Extremities are angulate in most Philippine species, i.e. the sister group of *D. ephippiata* from Sulawesi.

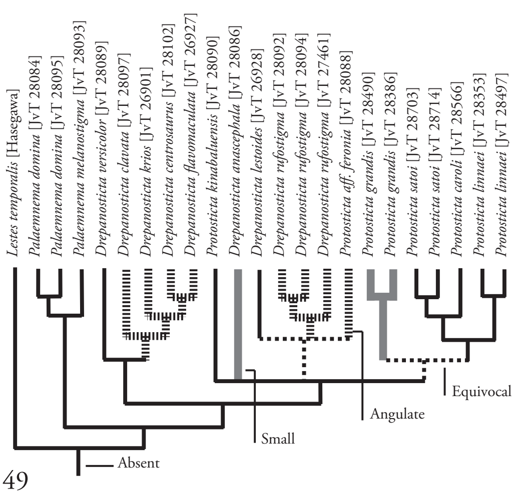
Wings. – Several characters in the Platystictidae show distinct evolutionary patterns on the strict consensus tree based on morphological characters.

All Platystictidae have one or more Cux, or 'post-cubital cross-veins' (character M13) (not illustrated), a unique apomorphy of this family.

The position of IR3 in relation to the subnodus is a traditional character to distinguish the Palaemnematinae (character M17, Fig. 52). In the outgroup IR3 is situated far proximal to the subnodus, while it is at the level of the subnodus in the Palaemnematinae (included in the molecular analysis), and in the Sinostictinae, *Platysticta* and *Drepanosticta dorcadion* (all not included in the molecular analysis). In all other Platystictinae the IR3 vein arises distal to the subnodus.

In the outgroup and the Sinostictinae the CuP vein meets the hind margin of the fore wing distal to the origin of R3 (character M23) (not illustrated). As an apomorphy of the Platystictinae + Palaemnematinae, the CuP vein meets the hind margin of the fore wing at the level of R3, or even proximal to it. In all species in the sister group of *Drepanosticta nietneri* (i.e., the 'West Malesian clade' + 'East Malesian clade' (except *D. clavata*) this vein meets the hind margin of the wing proximal to the origin of R3.

The absence of the anal bridge vein (Fig. 51) is



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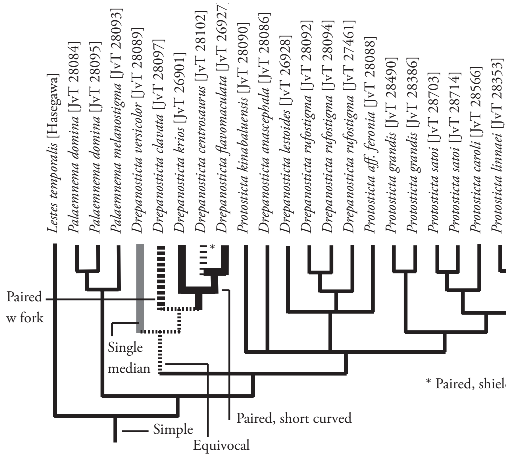

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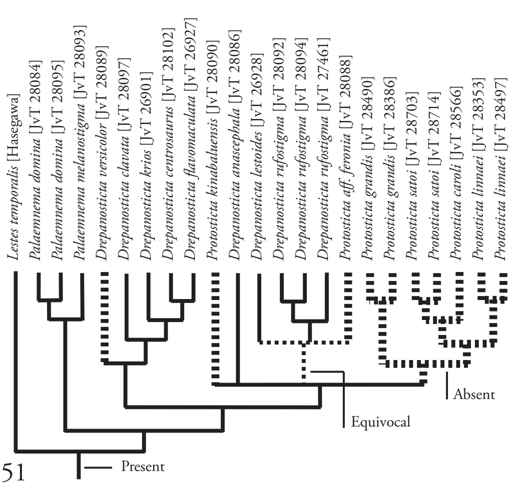

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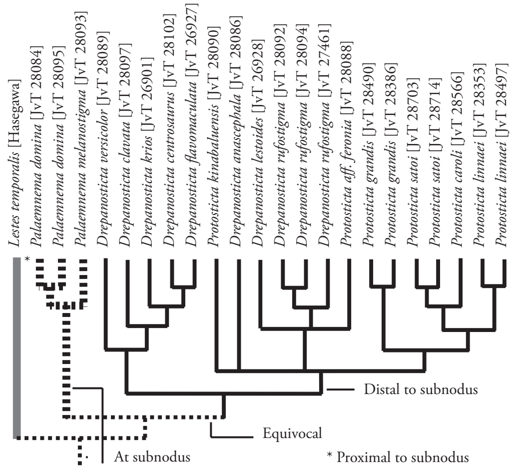

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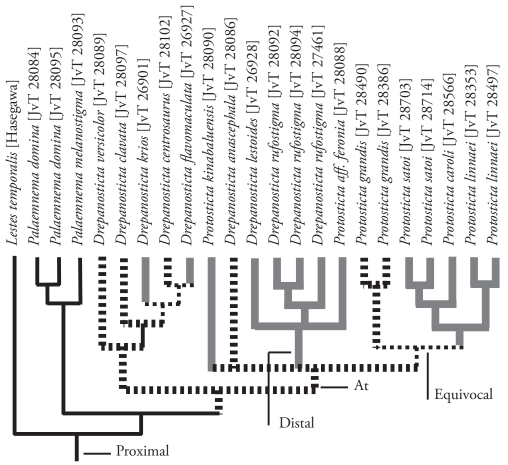

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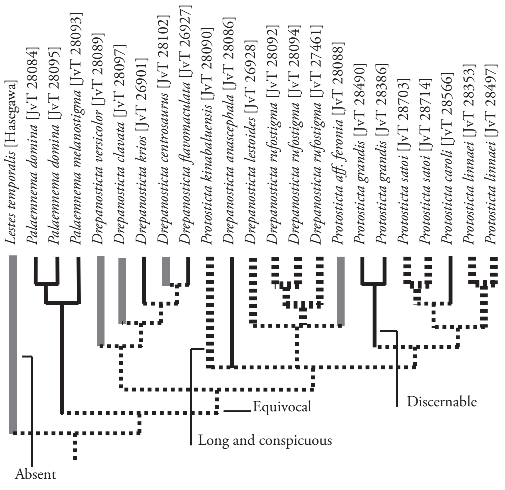

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a diagnostic character of the genus *Protosticta* as presently defined. This character defines the clade that is the sister group of *Drepanosticta sundana* (Krüger) (Java), which consists of all species of *Protosticta* plus *Drepanosticta anascephala* (Thailand) and *Sulcosticta striata* (Luzon). The anal bridge vein is also lacking in *Drepanosticta versicolor,* which was previously assigned to *Protosticta*. This species clusters in our analysis with *D. crenitis* and *D. ceratophora*; this result is consistent with the study by Orr (2003), who moved *Protosticta versicolor* to *Drepanosticta.*

Wing vein R4+5 (Fig. 53) is always situated proximal to the subnodus in the outgroup and in the Palaemnematinae, but is typically at or distal to the subnodus in the Platystictinae. During the evolution of the Platystictidae there is a distinct tendency for a more distal position (via 'at'), but this has occurred independently once in the West-Malesian and once in the East-Malesian clade. In the 'West Malesian clade' it is an apomorphy for the sister group of *Drepanosticta moorei* (7 in fig. 55), but there are two reversals, including the sister group of *P.* aff. *feronia*, consisting of *D. anascephala* + the species of *Protosticta* confined to Sulawesi. A reversal in the 'East Malesian clade' is an apomorphy of the clade named as '19' in Fig. 55, basically the group of *Drepanosticta* species that moved from Mindanao eastward to the northern Moluccas and New Guinea.

Structure male anal appendages. – The development of most characters of the male anal appendages do not well coincide with the tree based on molecular characters. An example is the presence and size of a dorsal denticle on the superior appendage (character M26, Fig. 54). It is 'discernable' in many species, or 'long and conspicuous', but closely related species seem to have different rather than similar dorsal denticles. This may indicate that this character plays a role in mating isolation of populations.

We found more structure in the distribution of character states of the sub-terminal tooth of the inferior appendage (not illustrated). It is absent in most Platystictidae (and the outgroup), but present in two lineages of the 'West Malesian clade'. The species of the sister group of *D. arcuata* ('9' in Fig. 55) all have a small or larger tooth (except *D. ceratophora*), as have the Bornean and Sulawesi species of *Protosticta* + *D. anascephala* that are the sister group of *Protosticta hearsayi* + *Sulcosticta striata*. Smaller, but apparently not homologous structures were observed in *Drepanosticta halterata* complex and *Platysticta apicalis*.

Structure male secondary genitalia (ligula). – The structure of the ligula appeared to be highly variable, and thus suitable for phylogenetic analysis. However, the phylogenetic signal of various characters appeared to differ significantly.

The shape of the cleft between the branches (character M33) of the ligula triangular / sharp is the plesiomorphic state. The 'West-Malesian clade' is characterized by a squarish cleft, but a reversal to a sharp cleft has occurred at least twice in this clade. Outside the West-Malesian clade we only found a squarish cleft in *D. clavata* (New Guinea). A rounded cleft occurs widely in the 'East Malesian clade', but seems to have developed at least three times. A wide and straight cleft is found in *Platysticta* and two New Guinean species of *Drepanosticta*, which also has developed independently in *Protosticta grandis*.

The horns of the ligula (character M36) show significant variation as well. It seems that long and slender horns (length more than two times segment length) are the plesiomorphic state. Nearly all other Platystictidae have horns with a length between half and two times the length of the segment. Very short horns occur, again, in *Platysticta deccanensis* + the two New Guinean *Drepanosticta* species, but developed also independently in *D. arcuata* and *D. quadrata*.

Left

Figures 49-54. Morphological character changes fitted on the tree based on molecular characters. – 49, Lateral extremities tranverse occipital carina (M01). – 50, Posterior margin of posterior lobe of pronotum (M06). – 51, Ab vein (M20). – 52, Position IR3 in relation to subnodus (M17). – 53, Position R4+5 in relation to subnodus (M16). – 54, Dorsal denticle on superior appendage (M26).

Other characters. – Most colour characters are very homoplastic. The antehumeral stripe (character M08) is absent in two species of this selection, *viz.*, *Protosticta* aff. *feronia* and *Protosticta grandis*, which are presumably not closely related. The pale brown base colour (character M10) occurs widely in the group with *D. krios*, but reversals have occurred as well. All other species are brownish black or black.

Our analysis indicates that the processes of the hind margin of the pronotum have evolved only once (character M06, Fig. 50). A process is present in all species of the group that includes *D. krios*. Due to insufficient data of Philippine species, based on the present analysis it is uncertain whether the single median process, as in *D. ceratophora*, evolved from an ancestor with paired process, or that the opposite is true.

3.5. **Biogeographical patterns**

For a reconstruction of the area relationships, we have substituted the names of the species for the areas in which they occur. The distribution of the taxa is given in Fig. 55.

In the limited taxon sample of which 16S and 28S rDNA was studied, the following pattern can be reconstructed. Middle+South America (represented by the Palaemnematinae, as in Fig. 49-54) is the sister group of Asia. The two sister groups of the sister clade of the Palaemnematinae show the following relationships: (Borneo,(S Philippines,W New Guinea), and ((Borneo, S Philippines),((Mainland, Borneo), Mainland)). In this scenario, the island of Borneo has a key position. From Borneo, the subfamily Platystictinae has dispersed to the Philippines and (then?) New Guinea.

The more extensive taxon sampling for our morphological analysis provides more details in biogeographical patterns. The scenarios are fully discussed below, but we mention here the following observations:

- The basal taxa are all confined to a region around the Indian Plate: *Sinosticta ogatai* (SE China), the genus *Platysticta* and *Drepanosticta nietneri* (both Sri Lanka),
- The clade including *Platysticta* also includes species of *Drepanosticta* confined to New Guinea, and the Palaemnematinae of Middle and South America,
- The rest of the taxa are Platystictinae; the basalmost taxa are distributed in the mainland of southeast Asia,
- From the mainland, two large clades are distinguished with distinct distributions: the so-called 'West Malesian clade' (WMC) (no. 5 in Fig. 55) and the 'East Malesian clade' (EMC) (no. 6 in Fig. 55),
- *Drepanosticta moorei* from Luzon forms a basal branch of the WMC,
- The sister group of *D. moorei* has apparently followed two routes into western Malesia. Branch '7a' first populated Sumatra, and then Borneo and from Borneo Palawan was occupied; speciation on the mainland continued,
- In branch '7b' the area relationships are as follows (mainland (Borneo + Sulawesi)); the Sulawesi species of *Protosticta* form one monophyletic clade,
- The EMC presumably used Java as the stepping stone; eastern Sulawesi + southern Moluccan species of *Drepanosticta* are the sister group of the rest of the EMC,
- The sister group of the Javan *D. gazella* Lieftinck is a large assemblage of species occurring in Sulawesi (basal), the southern Philippines (*D. krios* and related species); more terminal taxa are distributed in the northern Moluccas and New Guinea.

The relationship between these patterns, and the palaeogeography, is further discussed below.

4. Discussion

4.1. **Relationships of families of Zygoptera**

The resulting tree of our Bayesian analysis of 52 species of zygopteran odonates, one species of 'Anisozygoptera' and two species of Anisoptera, based on molecular characters, is essentially congruent with the Zygoptera part of the tree as published by Bybee *et al.* (2008). We designated the Epiprocta of this selection, *i.e., Epiophlebia* and the *Sympetrum* species, as outgroup. *Lestes temporalis,* representing the superfamily Lestoidea, appeared as the sister group of all other Zygoptera. This analysis also confirmed the sister group relationship of the Platystictidae with the remaining Zygoptera, although we found a trichotomy with *Sinocnemis yangbingi*, which was not included in Bybee *et al.* (2008). Wilson & Zhou (2000) considered *Sinocnemis* a member of the Platycnemididae, but it was recently assigned to the Megapodagrionidae (Kalkman 2008). Our analysis a least shows that *Sinocnemis* does not cluster with 'genuine' platycnemidid genera, such as *Coeliccia*, *Platycnemis* or *Copera*. On the other hand, the relationships of the 'Megapodagrionidae' are presently poorly understood, as also appears from our analysis.

The topology of the Platystictidae part of the tree will be further discussed below. The strict parsimony analysis of our molecular dataset shows a somewhat different topology, in which the Platystictidae are monophyletic, and appear as sister group of *Sinocnemis*. These two taxa together are a member of a polytomy with taxa of different hierarchical position. We will further only discuss the results of the majority rule consensus tree of the Bayesian analysis.

The topology of the rest of the Zygoptera differs between our study and Bybee *et al.* (2008), even when our more restricted taxon sampling is taken into account. Our analysis revealed the monophyly of the families Protoneuridae and Platycnemididae as presently defined, although the monophyly of the Platycnemididae is weakly supported. Both families are sister groups as well. This result differs from Bybee *et al.* (2008), in which the Calicnemiinae (represented by *Coeliccia*) is the sister group of the Platycnemidinae + Old World Protoneuridae (viz. *Nososticta* Selys, 1860 and *Phylloneura* Fraser, 1922). Another part of the Protoneuridae, viz. *Neoneura* Selys, 1860 + *Protoneura* Selys, 1857 (all New World taxa), is the sister group of most Coenagrionidae in Bybee *et al.* (2008). New World species were not part of our analysis.

We included only one species of Coenagrionidae, *Ischnura elegans*, and one species of Lestoideidae, *Philoganga vetusta* Ris, 1912. Both species can be found among a group of species traditionally assembled in the Megapodagrionidae. However, both branches are poorly supported.

The topology of the Platycnemididae branch of our tree confirms the monophyly of the Platycnemidinae, but the Calicnemiinae are paraphyletic, since *Risiocnemis* forms a trichotomy with the Platycnemidinae and the rest of the Calicnemiinae. It must be mentioned here that the strict parsimony analysis of this dataset did confirm the monophyly and sister group relationship of the Platycnemidinae and the Calicnemiinae.

Based on morphological characters, the two subfamilies of the Platycnemididae have been commonly distinguished since Fraser (1957). In a recent cladistic analysis based on morphological characters, the sister group relationship of the Platycnemidinae and the Calicnemiinae had to be left open, since no synapomorphy of the Calicnemiinae could be revealed (Gassmann 2005).

