Phylogeny and biogeography of the Platystictidae (Odonata)

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Jan van Tol

Phylogeny and biogeography of the Platystictidae (Odonata)

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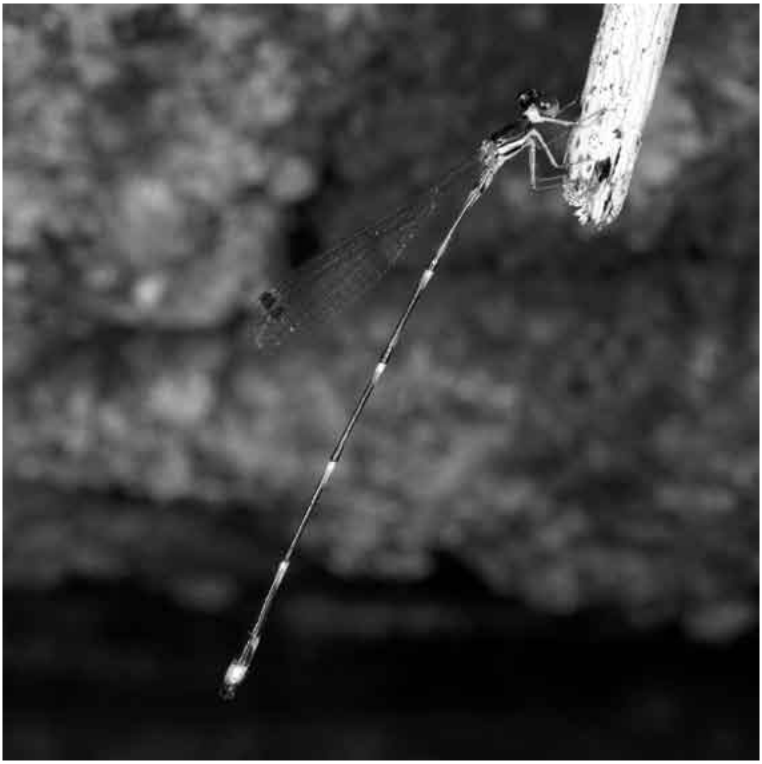


One of the more ‘colourful’ species of Platystictidae: *Protosticta linnaei* van Tol. Vietnam, Chu Yang Sin National Park, 2007.

Introduction

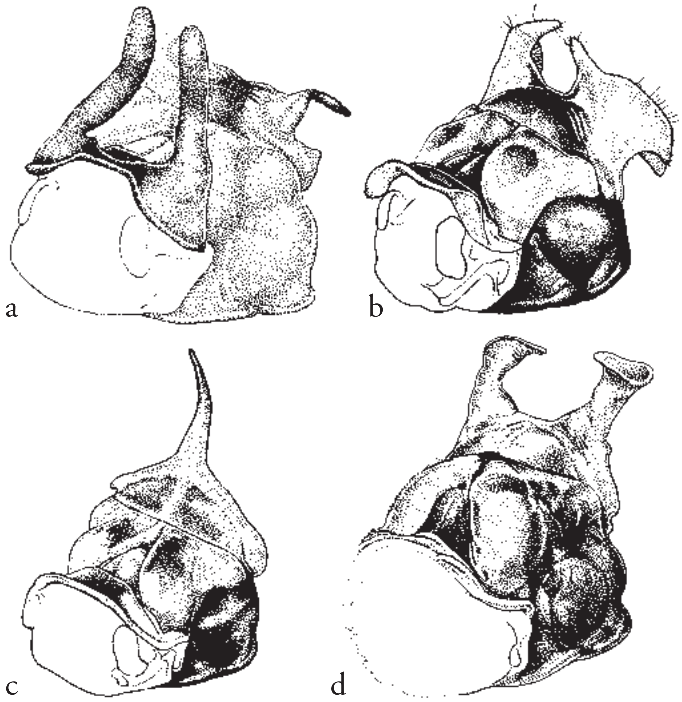
Tropical odonates are well-known for their brilliant colours, their size and conspicuous behaviour. Indeed, the scarlet abdomen, or the iridescent colours in the wings of some dragonflies and damselflies attract the attention of even the general naturalist when visiting a tropical lake or stream. The eye-catching display and agonistic behaviour of tropical calopterygoids and other damselflies also contribute to this general notion.

The species of the family Platystictidae, also known as forest damselflies or shadowdamsels, the subject of this publication, differ in nearly all aspects from this general impression of tropical odonates. Although platystictids are restricted to the tropics, they are dull-coloured, small insects with elusive behaviour. In the larval stage, they typically live in seepages or small streams deep in dark forest, while the imagos seem to hang all day from the tips of branches or leaves of trees and shrubs in gullies or along streams. The adults are poor flyers, and take the wing only when they are disturbed, to catch a prey, or are attracted by the opposite sex. They are underrepresented in many entomological collections, since they are simply not noticed by the general insect collector.

The family Platystictidae is known from southeast Asia (Sri Lanka and India eastwards to the Papuan region) and from Central and the northern part of South America. Most species are island endemics, or are even confined to parts of these islands only. The overall similar general appearance of dull brownish species with a blue tip of the abdomen conceals the huge variation in such structures as the pronotum, male anal appendages and secondary genitalia. This combination of characters makes the family Platystictidae a group of choice for a contribution to our understanding of the history of the aquatic biotas of the tropics. This thesis focuses on the following research questions:

(a) what is the diversity of the family Platystictidae at the species level, especially in southeast Asia, and what is the distribution of each species?
(b) which morphological and molecular characters can be used to reconstruct the phylogeny of this group of odonates?
(c) is the family Platystictidae a monophyletic group, and what are the relationships to other families of Zygoptera?
(d) what are the phylogenetic relationships of the species of the Platystictidae, based on the analysis of both morphological and molecular characters?
(e) which areas of endemism can be recognized based on the distributions of the species of Platystictidae?
(f) what are the relationships of the areas of endemism as defined by the distributions and phylogenetic relationships of the species of Platystictidae, and what is the relation to area cladograms based on other taxa?
(g) how did the present distributional pattern of the Platystictidae evolve, *e.g.*, in relation to the palaeogeography and palaeoclimatology?

Research questions (a) and (b) are treated in the second part (chapters 3 to 8) of this publication. This part includes several regional revisions of Platystictidae, including descriptions of 46 species new to science. Special attention was paid to the species of the Philippines, Sulawesi, and the Moluccas. A smaller paper was devoted to the fauna of Vietnam. These revisions were based on a significant amount of new material available in the National Museum of Natural History Naturalis, which was partly collected by myself



Platystictidae show bizarre variation in subtle structural details. Pronotum of Philippine *Drepanosticta* species. (a) *D. trachelocele* van Tol (Samar); (b) *D. centrosaurus* van Tol (Mindanao); (c) *D. ceratophora* Lieftinck (Balabac); (d) *D. myzouris* van Tol (Luzon) [not to scale].
For details, see Chapter 5 (Illustrations by E.J. Bosch and I.M. van Noortwijk).

during fieldwork in Vietnam and Indonesia. It was, for instance, exciting to study the bizarre variation in the processes of the pronotum of the species of *Drepanosticta* Laidlaw in the Philippines (this page and chapter 5). In other parts of the range, species mainly differ in the anal appendages of the male, e.g. in the genus *Protosticta* Selys of Sulawesi (chapter 6). These taxonomic papers also include discussions of characters.

The full variation of this family was taken into account for a reconstruction of the phylogeny and the historical biogeography of this family (Part 1, chapter 1). Chapter 2 reviews present knowledge of the zoogeography of freshwater invertebrates of southeast Asia, with special attention to Odonata. It also includes a rather extensive summary of the regional palaeogeography of the region during the Cenozoic. Unfortunately, well-founded phylogenetic reconstructions of aquatic insects of southeast Asia are still scarce, while such reconstructions are a prerequisite for biogeographical analyses.

The present biogeographical reconstruction based on Platystictidae is one of the first based on extensive taxon sampling and character analysis, and thus contributes to our understanding of the evolution of the aquatic biotas of southeast Asia. Platystictidae occur in Central and northern South America (subfamily Palaemnematinae), and the Oriental and Papuan regions (subfamilies Platystictinae and Sinostictinae). The reconstruction of the phylogeny of 53 species is based on morphological characters, while a preliminary analysis based on molecular characters (16S and 28S rDNA) is restricted to 55 samples of 44 species, including 22 samples representing 16 species of Platystictidae. The reconstruction of the phylogeny is used for an analysis of the historical biogeography of this family. The sister-group relationships at the base of the tree suggest that the New World and Old World taxa diversified already early during their evolution, presumably before the end of the Cretaceous (65 Ma). It is further concluded that the group may have evolved in Africa, that a tropical Europe during the Eocene has played a remarkable role as a pathway for forest damselflies to the New World, and that the taxa of southeast Asia all have evolved from a centre at the border of the Indian plate and Laurasia.

Leiden, October 2008.

Part 1

Phylogeny and biogeography

1. Phylogeny and biogeography of the Platystictidae (Odonata)

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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

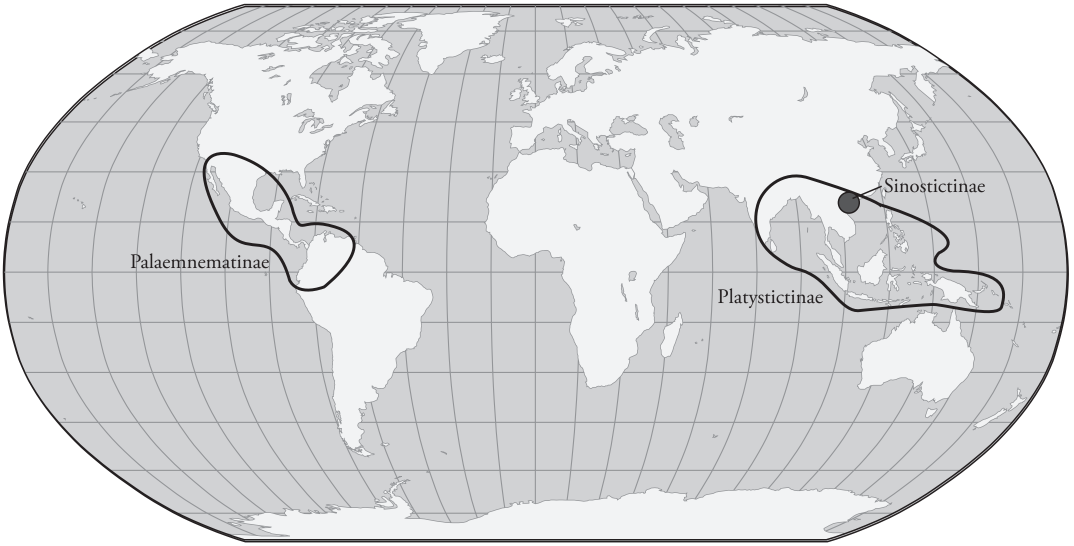

Figure 1. Global distribution of Platystictidae. The subfamily Platystictinae is confined to southeast Asia, and the subfamily Palaemnematinae to Central and northern South America. The Sinostictinae are only known from southeastern China.

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).

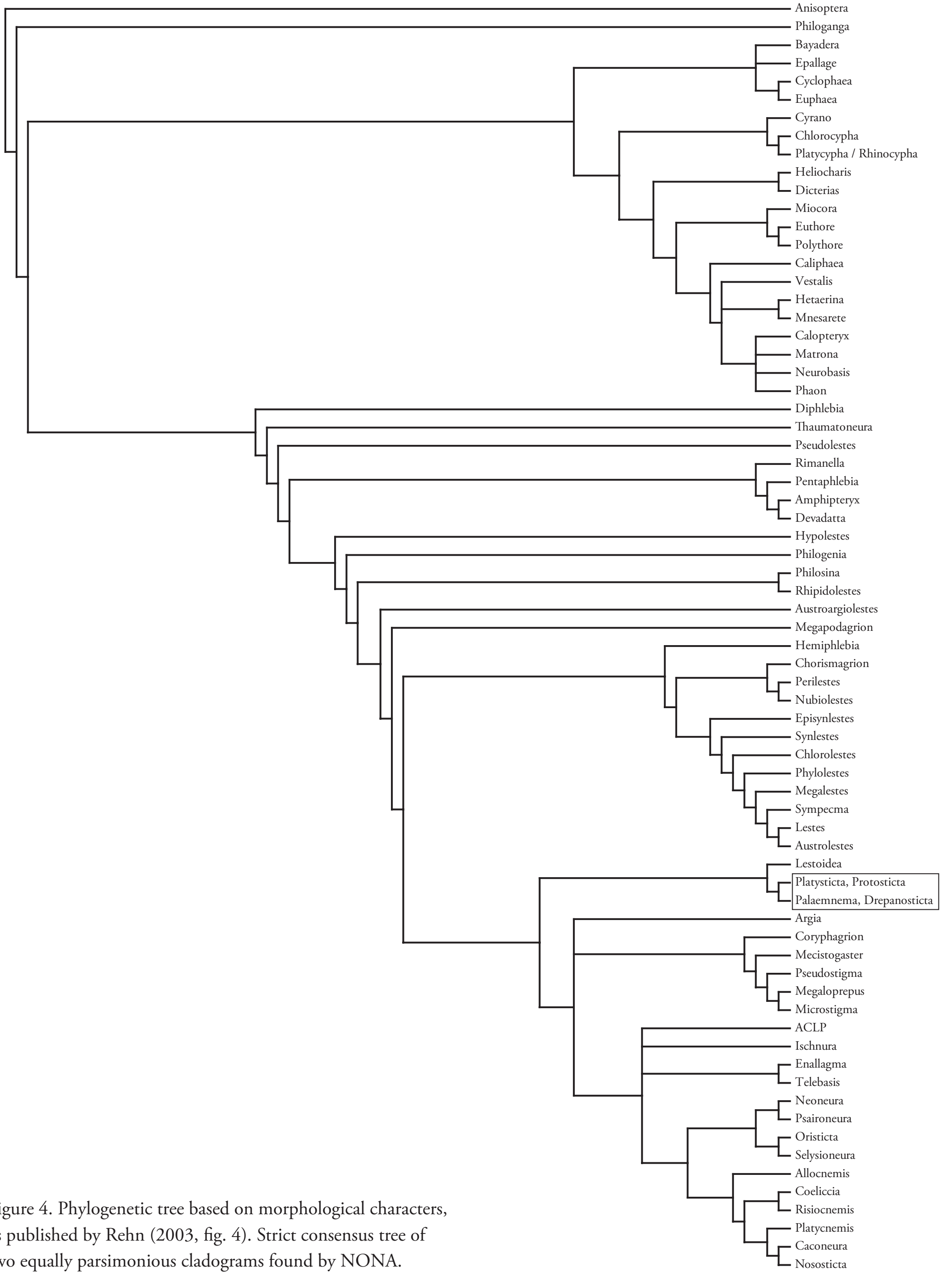

Figure 4. Phylogenetic tree based on morphological characters, as published by Rehn (2003, fig. 4). Strict consensus tree of two equally parsimonious cladograms found by NONA.