The results of our study and those of Bybee *et al.* (2008) on the phylogenetic relationships of the non-calopterygoid families differ significantly from previously published trees based on morphological characters only (e.g. Bechly 1996, Trueman 1996, Rehn 2003) (see also Fig. 5). Bechly's phylogenetic reconstruction of the extant families can be summarized as ((((((Megalestidae+Lestidae), Synlestidae), Perilestidae), Chorismagrionidae), Hemiphlebiidae), ('Megapodagrionidae', (((Coenagrionidae, Platycnemididae + Protoneuridae), Pseudostigmatidae + *Coryphagrion* Morton, 1924), Platystictidae))). Bechly was criticized by Rehn for his irreproducible results since he used 'head and brain' phylogenetic systematics, rather than 'modern computer cladistics', but he correctly considered the Megapodagrionidae as a paraphyletic assemblage, and the Platycnemididae and Protoneuridae as sister groups. However, Bechly's reconstruction of the other sister group relationships does not agree with our tree, and especially the basal position of the Platystictidae in the coenagrionoid clade is not confirmed. The tree by Trueman (1996), (*Perilestes*, (*Chorismagrion*, (*Synlestes*, (*Pseudostigma*, (*Xanthagrion*, (*Platycnemis*, ((*Neosticta*, (*Platysticta*, *Protoneura*)), (*Austroargiolestes*, (*Austrolestes*, (*Lestoidea*, (*Pseudolestes*, Caloptera)))))))))))), based on odonate wing venation, shows hardly any congruence with our tree. Rehn's preferred tree (Fig. 5) is largely incongruent with the present results as well.

We appreciate that our results should be considered an initial framework for future analyses, since the study is based on a preliminary and incomplete dataset of non-calopterygoid Zygoptera, mainly to establish the monophyly of the Platystictidae. It is also noteworthy to mention some significant differences between our results and those of Bybee *et al*. (2008). The latter study is based on a larger taxon sample, on six rather than two genes, and on morphological characters as well. Most sequences produced by Bybee *et al*. were not available to us at the time of our analysis. Besides, a random sample of Bybee's dataset appeared to consist of such short sequences of several genes that we were unable to align them with our dataset.

4.2. Relationships of the Platystictidae

As explained in 1.2 above, little information is available on the phylogenetic relationships of the species assigned to the Platystictidae. Analyses published up to now included only very few species of this family. Rehn (2003) studied two species of *Palaemnema*, two species of *Drepanosticta*, and one species of both *Platysticta* and *Protosticta*. Bybee *et al*. (2008) only had *Palaemnema melanostigma* and *Protosticta sanguinostigma* available for their molecular study.

The sister group relationship of the Palaemnematinae and Platystictinae has been implicitly assumed in classifications since Fraser (1957), but the status of the Sinostictinae remained uncertain. Within the Asian Platystictinae, the status of the genera has been frequently questioned. Lieftinck (1933) expressed his concerns on the close morphological similarity of *Protosticta feronia* and *Drepanosticta dupophila*, to be assigned to different genera based on one wing venational character, while their morphology was generally similar. Orr (2003) showed no confidence in the two 'poorly defined genera *Drepanosticta* and *Protosticta*', and recognized four 'main forms' with members of both genera. Van Tol (2005) attempted to group closely related species in the Philippines, indicating that similar species also occurred in Borneo, or in the Moluccas and New Guinea. He erected a new genus, *Sulcosticta*, for species not assignable to *Protosticta* nor to *Drepanosticta*, but the phylogenetic position of that genus was not discussed.

Our results based on molecular characters confirm the supposed sister group relationship of the American Palaemnematinae and Asian Platystictinae. The position of the genus *Platysticta* (Platystictinae), which was not available for molecular studies, needs further study. Our study of the morphology of these taxa indicates that *Palaemnema*, *Platysticta* and some species of *Drepanosticta* from New Guinea form a monophyletic group, in which one species of *Platysticta* is the sister taxon of *Palaemnema*, and another species to some New Guinean *Drepanosticta* species.

The monophyly of the genera *Drepanosticta* and *Protosticta* (both Platystictinae), as presently defined, could not be confirmed by the results of our analysis of the small dataset sampled for 16S and 28S rDNA, nor by the analysis based on morphological characters. In our analysis of the molecular dataset, we found that '*Protosticta*' aff. *feronia* (Borneo) appears in a trichotomy with *Drepanosticta rufostigma* and *D. lestoides* (Philippines). In our morphological analysis, it is a member of the '*Protosticta*'-clade. However, it is morphologically very similar to *Drepanosticta dupophila*, occurring in the same region (Lieftinck 1933: 285, and text on p. 8). Unfortunately, no material of *D. dupophila* was available for our molecular study. Based on the fact that both nominal species are syntopic and share all morphological characters except wing venation, we predict that both names are synonyms.

Drepanosticta anascephala (mainland southeast Asia) appears to be a member of a clade including all species presently assigned to *Protosticta* in both our molecular and morphological analyses.

4.3 Biogeography

Vicariance and dispersal. – The historical biogeography of southeast Asia has attracted much attention for more than a century (Wallace 1860, 1863). The geological history of this region has become much better known during the last thirty years (*e.g.*, Hamilton 1979, Pigram & Davies 1987, Hall 2002, Hill & Hall 2003), and this has also been summarized in a biogeographical context several times (de Boer 1995, de Boer & Duffels 1996, Beuk 2002; for aquatic organisms see, *e.g.*, Polhemus 1996, Polhemus & Polhemus 1998, van Tol & Gassmann 2007). Essentially, most islands in the region consist of amalgamations of island arc terranes, which successively accreted since the Late Cretaceous. This process actually continues up to today. Since many of these micro-continental fragments have had a subaerial history for millions of years, floral en faunal elements that dispersed to these fragments have been able to survive, and evolve in isolation. The composition of the fauna of such islands as Mindanao, Sulawesi, and especially New Guinea, may thus be a mixture of clades that became separated up to 40 to 50 million years ago, and re-assembled on one island only ten to twenty million years ago. The present distributions of such organisms, and their evolution since the docking of the palaeo-island on which they lived with a larger land mass, depend on the biology of the species (ecology, dispersal power), and the time since the amalgamation of fragments of land.

In many groups of organisms in the Malay archipelago, species have distributional ranges of a few hundred square kilometers only. Such small ranges have a high potential to define areas of endemism. The reconstruction of the phylogenetic relationships of the taxa is thus a powerful tool for the reconstruction of area relationships. Nevertheless, the reconstruction of the common history of the areas of endemism based on cladistic analyses of various groups of organisms has proved to be unsuccessful up to now (*e.g.*, Turner *et al.* 2001), although parsimony-based tree-fitting methods using phylogenetic reconstructions and geological area cladograms in the Malay archipelago (Sanmartín & Ronquist 2004) have not been attempted as yet. The use of component analysis is hampered since areas of endemism are usually defined too large and are based on multicentric biotas, so that areas of endemism are actually composite areas (Polhemus & Polhemus 2002). Progress in our knowledge of area cladistic relationships can only be expected when cladograms with *absolute* timing of clade splitting in different lineages will become available.

Our present taxon sampling does not allow for a detailed analysis of the historical relationships of small areas of endemism. So, in our cladogram of the Platystictidae based on morphological characters we have substituted the areas for the taxa, revealing relationships between the areas defined by the distributional ranges of the taxa (Fig. 55).

Old en New World relationships

Patterns. – The basal division in the tree based on the molecular analysis, of the Platystictidae revealing Palaemnematinae and Platystictinae as sister groups, recognizes the New and Old World as sister areas. In our morphological analysis (Fig. 55) the interpretation of the tree is somewhat more complicated. *Sinosticta ogatai* from southeastern China is the sister taxon of all other Platystictidae. The next branching separates most species of the Platystictinae from a clade including the Palaemnematinae (America), *Platysticta* (Sri Lanka, southern India) and two species of *Drepanosticta* confined to New Guinea. We notice that the basalmost branch in the Platystictinae (excluding the two New Guinean species) separates *Drepanosticta nietneri* from Sri Lanka from the remaining species.

Processes. – The sister group relationship of the Sinostictinae, presently known from SE China only, to all other Platystictidae (= subfamilies Platystictinae + Palaemnematinae) suggests that the ancestors of the Platystictidae evolved at the border of the Oriental and Palaearctic regions, or, in the region where the ancestors of the sister group lived, *viz.*, Central and northern South America (Palaemnematinae), Sri Lanka and southernmost India (genus *Platysticta*, and basal *Drepanosticta*), and possibly New Guinea. A final conclusion has to await a reconstruction of the phylogeny including the identification of the immediate ancestor of the Platystictidae.

A distribution pattern as we presently find in the Platystictidae, is also known in other groups of tropical organisms. This pattern was named 'tropical amphi-transpacific distribution' by van Steenis (1962). It is mainly found in rain forest trees and herbs. The evolution of this pattern has been attributed to dispersal from Africa (during the Late Cretaceous) to the northern hemisphere with later extinction in Africa due to Neogene aridity (Raven & Axelrod 1974). The route for the exchange of biotas theoretically includes dispersal via Europe into Asia, or via India. More recent studies have emphasized the function of India as a dispersal route to reach southeast Asia from Africa / Madagascar, such as several groups of amphibians (Bossuyt & Milinkovitch 2001). Besides, the general notion of an isolated India during the Cretaceous is also under discussion by geologists. Briggs (2003) recently suggested that dispersal routes between southeast Asia and eastern Africa via India may have existed during most of the Cretaceous, mainly since the northern margin of India must have been much larger then known up to now. Nearly all material now forming the Himalayas once formed the northern margin of the Indian continent, and new calculations suggest a crustal shortening in northern India of 1500 km (Patzelt *et al* 1996) up to even 4000 km (Zaman & Torii 1999) during the formation of the Himalayas. Ali & Aitchison (2008), however, state that the marine barrier between Asia and India was at least 1000 km during the Late Cretaceous.

Origin of the Platystictidae. – Based on the presence of basal lineages in the New World (*Palaemnema*), Sri Lanka (*Platysticta* and some *Drepanosticta*) and south-eastern China (Sinostictinae), we hypothesize a scenario with an origin of the Platystictidae in eastern Africa. Gondwana is the ancestral area of the outgroup, the superfamily Lestoidea (see Fig. 5), with groups in South America, southern Africa and Australia. The common ancestor of (i) species presently assigned to *Platysticta* and only surviving in Sri Lanka and southernmost India, plus (ii) New World *Palaemnema* plus (iii) some *Drepanosticta* species of New Guinea, must have lived in a tropical region with dispersal routes to the aforementioned areas. This pattern can be understood with an ancestral area in the eastern part of Gondwana, and subsequent (i) dispersal into South America, presumably via Europe (see below), (ii) drifting with, or dispersal, via India / Sri Lanka to Asia, (iii) dispersal into the Asian mainland, (iv) dispersal via a 'pre-Eocene island arc' from eastern Asia to New Guinea (v) extinction in Africa.

A further study of the phylogenetic position of some species of *Drepanosticta* in New Guinea is needed to judge an alternative scenario for this group, *viz.*, via a southern Gondwana connection (see Fig. 56).

Origin of the Palaemnematinae. – Based on the restricted range of the Palaemnematinae in South America, we hypothesize an arrival of the Palaemnematinae in America only after the break-up of the Central American land bridge, but before the climate of the northern hemisphere became unsuitable for tropical organisms. A direct dispersal between Africa and South America is considered less likely, although dispersal routes between Africa and South America have existed longer than the break-up of the connection between these continents between 106 and 84 Ma. According to Morley & Dick (2003) trans-atlantic dispersal of angiosperms must have been possible via island chains such as the Rio Grande – Walvis ridge throughout the Late Cretaceous.

The ancestors of the Palaemnematinae of the Americas were presumably elements of the so-called 'Northern Hemisphere Boreotropical province' during the Late Paleocene and Early Eocene. They may have reached the European region from Africa. Van Tol & Müller (2003) (Chapter 4) dated the division between the New World Palaemnematinae and the Platystictinae of the Old World back to the Late Cretaceous (65 Ma), but after the termination of trans-oceanic dispersal routes between Africa and South America (84-65 Ma). This estimate seems to be corroborated by the present reconstruction, since an extensive moist megathermal zone was available at northern latitudes during the Late Cretaceous. Similar distribution patterns as in Platystictidae are also known in other groups of tropical organisms, and the timing of floral or faunal exchange between northwestern Laurasia and northern America is usually placed in late Paleocene or early Eocene (ca.

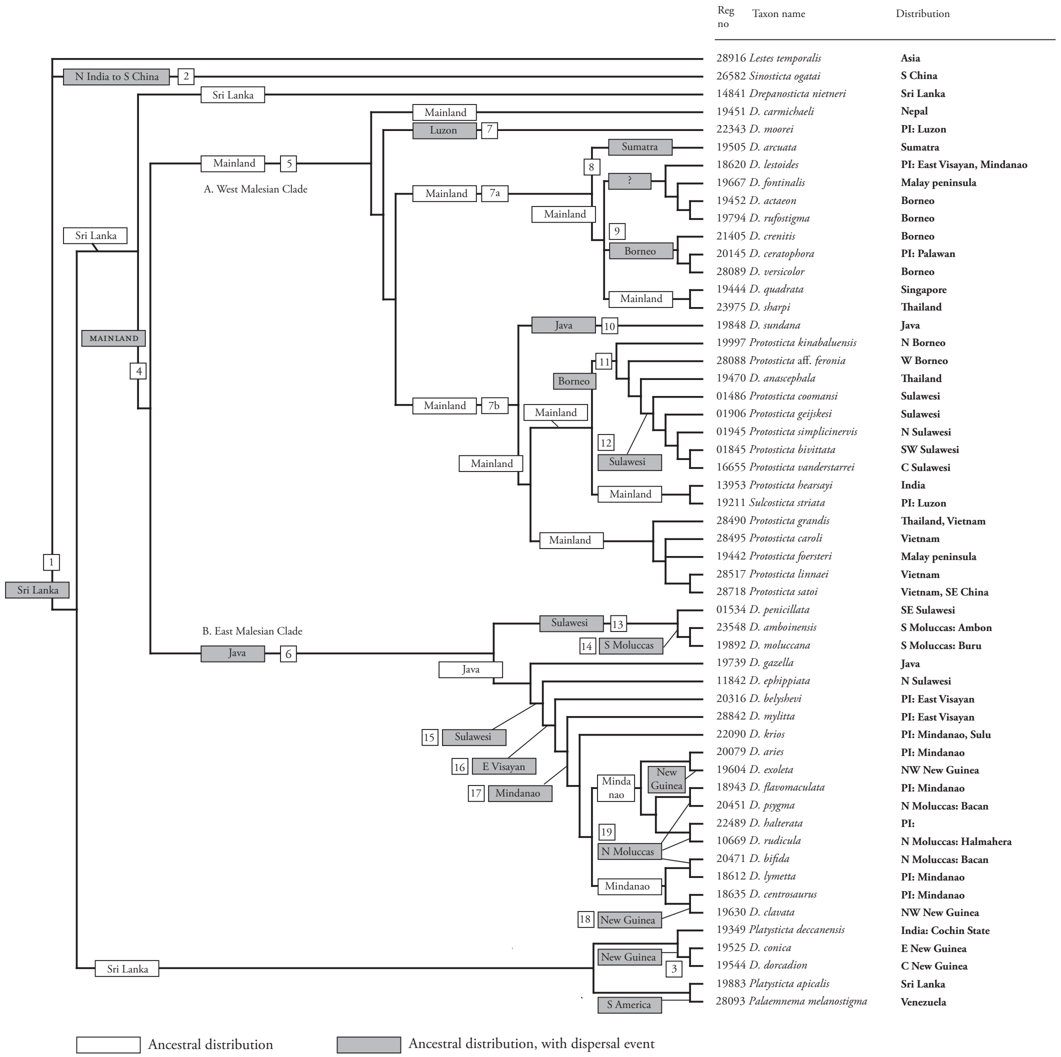

Figure 55. Strict consensus tree of ten most parsimious trees of 53 species of Platystictidae plus one Lestidae (*Lestes temporalis*) (morphological dataset). The distribution of each species is given to the right of the species name. Names in blocks indicate presumed ancestral areas. Dark blocks indicate dispersal event. Numbers in blocks indicate clades discussed in the text.

55 Ma) (information mainly based on Morley 2000). Only during the Early Paleogene multistratal tropical rain forests developed in the so-called Boreotropical zone (Fig. 6), presumably in relation to the extinction of the large herbivorous dinosaurs by the end of the Cretaceous, and the subsequent evolution of fruit and seed eating and dispersing mammals. Especially during the Eocene (50 Ma) the climatic conditions were tropical and considered suitable for migrations via the 'North Atlantic Land Bridge' sensu Tiffney (1985a, b), which is a connection from northern North America to northern Europe, which at least is supposed to have existed during the Early Eocene (54-49 Ma). A migration route from Asia via Beringia is considered an alternative for the North Atlantic Land Bridge, but the climate was probably too cool at the high latitude of this route to support tropical species.

Our scenario, with evolution of the Platystictidae in

Africa, dispersal from Africa into Asia via India, and dispersal to the New World via Europe, and subsequent extinction in Africa, has parallels in other groups of plants and animals, including other odonates.