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).

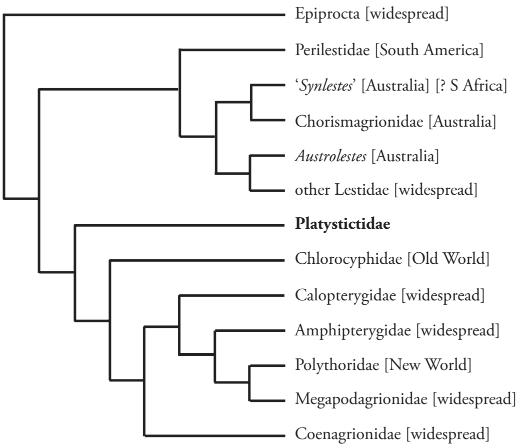

Figure 5. Simplified version of Hypothesis I of phylogenetic relationships of Odonata by Bybee et al. (2008: fig. 6 and 2). African Synlestinae were not studied.

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.

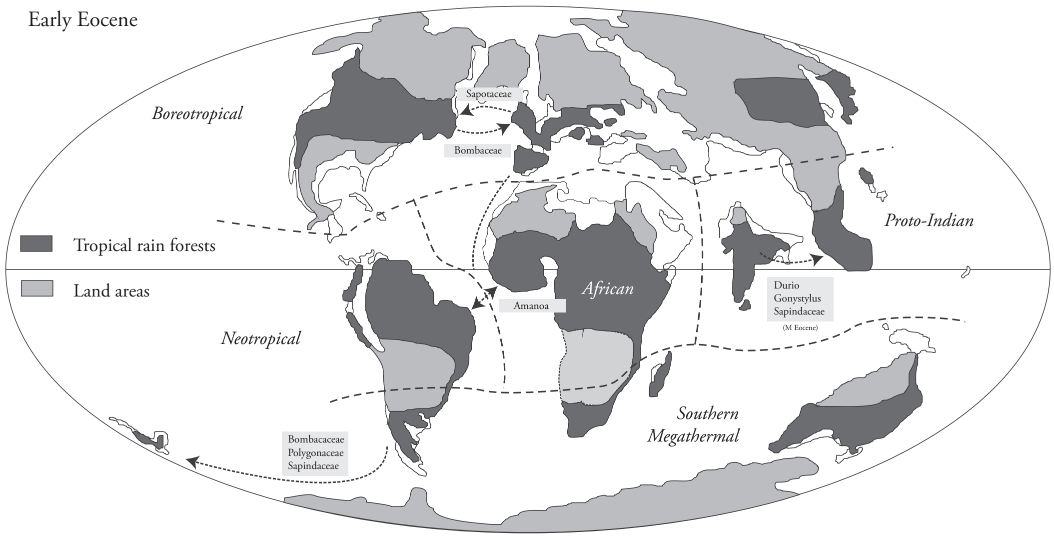

Figure 6. Distribution of closed-canopy tropical rain forests during the Late Paleocene / Early Eocene thermal maximum. Redrawn after Morley (2000, fig. 13.3), names of plant genera and families omitted. Arrows indicate 'noteworthy dispersals of megathermal plants relating to the thermal maximum, and 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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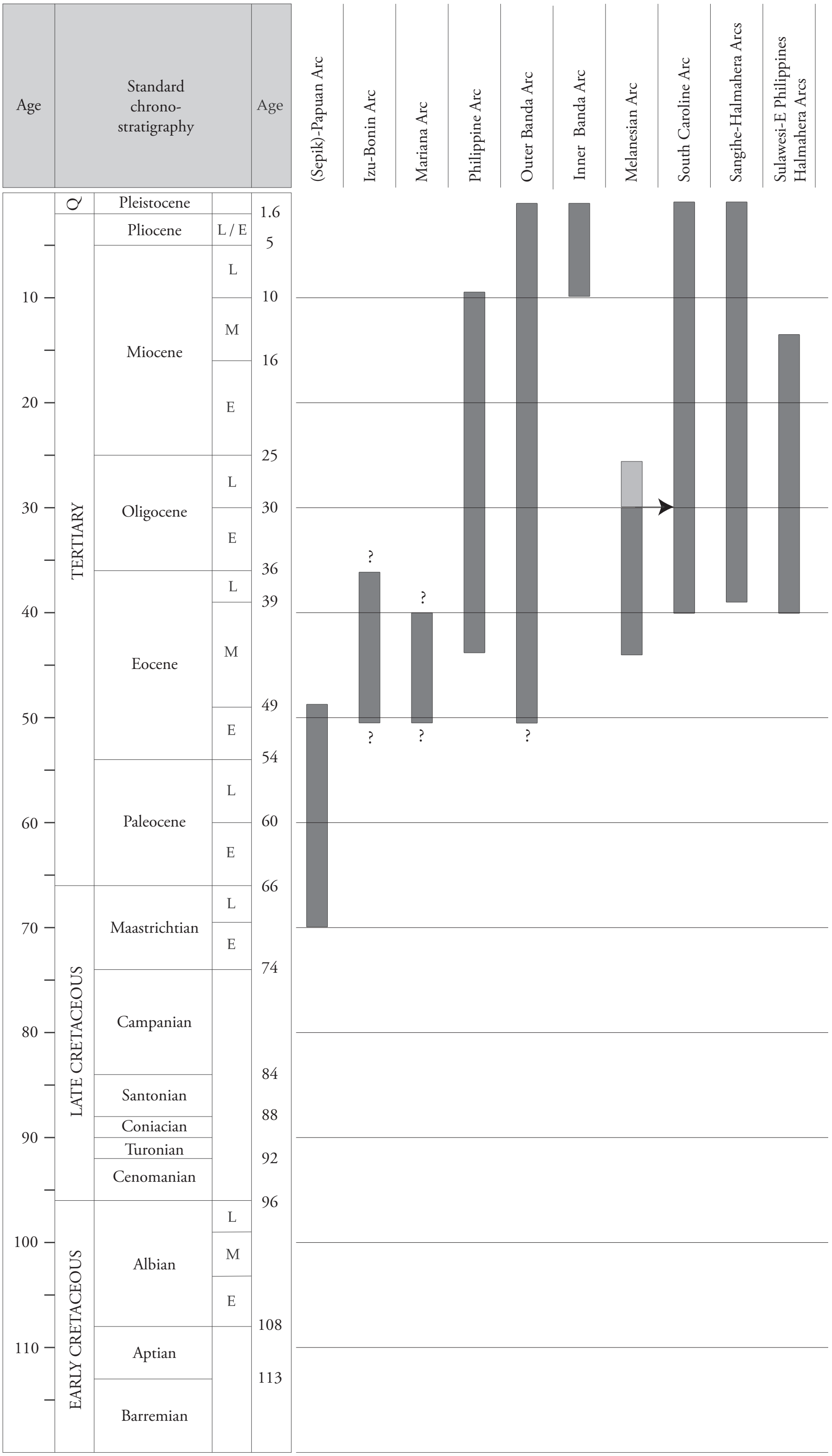
Right
Figure 7. The history of island arcs of southeast Asia and the western Pacific.


Age
Standard chrono-stratigraphy
Age
(Sepik)-Papuan Arc
Izu-Bonin Arc
Mariana Arc
Philippine Arc
Outer Banda Arc
Inner Banda Arc
Melanesian Arc
South Caroline Arc
Sangihe-Halmahera Arcs
Sulawesi-E Philippines Halmahera Arcs
Q
TERTIARY
LATE CRETACEOUS
EARLY CRETACEOUS
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
L / 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**

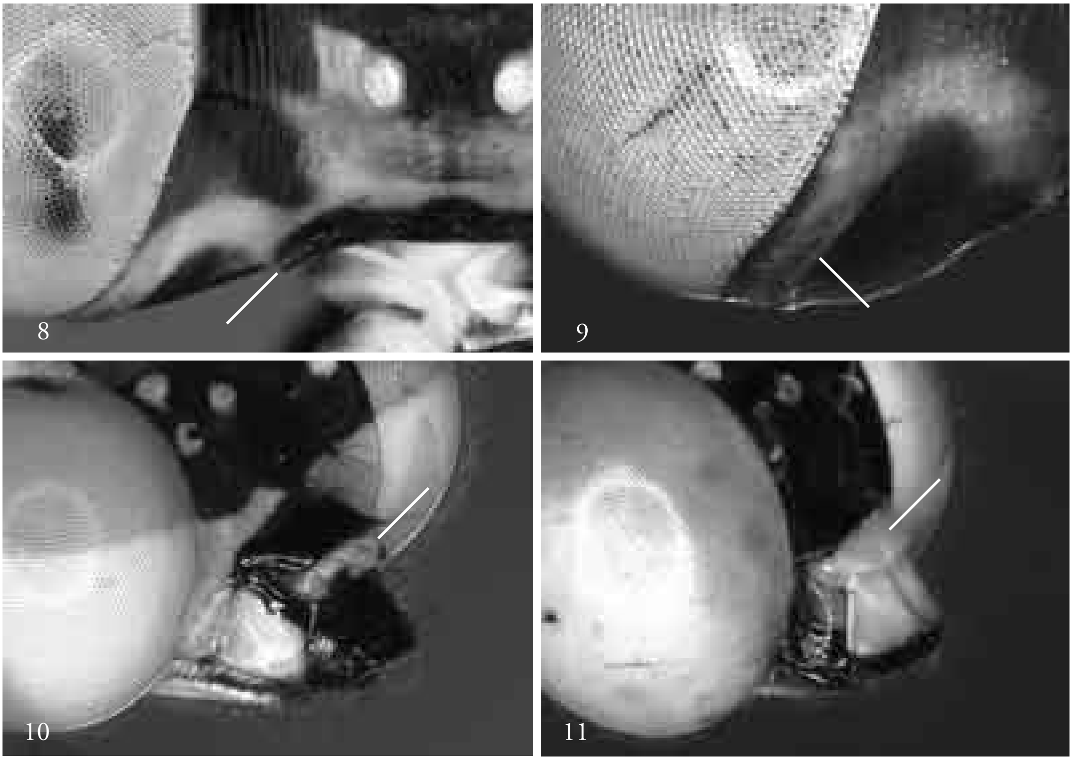
The characters chosen for our phylogenetic analysis were partly derived from previous analyses as published in systematic papers (Calvert 1931; Rehn 2003), supplemented with characters not studied systematically before, including the ligula of the male. The datamatrix is presented in Appendix 2, with 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.

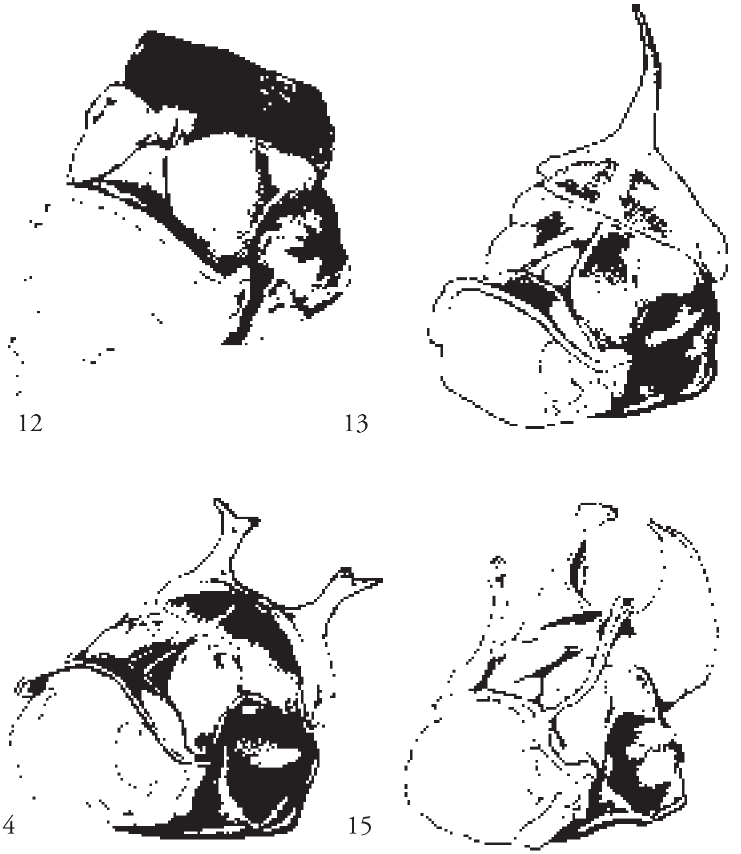
M02 Head: parorbital carina. – (0) absent, (b) present. Seems to be a unique apomorphy of all Platystictidae (Fig. 9).

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.