The Pseudostigmatidae (Odonata) are presently known from South and Middle America in roughly the same area as the Palaemnematinae. Recently, a species from eastern Africa, *Coryphagrion grandis* Morton, 1924 was recognized as a sister group of the American Pseudostigmatidae (Groeneveld *et al.* 2007). Dijkstra (2007: 163) describes a scenario for the survival of the ecosystem of *C. grandis* since the Eocene. He, however, presumes a much later, direct exchange (at the Eocene–Oligocene boundary, c. 34 Ma) of the Pseudostigmatidae s.l. from South America to Africa, referring to a study of monkeys by Opazo *et al.* (2006). New World monkeys, which have African ancestors, began to radiate in South America from c. 25 Ma, suggesting exchange of faunas between Africa and South America even well into the Oligocene.

We can, however, not exclude the scenario that the monkeys of South America also have used the 'North Atlantic Land Bridge', and reached South America during the Oligocene from North America. Dijkstra (2007) presumes a dispersal of the Pseudostigmatidae from South America to Africa, based on the record of a fossil *Euarchistigma* Carle & Wighton, 1990 from western Brasil. Dating of splitting based on molecular characters supporting the dating of phylogenetic reconstructions of the Zygoptera, is needed for a better understanding of these patterns. According to Morley (2000), several groups of plants show a pattern of repeated dispersal in both directions.

The origin of various tropical groups in Africa has also been found in several groups of rain forest plants. Since Platystictidae are restricted to tropical rain forest, we may refer to phytogeographical studies, which can frequently use fossil data as well. According to Morley (2000, p. 260-262) (see also Morley & Dick 2003) three centres of tropical flowering plant diversification during the Late Cretaceous and earliest Tertiary can be distinguished: (1) one across northern mid-latitudes (Laurasia), (2) an equatorial centre (West Gondwana), (3) a southern mid-latitude centre (southern Gondwana). 'The northern hemisphere centre is particularly noteworthy because many of its modern taxa display amphi-Pacific distributions (being confined to the Neotropics and southeast Asia, but absent from Africa), or are relict to southeast Asia' (Morley & Dick 2003: 1638). These patterns appeared when global climates deteriorated during the mid-Tertiary (Morley 2000) and rain forest species were forced to lower latitudes. The poor representation of many rain forest taxa (of plants) in Africa is attributed to Late Tertiary extinctions due to intermittent dry climates in that region. Under such conditions, we consider a scenario with a local extinction in Africa of a characteristic rain forest inhabiting insect family as realistic.

Again according to information in Morley (2000), the alternative scenario of an origin of the Palaemnematinae in southeast Asia, and subsequent dispersal to the New World is less likely, since exchange of biota between Europe and southeast Asia was actually impossible during the Oligocene. Around 55 Ma the forests of eastern Asia 'developed somewhat in isolation' (Morley 2000: 264), as they were separated from Europe by a large epicontinental sea, the Turgai Straits, and central Asia was characterized by very dry conditions. The Turgai Straits only closed around 35 Ma, and a short-lived dispersal route for megathermal biotas may have been realized along the northern shores of the Tethys at the end of the Eocene, before the temperatures dropped during the Oligocene.

Origin of the Sinostictinae and Platystictinae. – As explained above, we presume that the ancestors of the subfamilies Sinostictinae and Platystictinae arrived via the Indian subcontinent in southeast Asia. India separated from Madagascar about 84-96 Ma, and collided with Eurasia from ca. 60-65 to 42-55 Ma. Based on new geological evidence, the timing of collision of India to southeast Asia, and the timing of extant dispersal routes, may prove to differ significantly from present textbook information. Anyhow, India is considered to take a central position in the history of the platystictids, since the basal genus *Platysticta* of the subfamily Platystictinae is virtually restricted to Sri Lanka. Also the present distribution in southeast

China of the genus *Sinosticta* (Sinostictinae) can be understood if we presume an origin at the northern margin of the Indian subcontinent.

Anyway, in our scenario Platystictidae were widely distributed in the extensive tropical forests of eastern Asia during the Eocene (c. 50 Ma), while they had also crossed the North Atlantic Land Bridge into North America.

The Platystictinae must have lived in the southern part of the Indian continent as well, now the island of Sri Lanka. The species of Sri Lanka, assigned to *Platysticta* and *Drepanosticta*, appear as basal lineages in our phylogenetic reconstruction based on morphological characters. Also in various other groups ancient lineages are represented on this island (Bossuyt *et al.* 2004, 2005). The sister group relationship of *Platysticta apicalis* to *Palaemnema* is remarkable and should be further investigated. Their close relationships were already noticed by Laidlaw (1951), who also considered *Platysticta* 'probably a surviving remnant of an ancient fauna which now has no other representatives in the area'.

Also the basal *Drepanosticta* lineage of New Guinea, including *D. dorcadion* and *D. conica*, asks for a more detailed study in future. It presently appears as the sister group of *P.* (*maculata*) *deccanensis* from southernmost India. It may, however, prove to be not an artefact, since a pattern with basal lineages in New Guinea also has parallels in other groups. Polhemus & Polhemus (1987) found a sister group relationship between sagocorine Naucoridae (aquatic Heteroptera) of the Philippines (Luzon) and New Guinea. Polhemus (1995) described Papuan species groups of *Rhagovelia* Mayr, 1865 (Veliidae, semi-aquatic Heteroptera) in the southern and central Philippines. These patterns were explained by the existence of an eastward migrating arc system including the southern Philippines and parts of New Guinea. This pre-Eocene arc system once extended from New Zealand, the Solomon islands, the northern margin of the Australian plate which is now part of New Guinea, and westward to what is now Mindanao. Indications of such an arc, such as arc-related deposits of Cretaceous age, have been found in New Guinea and southern Mindanao (Hamilton 1989), but there is much uncertainty on timing and the presumed subaerial history. The alternative scenario, where biotas may have reached New Guinea via Australia after the break-up of Gondwana, is less likely since most ancient lineages are restricted to parts of New Guinea that only recently amalgamated with the Australian Plate.

Relationships from mainland southeast Asia into the Malay archipelago

Patterns. – In the reconstruction based on *molecular* characters, viz., 16S and 28S genes, we found a well-supported branching of a monophyletic group of three species confined to the Philippines plus one species from Borneo (*D. versicolor*), and one from New Guinea (*D. clavata*), named the 'East Malesian clade' (EMC). The other branch includes a group of species distributed in the mainland, on Borneo and one species in the Philippines, for which the name 'West Malesian clade' (WMC) was used. This WMC has two major clades, one consisting of *Protosticta* species, and one species of *Drepanosticta*, to be found on the mainland and on Borneo, and another clade consisting of *Drepanosticta* species from Borneo and the Philippines. The status of '*Protosticta*' *feronia* in the genus *Protosticta* was already discussed above.

The cladogram based on a very restricted number of species sampled for molecular characters only reveals a rough outline of the biogegraphical history of this group. The EMC presumably reached the Philippines via Java, while the species of New Guinea is a recent sister group of a species endemic to Mindanao. One branch of the WMC is strongly represented with a great diversity of species in the mainland. The evolution of the sister group of the mainland clade must be dated quite early in the geological history. Members of this clade are found on Borneo and in the Philippines.

Based on *morphological* characters, the division in the cladogram of the Platystictinae in the WMC and the EMC is distinct (Fig. 55). Due to more extensive taxon sampling, the dispersal pattern is more detailed than in the cladogram based on molecular characters. However, we recognize that both cladograms are not fully

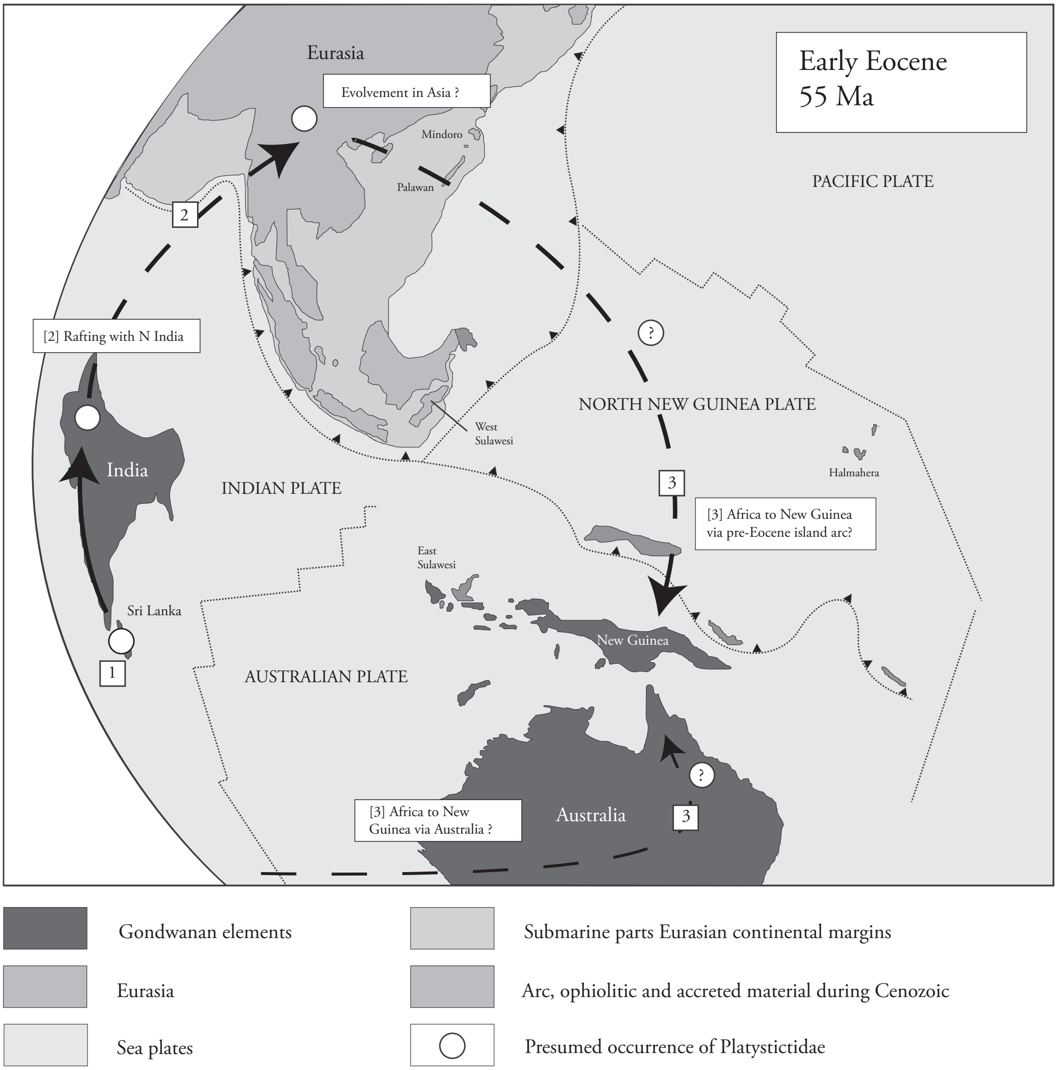

Figure 56. Distribution and dispersal events of Platystictidae during Early Eocene (see text). Geological reconstruction redrawn after Hall (2002).

congruent, and partly suggest a different scenario.
The sister group of the WMC+EMC is *Drepanosticta nietneri*, an endemic from Sri Lanka. The ancestors of the WMC (Fig. 55: '5') definitely lived in the mainland of southeast Asia. One of the basal branchings concerns *Drepanosticta moorei* from Luzon, presumably an early dispersal. The sister taxon apparently entered the Greater Sunda islands more than one time. One clade (Fig. 55: '7a') is found on Sumatra and Borneo, and has one species, *D. lestoides*, in the Philippines. A close relative of the last species is not known from the Philippines. The sister group (Fig. 55: '7b') also entered the Malay archipelago more than once. It mainly includes the species assigned to *Protosticta*. One lineage dispersed from the mainland to Borneo, and then to Sulawesi, where this group radiated significantly (van Tol 2000). The EMC apparently started with a dispersal to Java, from where one clade reached (Central?) Sulawesi, and

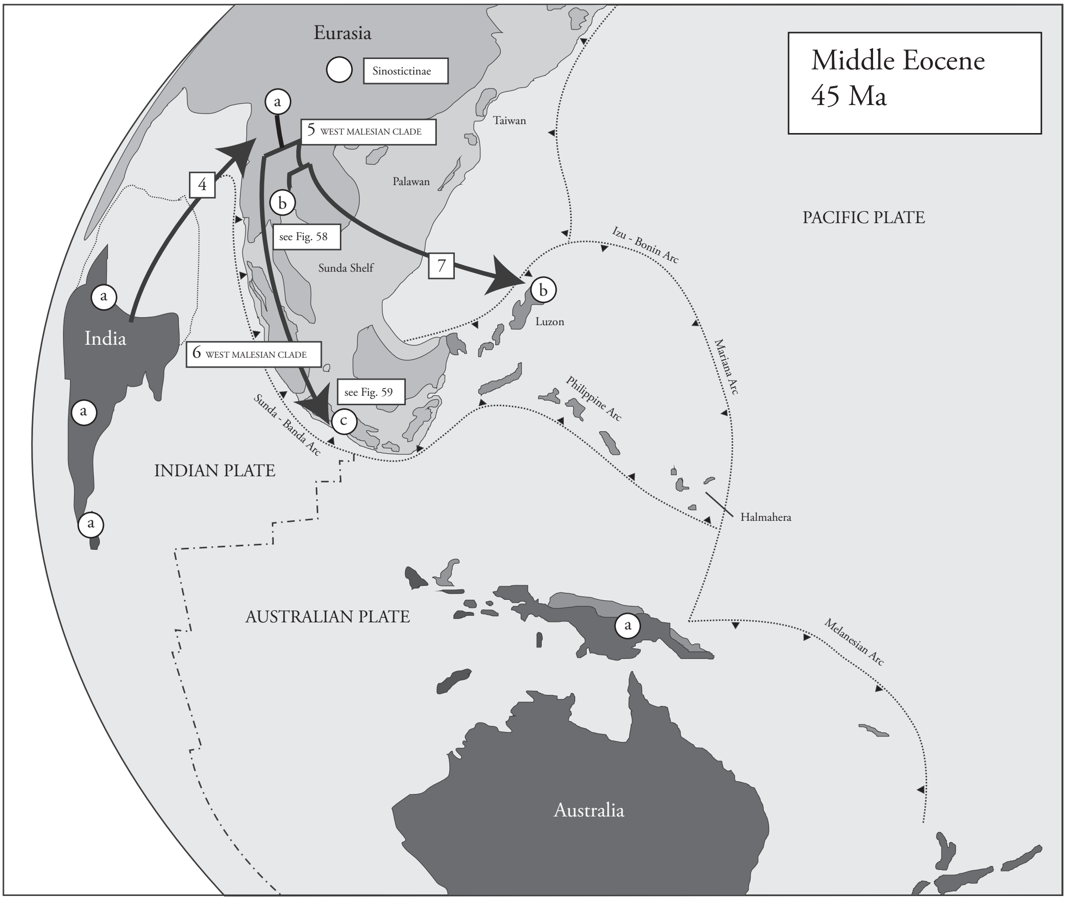

Figure 57. Distribution and dispersal events of the Platystictidae during Middle Eocene (see text). 'b' represents West Malesian Clade (WMC) and 'c' the East Malesian Clade (EMC). Geological reconstruction redrawn after Hall (2002).

from there the southern Moluccas. The other clade also dispersed to Sulawesi (Fig. 55: 15), and from there to the southern Philippines (Fig. 55: '16' and '17'). Species closely related to the species flock of the southeastern Philippines are found in the northern Moluccas and on New Guinea. In our morphological analysis, these species show complex sister group relationships (Fig. 55: '18' and '19'), which indicate a relatively recent eastward dispersal. Although the phylogenetic reconstructions of the relationships of the species of the Philippines and New Guinea based on molecular and morphological data are not fully congruent, they confirm the picture of a recent eastward dispersal from the Philippines towards New Guinea (*D. clavata* as the sister species of *D. krios*, while the sister group of this clade is confined to the Philippines).

Processes. – There is still considerable disagreement about the time that dispersal of biotas from India into the mainland of Asia was possible. Morley (2000, his fig. 13.3) indicates a timing since the Middle Eocene based on various groups of plants, and it seems that also mammals dispersed into Asia from India by the Middle Eocene (Hallam 1994). The palaeogeography of southeast Asia, India and Africa, was already discussed above. Tropical rain forest subsequently retreated to a narrow zone which now includes southeastern China,

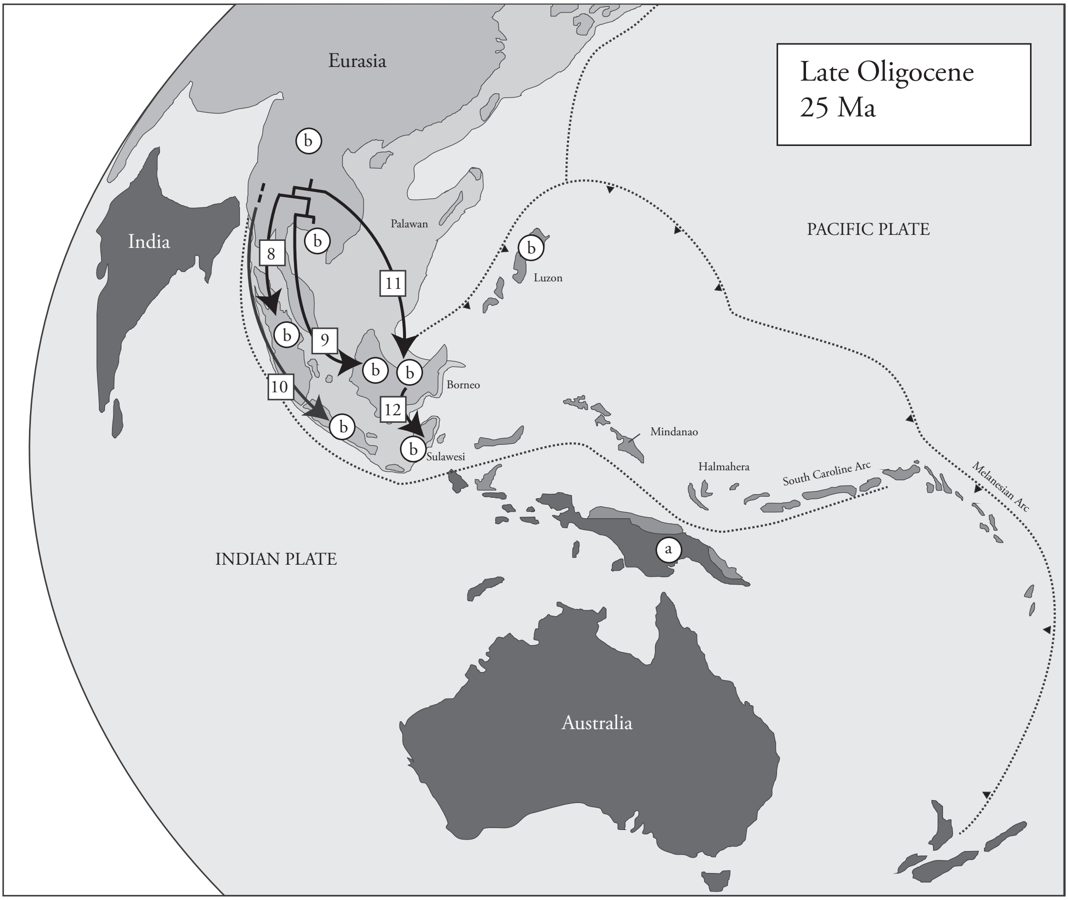

Figure 58. Distribution and dispersal events of 'West Malesian clade' (WMC) of the Platystictidae during Late Oligocene (see text). Geological reconstruction redrawn after Hall (2002).

plus a significant part of eastern India during the Oligocene (see Morley 2000: fig. 13.4). Only during a new thermal maximum of the Middle Miocene (10-16 Ma), rain forests became more widespread in southeast Asia again (Morley 2000: fig. 13.5). It is thus likely that dispersal into the archipelago antedates the Oligocene cooling. The first dispersal of Platystictidae into Asia may thus have been possible about 50-40 Ma (Fig. 57). The Greater Sunda islands were approximately in the same position as today, and a subaerial history is generally assumed (data mainly based on Hall 2002). For most of the time and until the Early Miocene, a land connection existed to Borneo through the central Java Sea (Hall 2002: 371). The southwestern arm of Sulawesi also had a position as today, although palaeontological data suggest that it was at least partly submerged. The palaeogeographical history of the northern arm of Sulawesi is still poorly understood. In a reconstruction by Wilson & Moss (1999: fig. 6), this northern arm was already connected to the southwestern arm since the Early Eocene, although presumably at least partly submerged. We presume that members of the EMC may have reached Java by the Late Eocene, and *Drepanosticta moorei,* the sister taxon all members of the WMC except *D. carmichaeli*, had crossed to Luzon (mechanism unknown). By the end of the Eocene, the ancestors of

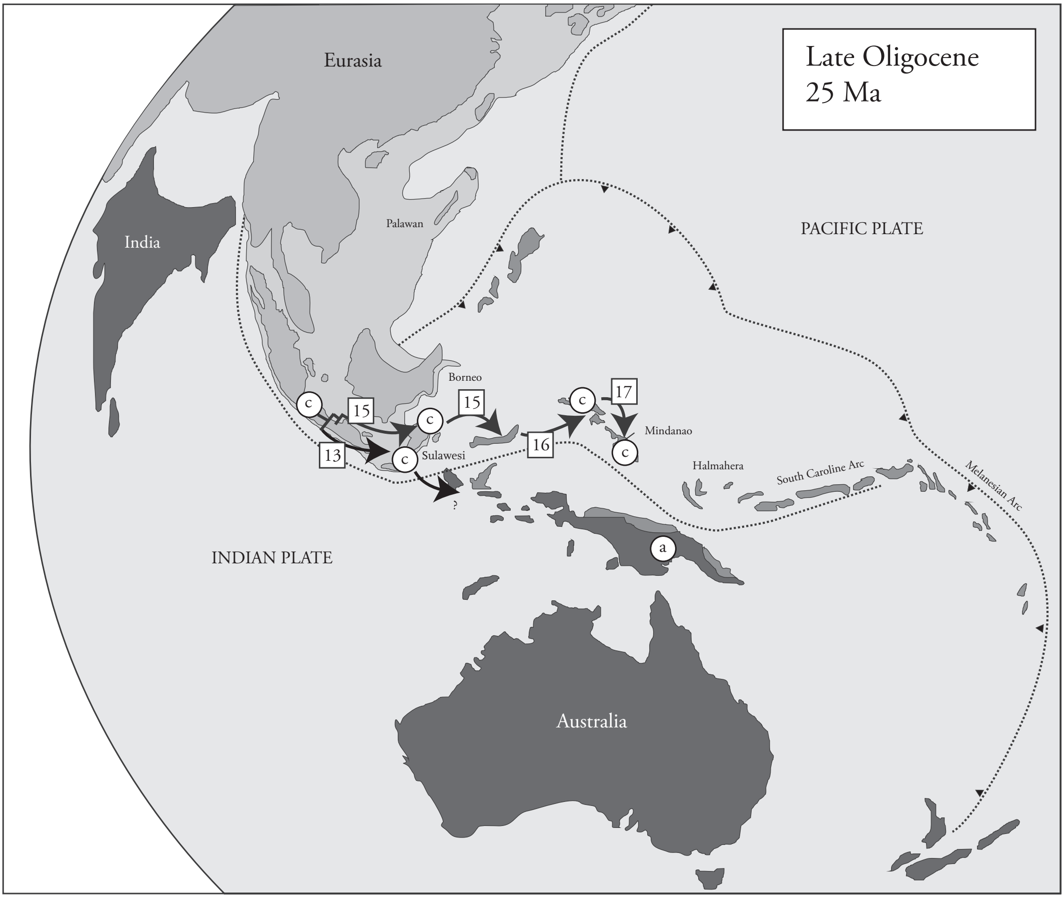

Figure 59. Distribution and dispersal events of 'East Malesian clade' of the Platystictidae during Late Oligocene (see text). Geological reconstruction redrawn after Hall (2002).

the present Platystictidae thus inhabited Africa, Eurasia (including Europe), the northern part of North America, the mainland of southeast Asia, the Greater Sunda islands, Luzon, and had reached New Guinea via the Papuan Arc (sensu Polhemus).

We now follow the WMC first (Fig. 58). This clade partly evolved further on the mainland, but also entered the Greater Sunda islands. Especially the dispersal into Sulawesi via Borneo (Fig. 58: '12') of the *Protosticta* lineage proved to be successful, since this group radiated significantly on that island. This colonization of Sulawesi may have taken place during the Oligocene, or at least before the Late Miocene, when the eastern arms of Sulawesi merged with the southwestern, or southwestern + northern arm. This is based on the observation that the highest diversity of this group is still found in the central region, which previously formed the northern extension of the southwestern arm. The fauna of the eastern arms distinctly reflects the fact that these palaeo-islands became relatively recently part of Sulawesi, although an exception must be made for the western mountain ridge of the southeast arm (based on biogeographical data of other Zygoptera). A more detailed scenario of the WMC has to await a further study based on molecular data.

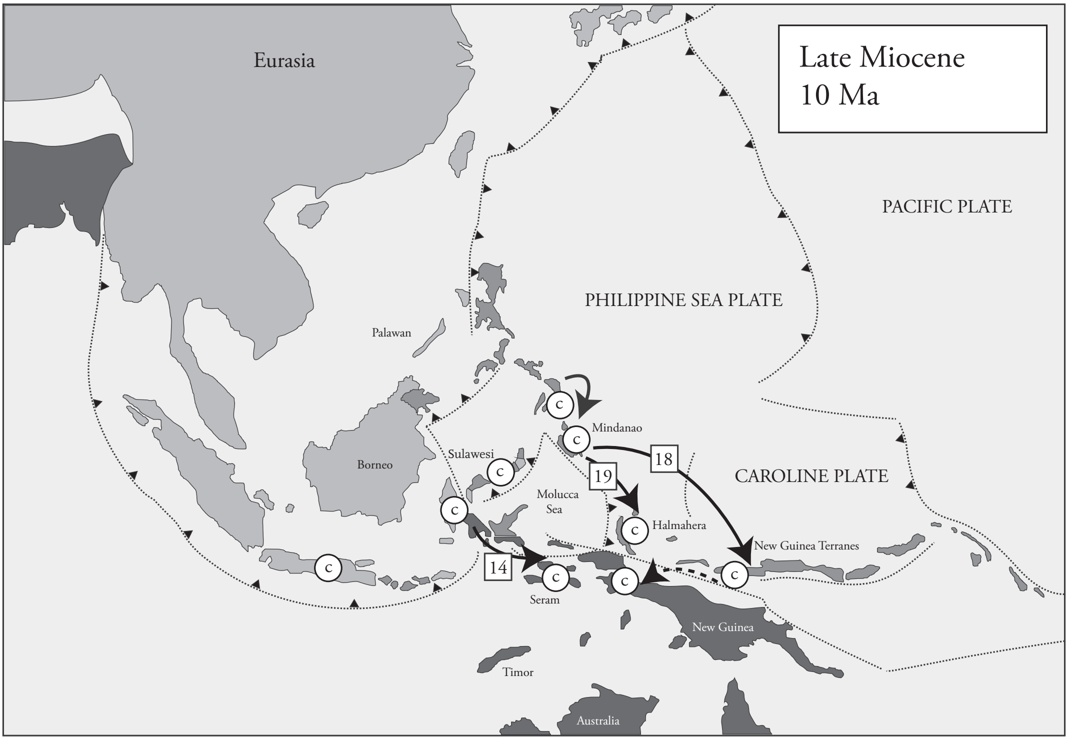

Figure 60. Distribution and dispersal events of 'East Malesian clade' of the Platystictidae during Late Miocene (see text). Geological reconstruction redrawn after Hall (2002).

The EMC started with dispersal to Java, possibly already during the Eocene. One lineage (Fig. 60: '14') dispersed towards the southern Moluccas via Sulawesi, but dispersal into the Moluccas via the Inner Banda Arc is presumably of rather recent age, since this vulcanic arc has been active since the Late Miocene only. Also the Outer Banda Arc, with an origin at the margin of the Australian and Asian plates, became more apparent at that time.

Another lineage of the EMC (Fig. 59: '15') dispersed to (? northern) Sulawesi, and will have reached the Philippines (Fig. 59: '16' and '17') at a time when the islands of the South Caroline Arc along the southern margin of the Philippine Plate 'passed' northern Sulawesi. This clade has significantly radiated in the Philippines, and further dispersed in eastern direction to Halmahera and other islands of the north Moluccas, and also New Guinea (Fig. 60: '18' and '19').

4.4. **Classification**

Classification has to reflect phylogenetic relationships. The classification of the Platystictidae has recently been discussed several times. Wilson (1997) revealed the special character of the species described as *Drepanosticta ogatai*, for which he erected a new genus and subfamily (*Sinosticta*, Sinostictinae). Also, the phylogenetic relevance of the diagnostic characters of the genera *Protosticta* and *Drepanosticta* has been questioned and discussed more than once (e.g., Orr 2003: 69; van Tol 2005: 199).

Based on the present results, some of these recent proposals for an updated classification seem to be justified. The subfamily status of the Sinostictinae is validated by the position of *Sinosticta* in our phylogenetic reconstruction. Orr (2003) assigned *Protosticta versicolor* from Borneo to the genus

Drepanosticta, which is also confirmed by the present phylogenetic analysis. The species presently assigned to *Protosticta* now generally form a monophyletic group, as a sister group to *Drepanosticta sundana*.

If the results of our analysis can be confirmed by a more extensive taxon sampling based on molecular characters, the classification of the Platystictidae needs further changes. For instance, if the genera *Palaemnema* and *Platysticta* indeed form a monophyletic group with some New Guinean species of *Drepanosticta*, the definition of the Palaemnematinae needs revision.

Our analysis suggests that the West and East Malesian clades of the Platystictinae have a long separate history, but no unique apomorphy for any of these groups has been found up to now. When such a (morphological) character is lacking for a clade, a basis for defining a higher level taxon in classification is lacking. Furthermore, the status of some species of Sri Lanka and southern India, should be reinvestigated, since *D. nietneri* from Sri Lanka appears to be the sister group of the West and East-Malesian clades, and may need a separate status.

At the generic level, *Protosticta* clusters as one clade as a sister group of *Drepanosticta sundana*, although it includes *Drepanosticta anascephala* and *Sulcosticta striata*. In the most conservative re-arrangement of a classification, new genus names would be necessary for the *D. nietneri* group, and the East Malesian clade. The name of the West Malesian group would be *Protosticta.* If the two main groups of this clade need separate generic names, the name *Drepanosticta* is available for those species that split off basally, including the type species of *Drepanosticta*, viz. *D. carmichaeli*.

Since our analysis of molecular characters is still based on too limited taxon sampling, we have refrained from introducing a new classification here. A further analysis shall at least include species of the presently recognized genera *Platysticta* and *Sulcosticta*, plus additional species of *Protosticta* from India, the Philippines and Sulawesi. Therefore, the names used in this paper follow the traditional classification, as implemented in, e.g., Tsuda (2000) and van Tol (2007a).

5. **Conclusions**

Methods. – We used both morphological and molecular characters for our phylogenetic analyses. Although the most parsimonious tree of the morphological character set showed many homoplasies, the strict consensus tree of the parsimony analysis was highly resolved, although the branches are poorly supported. However, we consider the significant congruence of this consensus tree with a tree based on molecular characters of a smaller taxon sample, a distinct indication of the robustness of the morphological character analysis.

Relationships. – To establish the relationships and estimate the age of the odonate family Platystictidae, we studied a wide assemblage of species of southeast Asia representing the Zygoptera families Lestidae, Platystictidae, Platycnemididae, Protoneuridae, Megapodagionidae and Coenagrionidae. Based on molecular characters, we ascertained that the Platystictidae represents an ancient monophyletic lineage of the Zygoptera. We confirmed the monophyly of the Platycnemididae, and the sister group relationship of the presently recognized subfamilies. The Protoneuridae were established as the sister group of the Platycnemididae. The family Megapodagrionidae seems to be a para- or even polyphyletic assemblage, which clearly needs further revision. Previous studies, such as Rehn (2003), found a different topology in the phylogenetic reconstruction of the Zygoptera, but our results agree broadly with Bybee *et al.* (2008), who added molecular characters to the morphological dataset of Rehn (2003). For a further understanding of the phylogeny of Zygoptera, we suggest inclusion of various small families of southeast Asia, such as the Isostictidae, a further expansion of the Coenagrionidae taxon sampling, and, in our set, addition of taxa of the New World.

The subfamily Sinostictinae (only studied on morphology)[4] represents the most basal clade in the phylogeny of the Platystictidae. The Palaemnematinae

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[4] See note on p. 29.

of the New World are the sister group of the Platystictinae in our analysis based on a limited taxon sample. Based on our morphological study, it appeared that the Palaemnematinae are not monophyletic, but share a common ancestor with the genus *Platysticta* (Sri Lanka) and some species of *Drepanosticta* confined to New Guinea.

Characters. – We have used the topology of the phylogenetic tree based on molecular characters to analyse the changes in character states of the morphological characters. We found that not many morphological characters exclusively define monophyletic groups as based on the molecular character set. Parallel development of the same character state appeared to be a common phenomenon. This conclusion was confirmed by our independent analysis of the morphological data set plotted on the tree based on molecular characters.