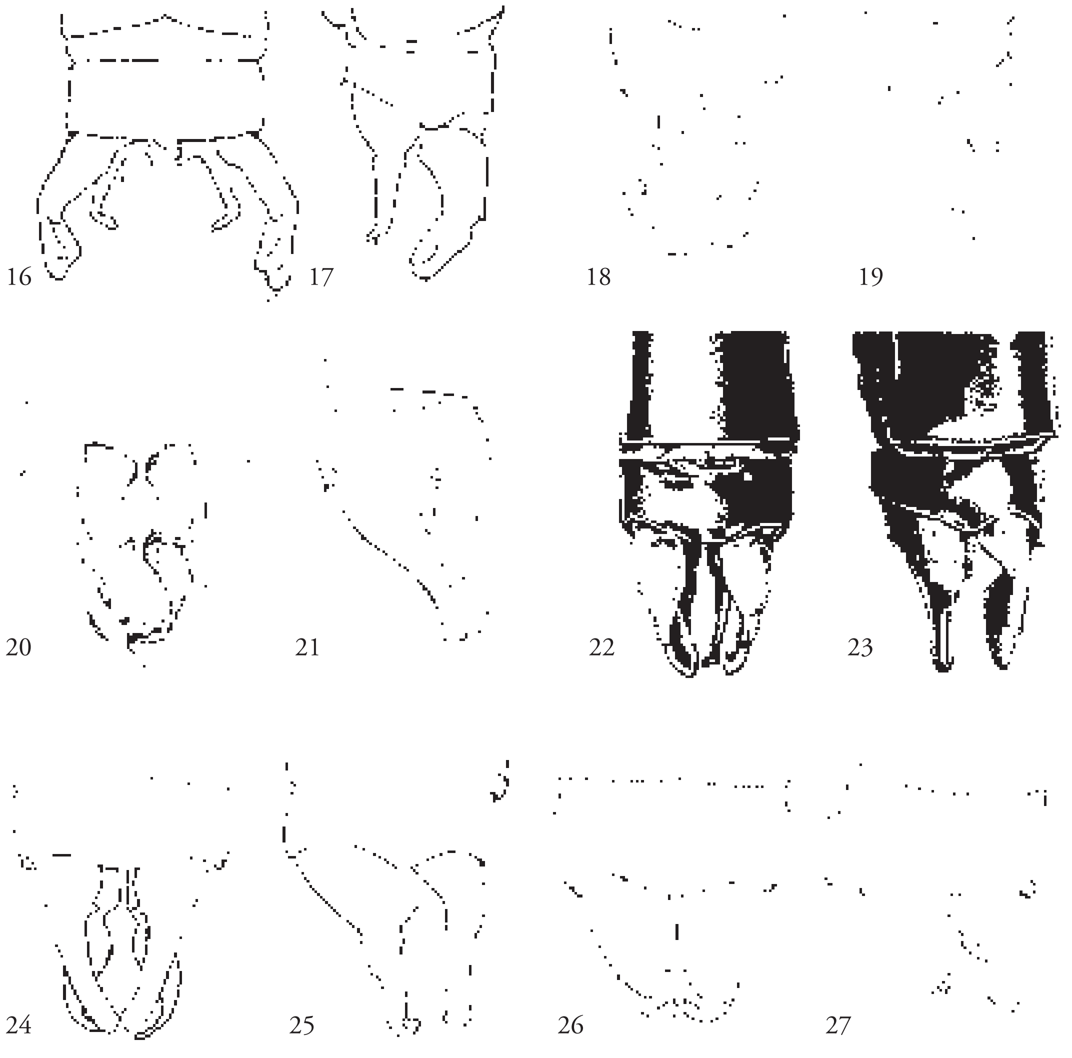
M09 Synthorax: colour venter. – (0) pale, (1) black, (2) variegate, (3) bicolorous. In most species the synthorax is pale. Coded as ‘bicolorous’ if distinctly different in anterior and posterior part, otherwise coded as ‘variegate’, e.g. for longitudinal dark stripes. Unordered.

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

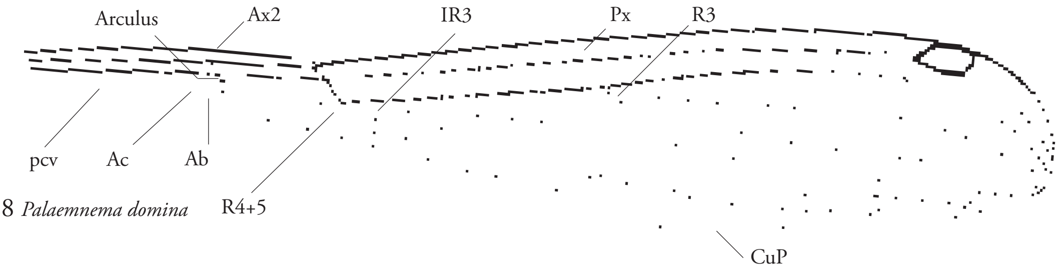


Figures 16-27. Anal appendages of male Platystictidae. – 16-17, *Palaemnema melanostigma* Hagen, dorsal and left lateral view (from Calvert 1931, figs. 57a, b). – 18-19, *Protosticta feronia* Lieftinck, dorsal and right lateral view (from Lieftinck 1965, fig. 1). – 20-21, *Protosticta geijskesi* van 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).

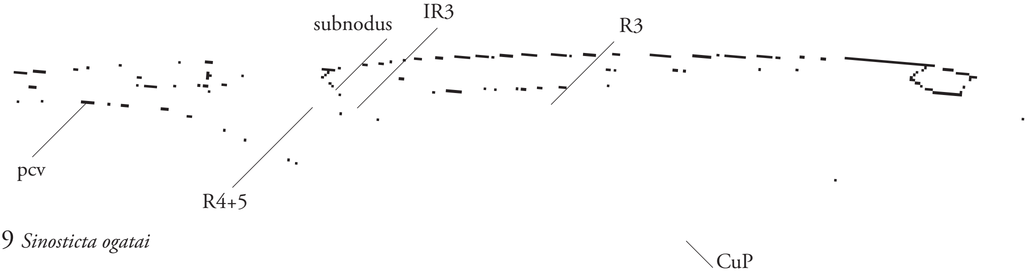
assigned to the Platystictidae. In rare cases there is more than pcv, but in the aberrant *Sinosticta ogatai* three or even four of these cross-veins may be present (Fig. 29).

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.

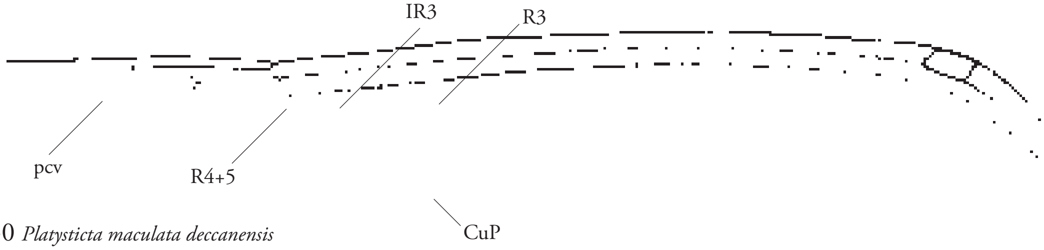
M15 Number of postnodal cross-veins (hind wing) (Fig. 28). – (0) 10-12, (1) 13-15, (2) 16-18. (3) 19-21, (4) 22-24, (5) 25-27, (6) more than 27, (7) less than 10. Ordered.



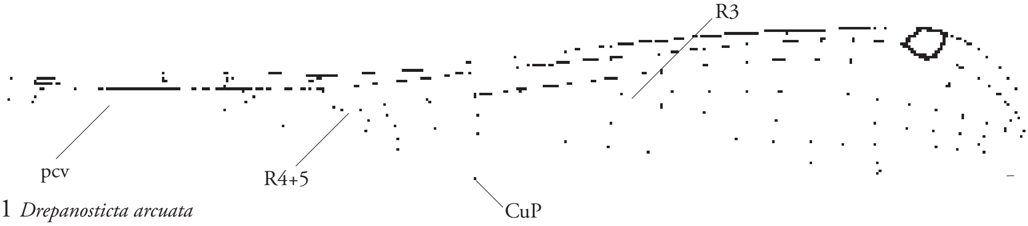
28 *Palaemnema domina*



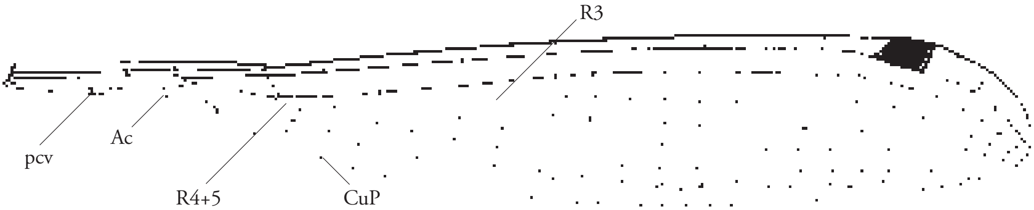
29 *Sinosticta ogatai*



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).

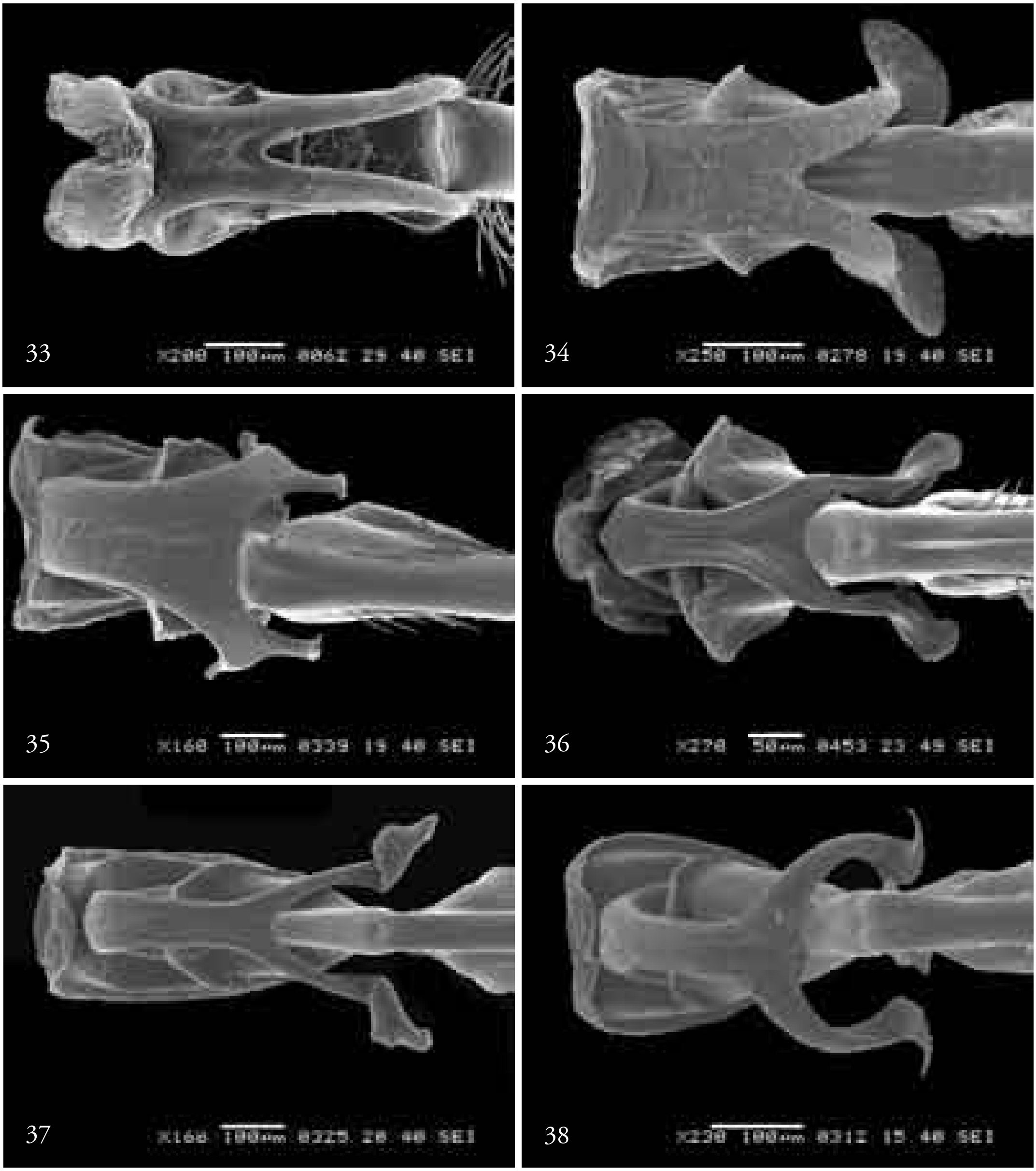
M34 Ligula, last segment medially. – (0) straight or concave, (1) convex.

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.

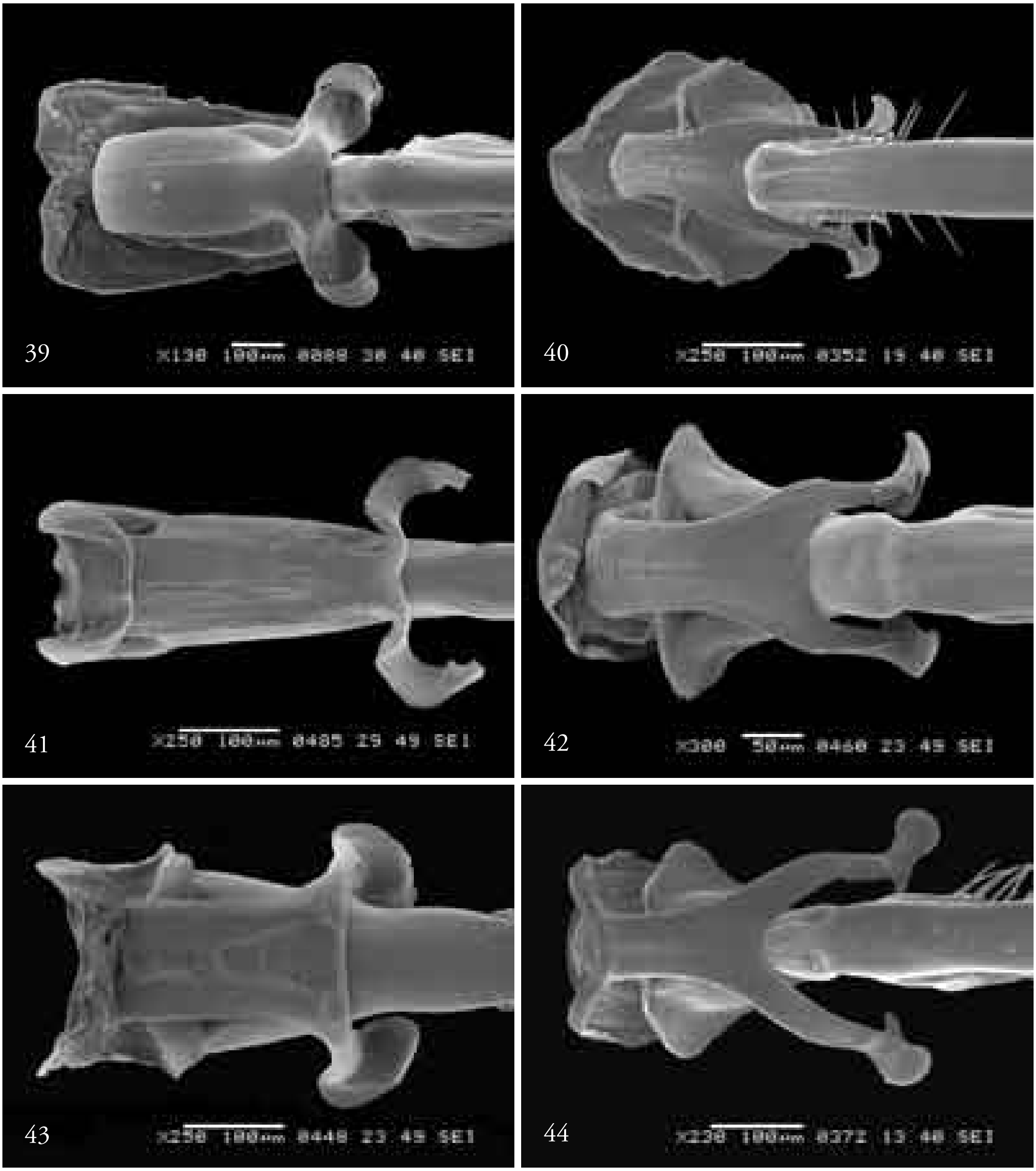
Amplification and sequencing. – The DNA thus obtained was used for direct amplification by PCR of partial 16S and 28S rDNA sequences. The following primers were used for PCR and sequencing reactions: 16S: LR-J-12887 (5' - CCG GTC TGA ACT CAG ATC ACG T-3') and LR-N-13398 (5' – CGC CTG TTT AAC AAA AAC 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