Our results confirmed the supposition by Orr (2003) that *Protosticta* Selys sensu Davies & Tobin (1984) cannot be considered an monophyletic group. The reduction of the Ab vein has occurred several times during evolution (Fig. 51). On the other hand, some other wing venational character states, such as the position of the IR3, only developed once. Somewhat unexpectedly, also some characters of the anal appendages appeared to be very homoplastic. A long and conspicuous dorsal denticle on the superior appendage of the male evolved various times. For a further understanding of the phylogeny of the Platystictidae, we suggest a more extensive taxon sampling first, and an increased number of genetic markers in the molecular analyses.

Biogeography. – The present 'tropical amphi-transpacific distribution' of the Platystictidae evolved from African ancestors that reached Asia via India, and the New World via the 'North Atlantic Land Bridge'. The evolution of the subfamily Platystictinae can be understood in relation to the palaeogeography of the Malesian region since the Eocene.

Our limited taxon sample for molecular characters permitted only a very rough indication of a biogeographical scenario. Our reconstruction of the phylogeny based on the morphological characters, including more species of Platystictidae, permitted a more detailed scenario.

Based on the occurrence of basal clades in southeast China (Sinostictinae) and Sri Lanka (*Platysticta* and some *Drepanosticta*), in combination with the presence of this family in the New World, we consider an origin of the ancestors of this family in Africa (where it does not occur at present) as the most likely scenario. The American taxa must have dispersed from Eurasia (Europe) via the North Atlantic Land Bridge during the Eocene, while the Asian clade dispersed into the region after India and Asia made their first contact about 50 Ma. Whether the species of New Guinea used a route via Asia (pre-Eocene Papuan Arc, suggesting evolution of the family in Asia), or via Australia (no recent representative in that continent), needs further study, including estimates of cladogenesis using a molecular clock. The cladogram of the Platystictinae and the present distribution of the species, indicate an eastward dispersal in which Sulawesi has played a prominent role. The widespread occurrence of one lineage from the Philippines to the northern Moluccas and New Guinea is presumably due to a geologically recent dispersal, probably during the Miocene or later.

This study of the Platystictidae confirms the complicated nature of the historical biogeography of southeast Asia. A similar study of the Calicnemiinae (Platycnemididae) (Gassmann 2005, van Tol & Gassmann 2007) revealed a different scenario. The family Platycnemididae is very diverse at the genus level in New Guinea, is very speciose with two closely related genera in the Philippines, but is unknown from Sulawesi and Halmahera. New Guinea was apparently populated from the mainland of southeast Asia via the Izu-Bonin Arc, whereafter this group dispersed into western direction to reach the Philippines. Ancient lineages of the Calicnemiinae are found on New Guinea, as is also the case in the Platystictidae and various other groups of aquatic insects. Polhemus (1995) has stressed the role of a 'pre-Eocene' arc for aquatic Heteroptera. Such an arc may also have played a role in the origin of present distribution patterns in the Calicnemiinae and the Platystictidae.

The historical biogeography of Malesia certainly asks for more, well-founded phylogenies of groups with similar ecology. The importance of estimates of timing of cladogenesis of those groups should be emphasized. This is considered the most reliable method to study the congruence between different cladograms, and area cladograms, in order to arrive at a reconstruction of the distributional history of the biotas of southeast Asia and the West Pacific.

Species diversity. – Finally, it is an intriguing question how the huge diversity of the endemic flora and fauna of Malesia evolved. The present and palaeo-geography of the region strongly suggest that dispersal is the overwhelmingly universal mechanism in which the islands of Malesia were populated. Species with high dispersal power will be most successful in populating vacant islands, and are the most likely candidates as inhabitants of isolated islands. However, dispersive species frequently reach the same places, so that even such relatively isolated populations cannot evolve isolating mechanisms due to frequent gene flow between populations. Thus, dispersive species usually have large distributional ranges. On the other hand, it is unlikely that species with low dispersal power will ever reach isolated islands.

The composition of island biotas was described in the dynamic equilibrium model of island biogeography by MacArthur & Wilson (1963, 1967), which is mainly a theory on an ecological time scale. Whittaker *et al.* (2008) recently proposed 'a general dynamic theory of oceanic island biogeography', in which also the geological life cycle of islands is incorporated. During the life cycle of an island, the complexity of habitats increases in relation to the development of an increasingly complex topography. Such conditions may provide opportunities for radiation of local plant and animal groups, as well as for individuals that newly reach the island.

Small distributional ranges in Malesia are common in very different groups of plants and animals. The present distributional patterns of biotas are supposed to reflect events in the geological past, and congruent patterns of area relationships are frequently found in southeast Asia. Such patterns are usually attributed to vicariance events, but palaeogeographical data of southeast Asia hardly support the hypothesis that splitting of islands has frequently occurred. We presume that the dynamics of origin, movements with the continental plates, and final disappearance of the islands of the archipelago have been a more dominant driving force in the evolution of taxa. The resulting variation in proximity of islands to other islands or continental fragments during their geological history provided an environment in which completely different biotas could be 'exchanged'. This aspect provides a further dimension in Whittaker's *et al.* (2008) theory on island biogeography.

Apparently, the biotas of Malesia evolved in a fragile balance, in which rare occasions of (common) dispersal events were interrupted with long periods without dispersal and radiation of local populations. The isolation of the islands in the Indo-Australian region during the Cenozoic strongly depended on the continuous reorganisation of the islands. During periods of low colonization rate, founder populations usually evolve isolating mechanisms (see Heaney, 2000). Specimens from new dispersal events, even from the same source population, may then no longer be able to mix with descendants of previous dispersal events, enabling the evolvement of new species in the same area.

In some cases, the flora and fauna of present-day larger islands, such as Sulawesi and New Guinea, which are themselves combinations of palaeo-islands that merged in the geological past, reflect the highly complex nature of evolution on the palaeo-islands, and the subsequent evolution of the biotas after the amalgamation of their habitats.

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Appendix 1

List of specimens used for the analyses, with registration numbers, and localities.

All specimens are kept in RMNH Leiden. The RMNH collection includes the collections of Matti Hämäläinen and Roland A. Müller. Other material deposited in RMNH by gift or exchange is usually mentioned under 'Remarks'.

JvT nos indicate numbers with collection specimens. Columns 'Mol', 'Mor' and 'Lig' indicate whether specimens were used for the molecular analysis, morphological characters coding (except ligula), and ligula characters (SEM photographs available). Locality data usually give country and province. 'Year' and 'leg' are year of collecting, and collector. 'Det' indicates specialist responsible for identification. Names under 'Mol analysis' indicates co-author responsible for the molecular analysis. 'Identification' provides reference to original description, later revision or comparison with specimens in collection. Any other data are summarized under 'Remarks', including original field numbers.

Family	Species	JvT-no	Mol	Mor	Lig	Locality
Libellulidae	*Sympetrum eroticum* (Selys, 1883)	Haseg.	Mol			Japan: Ohita
Libellulidae	*Sympetrum depressiusculum* (Selys, 1841)	Haseg.	Mol			Japan: Niigata
Epiophlebiidae	*Epiophlebia superstes* (Selys, 1889)	Haseg.	Mol			Japan: Hokkaido
Lestidae	*Lestes temporalis* Selys, 1883	Haseg.	Mol			Japan: Ooita
Lestidae	*Lestes temporalis* Selys, 1883	28 916		Mor	Lig	Japan: Ehime
Lestoideidae	*Philoganga vetusta* Ris, 1912	28 428	Mol			Vietnam: Dak Lak
Megapodagrionidae	*Agriomorpha fusca* May, 1933	28 706	Mol			Vietnam: Tam Dao
Megapodagrionidae	*Argiolestes amphistylus* Lieftinck, 1949	28 101	Mol			Indonesia: Papua
Megapodagrionidae	*Argiolestes sponsus* Lieftinck, 1956	28 099	Mol			Indonesia: Papua
Megapodagrionidae	*Burmargiolestes melanothorax* (Selys, 1891)	28 104	Mol			Thailand: Chiang Mai
Megapodagrionidae	*Mesopodagrion tibetanum* McLachlan, 1896	28 105	Mol			China: Sichuan
Megapodagrionidae	*Podolestes orientalis* Selys, 1862	28 098	Mol			Brunei
Megapodagrionidae	*Rhinagrion mima* (Karsch, 1891)	28 096	Mol			Thailand: Ranong
Megapodagrionidae	*Rhinagrion* cf. *yokoii* Sasamoto, 2003	28 374	Mol			Vietnam: Dak Lak
Megapodagrionidae	*Rhinagrion* cf. *yokoii* Sasamoto, 2003	28 522	Mol			Vietnam: Dak Lak
Megapodagrionidae	*Sinocnemis yangbingi* Wilson &Zhou, 2000	28 103	Mol			China: Emeishan
Megapodagrionidae	*Nososticta fonticola* (Lieftinck, 1932)	28 100	Mol			Indonesia: Papua
Protoneuridae	*Prodasineura integra* (Selys, 1882)	26 843	Mol			Philippines: Mindanao
Protoneuridae	*Prodasineura* aff. *collaris* (Selys, 1860)	28 524	Mol			Vietnam: Dak Lak
Protoneuridae	*Prodasineura* aff. *collaris* (Selys, 1860)	28 526	Mol			Vietnam: Dak Lak
Platycnemididae	*Calicnemia* cf. *eximia* (Selys, 1863)	28 402	Mol			Vietnam: Dak Lak
Platycnemididae	*Calicnemia* sp. n. Tam Dao	28 720	Mol			Vietnam: Tam Dao
Platycnemididae	*Coeliccia dinoceras* Laidlaw, 1925	26 847	Mol			Philippines: Mindanao
Platycnemididae	*Coeliccia* sp. n. Chu Yang Sin	28 372	Mol			Vietnam: Dak Lak
Platycnemididae	*Coeliccia* sp. n. Chu Yang Sin	28 485	Mol			Vietnam: Dak Lak
Platycnemididae	*Coeliccia* sp. n. Chu Yang Sin	28 568	Mol			Vietnam: Dak Lak
Platycnemididae	*Indocnemis ambigua* (Asahina, 1997)	28 668	Mol			Vietnam: Tam Dao
Platycnemididae	*Indocnemis ambigua* (Asahina, 1997)	28 684	Mol			Vietnam: Tam Dao
Platycnemididae	*Copera vittata* (Selys, 1863)	28 425	Mol			Vietnam: Dak Lak
Platycnemididae	*Copera* sp.	28 553	Mol			Vietnam: Dak Lak
Platycnemididae	*Indocnemis orang* (Foerster, 1907)	28 399	Mol			Vietnam: Dak Lak
Platycnemididae	*Platycnemis pennipes* (Pallas, 1771)	28 273	Mol			Nederland: Drenthe
Platycnemididae	*Risiocnemis flammea* (Selys, 1882)	26 855	Mol			Philippines: Mindanao
Platystictidae	*Drepanosticta actaeon* Laidlaw, 1934	19 452		Mor	Lig	Sabah: Kinabalu
Platystictidae	*Drepanosticta amboinensis* van Tol, 2007c	23 548		Mor	Lig	Indonesia: Ambon
Platystictidae	*Drepanosticta anascephala* Fraser, 1933c	28 086	Mol			Thailand: Chiang Mai
Platystictidae	*Drepanosticta anascephala* Fraser, 1933c	19 470		Mor		Thailand: Chiang Mai
Platystictidae	*Drepanosticta arcuata* Lieftinck, 1934	19 484			Lig	Indonesia: S Sumatra
Platystictidae	*Drepanosticta arcuata* Lieftinck, 1934	19 505		Mor		Indonesia: S Sumatra
Platystictidae	*Drepanosticta aries* Needh. & Gyger, 1941	20 079		Mor	Lig	Philippines: Mindanao

Year	Leg	Det	Mol analysis	Identification	GenBnk 16S	GenBnk 28S	Remark
?	?	Hasegawa	Hasegawa	?	AB 127 056	AB 127 408	
?	?	Hasegawa	Hasegawa	as *S. frequens*	AB 127 057	AB 127 409	
?	?	Hasegawa	Hasegawa		AB 127 062	AB 127 421	
?	?	Hasegawa	Hasegawa	as *L. japonicus*	AB 127 074	AB 127 422	
1988	Matsumaya	Barlow	n/a	RMNH collection			
2007	van Tol	van Tol	Reijnen	Ris 1912			Leg only
2007	van Tol	van Tol	Reijnen	RMNH collection			
2006	Kalkman	Kalkman	Thomassen	Lieftinck 1956			
2006	Kalkman	Kalkman	Thomassen	Lieftinck 1956			
?	Hämäläinen	Hämäläinen	Thomassen	RMNH collection			
2005	Kalkman	Kalkman	Thomassen	RMNH collection			
2004	Dijkstra	Kalkman	Thomassen	Lieftinck 1950			
2002	Hämäläinen	Hämäläinen	Thomassen	RMNH collection			
2007	van Tol	van Tol	Reijnen	Sasamoto 2003			
2007	van Tol	van Tol	Reijnen	Sasamoto 2003			Leg only
2005	Kalkman	Kalkman	Thomassen	Wilson & Zhou 2000			
2006	Kalkman	Kalkman	Thomassen	RMNH collection			
2004	van Tol	van Tol	Thomassen	RMNH collection			
2007	van Tol	van Tol	Reijnen	RMNH collection			
2007	van Tol	van Tol	Reijnen	RMNH collection			
2007	van Tol	Gassman	Reijnen	RMNH collection			
2007	van Tol	Gassmann	Reijnen	RMNH collection			
2004	van Tol	van Tol	Thomassen	RMNH collection			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			
2007	van Tol	van Tol	Reijnen	Asahina 1997a			Leg only
2007	van Tol	van Tol	Stokvis	van Tol 2002			
2004	van Tol	Gassmann	Thomassen	RMNH collection			
1994	Hämäläinen	Hämäläinen	n/a	Laidlaw 1934			
1948	Lieftinck	van Tol	n/a	van Tol 2007c			
1991	Hämäläinen	Hämäläinen	Thomassen	RMNH collection			
1991	Hämäläinen	Hämäläinen	n/a	RMNH collection			
1934	Lieftinck	Lieftinck	n/a	RMNH collection			
1940	Lieftinck	Lieftinck	n/a	RMNH collection			
1995	Müller	Hämäläinen	n/a	van Tol 2005			

Family	Species	JvT-no	Mol	Mor	Lig	Locality
Platystictidae	*Drepanosticta belyshevi* Hämäläinen, 1991	20 316		Mor	Lig	Philippines: Bohol
Platystictidae	*Drepanosticta bifida* van Tol, 2007c	20 471		Mor		Indonesia: Bacan
Platystictidae	*Drepanosticta bifida* van Tol, 2007c	23 670			Lig	Indonesia: Bacan
Platystictidae	*Drepanosticta carmichaeli* (Laidlaw, 1915a)	19 451		Mor	Lig	Nepal: Biritante
Platystictidae	*Drepanosticta centrosaurus* van Tol, 2005	28 102	Mol			Philippines: Mindanao
Platystictidae	*Drepanosticta centrosaurus* van Tol, 2005	18 635		Mor		Philippines: Mindanao
Platystictidae	*Drepanosticta centrosaurus* van Tol, 2005	18 683			Lig	Philippines: Mindanao
Platystictidae	*Drepanosticta ceratophora* Lieftinck, 1974	20 145		Mor	Lig	Philippines: Palawan
Platystictidae	*Drepanosticta clavata* Lieftinck, 1932	28 097	Mol			Indonesia: Yapen
Platystictidae	*Drepanosticta clavata* Lieftinck, 1932	19 630		Mor		Indonesia: Hollandia
Platystictidae	*Drepanosticta clavata* Lieftinck, 1932	23 449			Lig	Indonesia: Hollandia
Platystictidae	*Drepanosticta conica* (Martin, 1909)	19 525		Mor	Lig	Papua New Guinea
Platystictidae	*Drepanosticta crenitis* Lieftinck, 1933	21 405		Mor	Lig	Indonesia: Singkawang
Platystictidae	*Drepanosticta dorcadion* Lieftinck, 1949	19 544		Mor		Indonesia: New Guinea
Platystictidae	*Drepanosticta dorcadion* Lieftinck, 1949	19 540			Lig	Indonesia: Ben. Mistcamp
Platystictidae	*Drepanosticta ephippiata* Lieftinck, 1937	11 842		Mor	Lig	Indonesia: Sulawesi
Platystictidae	*Drepanosticta exoleta* Lieftinck, 1932	19 604		Mor	Lig	Indonesia: New Guinea
Platystictidae	*Drepanosticta flavomaculata* van Tol, 2005	26 927	Mol			Philippines: Mindanao
Platystictidae	*Drepanosticta flavomaculata* van Tol, 2005	18 943		Mor		Philippines: Mindanao
Platystictidae	*Drepanosticta flavomaculata* van Tol, 2005	18 913			Lig	Philippines: Mindanao
Platystictidae	*Drepanosticta fontinalis* Lieftinck, 1937	19 667		Mor	Lig	Malaysia: Templer Park
Platystictidae	*Drepanosticta gazella* Lieftinck, 1929	19 739		Mor		Indonesia: Java
Platystictidae	*Drepanosticta gazella* Lieftinck, 1929	19 913			Lig	Indonesia: Java
Platystictidae	*Drepanosticta halterata* complex	22 489		Mor	Lig	Philippines: Negros
Platystictidae	*Drepanosticta krios* van Tol, 2005	26 901	Mol			Philippines: Mindanao
Platystictidae	*Drepanosticta krios* van Tol, 2005	22 090		Mor		Philippines: Tawi Tawi
Platystictidae	*Drepanosticta krios* van Tol, 2005	20 179			Lig	Philippines: Tawi Tawi
Platystictidae	*Drepanosticta lestoides* (Brauer, 1868)	26 928	Mol			Philippines: Mindanao
Platystictidae	*Drepanosticta lestoides* (Brauer, 1868)	18 620		Mor	Lig	Philippines: Mindanao
Platystictidae	*Drepanosticta lymetta* Cowley, 1936	18 612		Mor	Lig	Philippines: Mindanao
Platystictidae	*Drepanosticta moluccana* Lieftinck, 1938	19 892		Mor	Lig	Philippines: Buru
Platystictidae	*Drepanosticta moorei* v. Tol & Müller, 2003	22 343		Mor		Philippines: Luzon
Platystictidae	*Drepanosticta moorei* v. Tol & Müller, 2003	22 227			Lig	Philippines: Luzon
Platystictidae	*Drepanosticta mylitta* Cowley, 1936	28 842		Mor	Lig	Philippines: Cebu
Platystictidae	*Drepanosticta nietneri* (Fraser, 1931)	14 841		Mor	Lig	Ceylon: Ratnapura
Platystictidae	*Drepanosticta penicillata* van Tol, 2007b	01 534		Mor	Lig	Indonesia: Sulawesi
Platystictidae	*Drepanosticta psygma* van Tol, 2007c	23 451		Mor		Indonesia: Bacan
Platystictidae	*Drepanosticta psygma* van Tol, 2007c	23 524			Lig	Indonesia: Bacan
Platystictidae	*Drepanosticta quadrata* (Selys, 1860)	19 444		Mor	Lig	Singapore
Platystictidae	*Drepanosticta rudicula* van Tol, 2007c	10 669		Mor	Lig	Indonesia: Halmahera