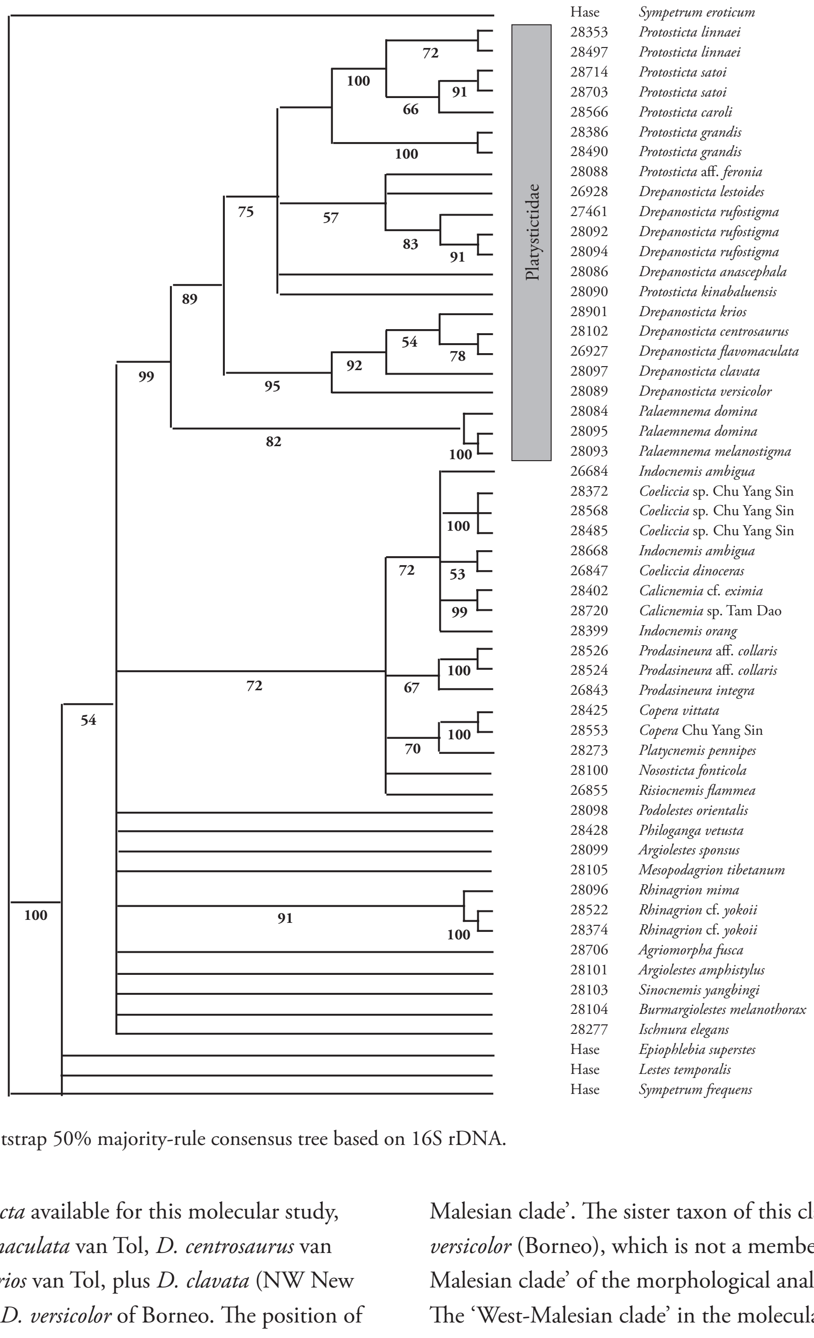


Figure 45. Bootstrap 50% majority-rule consensus tree based on 16S rDNA.

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

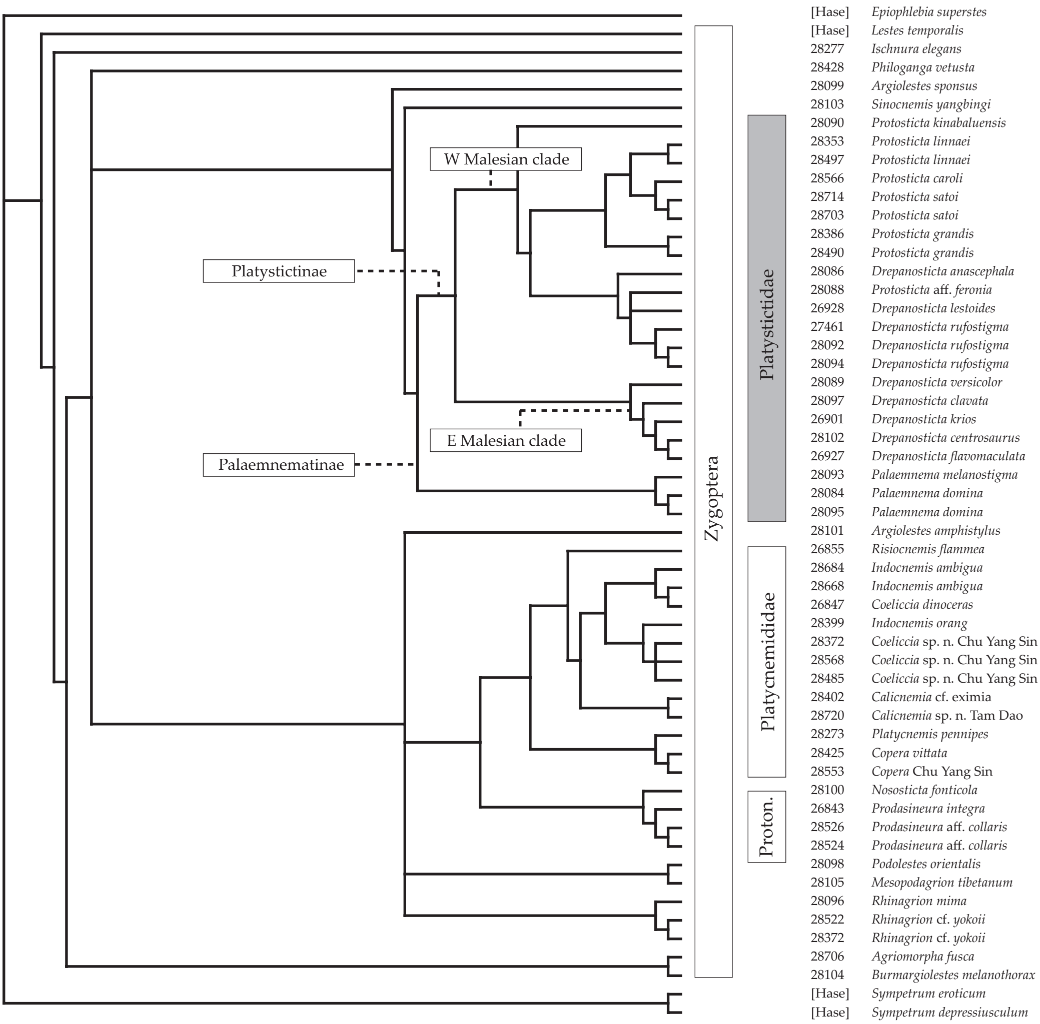


Figure 46. Strict consensus tree of 37 most parsimonious trees of a heuristic search of the 16S28S rDNA data. 'Hase' refers to data from Hasegawa & Kasuya (2006). 'Proton' = Protoneuridae.

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

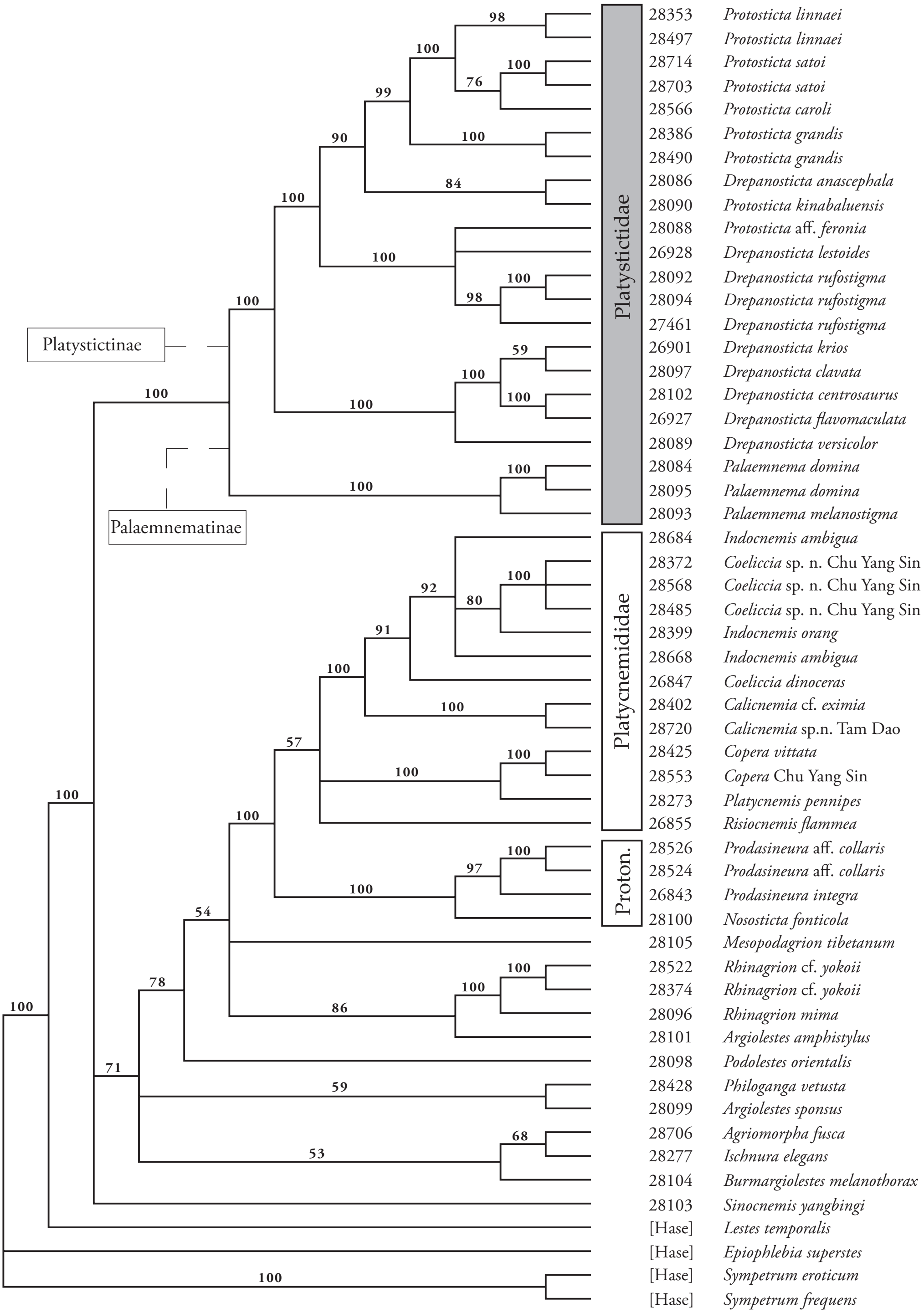


Fig. 47. Majority rule consensus tree of Bayesian analysis of 16S and 28S rDNA data of 54 taxa. Numbers of branchs refer to percentage of trees which supported the clade. 'Hase' refers to data from Hasegawa & Kasuya (2006). 'Proton' = Protoneuridae.

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.

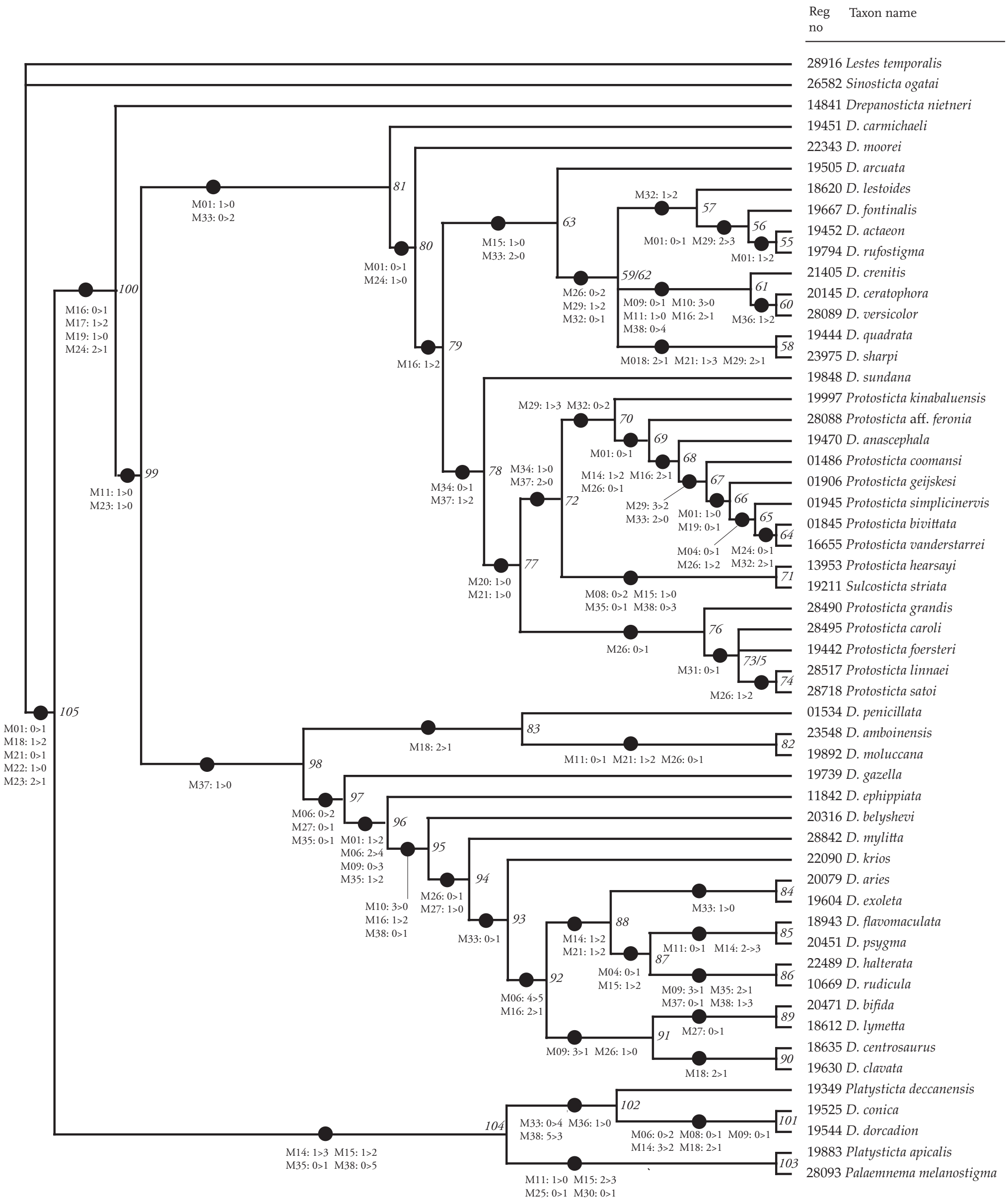


Figure 48. Strict consensus tree of ten most parsimious trees of 53 species of Platystictidae plus one Lestidae (*Lestes temporalis*) (morphological dataset). Character changes of morphological characters (except for terminal taxa). Numbers of nodes in italics. See Appendix 3 for complete change list.

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.

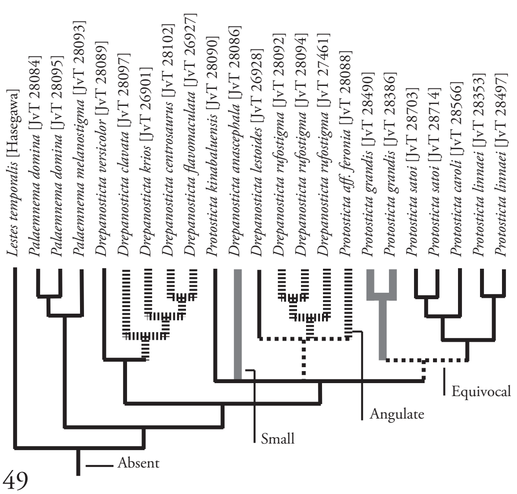
Wings. – Several characters in the Platystictidae show distinct evolutionary patterns on the strict consensus tree based on morphological characters.

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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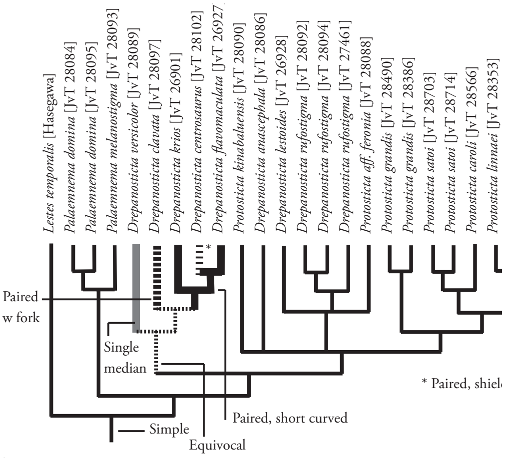

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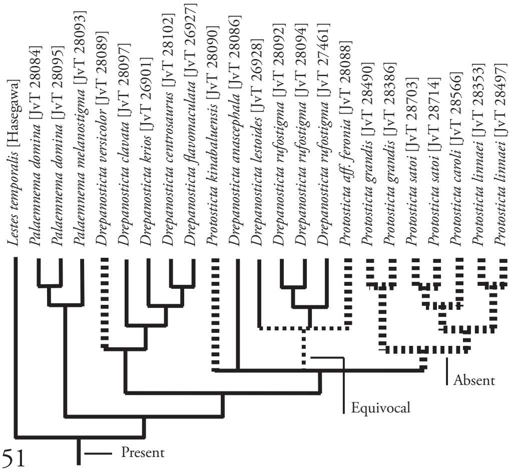

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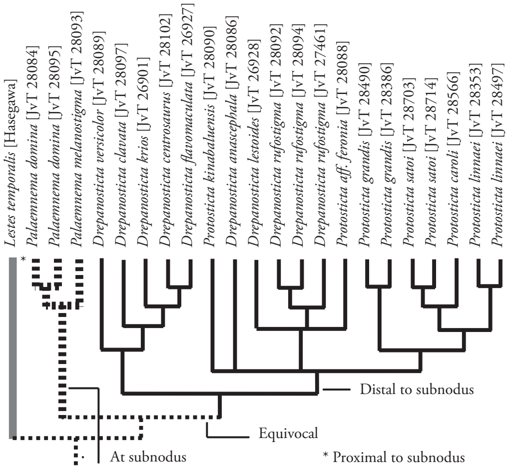

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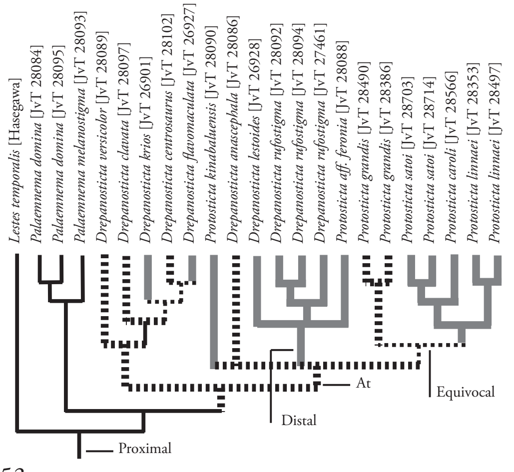

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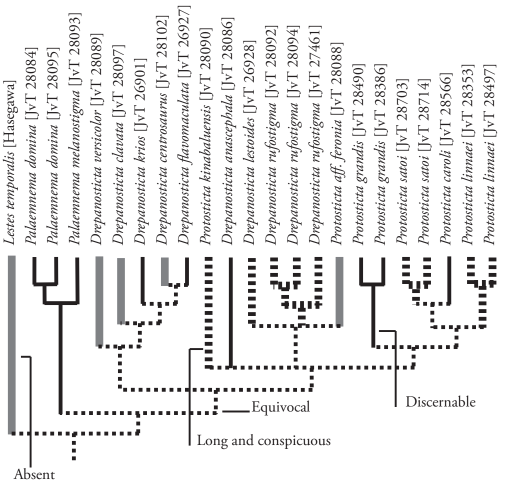

54

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 amphitranspacific 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.

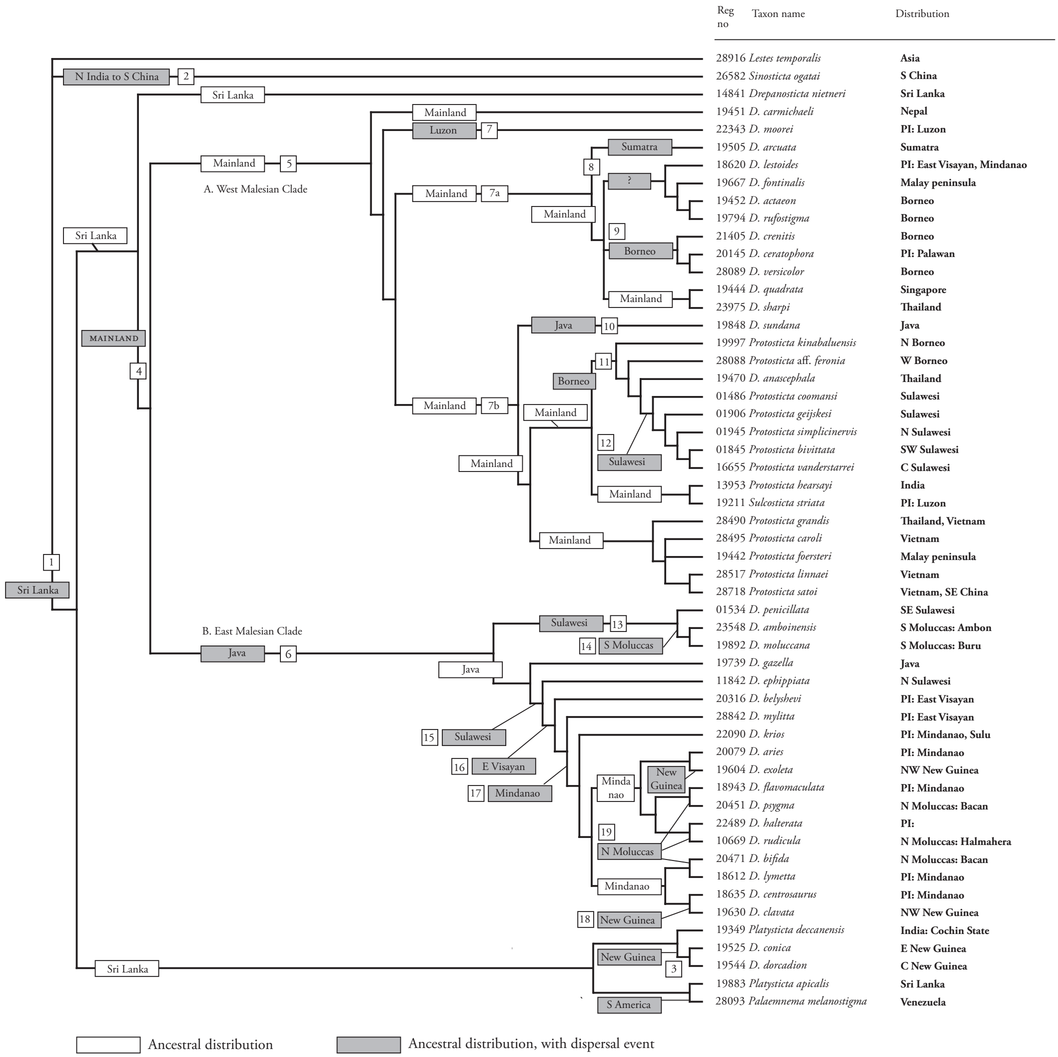

Figure 55. Strict consensus tree of ten most parsimious trees of 53 species of Platystictidae plus one Lestidae (*Lestes temporalis*) (morphological dataset). The distribution of each species is given to the right of the species name. Names in blocks indicate presumed ancestral areas. Dark blocks indicate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

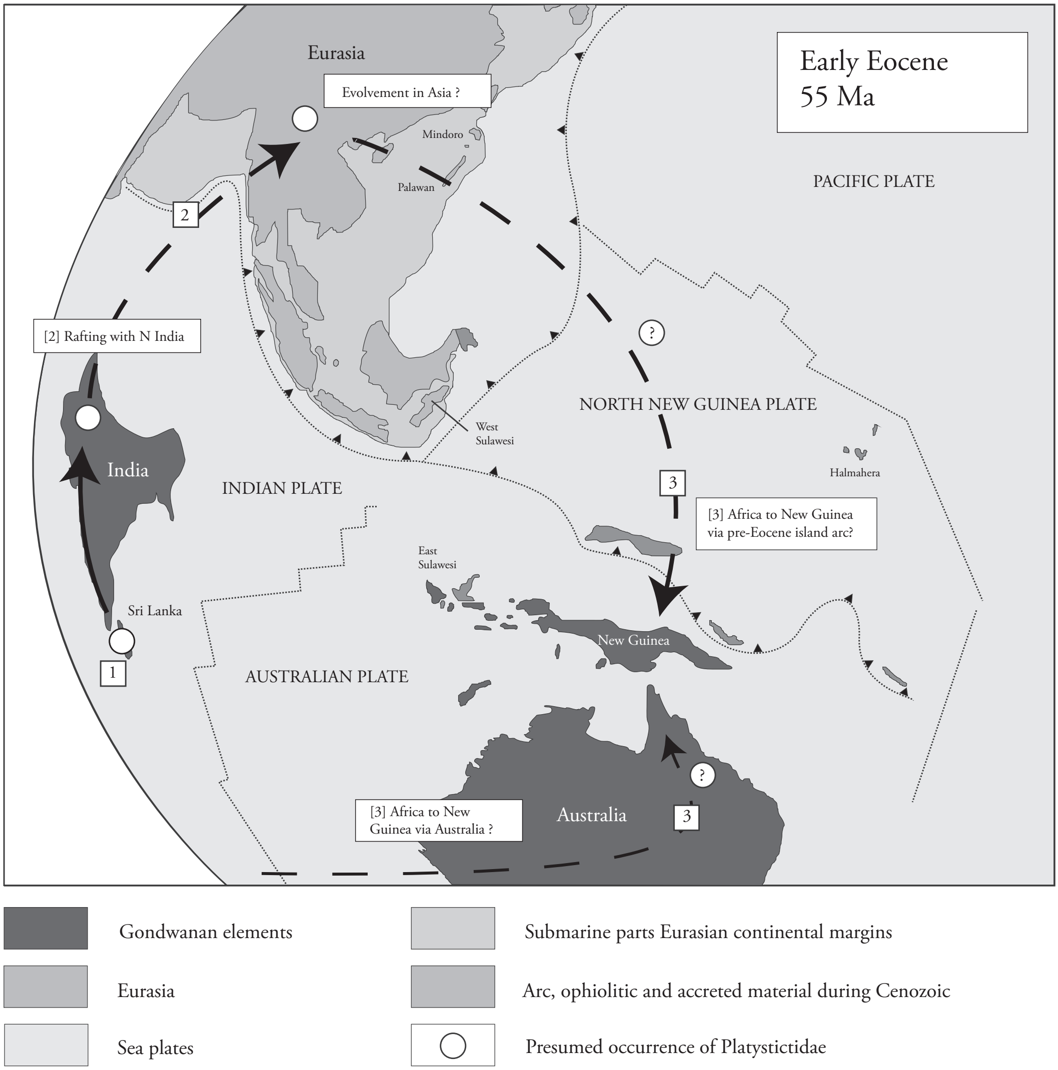

Figure 56. Distribution and dispersal events of Platystictidae during Early Eocene (see text). Geological reconstruction redrawn after Hall (2002).