Year	Leg	Det	Mol analysis	Identification	GenBnk 16S	GenBnk 28S	Remark
1989	Catal	Hämäläinen	n/a	van Tol 2005			
1985	Rozendaal	van Tol	n/a	van Tol 2007c			
1953	Wegner	van Tol	n/a	van Tol 2007c			
1987	ex coll Vick	Hämäläinen	n/a	RMNH collection			
2006	Villanueva	van Tol	Thomassen	van Tol 2005			
1995	Buenafe	van Tol	n/a	van Tol 2005			
1995	Müller	van Tol	n/a	van Tol 2005			
1991	Hämäläinen	Hämäläinen	n/a	van Tol 2005			
2006	Kalkman	van Tol	Thomassen	Lieftinck 1932			
1930	Stüber	Lieftinck	n/a	Lieftinck 1932			
1931	Stüber	Lieftinck	n/a	Lieftinck 1932			
1972	Donnelly	Lieftinck	n/a	Lieftinck 1949			
1932	Coomans dR	Lieftinck	n/a	Lieftinck 1933			
1939	Toxopeus	Lieftinck	n/a	Lieftinck 1949			
1939	Toxopeus	Lieftinck	n/a	Lieftinck 1949			
1940	van der Starre	van Tol	n/a	van Tol 2007c			
1931	Stüber	Lieftinck	n/a	Lieftinck 1932			
2004	van Tol	van Tol	Thomassen	van Tol 2005			
1996	Müller	van Tol	n/a	van Tol 2005			
1995	Buenafe	van Tol	n/a	van Tol 2005			
1963	Lieftinck	Lieftinck	n/a	Lieftinck 1965			
1931	Lieftinck	Lieftinck	n/a	Lieftinck 1929			
1936	Toxopeus	Lieftinck	n/a	Lieftinck 1929			
1995	Buenafe	van Tol	n/a	RMNH collection			
2004	van Tol	van Tol	Thomassen	van Tol 2005			
1990	Müller	van Tol	n/a	van Tol 2005			
1990	Müller	van Tol	n/a	van Tol 2005			
2004	van Tol	van Tol	Thomassen	van Tol 2005			
1996	Müller	van Tol	n/a	van Tol 2005			
1995	Buenafe	van Tol	n/a	van Tol 2005			
1941	van der Starre	van Tol	n/a	van Tol 2007c			
1991	Müller	van Tol	n/a	van Tol 2005			
1991	Müller	van Tol	n/a	van Tol 2005			
2007	Villanueva	van Tol	n/a	van Tol 2005			
1970	Flint	Lieftinck	n/a	RMNH collection			
1993	van Tol	van Tol	n/a	van Tol 2007b			
1953	Wegner	van Tol	n/a	van Tol 2007c			
1953	Wegner	van Tol	n/a	van Tol 2007c			
1985	Murphy	Hämäläinen	n/a	Lieftinck 1965			
1995	van Tol	van Tol	n/a	van Tol 2007c			

Family	Species	JvT-no	Mol	Mor	Lig	Locality
Platystictidae	*Drepanosticta rufostigma* (Selys, 1886)	27 461	Mol			Indonesia: Borneo
Platystictidae	*Drepanosticta rufostigma* (Selys, 1886)	28 092	Mol			Brunei
Platystictidae	*Drepanosticta rufostigma* (Selys, 1886)	28 094	Mol			Brunei
Platystictidae	*Drepanosticta rufostigma* (Selys, 1886)	19 794		Mor	Lig	Indonesia: Borneo
Platystictidae	*Drepanosticta sharpi* (Laidlaw, 1907)	23 975		Mor	Lig	Thailand: Krabi
Platystictidae	*Drepanosticta sundana* (Krüger, 1898)	19 848		Mor		Indonesia: Java
Platystictidae	*Drepanosticta sundana* (Krüger, 1898)	19 855			Lig	Indonesia: Java
Platystictidae	*Drepanosticta versicolor* (Laidlaw, 1913)	28 089	Mol	Mor	Lig	Brunei
Platystictidae	*Palaemnema domina* Calvert, 1903	28 084	Mol			Mexico: Colima State
Platystictidae	*Palaemnema domina* Calvert, 1903	28 095	Mol			Mexico: Morelos
Platystictidae	*Palaemnema melanostigma* (Hagen, 1860)	28 093	Mol	Mor	Lig	Venezuela
Platystictidae	*Platysticta apicalis* Kirby, 1894	19 883		Mor	Lig	Sri Lanka: Kandy
Platystictidae	*Platysticta deccanensis* Laidlaw, 1915a	19 349		Mor	Lig	Sri Lanka: Kavalai
Platystictidae	*Protosticta bivittata* Lieftinck, 1939	01 845		Mor	Lig	Indonesia: S Sulawesi
Platystictidae	*Protosticta caroli* van Tol, 2008	28 566	Mol			Vietnam: Dak Lak
Platystictidae	*Protosticta caroli* van Tol, 2008	28 495		Mor	Lig	Vietnam: Dak Lak
Platystictidae	*Protosticta coomansi* van Tol, 2000	01 486		Mor	Lig	Indonesia: Sulawesi
Platystictidae	*Protosticta* aff. *feronia* Lieftinck, 1933	28 088	Mol	Mor	Lig	Brunei
Platystictidae	*Protosticta foersteri* Laidlaw, 1902	19 442		Mor	Lig	Malaysia: Pahang
Platystictidae	*Protosticta geijskesi* van Tol, 2000	01 906		Mor	Lig	Indonesia: Sulawesi
Platystictidae	*Protosticta grandis* Asahina, 1985	28 386	Mol	Mor		Vietnam: Dak Lak
Platystictidae	*Protosticta grandis* Asahina, 1985	28 490			Lig	Vietnam: Dak Lak
Platystictidae	*Protosticta hearsayi* Fraser, 1922	13 953		Mor		India: Travancore
Platystictidae	*Protosticta hearsayi* Fraser, 1922	23 664			Lig	India: Madras
Platystictidae	*Protosticta kinabaluensis* Laidlaw, 1915b	28 090	Mol			Sabah: Mt Kinabalu
Platystictidae	*Protosticta kinabaluensis* Laidlaw, 1915b	19 997		Mor	Lig	Sabah: Mt Kinabalu
Platystictidae	*Protosticta linnaei* van Tol, 2008	28 353	Mol			Vietnam: Dak Lak
Platystictidae	*Protosticta linnaei* van Tol, 2008	28 497	Mol			Vietnam: Dak Lak
Platystictidae	*Protosticta linnaei* van Tol, 2008	28 517		Mor	Lig	Vietnam: Dak Lak
Platystictidae	*Protosticta satoi* Asahina, 1997b	28 703	Mol			Vietnam: Tam Dao
Platystictidae	*Protosticta satoi* Asahina, 1997b	28 714	Mol			Vietnam: Tam Dao
Platystictidae	*Protosticta satoi* Asahina, 1997b	28 718		Mor	Lig	Vietnam: Tam Dao
Platystictidae	*Protosticta simplicinervis* (Selys, 1885)	01 945		Mor		Indonesia: Sulawesi
Platystictidae	*Protosticta simplicinervis* (Selys, 1885)	02 044			Lig	Indonesia: Sulawesi
Platystictidae	*Protosticta vanderstarrei* van Tol, 2000	16 655		Mor		Indonesia: C Sulawesi
Platystictidae	*Protosticta vanderstarrei* van Tol, 2000	16 636			Lig	Indonesia: C Sulawesi
Platystictidae	*Sinosticta ogatai* (Matsuki & Saito, 1996)	26 582		Mor	Lig	China: Hong Kong
Platystictidae	*Sulcosticta striata* van Tol, 2005	19 211		Mor		Philippines: Luzon
Platystictidae	*Sulcosticta striata* van Tol, 2005	19 224			Lig	Philippines: Luzon
Coenagrionidae	*Ischnura elegans* (Vander Linden, 1820)	28 277	Mol			Nederland: Drenthe

Year	Leg	Det	Mol analysis	Identification	GenBnk 16S	GenBnk 28S	Remark
2005	van Tol	van Tol	Thomassen	Lieftinck 1933			
2004	Dijkstra et al.	van Tol	Thomassen	Lieftinck 1933			KDD.04.0221
2004	Dijkstra et al.	van Tol	Thomassen	Lieftinck 1933			KDD.04.0163
1932	Coomans dR	Lieftinck	n/a	Lieftinck 1933			
2001	van Tol	van Tol	n/a	Lieftinck 1965			
1938	Lieftinck	Lieftinck	n/a	RMNH collection			
1940	Unknown	Lieftinck	n/a	RMNH collection			
2004	Dijkstra et al.	van Tol	Thomassen	Lieftinck 1933			
2006	Gonzalez	Gonzalez	Thomassen	Calvert 1931			
2001	Novelo	Gonzalez	Thomassen				larva
?	de Marmels	de Marmels	Thomassen	de Marmels pers. c.			
1975	Messersmith	Lieftinck	n/a	Fraser 1933a			ex USNM
1929	? Fraser	Fraser	n/a	Fraser 1933a			ex Fraser
1983	Pariwono	Lieftinck	n/a	van Tol 2000			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	n/a	van Tol 2008			
1993	van Tol	van Tol	n/a	van Tol 2000			
2004	Dijkstra et al.	van Tol	Thomassen	RMNH collection			KDD.04.0201
1997	Hämäläinen	Hämäläinen	n/a	Laidlaw 1907			
1989	van Tol	van Tol	n/a	van Tol 2000			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
1932	Fraser	Fraser	n/a	RMNH collection			ex Fraser
1964	Nathan	van Tol	n/a	RMNH collection			
2004	Dijkstra et al.	van Tol	Thomassen	Laidlaw 1915			KDD.04.0154
2000	van Tol	van Tol	n/a	Laidlaw 1915			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	n/a	van Tol 2008			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	Reijnen	van Tol 2008			
2007	van Tol	van Tol	n/a	van Tol 2008			
1985	de Jong	van Tol	n/a	van Tol 2000			
1993	Yohan R.	van Tol	n/a	van Tol 2000			
1997	van Tol	van Tol	n/a	van Tol 2000			
1997	van Tol	van Tol	n/a	van Tol 2000			
1996	Wilson	Wilson	n/a	Wilson 1997			ex Wilson
1997	Müller	van Tol	n/a	van Tol 2005			
1997	Müller	van Tol	n/a	van Tol 2005			
2007	van Tol	van Tol	Stokvis	van Tol 2002			

Appendix 2

Datamatrix of morphological characters of Platystictidae, plus *Lestes temporalis*, for the phylogenetic analysis.

					5					10					15				
28916 Lestes temporalis	0	0	0	0	0	0	0	0	0	3	2	0	0	1	0	0	0	1	1
19452 Drepanosticta actaeon	2	1	1	0	0	0	0	0	0	3	0	0	1	1	0	2	2	2	0
23548 Drepanosticta amboinensis	1	1	1	0	0	2	0	0	3	0	1	0	1	1	1	1	2	1	0
19470 Drepanosticta anascephala	1	1	1	0	0	0	1	0	0	3	0	0	1	2	1	1	2	2	2
19505 Drepanosticta arcuata	0	1	1	0	0	2	0	0	0	3	0	0	1	1	0	2	2	2	0
20079 Drepanosticta aries	2	1	1	0	0	5	0	0	3	0	0	0	1	2	1	1	2	2	0
20316 Drepanosticta belyshevi	2	1	1	2	0	4	0	0	3	2	1	0	1	1	1	2	2	2	0
20471 Drepanosticta bifida	2	1	1	0	0	5	0	0	1	0	1	0	1	2	1	1	2	2	0
19451 Drepanosticta carmichaeli	1	1	1	0	0	0	0	1	2	3	0	0	1	1	1	1	2	2	0
18635 Drepanosticta centrosaurus	2	1	1	0	0	6	0	0	1	0	0	0	1	1	1	1	2	1	0
20145 Drepanosticta ceratophora	0	1	1	0	0	1	0	0	1	0	1	0	1	1	1	1	2	1	0
19630 Drepanosticta clavata	2	1	1	1	0	5	0	0	1	2	1	0	1	1	1	1	2	1	0
19525 Drepanosticta conica	2	1	1	0	0	2	0	1	1	3	0	0	1	2	2	0	2	1	1
21405 Drepanosticta crenitis	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1	2	2	1
19544 Drepanosticta dorcadion	1	1	1	0	0	5	0	1	1	3	1	0	1	2	2	0	1	1	1
11842 Drepanosticta ephippiata	2	1	1	0	0	4	0	0	3	3	0	0	1	2	1	1	2	2	0
19604 Drepanosticta exoleta	2	1	1	0	0	5	0	0	0	3	0	0	1	2	1	1	2	2	0
18943 Drepanosticta flavomaculata	2	1	1	1	0	4	0	0	3	1	1	0	1	3	2	2	2	2	0
19667 Drepanosticta fontinalis	1	1	1	0	0	0	0	0	0	3	0	0	1	1	0	2	2	2	0
19739 Drepanosticta gazella	1	1	1	0	0	2	0	0	0	3	0	0	1	1	1	1	2	2	0
22489 Drepanosticta halterata	0	1	1	1	0	3	0	0	1	2	0	0	1	2	2	1	2	2	0
22090 Drepanosticta krios	2	1	1	0	0	4	0	0	3	0	0	0	1	1	1	2	2	1	0
18620 Drepanosticta lestoides	0	1	1	0	0	0	0	0	0	3	?	0	1	1	0	2	2	?	?
18612 Drepanosticta lymetta	1	1	1	0	0	5	0	0	1	0	0	0	1	1	1	1	2	2	0
19892 Drepanosticta moluccana	0	1	1	0	0	0	0	0	0	3	1	0	1	1	1	1	2	1	0
22343 Drepanosticta moorei	0	1	1	2	0	6	0	0	1	3	0	0	1	1	1	1	2	2	0
28842 Drepanosticta mylitta	2	1	1	0	0	2	0	0	1	0	0	0	1	1	1	2	2	2	0
14841 Drepanosticta nietneri	2	1	1	0	0	0	0	0	0	?	1	0	1	1	1	1	2	2	0
01534 Drepanosticta penicillata	1	1	1	0	0	0	0	0	0	3	0	0	1	1	1	1	2	1	0
20451 Drepanosticta psygma	2	1	1	1	0	5	0	0	0	0	1	0	1	1	3	1	2	2	0
19444 Drepanosticta quadrata	0	1	1	0	0	0	0	0	0	3	0	0	1	1	0	1	2	1	0
10669 Drepanosticta rudicula	2	1	1	1	0	5	0	0	1	0	0	0	1	2	2	1	2	1	0
19794 Drepanosticta rufostigma	2	1	1	0	0	0	0	0	0	3	0	0	1	1	0	2	2	1	0
23975 Drepanosticta sharpi	1	1	1	0	0	0	0	0	0	3	0	0	1	1	1	2	2	1	0
19848 Drepanosticta sundana	0	1	1	0	0	3	0	0	0	3	0	0	1	1	1	2	2	2	0
28089 Drepanosticta versicolor	0	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	2	2	0
28093 Palaemnema melanostigma	0	1	1	0	0	0	0	0	0	2	0	0	1	4	3	0	1	2	1
19883 Platysticta apicalis	1	1	1	0	1	0	0	0	0	3	0	0	1	3	3	0	1	2	1
26585 Platysticta deccanensis	1	0	1	0	0	0	0	0	0	0	1	0	1	3	2	0	1	2	1
01845 Protosticta bivittata	0	1	1	1	0	2	0	1	0	3	0	0	1	2	1	1	2	2	1
28495 Protosticta caroli	0	1	1	0	0	0	0	0	0	3	0	0	1	1	1	2	2	2	0
01486 Protosticta coomansi	1	1	1	1	0	0	0	0	0	3	0	0	1	3	3	0	2	2	0
28088 Protosticta aff feronia	2	1	1	0	0	0	2	1	0	3	0	0	1	0	0	2	2	2	0
19442 Protosticta foersteri	0	1	1	0	0	0	0	0	0	3	1	0	1	1	1	2	2	2	0
01906 Protosticta geijskesi	0	1	1	0	0	2	0	0	0	3	0	0	1	2	1	1	2	2	1
28490 Protosticta grandis	1	1	1	0	0	0	0	1	0	3	?	0	1	1	1	1	2	1	0
13953 Protosticta hearsayi	0	1	1	0	0	0	0	0	2	3	0	0	1	0	0	2	2	2	0
19997 Protosticta kinabaluensis	0	1	1	0	0	0	0	0	0	3	0	0	1	1	1	2	2	2	0
28517 Protosticta linnaei	0	1	1	0	0	0	0	0	0	3	0	0	1	1	0	2	2	2	0
28718 Protosticta satoi	0	1	1	0	0	0	0	0	3	2	0	0	1	3	2	2	2	2	0
01945 Protosticta simplicinervis	0	1	1	1	1	0	0	0	0	3	0	0	1	2	1	0	2	1	1
16655 Protosticta vanderstarrei	0	1	1	0	0	0	0	0	1	2	0	0	1	2	1	1	2	2	1
26582 Sinosticta ogatai	0	1	1	0	0	0	0	1	0	2	1	0	1	2	1	0	1	1	1