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

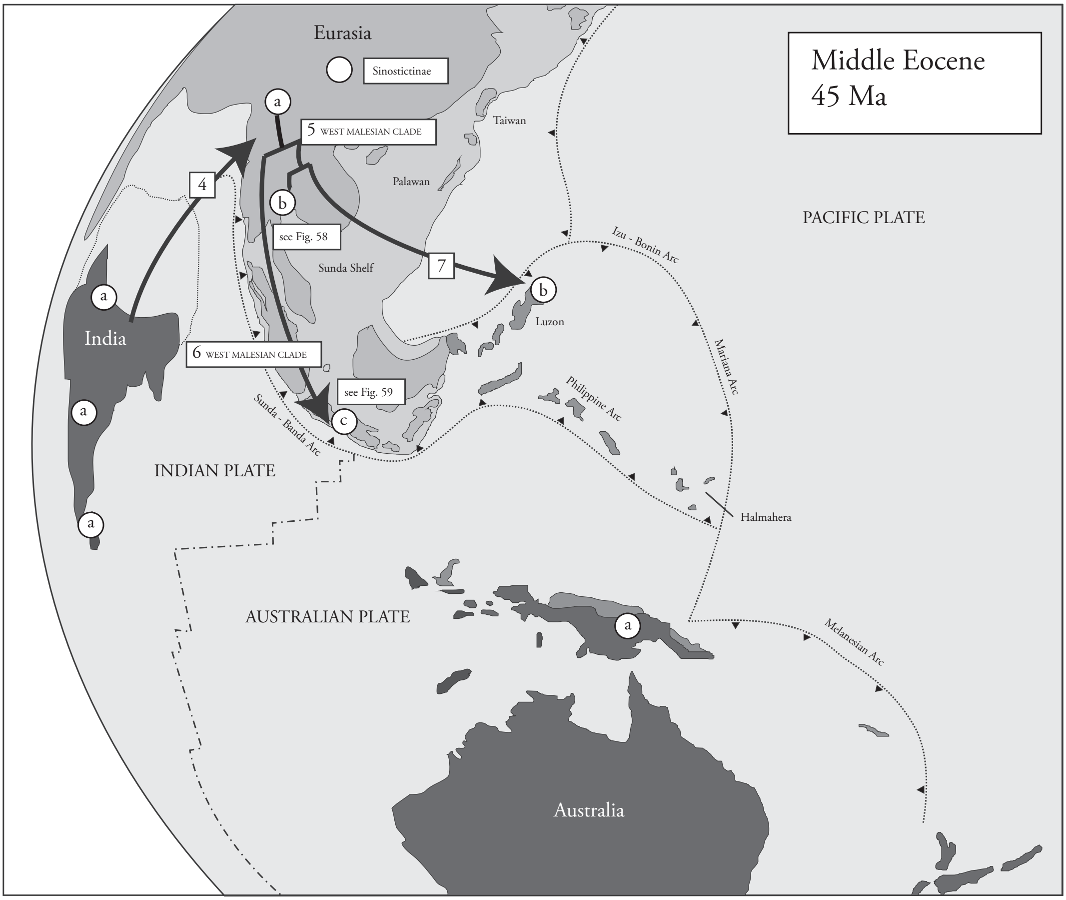

Figure 57. Distribution and dispersal events of the Platystictidae during Middle Eocene (see text). 'b' represents West Malesian Clade (WMC) and 'c' the East Malesian Clade (EMC). Geological reconstruction redrawn after Hall (2002).

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,

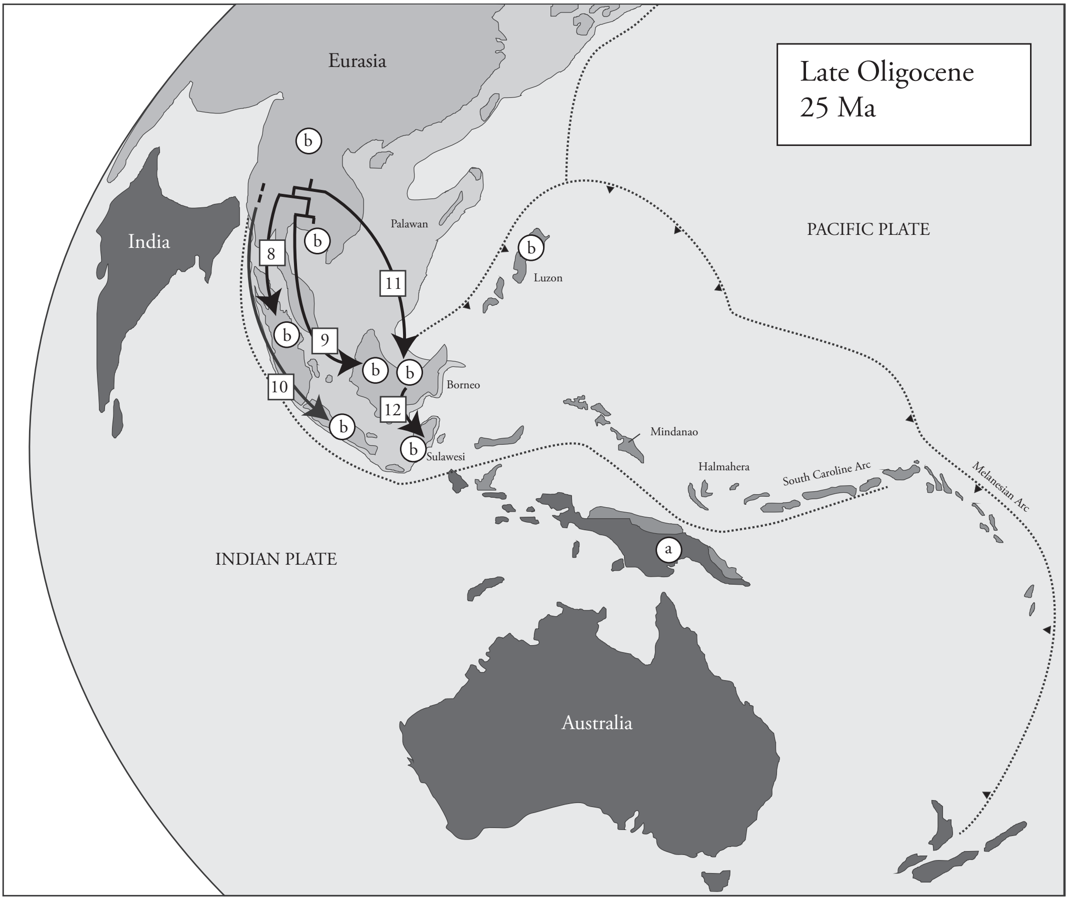

Figure 58. Distribution and dispersal events of 'West Malesian clade' (WMC) of the Platystictidae during Late Oligocene (see text). Geological reconstruction redrawn after Hall (2002).

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

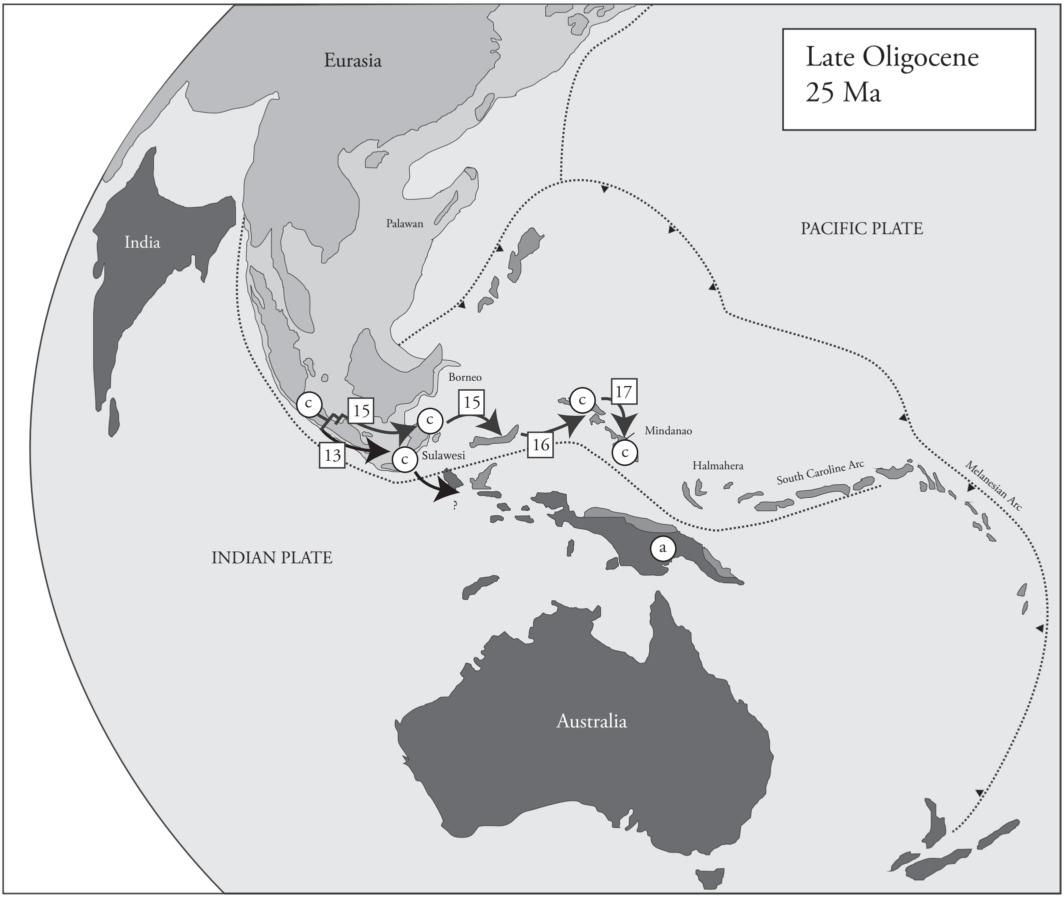

Figure 59. Distribution and dispersal events of 'East Malesian clade' of the Platystictidae during Late Oligocene (see text). Geological reconstruction redrawn after Hall (2002).

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.

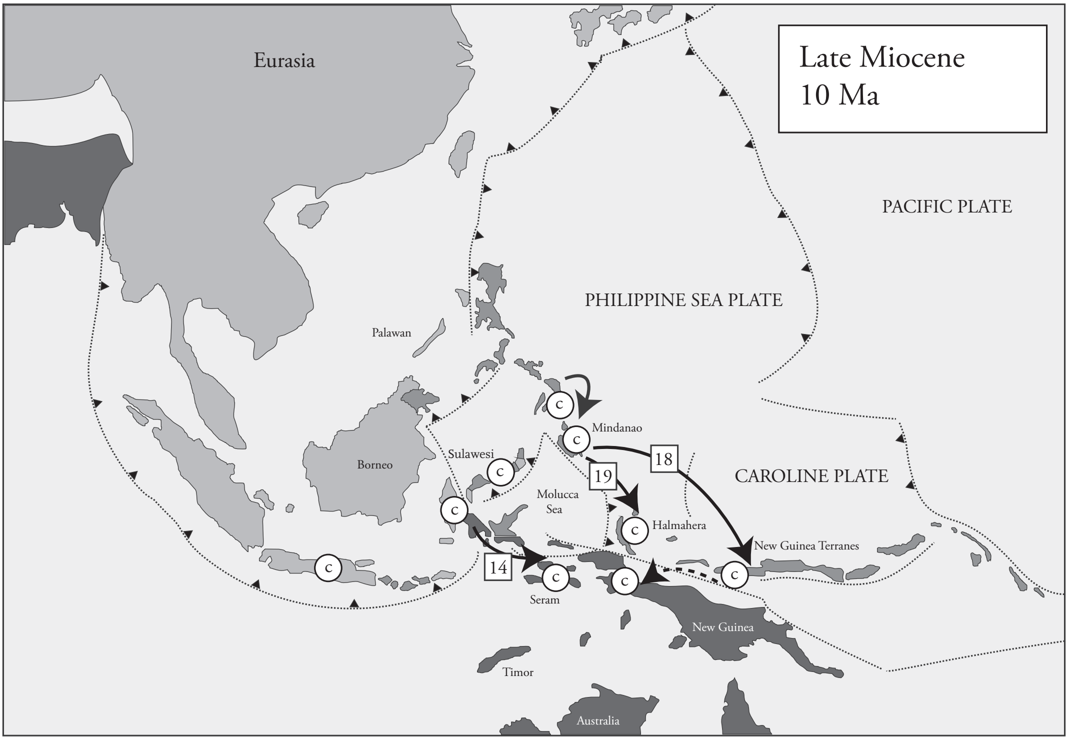

Figure 60. Distribution and dispersal events of 'East Malesian clade' of the Platystictidae during Late Miocene (see text). Geological reconstruction redrawn after Hall (2002).

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*.

2. Zoogeography of freshwater invertebrates of southeast Asia, with special reference to Odonata

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Abstract

The present knowledge of the historical biogeography of aquatic invertebrate groups is reviewed. Most orders of aquatic insects have a fossil record starting in the Early Permian, or Middle Carboniferous (Odonata), making even the break-up of Gondwana (Late Jurassic) relevant to understanding present distributional patterns.

The complex geological history of southeast Asia is summarized, and geological area cladograms presented. Biogeographical studies are seriously hampered by the limited information on subaerial history of the various islands and terranes. The historical biogeography of the Platycnemididae (Odonata), with special reference to the subfamily Calicnemiinae, is presented as one of the first examples of such a study of a widespread group. The species of southeast Asia derived from African Platycnemididae. Malesian Calicnemiinae derived from ancestors on the mainland of Asia, and may have dispersed along the Izu-Bonin Arc (40-50 Ma), or along the Late Cretaceous 'Inner Melanesian Arc' sensu Polhemus. A clade of the genera *Lieftinckia* and *Risiocnemis* (Solomon Islands and the Philippines) represents a more recent westward dispersal of the Calicnemiinae, via the Caroline and Philippine Arcs during the Oligocene.

Various other more limited phylogenetic reconstructions and biogeographical analyses of other freshwater invertebrates, particularly Odonata and Hemiptera, are discussed. Areas of endemism on New Guinea are generally congruent with geological entities recognized, e.g., the microterranes along the northern margin of New Guinea. Special attention is paid to the fauna of Sulawesi. Area cladistic reconstructions based on distribution patterns and phylogenetic reconstructions of, e.g., *Protosticta* Selys (Odonata, Platystictidae) and genera and species of Chlorocyphidae (Odonata), show a pattern of (northern arm (southwest arm – central and southeastern arm)), which is a reflection of the geological history of the island.

Biogeographical patterns recognized in freshwater invertebrates of Malesia do not principally differ from those found in strictly

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terrestrial taxa. The distribution of land and water seems to be the driving force in speciation during the Cenozoicum. It is unresolved whether rafting of biotas on the various island arcs, or congruent patterns in dispersal, are to be considered the underlying principle. The extreme habitat requirements and poor dispersal power of many species involved seem to make a dispersal scenario unlikely. However, recent studies show that such habitat specialization may develop rapidly.

> *Facts such as these can only be explained by a bold acceptance of vast changes in the surface of the earth.*
> (Wallace, 1860: 177)

1. Introduction

Recently, de Bruyn et al. (2004) found extensive genetic divergence between wild populations of the giant freshwater prawn *Macrobrachium rosenbergii* (De Man) in southeast Asia. This species of prawn occurs in the wild from Pakistan to Australia and on some Pacific islands, and it is cultured widely around the world in more than 40 countries (Mather and de Bruyn 2003). It is of high economic importance for some regions in southeast Asia, with harvesting of wild populations alone exceeding a value of US$ 800 million in 1998. In the 1990s, harvest of several stocks in culture experienced a decline, presumably due to inbreeding. Consequently, wild populations are important sources of genetic diversity to overcome inbreeding problems, but *M. rosenbergii* is rapidly declining in the wild due to overharvesting and habitat loss. Mating between specimens of different parts of the species range resulted in reduced larval survival, although heterosis (hybrid vigour) was found for other populations from the same region. Obviously, a better understanding of the genetic diversity is needed to contribute to improved aquaculture of this species. Study of the variation in 16S ribosomal DNA (de Bruyn et al. 2004) proved to be successful in describing the evolutionary relationships in this species, and supported previous allozyme and morphological work that had identified an eastern and a western form (Holthuis 1995). The boundary between both 'forms' proved to be Huxley's (1868) line (Fig. 1), the biogeographically based division of the Oriental and Australian regions running between Palawan and the rest of the Philippines in the north, then southward between Borneo and Sulawesi (Celebes), and between Bali and Lombok. It only differs from Wallace's (1863) line in the position of the Philippines. Recent data, based on morphological studies, show that the distribution of these species differs in details from a division as by Huxley's line (Wowor 2004, cf. Fig. 1). While it may be true that not all lack of knowledge on the zoogeography and phylogenetic relationships of species has similar economical implications as the example of *M. rosenbergii*, it may serve as an example that the historical relationships of aquatic invertebrates and their distributions are still poorly examined even for better known species. It may also demonstrate that phylogenetic and biogeographical understanding is not only a scientific problem, but may also have practical, e.g., economic, consequences.

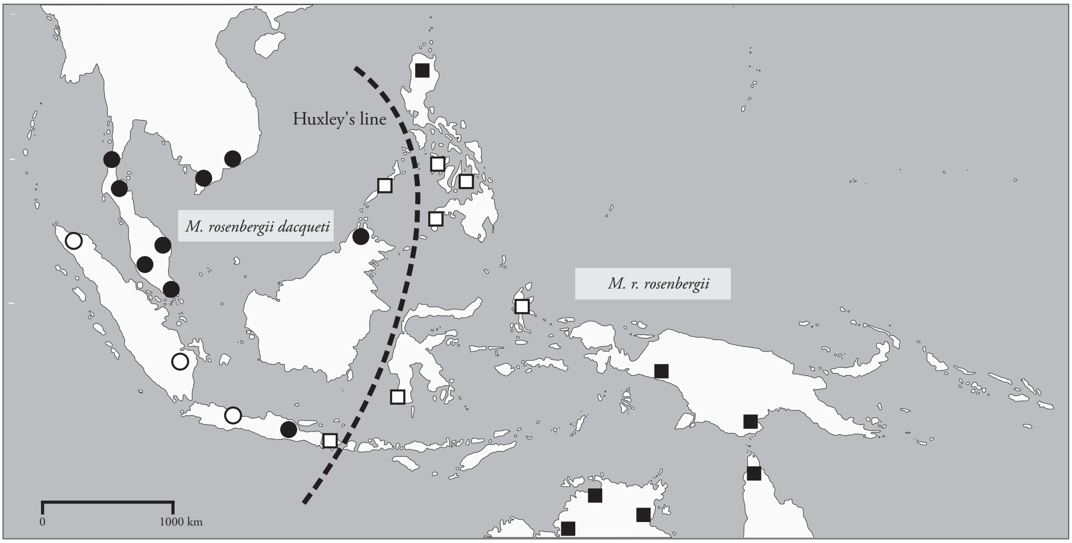
The example of *Macrobrachium* also raises another issue, namely the mechanism or mechanisms by which present patterns have evolved. Based on current knowledge of the palaeogeography of the region, island-hopping along terranes or island arcs during the Cenozoicum has been hypothesized to explain the present patterns in some groups. Such a mechanism may seem likely for groups such as birds, butterflies, cicadas, and can even be defended for mostly aquatic groups with a terrestrial adult stage such as the caddisflies. However, such a mechanism seems less likely for prawns such as *Macrobrachium*, although they are also known from some Pacific islands. *M. rosenbergii* has a tolerance for salt, which potentially increases the dispersal power, but distribution patterns of marine organisms in the Indo-West Pacific are typically related to patterns of ocean currents (Briggs 1974; Hoeksema this volume). A study at the molecular level could possibly unravel whether 'human-mediated dispersal' may have played a role (Diamond 1988). A similar unlikely distribution pattern was studied by Austin (1999) in the lizard *Lipinia noctua* (Lesson), which does occur in human settlements, and was probably transported in canoes by the Polynesians as far as the Marquesas Islands, Tuamotu and Hawaii.

In this paper we will examine the distribution patterns of aquatic invertebrates in southeast Asia, especially in relation to the geological history of the region. The historical relationships and the present distributions of most groups of aquatic invertebrates are insufficiently known to follow the example of Turner et al. (2001) in reconstructing generalized area cladistic relationships based on aquatic invertebrates. We here present a summary of the much-scattered knowledge of various taxonomic groups, and also demonstrate the congruences of various area cladograms based on reconstructions of phylogenies as compared to palaeogeographical reconstructions. Special attention will be paid to Odonata, the dragonflies and damselflies. New data are available for this order of insects, especially those obtained by the junior author for the calicnemiine Platycnemididae. We will also summarize results of some more limited studies of the senior author and others. Finally, the data from aquatic invertebrates will be compared with present knowledge of the area relationships obtained from other groups.

Schuh and Stonedal (1986), and more recently Turner et al. (2001), tried to reconstruct the historical biogeography of the southeast Asian region. Turner et al. used such diverse groups as plants of the families Sapindaceae, Euphorbiaceae, and Rubiaceae, and insects including cicadas (Homoptera, Cicadidae), semiaquatic bugs (Hemiptera, *Haloveloides*, *Halobates*, *Halovelia*, and *Xenobates*) and several genera of beetles. Although the examples were selected for carefully reconstructed phylogenies at the species level and detailed information on distribution, the 'general patterns that emerged were weakly supported and [did] not allow general conclusions'. The authors did not analyse why the reconstruction failed, but they described the complicated geological history of the region, and mentioned the process of active dispersal of biotas along island arcs.

The geological history of southeast Asia is one of the most complicated on earth. Reconstructions of the palaeogeography of the region since the Mesozoicum have been the subject of several research groups (e.g., Hall 1998, 2001, 2002; Hamilton 1979; Hill and Hall 2003; Kroenke 1996; Rangin et al. 1990; Yan and Kroenke 1993) and have thus greatly improved in details, but information on the scale necessary for biogeographical studies of terrestrial organisms is still scarce. It is, for instance, still poorly known which areas

Figure 1. Distribution of *Macrobrachium rosenbergii* (de Man) and *M. dacqueti* (Sunier) in southeast Asia (black symbols, after de Bruyn et al (2004); some essential records from Wowor (2004) with open symbols).



were submerged for a shorter or longer period of time during their history. And, although it is known that some islands in the region have moved along the Pacific or Philippine plates over a long distance during the last 10-15 My, their positions during this period differ significantly between the various studies. The analysis is further complicated by island arcs of the past that have been (nearly) fully absorbed by plate movements later in the geological history. We will describe present knowledge of land masses, microcontinents and island arcs as far as relevant for the present study. Since many extant families of some insect orders, e.g., the Odonata, are already known since the Jurassic, even details of the break-up of Pangaea are relevant. The palaeogeography of the Cenozoicum of the Malay archipelago and the West Pacific is described in more detail to enable comparison of the area cladograms at the generic or species group level in selected families.

2. History of aquatic invertebrates

It may be questioned how far a geological history may be traced back in patterns of extant taxa. Is it reasonable to reconstruct distributional histories of groups from as long ago as the break-up of Pangaea? Apart from knowledge of palaeogeography, it is necessary to know how long families, or even genera and species, have existed. Since estimates based on molecular data are sparse and their reliability under discussion, we are dependent on data of the fossil record up to now.

Several observations indicate that even species may persist for many millions of years. Kathirithamby and Grimaldi (1993) mention a record of *Bohartilla megalognata* Kinzelbach, an extant species of Strepsiptera, from the Miocene Dominican amber (20 Ma), while Rasnitsyn (2002) mentions that such examples are even available for Baltic amber (*c.* 40 Ma). It is generally known that the fossil record is incomplete and biased. Carle (1995), for instance, discussed the overwhelming abundance of dragonflies of lentic habitats in the fossil record, while most species of extant anisopteran families are obligate inhabitants of streams and seepage areas. Such species are, however, rarely preserved as fossils, since they have small population sizes and their habitats are less suitable for preservation of fossil specimens. Since small stream habitats have permanently existed at least since the Jurassic, the inhabitants of this habitat have been able to survive up to today without significant morphological change, while faunas of lentic habitats became extinct when ponds and lakes dried up. Consequently, when a new lentic habitat developed, the settlement of other biotic lineages provided new opportunities for local evolution.

Here we will examine the data of the age of various groups of invertebrates, especially insects, based on the fossil record. The affinities of the orders of the Insecta have recently been extensively discussed by Wheeler et al. (2001), while Rasnitsyn and Quicke (2002) provide a thorough summary of the knowledge of the geological history of the insect orders. Sinitshenkova (2002b) provides a summary for the aquatic insect orders in chronological order, including an interpretation in ecological context.

Many orders of aquatic insects, or at least those with aquatic larval stages, are known in the fossil record as early as the Early Permian, namely in the terminology of Rasnitsyn and Quicke (2002), Ephemerida, Hemiptera, Coleoptera, Neuroptera, and Trichoptera. The earliest fossils are those of Libellulida (i.e., Odonata) from the middle Carboniferous (*c.* 325 Ma). Somewhat later in the fossil record appear the Corydalida and Perlida (i.e., Plecoptera), from middle Permian (c. 299-250 Ma), while the Diptera are not known from the Palaeozoicum, but only from the Middle Triassic (*c.* 228-245 Ma) onwards. We do not discuss extinct orders with aquatic stages in the present context.

Not only many of the present orders, but also many extant superfamilies have a long geological record, and are known from the Mesozoicum. Most superfamilies of the Odonata are recorded from the Late Jurassic or Early Cretaceous (150-135 Ma) (Rasnitsyn and Pritykina 2002). New studies of fossils show that all superfamilies of the Odonata had developed before the Cretaceous (135 Ma). Various extant families of the suborder Calopterygina are known from the supercontinents Gondwana (Brazil) as well as from Laurasia (England) from that period.

For the other groups of aquatic insects that will be discussed below, the following data are available.

Ephemerida (i.e., Ephemeroptera). Several superfamilies (Oligoneuroidea, Ephemeroidea, Leptophlebioidea) are known from the Early Cretaceous (Kluge and Sinitshenkova 2002).

Perlida (i.e., Plecoptera). A group with many plesiomorphic characters. Fossils are uncommon in most deposits, since virtually all species are rheophilic and such species hardly enter the fossil record (see above). The oldest fossils known are Permian (c. 299-250 Ma) (Sinitshenkova 2002a). Recent families seem to be much younger. Nemouridae are only known from the Early Cretaceous. Permian stoneflies were widely distributed and are known from both the northern and southern hemisphere, including Australia, South Africa, and Antarctica. Stoneflies were common during the Jurassic.

The superfamilies of the aquatic hemipteran infraorder Nepomorpha all appear in the fossil record in the Late Triassic (*c.* 210 Ma), while the earliest Gerromorpha (semiaquatic water bugs of the superfamily Hydrometroidea) are known from the Early Cretaceous (Shcherbakov and Popov 2002). Fossils from the Santana formation of Brazil indicate that all modern families of Heteroptera had evolved by at least the Cretaceous (D.A. Polhemus, personal communication, 2005).

Although the order Trichoptera is known from the early Permian onwards, extant families appear later in the fossil record, e.g., Rhyacophilidae from Middle Jurassic, and most other groups even much later (e.g., Hydropsychidae from the Eocene, *c.* 50 Ma, only) (Ivanov and Sukatsheva 2002).

In summary, the fossil record indicates that most groups of insects had developed as early as 150-200 Ma. During the break-up of Gondwana, that started in the Late Jurassic (*c.* 152 Ma) (cf. McLoughlin 2001), but continued in more extensive form during the Cretaceous, most families here under discussion were represented.

3. Geological history of southeast Asia

3.1. Geological history of the southeast Asian continent, the Malay Archipelago, and the West Pacific

Since most groups had developed as early as the end of the Palaeozoicum, much of the present knowledge on the geological history of the region is relevant for the reconstruction of the history of present distributions. The study of the geological and tectonic evolution of southeast Asia has been intensified during the last decades. Various summarizing papers, also by biogeographers, are available, and an intriguing picture is emerging of the historical relationships of the presently existing land masses. The summary below will focus on the general patterns and on some details relevant for the distribution patterns of groups discussed. Few regions of the earth have changed so dramatically as southeast Asia during the last 100 My. Besides, this process of rapid change continues up to today. Not more than 10 Ma the position of the island of Halmahera (Moluccas) was northeast of the Bird's Head Peninsula of New Guinea, and Halmahera approximately had the position of Manus Island today by the end of the Oligocene (25 Ma) (Hall 2002: 407, see also Fig. 4). These data add a new dimension to our understanding of the evolution of the present distribution patterns of biotas. After our summary of the palaeogeography, the historical relationships of the various 'areas of endemism' based on the geological reconstructions are discussed. These relationships are described in a so-called geological area cladogram.