	20					25					30					35			
28916 Lestes temporalis	1	0	1	2	2	0	0	0	0	1	0	0	0	-	-	-	-	-	-
19452 Drepanosticta actaeon	1	1	0	0	0	0	2	0	0	3	0	0	2	2	1	0	1	2	0
23548 Drepanosticta amboinensis	1	2	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	0	3
19470 Drepanosticta anascephala	1	3	0	0	0	0	1	0	0	3	0	0	2	2	0	0	0	1	2
19505 Drepanosticta arcuata	1	1	0	0	0	0	0	0	0	1	0	0	0	4	0	0	0	1	2
20079 Drepanosticta aries	1	2	0	0	1	0	1	0	0	1	0	0	0	0	0	2	1	0	1
20316 Drepanosticta belyshevi	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	2	1	0	1
20471 Drepanosticta bifida	1	1	0	0	2	0	0	1	0	1	0	0	0	1	0	2	1	0	1
19451 Drepanosticta carmichaeli	1	3	0	0	2	0	0	0	0	0	1	0	0	2	0	0	1	1	0
18635 Drepanosticta centrosaurus	1	1	0	0	1	0	0	2	0	1	0	0	0	1	0	2	1	0	1
20145 Drepanosticta ceratophora	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	1	4
19630 Drepanosticta clavata	1	1	0	1	1	0	0	0	0	1	0	0	0	2	0	2	1	0	1
19525 Drepanosticta conica	1	1	0	2	2	0	0	0	0	1	0	0	0	4	0	1	0	1	3
21405 Drepanosticta crenitis	1	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	1	1	4
19544 Drepanosticta dorcadion	1	1	0	1	2	0	0	0	0	1	0	0	0	4	0	1	0	1	3
11842 Drepanosticta ephippiata	1	1	0	0	2	0	0	1	0	1	0	0	0	0	0	2	1	0	0
19604 Drepanosticta exoleta	1	2	0	0	2	0	1	0	0	1	0	0	0	0	0	0	1	0	1
18943 Drepanosticta flavomaculata	1	1	0	0	1	0	1	0	0	1	0	0	0	1	0	2	1	0	1
19667 Drepanosticta fontinalis	1	1	0	0	0	0	2	0	0	3	0	0	2	0	0	0	1	1	0
19739 Drepanosticta gazella	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0
22489 Drepanosticta halterata	1	2	0	0	1	0	1	0	0	1	0	0	1	0	0	1	1	1	3
22090 Drepanosticta krios	1	1	0	0	1	0	1	0	0	1	0	0	0	1	0	2	1	0	1
18620 Drepanosticta lestoides	1	2	0	0	0	0	2	0	0	2	0	0	2	3	0	0	1	1	0
18612 Drepanosticta lymetta	1	2	0	0	1	0	0	1	0	1	0	0	0	1	0	2	1	0	1
19892 Drepanosticta moluccana	1	2	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0
22343 Drepanosticta moorei	1	1	0	0	0	0	0	0	1	1	0	0	0	2	0	2	1	0	1
28842 Drepanosticta mylitta	1	3	0	0	1	0	1	0	0	1	0	0	0	0	0	2	1	1	0
14841 Drepanosticta nietneri	1	1	0	1	0	0	0	0	0	4	1	0	0	0	0	0	1	1	0
01534 Drepanosticta penicillata	1	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0
20451 Drepanosticta psygma	1	2	0	0	2	0	1	0	0	1	0	0	0	1	0	2	1	0	1
19444 Drepanosticta quadrata	1	3	0	0	0	0	2	0	0	4	0	0	1	0	0	0	0	1	0
10669 Drepanosticta rudicula	1	2	0	0	2	0	1	1	0	1	0	0	0	1	0	1	1	1	3
19794 Drepanosticta rufostigma	1	1	0	0	0	0	2	0	0	3	0	0	2	0	0	0	1	1	4
23975 Drepanosticta sharpi	1	3	0	0	0	0	2	0	0	1	1	0	1	0	0	0	1	1	0
19848 Drepanosticta sundana	1	1	0	0	0	0	0	0	0	4	0	0	0	1	1	0	1	2	0
28089 Drepanosticta versicolor	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	2	1	4
28093 Palaemnema melanostigma	1	2	0	2	2	1	1	0	0	1	1	0	0	0	0	1	1	1	5
19883 Platysticta apicalis	1	1	0	1	2	1	0	0	0	2	1	0	1	0	0	2	1	1	5
26585 Platysticta deccanensis	1	1	0	1	1	0	1	0	0	1	0	0	0	4	0	2	0	0	5
01845 Protosticta bivittata	0	0	0	0	1	0	2	0	0	2	0	0	1	0	0	0	1	0	0
28495 Protosticta caroli	0	0	0	0	0	0	1	0	0	7	0	1	0	2	1	0	1	1	0
01486 Protosticta coomansi	0	0	0	0	2	0	1	0	0	2	0	0	2	0	0	0	1	0	0
28088 Protosticta aff feronia	0	0	0	0	0	0	0	2	0	4	0	0	2	3	0	0	1	0	0
19442 Protosticta foersteri	0	0	0	0	0	0	1	0	0	1	0	1	0	?	?	?	?	?	?
01906 Protosticta geijskesi	0	0	0	0	0	0	1	0	0	2	0	0	2	3	0	0	1	0	0
28490 Protosticta grandis	0	0	0	0	0	0	1	0	1	1	0	0	0	4	1	0	1	2	0
13953 Protosticta hearsayi	0	0	0	0	0	0	2	0	0	1	1	0	0	2	0	1	1	0	3
19997 Protosticta kinabaluensis	0	0	0	0	0	0	2	0	1	3	1	0	2	2	0	0	1	0	0
28517 Protosticta linnaei	0	0	0	0	0	0	2	0	0	1	0	1	0	2	1	0	1	2	0
28718 Protosticta satoi	0	0	0	0	0	0	2	0	0	7	0	1	0	2	1	0	1	2	0
01945 Protosticta simplicinervis	0	0	0	0	0	0	2	0	0	1	0	0	2	0	0	1	1	1	0
16655 Protosticta vanderstarrei	0	0	0	0	1	0	2	0	1	2	1	0	1	3	0	0	1	0	0
26582 Sinosticta ogatai	1	2	1	2	2	0	0	0	0	5	0	0	0	0	0	0	2	1	6

Appendix 3

Description of morphological characters used in phylogenetic analysis

M01. *Lateral extremities transverse occipital carina*: **(0)** Absent ; **(1)** Small ; **(2)** Angulate.

M02. *Parorbital carina*: **(0)** Absent ; **(1)** Present .

M03. *Shape of clypeus*: **(0)** Rectangular, ante and postclypeus forming distinct faces; **(1)** Flattened, anteclypeus tilted back.

M04. *Prothorax: anterior margin*: **(0)** Simple ; **(1)** Partly widened ; **(2)** With processes.

M05. *Prothorax: median lobe with protuberances*: **(0)** Absent ; **(1)** Present .

M06. *Prothorax: posterior margin posterior lobe* : **(0)** Simple; **(1)** Single median process ; **(2)** Paired process triangular; **(3)** Paired process, round and straight; **(4)** Paired process, short and curved; **(5)** Paired process, straight with knob or fork; **(6)** Paired process, shields.

M07. *Prothorax: posterior lobe with lateral appendage*: **(0)** Absent ; **(1)** Present, short ; **(2)** Present, at least two times as long as wide.

M08. *Synthorax: antehumeral stripe*: **(0)** Absent ; **(1)** Present .

M09. *Synthorax: colour venter*: **(0)** Pale ; **(1)** Black ; **(2)** Variegate; **(3)** Bicolorous.

M10. *Synthorax: metepisternum*: **(0)** Dark ; **(1)** Short pale anterior stripe ; **(2)** Idem, posterior stripe; **(3)** Long pale stripe; **(4)** Fully pale.

M11. *Synthorax: base colour*: **(0)** Brownish black or black; **(1)** Pale brown; **(2)** Metallic green.

M12. *Wings: Ax number*: **(0)** Two; **(1)** More than 2.

M13. *Wings: Cux*: **(0)** Absent ; **(1)** Present .

M14. *Wings: Px fore wing (number)*: **(0)** Px 10 11 12 ; **(1)** Px 13 14 15 ; **(2)** Px 16 17 18; **(3)** Px 19 20 21; **(4)** Px 22 23 24; **(5)** Px 25 26 27; **(6)** Px more than 27; **(7)** Less than 10.

M15. *Wings: Px hind wing (number)*: **(0)** Px 10 11 12 ; **(1)** Px 13 14 15 ; **(2)** Px 16 17 18; **(3)** Px 19 20 21; **(4)** Px 22 23 24; **(5)** Px 25 26 27; **(6)** More than 27; **(7)** Less than 10.

M16. *Wings: Position R4+5 re subnodus (hind wing)*: **(0)** Proximal ; **(1)** At ; **(2)** Distal.

M17. *Wings: IR3*: **(0)** Far proximal to subnodus; **(1)** At subnodus; **(2)** Distal to subnodus.

M18. *Wings: Position Arculus re Ax2*: **(0)** Proximal; **(1)** At ; **(2)** Distal.

M19. *Wings: Arculus*: **(0)** Stalked; **(1)** Sessile / Divided.

M20. *Wings: Ab vein*: **(0)** Absent ; **(1)** Present .

M21. *Wings: Y-vein*: **(0)** Absent ; **(1)** Sessile ; **(2)** Stalked; **(3)** Divided.

M22. *For wings: quadrangle distal side*: **(0)** Rectangular; **(1)** Oblique; **(2)** Sharp.

M23. *Wings: CuP meeting hind margin of fore wing*: **(0)** Proximal to origin of R3; **(1)** At ; **(2)** Distal to.

M24. *Wings: CuP meeting hind margin of hw at*: **(0)** Proximal to origin of R3; **(1)** At; **(2)** Distal to.

M25. *Wings: Terminal part of wing*: **(0)** Hyaline ; **(1)** Opaque .

M26. *Abdomen: dorsal denticle app sup*: **(0)** Absent ; **(1)** Discernable ; **(2)** Long and conspicuous.

M27. *Abdomen: Ventral denticle of app sup*: **(0)** Absent ; **(1)** Discernable ; **(2)** Long and conspicuous.

M28. *App sup with distal half*: **(0)** Rounded or somewhat flattened; **(1)** Extremely flat and large.

M29. *App inf with tip*: **(0)** Rounded ; **(1)** Sharp ; **(2)** Boxing glove; **(3)** Long bifid; **(4)** Short bifid; **(5)** Bent apicad; **(6)** Reduced; **(7)** Cup-shaped.

M30. *App inf with basal tooth*: **(0)** Absent; **(1)** Present.

M31. *App inf with terminal tuft of setae*: **(0)** Absent; **(1)** Present.

M32. *Inferior appendage sub-terminal tooth*: **(0)** Absent ; **(1)** Small ; **(2)** Large.

M33. *Ligula cleft between branches*: **(0)** Triangular, sharp; **(1)** Rounded; **(2)** Squarish; **(3)** Convex; **(4)** Wide and straight.

M34. *Last segment in middle*: **(0)** Straight or concave; **(1)** Convex; **(2)** Not used.

M35. *Ligula: shape of tip of branch*: **(0)** Sharp; **(1)** Spoon-shaped; **(2)** Hook-shaped / bifid.

M36. *Horns of ligula*: **(0)** Less than half of segment; **(1)** Half to twice segment length; **(2)** More than twice segment length.

M37. *Segment at base of horns*: **(0)** Widened; **(1)** Straight; **(2)** Constricted.

M38. *Shape of horns*: **(0)** Long, tip curved upwards; **(1)** Long, tip in bird's head; **(2)** Short, curved upward; **(3)** Ending in disc; **(4)** Ending in threadlike structure; **(5)** Ending in short bifid structure; **(6)** Sharp, curved downwards.

Character change of morphological characters on morphological trre

Tree number 1 (rooted using default outgroup). Tree length = 308; Consistency index (CI) = 0.2597; Homoplasy index (HI) = 0.7403; CI excluding uninformative characters = 0.2549; HI excluding uninformative characters = 0.7451; Retention index (RI) = 0.5624; Rescaled consistency index (RC) = 0.1461

Character change lists (Character, CI steps, Changes)

M01: 0.118. — 1, node_106 0 ➔1 node_105; 1, node_81 1 ➔ 0 node_80; 1, node_57 0 ➔ 1 node_56; 1, node_56 1 ➔ 2 node_55; 1, node_58 0 ➔ 1 23975 *D sharpi*; 1, node_70 0 ➔ 1 node_69; 1, node_67 1 ➔ 0 node_66; 1, node_69 1 ➔ 2 28088 *P* aff *feronia*; 1, node_76 0 ➔ 1 28490 *P grandis*; 1, node_82 1 ➔ 0 19892 *D moluccana*; 1, node_97 1 ➔ 2 node_96; 2, node_86 2 ➔ 0 22489 *D halterata*; 1, node_89 2 ➔ 1 18612 *D lymetta*; 1, node_100 1 ➔ 2 14841 *D nietneri*; 1, node_101 1 ➔ 2 19525 *D conica*; 1, node_103 1 ➔ 0 28093 *P melanostigma*.

M02: 0.500. — 1, node_106 1 ➔ 0 28916 *Lestes temporalis*; 1, node_102 1 ➔ 0 26585 *P deccanensis*.

M03: 1.000. — 1, node_106 1 ➔ 0 28916 *Lestes temporalis*.

M04: 0.250. — 1, node_66 0 ➔ 1 node_65; 1, node_64 1 ➔ 0 16655 *P vanderstarrei*; 1, node_71 0 ➔ 2 19211 *S striata*; 1, node_73 0 ➔ 1 19442 *P foersteri*; 1, node_80 0 ➔ 2 22343 *D moorei*; 1, node_88 0 ➔ 1 node_87; 1, node_90 0 ➔ 1 19630 *D clavata*; 1, node_95 0 ➔ 2 20316 *D belyshevi.*

M05: 0.500. — 1, node_65 0 ➔ 1 01945 *P simplicinervis*; 1, node_103 0 ➔ 1 19883 *P apicalis.*

M06: 0.375. — 1, node_61 0 ➔ 1 node_60; 1, node_63 0 ➔ 2 19505 *D arcuata*; 1, node_64 0 ➔ 2 01845 *P bivittata*; 1, node_66 0 ➔ 2 01906 *P geijskesi*; 1, node_78 0 ➔ 3 19848 *D sundana*; 1, node_80 0 ➔ 6 22343 *D moorei*; 1, node_82 0 ➔ 2 23548 *D amboinensis*; 1, node_98 0 ➔ 2 node_97; 1, node_97 2 ➔ 4 node_96; 1, node_93 4 ➔ 5 node_92; 1, node_85 5 ➔ 4 18943 *D flavomaculata*; 1, node_86 5 ➔ 3 22489 *D halterata*; 1, node_90 5 ➔ 6 18635 *D centrosaurus*;1, node_94 4 ➔ 2 28842 *D mylitta*; 1, node_102 0 ➔ 2 node_101; 1, node_101 2 ➔ 5 19544 *D dorcadion*.

M07: 0.667. — 1, node_68 0 ➔ 1 19470 *D anascephala*; 1, node_69 0 ➔ 2 28088 *P* aff *feronia*; 1, node_71 0 ➔ 1 19211 *Sulcosticta striata.*

M08: 0.167. — 1, node_64 0 ➔ 1 01845 *P bivittata*; 1, node_69 0 ➔ 1 28088 *P* aff *feronia*; 1, node_76 0 ➔ 1 28490 *P grandis*; 1, node_81 0 ➔ 1 19451 *D carmichaeli*; 1, node_102 0 ➔ 1 node_101; 1, node_106 0 ➔ 1 26582 *S ogatai*.

M09: 0.200. — 1, node_62 0 ➔ 1 node_61; 1, node_64 0 ➔ 1 16655 *P vanderstarrei*; 1, node_72 0 --> 2 node_71; 1, node_71 2 ➔ 3 19211 *S striata*; 1, node_74 0 ➔ 3 28718 *P satoi*; 1, node_80 0 ➔ 1 22343 *D moorei*; 1, node_81 0 ➔ 2 19451 *D carmichaeli*; 1, node_82 0 ➔ 3 23548 *D amboinensis*; 1, node_97 0 ➔ 3 node_96; 1, node_84 3 ➔ 0 19604 *D exoleta*; 1, node_85 3 ➔ 0 20451 *D psygma*; 1, node_87 3 ➔ 1 node_86; 1, node_92 3 ➔ 1 node_91; 1, node_94 3 ➔ 1 28842 *D mylitta*; 1, node_102 0 ➔ 1 node_101.

M10: 0.231. — 1, node_62 3 ➔ 0 node_61; 1, node_64 3 ➔ 2 16655 *P vanderstarrei*; 1, node_74 3 ➔ 2 28718 *P satoi*; 1, node_82 3 ➔ 0 23548 *D amboinensis*; 1, node_96 3 ➔ 0 node_95; 1, node_84 0 ➔ 3 19604 *D exoleta*; 1, node_85 0 ➔ 1 18943 *D flavomaculata*; 1, node_86 0 ➔ 2 22489 *D halterata*; 1, node_90 0 ➔ 2 19630 *D clavata*; 1, node_95 0 ➔ 2 20316 *D belyshevi*; 1, node_102 3 ➔ 0 26585 *P deccanensis*; 1, node_103 3 ➔ 2 28093 *P melanostigma*; 1, node_106 3 ➔ 2 26582 *S ogatai*.

M11: 0.182. — 1, node_106 1 ➔ 2 28916 *Lestes temporalis*; 1, node_100 1 ➔ 0 node_99; 1, node_62 0 ➔ 1 node_61; 1, node_73 0 ➔ 1 19442 *P foersteri*; 1, node_83 0 ➔ 1 node_82; 1, node_87 0 ➔ 1, node_85; 1 node_89 0 ➔ 1 20471 *D bifida*; 1 node_90 0 ➔ 1 19630 *D clavata*; 1 node_95 0 ➔ 1 20316 *D belyshevi*; 1 node_101 1 ➔ 0 19525 *D conica*; 1 node_104 1 ➔ 0 node_103.

M13: 1.000. — 1 node_106 1 ➔ 0 28916 *Lestes temporalis*.

M14: 0.250. — 1 node_61 1 ➔ 0 21405 *D crenitis*; 1 node_69 1 ➔ 2 node_68; 1 node_67 2 ➔ 3 01486 *P coomansi*; 1 node_69 1 ➔ 0 28088 *P* aff *feronia*; 1 node_71 1 ➔ 0 13953 *P hearsayi*; 2 node_74 1 ➔ 3 28718 *P satoi*; 1 node_92 1 ➔ 2 node_88; 1 node_87 2 ➔ 3 node_85; 1 node_90 1 ➔ 2 18635 *D centrosaurus*; 1 node_96 1 ➔ 2 11842 *D ephippiata*; 2 node_105 1 ➔ 3 node_104; 1 node_102 3 ➔ 2 node_101; 1 node_103 3 ➔ 4 28093 *P melanostigma*; 1 node_106 1 ➔ 2 26582 *S ogatai*.

M15: 0.231 1 node_106 1 ➔ 0 28916 *Lestes temporalis*; 1 node_79 1 ➔ 0 node_63; 1 node_58 0 ➔ 1 23975 *D sharpi*; 1 node_60 0 ➔ 1 20145 *D ceratophora*; 2 node_67 1 ➔ 3 01486 *P coomansi*; 1 node_69 1 ➔ 0 28088 *P* aff *feronia*; 1 node_72 1 ➔ 0 node_71; 1 node_74 1 ➔ 0 28517 *P linnaei*; 1 node_74 1 ➔ 2 28718 *P satoi*; 1 node_88 1 ➔ 2 node_87; 1 node_105 1 ➔ 2 node_104; 1 node_104 2 ➔ 3 node_103.

M16: 0.182. — 1, node_105 0 ➔ 1 node_100; 1 node_80 1 ➔ 2 node_79; 1 node_58 2 ➔ 1 19444 *D quadrata*; 1 node_62 2 ➔ 1 node_61; 1 node_69 2 ➔ 1 node_68; 1 node_65 1 ➔ 0 01945 *P simplicinervis*; 1 node_67 1 ➔ 0 01486 *P coomansi*; 1 node_76 2 ➔ 1 28490 *P grandis*; 1 node_96 1 ➔ 2 node_95; 1 node_93 2 ➔ 1 node_92; 1 node_851 ➔ 2 18943 *D flavomaculata*.

M17: 0.667 1 node_106 1 ➔ 0 28916 *Lestes temporalis*; 1 node_105 1 ➔ 2 node_100; 1 node_101 1 ➔ 2 19525 *D conica.*

M18: 0.091 1 node_106 1 ➔ 2 node_105; 1 node_55 2 ➔ 1 19794 *D rufostigma*; 1 node_59 2 ➔ 1 node_58; 1 node_60 2 ➔ 1 20145 *D ceratophora*; 1 node_65 2 ➔ 1 01945 *P simplicinervis*; 1 node_76 2 ➔ 1 28490 *P grandis*; 1 node_98 2 ➔ 1 node_83; 1 node_86 2 ➔ 1 10669 *D rudicula*; 1 node_91 2 ➔ 1 node_90; 1 node_93 2 ➔ 1 22090 *D krios*; 1 node_102 2 ➔ 1 node_101.

M19: 0.333. — 1 node_105 1 ➔ 0 node_100; 1 node_61 0 ➔ 1 21405 *D crenitis*; 1 node_67 0 ➔ 1 node_66.

M20: 0.333. — 1 node_60 1 ➔ 0 28089 *D versicolor*; 1 node_78 1 ➔ 0 node_77; 1 node_68 0 ➔ 1 19470 *D anascephala*.

M21: 0.214. — 1 node_106 0 ➔ 1 node_105; 1 node_57 1 ➔ 2 18620 *D lestoides*; 1 node_59 1 ➔ 3 node_58; 1 node_60 1 ➔ 0 28089 *D versicolor*; 1 node_78 1 ➔ 0 node_77; 1 node_68 0 ➔ 3 19470 *D anascephala*; 1 node_81 1 ➔ 3 19451 *D carmichaeli*; 1 node_83 1 ➔ 2 node_82; 1 node_92 1 ➔ 2 node_88; 1 node_85 2 ➔ 1 18943 *D flavomaculata*; 1 node_89 1 ➔ 2 18612 *D lymetta*; 1 node_94 1 ➔ 3 28842 *D mylitta*; 1 node_103 1 ➔ 2 28093 *P melanostigma*; 1 node_106 0 ➔ 2 26582 *S ogatai*.

M22: 1.000. — 1 node_106 1 ➔ 0 node_105.

M23: 0.400 1 node_106 2 ➔ 1 node_105; 1 node_100 1 ➔ 0 node_99; 1 node_90 0 ➔ 1 19630 *D clavata*; 1 node_101 1 ➔ 2 19525 *D conica*; 1 node_103 1 ➔ 2 28093 *P melanostigma*.

M24: 0.154. — 1 node_105 2 ➔ 1 node_100; 1 node_81 1 ➔ 0 node_80; 1 node_65 0 ➔ 1 node_64; 2 node_67 0 ➔ 2 01486 *P coomansi*; 1 node_81 1 ➔ 2 19451 *D carmichaeli*; 1 node_84 1 ➔ 2 19604 *D exoleta*; 1 node_85 1 ➔ 2 20451 *D psygma*; 1 node_86 1 ➔ 2 10669 *D rudicula*; 1 node_89 1 ➔ 2 20471 *D bifida*; 1 node_96 1 ➔ 2 11842 *D ephippiata*; 1 node_100 1 ➔ 0 14841 *D nietneri*; 1 node_102 2 ➔ 1 26585 *P deccanensis*.

M25: 1.000. — 1 node_104 0 ➔ 1 node_103.

M26: 0.167. — 1 node_62 0 ➔ 2 node_59; 1 node_69 0 ➔ 1 node_68; 1 node_66 1 ➔ 2 node_65; 1 node_70 0 ➔ 2 19997 *P kinabaluensis*; 1 node_71 0 ➔ 2 13953 *P hearsayi*; 1 node_77 0 ➔ 1 node_76; 1 node_75 1 ➔ 2 node_74; 1 node_83 0 ➔ 1 node_82; 1 node_95 0 ➔ 1 node_94; 1 node_92 1 ➔ 0 node_91; 1 node_102 0 ➔ 1 26585 *P deccanensis*; 1 node_103 0 ➔ 1 28093 *P melanostigma*.

M27: 0.333. — 1 node_69 0 ➔ 2 28088 *P* aff *feronia*; 1 node_98 0 ➔ 1 node_97; 1 node_95 1 ➔ 0 node_94; 1 node_86 0 ➔ 1 10669 *D rudicula*; 1 node_91 0 ➔ 1 node_89; 1 node_90 0 ➔ 2 18635 *D centrosaurus*.

M28: 0.167. — 1 node_64 0 ➔ 1 16655 *P vanderstarrei*; 1 node_70 0 ➔ 1 19997 *P kinabaluensis*; 1 node_71 0 ➔ 1 19211 *S striata*; 1 node_76 0 ➔ 1 28490 *P grandis*; 1 node_80 0 ➔ 1 22343 *D moorei*; 1 node_83 0 ➔ 1 01534 *D penicillata*.

M29: 0.375. — 1 node_63 1 ➔ 2 node_62; 1 node_57 2 ➔ 3 node_56; 1 node_59 2 --> 1 node_58; 1 node_58 1 ➔ 4 19444 *D quadrata*; 1 node_72 1 ➔ 3 node_70; 1 node_68 3 ➔ 2 node_67; 1 node_65 2 ➔ 1 01945 *P simplicinervis*; 1 node_69 3 ➔ 4 28088 *P* aff *feronia*; 1 node_71 1 ➔ 4 19211 *S striata*; 1 node_73 1 ➔ 7 28495 *P caroli*; 1 node_74 1 ➔ 7 28718 *P satoi*; 1 node_78 1 ➔ 4 19848 *D sundana*; 1 node_81 1 ➔ 0 19451 *D carmichaeli*; 1 node_100 1 ➔ 4 14841 *D nietneri*; 1 node_103 1 ➔ 2 19883 *P apicalis*; 1 node_106 1 ➔ 5 26582 *S ogatai*.

M30: 0.143. — 1 node_58 0 ➔ 1 23975 *D sharpi*; 1 node_64 0 ➔ 1 16655 *P vanderstarrei*; 1 node_70 0 ➔ 1 19997 *P kinabaluensis*; 1 node_71 0 ➔ 1 13953 *P hearsayi*; 1 node_81 0 ➔ 1 19451 *D carmichaeli*; 1 node_100 0 ➔ 1 14841 *D nietneri*; 1 node_104 0 ➔ 1 node_103.

M31: 0.500. — 1 node_76 0 ➔ 1 node_75; 1 node_83 0 ➔ 1 01534 *D penicillata*.

M32: 0.286. — 1 node_63 0 ➔ 1 node_62; 1 node_59 1 ➔ 2 node_57; 1 node_60 1 ➔ 0 20145 *D ceratophora*; 1 node_72 0 ➔ 2 node_70; 1 node_65 2 ➔ 1 node_64; 1 node_86 0 ➔ 1 22489 *D halterata*; 1 node_103 0 ➔ 1 19883 *P apicalis*.

M33: 0.211. — 1 node_99 0 ➔ 2 node_81; 1 node_79 2 ➔ 0 node_63; 1 node_55 0 ➔ 2 19452 *D actaeon*; 1 node_57 0 ➔ 3 18620 D lestoide; 1 node_63 0 ➔ 4 19505 D arcuata; 1 node_68 2 ➔ 0 node_67; 1 node_64 0 ➔ 3 16655 *P vanderstarrei*; 1 node_66 0 ➔ 3 01906 *P geijskesi*; 1 node_69 2 ➔ 3 28088 *P* aff *feronia*; 1 node_71 2 ➔ 1 19211 *S striata*; 1 node_76 2 ➔ 4 28490 *P grandis*; 1 node_78 2 ➔ 1 19848 *D sundana*; 1 node_82 0 ➔ 1 19892 *D moluccana*; 1 node_94 0 ➔ 1 node_93; 1 node_88 1 ➔ 0 node_84; 1 node_86 1 ➔ 0 22489 *D halterata*; 1 node_90 1 ➔ 2 19630 *D clavata*; 1 node_97 0 ➔ 1 19739 *D gazella*; 1 node_104 0 ➔ 4 node_102.

M34: 0.333. — 1 node_55 0 ➔ 1 19452 *D actaeon*; 1 node_79 0 ➔ 1 node_78; 1 node_77 1 ➔ 0 node_72.

M35: 0.182. — 1 node_65 0 ➔ 1 01945 *P simplicinervis*; 1 node_72 0 ➔ 1 node_71; 1 node_80 0 ➔ 2 22343 *D moorei*; 1 node_82 0 ➔ 1 23548 *D amboinensis*; 1 node_98 0 ➔ 1 node_97; 1 node_97 1 ➔ 2 node_96; 1 node_84 2 ➔ 0 19604 *D exoleta*; 1 node_87 2 ➔ 1 node_86; 1 node_105 0 ➔ 1 node_104; 1 node_102 1 ➔ 2 26585 *P deccanensis*; 1 node_103 1 ➔ 2 19883 *P apicalis*.

M36: 0.333. — 1 node_58 1 ➔ 0 19444 *D quadrata*; 1 node_61 1 ➔ 2 node_60; 1 node_63 1 ➔ 0 19505 *D arcuata*; 1 node_68 1 ➔ 0 19470 *D anascephala*; 1 node_104 1 ➔ 0 node_102; 1 node_106 1 ➔ 2 26582 *S ogatai*.

M37: 0.182. — 1 node_55 1 ➔ 2 19452 *D actaeon*; 1 node_79 1 ➔ 2 node_78; 1 node_77 2 ➔ 0 node_72; 1 node_68 0 ➔ 1 19470 *D anascephala*; 1 node_65 0 ➔ 1 01945 *P simplicinervis*; 1 node_75 2 ➔ 1 node_73; 1 node_80 1 ➔ 0 22343 *D moorei*; 1 node_99 1 ➔ 0 node_98; 1 node_87 0 ➔ 1 node_86; 1 node_94 0 ➔ 1 28842 *D mylitta*; 1 node_102 1 ➔ 0 26585 *P deccanensis*.

M38: 0.462. — 1 node_55 0 ➔ 4 19794 *D rufostigma*; 1 node_62 0 ➔ 4 node_61; 1 node_63 0 ➔ 2 19505 *D arcuata*; 1 node_68 0 ➔ 2 19470 *D anascephala*; 1 node_72 0 ➔ 3 node_71; 1 node_80 0 ➔ 1 22343 *D moorei*; 1 node_82 0 ➔ 3 23548 *D amboinensis*; 1 node_96 0 ➔ 1 node_95; 1 node_87 1 ➔ 3 node_86; 1 node_94 1 ➔ 0 28842 *D mylitta*; 1 node_105 0 ➔ 5 node_104; 1 node_102 5 ➔ 3 node_101; 1 node_106 0 ➔ 6 26582 *S ogatai*.