3.2. Mesozoicum

By the end of the Permian (250 Ma) the continents were still connected as Pangaea. Several slivers of continent rifted northward towards Eurasia forming the Palaeotethys (between North China and the Cimmerian continent) and the Mesotethys (between the Cimmerian continent and the still connected continental parts of, e.g., Birma at southern latitudes) (Metcalfe 2001). The Cimmerian continent included the so-called Sibumasu terrane, now forming parts of

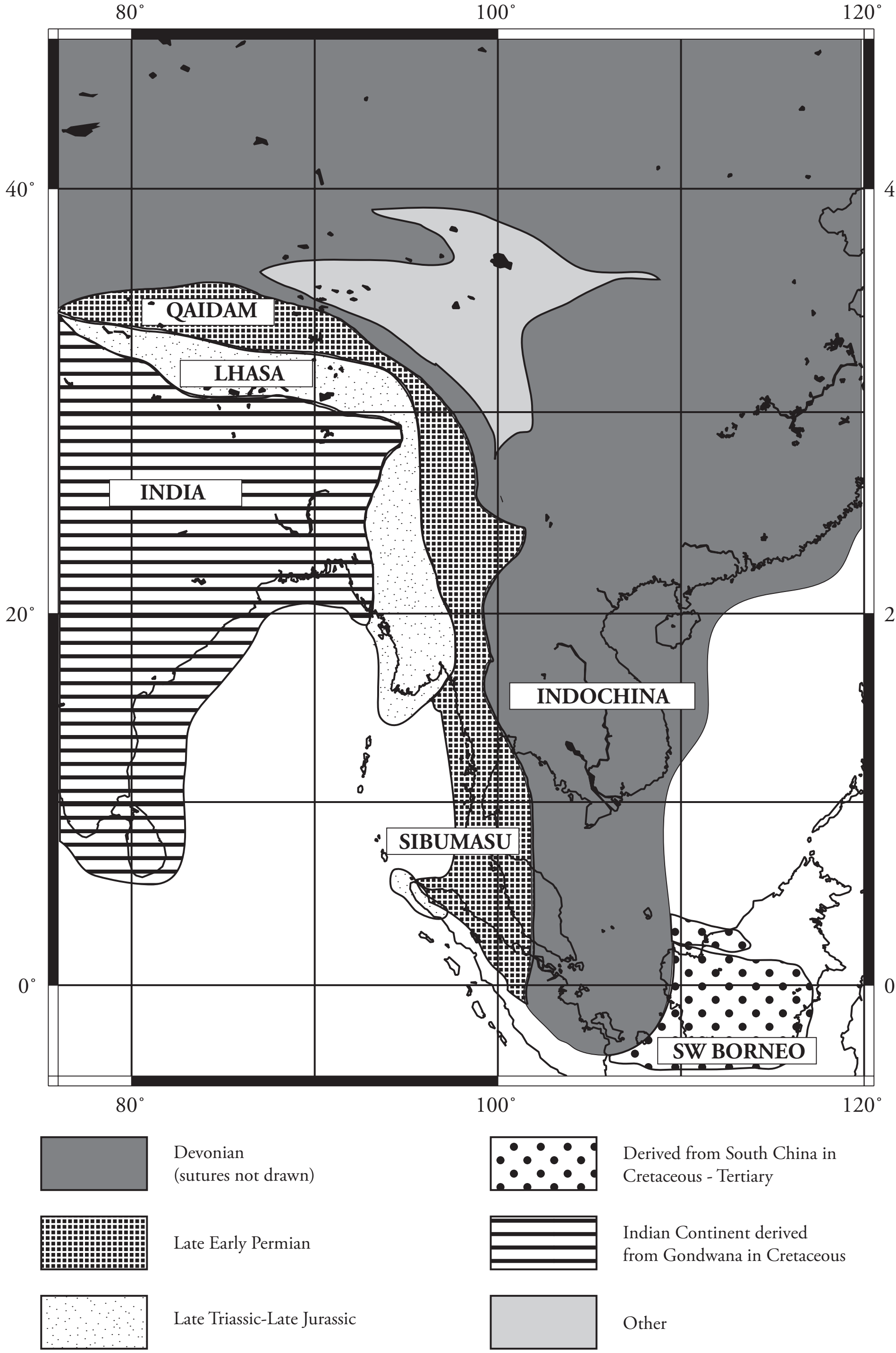


Figure 2. Distribution of principal terranes of east and southeast Asia. Sutures, especially of Devonian age, not indicated (simplified after Metcalfe 2001)

Thailand, the Malay Peninsula, and northern Sumatra (Fig. 2). The Sibumasu terrane amalgamated with Indochina and South China during the Triassic (200-250 Ma). Based on the fossil record, it is presumed that this terrane has had a history above sea level since the Triassic. Another sliver of continent or arc of terranes, including Lhasa, West Burma, and Western Sulawesi, was separated from Gondwana during the late Triassic, opening the Ceno-Tethys. These terranes accreted to the Sibumasu terrane during the Cretaceous. Southwestern Borneo had a position at the southeastern margin of the Eurasian continent at least since the Jurassic.

India (with Madagascar and the Seychelles) became isolated from Africa at *c*. 130 Ma, wherafter India and the Seychelles separated from Madagascar 88 Ma (cf. Bossuyt and Milinkovitch 2001). Eruption of the Deccan flood basalts resulted, among other things, in the separation of India and the Seychelles block at *c*. 65 Ma (Braithwaite 1984; McLoughlin 2001). The Seychelles block became fixed to the African continent from that time. Only during the collision of India with the southern Asia continent (between 65 and 56 Ma, but according to McLoughlin (2001) *c*. 43 Ma), the southeastern corner of Asia with Indochina and the former Sibumasu terrane turned clockwise to its present more north–south orientation.

Australia separated from Gondwana at *c*. 85 Ma and rifted northward (Metcalfe 2001; Hill and Hall 2003). The northern margin of the Australian plate included at least the southeastern parts of present-day Sulawesi, Buton, Buru, Seram, as well as parts of New Guinea. During the process of rifting during the Cretaceous, a series of continental slivers became isolated along the passive northern margin. Some of these fragments are now part of the Central Highlands of New Guinea. This series of fragments is known as the 'Inner Melanesian Arc' in biogeographical studies, and further discussed below under Cenozoicum, since it was presumably absorbed with the northern margin of the Australian craton during the Eocene.

3.3. **Cenozoicum**

The geological evolution of southeast Asia during the Cenozoicum has been extensively studied and discussed by Hall and collaborators (e.g., Hall 2001, 2002) and with special attention to the northern margin of the Australian continent by Hill and Hall (2003). Hall's reconstructions, and particularly the terminology, are not fully congruent with those of Yan and Kroenke (1993) and Kroenke (1996) for the West Pacific region. Quarles van Ufford and Cloos (2005: Fig. 2) summarize the different models for the Cenozoic plate-tectonic history of New Guinea, while also providing a new summary of the tectonic evolution. The Cenozoic palaeogeography of the region in relation to biogeographical problems has also been discussed various times (Beuk 2002b; Soulier-Perkins 2000).

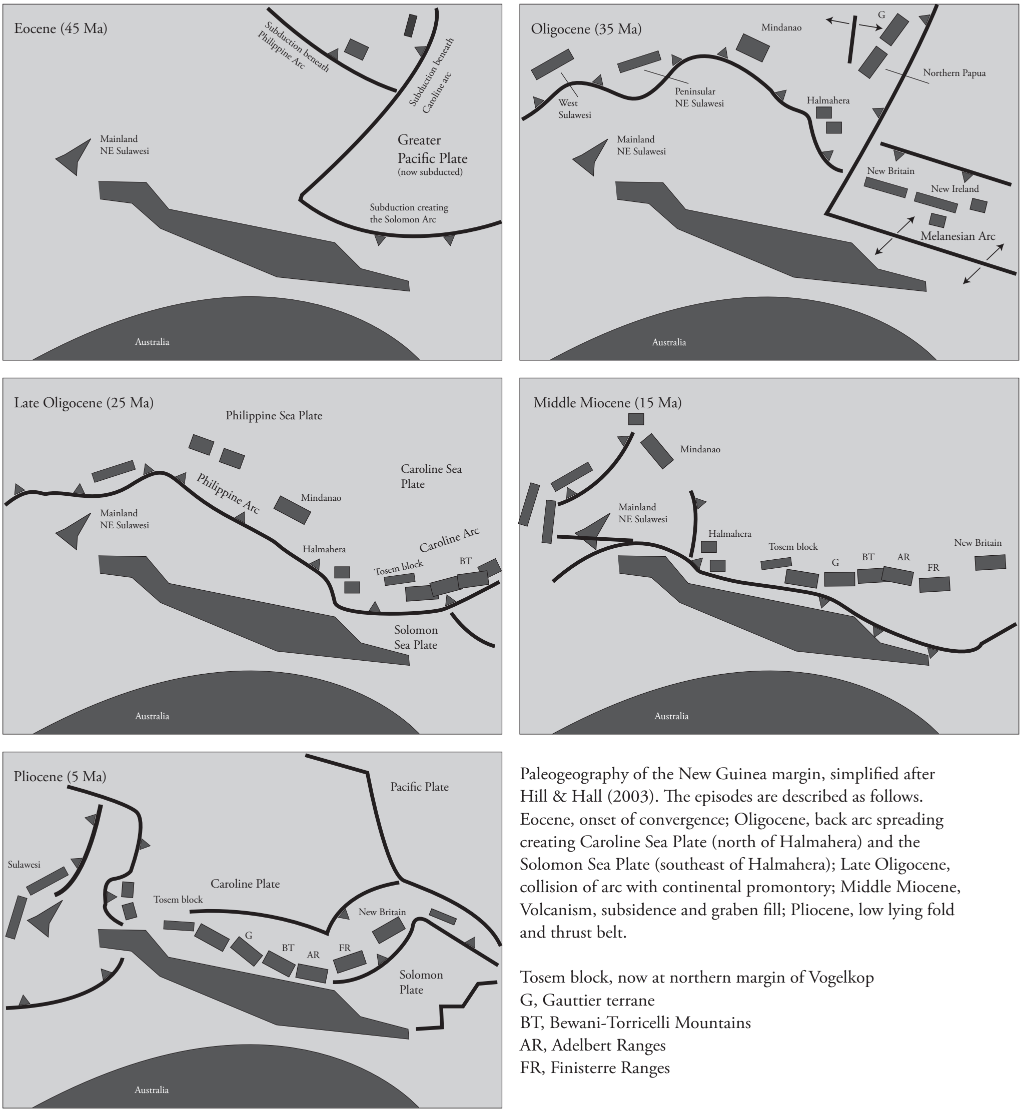
The geological history of smaller parts of this region in relation to biogeography has been analysed, e.g., southeast Asia, Borneo and Sulawesi (Moss and Wilson 1998). the Philippines (de Jong 1996), the West Pacific (Keast and Miller 1996; de Boer 1995, de Boer and Duffels 1996, 1997), or with special emphasis on New Guinea (e.g., Polhemus and Polhemus 1998, 2002).

The general pattern arising from recent reconstructions can be described as follows. The collision of India with the southern margin of the Asian continent significantly changed the structure of that area between 65 and 56 Ma. The collision resulted in the orogeny of the Himalayas. It may have increased the land surface as well, but the amount of crustal shortening is unknown. Recent data (Krause et al. 1999; Bossuyt and Milinkovitch 2001) suggest that the fauna that developed in India during that time has spread over the Oriental region since *c*. 60 Ma. The northward movement of Australia towards the Pacific plate that started 85 Ma has continued with relatively slow speed up to today, although the separation of Australia from Antarctica at *c*. 55 Ma increased the rate of convergence. From *c*. 43 Ma (Quarles van Ufford and Cloos 2005), a southwest directed subduction of the Pacific plate started two subduction systems, one at the Papuan–Rennell–New Caledonian trench system, and a more northerly subduction zone at the New Guinea–Manus–Kilinailau–Solomon trench system. Several arc systems were formed during subduction and rotation of the plates (see discussion below for

Figure 3. Palaeogeographic reconstruction of southeast Asia at 45 Ma (Middle Eocene) (from Hall, 2002). Note the position of southwestern Sulawesi approximately at its present position, of East Sulawesi at the northwestern corner of the Australian plate, and of northern Sulawesi at the margin of the Australian and the Philippine plates in an island arc with the east Philippines and Halmahera. The collision of the parts of Sulawesi only occurred during the Middle to Late Miocene (15-10 Ma).

more detailed geology of the New Guinea region). A subduction at the western margin of the Pacific plate, north of the equator, formed the Izu-Bonin–Mariana Arc system, while at the same time the Philippine plate became a separate entity between the Australian and Pacific plate. The Philippine plate itself has a 'complex rotation history' (Hall 2002: 378), with a rotation of 50° between 50 and 40 Ma (Fig. 3), whereafter a period without rotation continued up to 25 Ma.

The most important reorganization of the plate boundaries occurred at *c*. 25 Ma (Hall 2002). The New Guinea passive margin collided with the East Philippines–Halmahera–South Caroline Arc system, and the northwestern corner of the Australian plate collided with southeast Asia in the Sulawesi area. From that time on, the Pacific plate became the driving force of the regional tectonic events. The northward movement of Australia caused the accretion of microcontinents north of New Guinea. The final large change in the tectonics of the region, possibly due to



Paleogeography of the New Guinea margin, simplified after Hill & Hall (2003). The episodes are described as follows. Eocene, onset of convergence; Oligocene, back arc spreading creating Caroline Sea Plate (north of Halmahera) and the Solomon Sea Plate (southeast of Halmahera); Late Oligocene, collision of arc with continental promontory; Middle Miocene, Volcanism, subsidence and graben fill; Pliocene, low lying fold and thrust belt.

Tosem block, now at northern margin of Vogelkop
G, Gauttier terrane
BT, Bewani-Torricelli Mountains
AR, Adelbert Ranges
FR, Finisterre Ranges

Figure 4. Tectonic evolution of the New Guinea region (after Hill and Hall, 2003).

motion change of the Pacific plate, occurred at *c.* 5 Ma, with significant impact in the Taiwan–Philippine region, and uplift in southern Indonesia (Java to the Lesser Sunda islands).

Whether the events described above are relevant to the present distribution of freshwater invertebrates mainly depends on whether the area was subaerial for all the time. Although much new information has become available during the last 20 years, there is still much controversy. Examples are the palaeogeographic evolution of Sulawesi (Wilson and Moss 1999) and of the Melanesian Arc. Sulawesi consists of a complex of fragments that only merged into its present position during the last 5 My. The southwestern arm is considered a part of the Asian continent, with the same position in relation to Borneo for at least *c.* 45 My. East Sulawesi originated in the northwestern corner of continental Australia, probably as early as the Early Eocene (56-49 Ma) (Hall 2002, see also Fig. 3). The northern Sulawesi arm was formed much further north at the northern margin of the northward moving Australian plate in an island arc with the eastern Philippine islands at *c.* 45 Ma (Philippine Arc). It possibly docked with the southwestern arm in the Early Oligocene (34-29 Ma; Wilson and Moss, 1999), but alternatively as late as the Middle Miocene (*c.* 15 Ma) (Hill and Hall 2003). With the opening of the Celebes Sea (Early Oligocene, 34-29 Ma) the western part of the Philippines shifted to a more northern position, while on the clockwise rotating Philippine plate parts of the eastern Philippines moved more towards their present positions. The northwest movement of the Australian plate slowly pushed the central and southeastern parts of Sulawesi towards their present positions. The relatively fast rotation of the Philippine plate caused a rapid change of positions of the islands along its margin (eastern Philippines, Halmahera) during the Miocene. According to Wilson and Moss (1999) the eastern arms of Sulawesi collided with central Sulawesi in the Early Miocene (23-16 Ma), but Hill and Hall (2003) reconstructed a Pliocene collision of these island fragments (Fig. 4).

Along the subduction zones and partly induced by turning of the plates, several island arcs were formed, displaced, and (partly) accreted or subducted again. During the Eocene (56-34 Ma), the area converged due to northward movement of the Australian plate. While the Australian plate subducted under the Philippine plate, the Philippine Arc was formed. At least during the Oligocene (34-23 Ma), while this zone was running more or less west to east, this island arc included from west to east peninsular northwestern Sulawesi, Mindanao, and Halmahera, including other parts of the Moluccas. Also during the Eocene, along the eastern margin of the Philippine Plate the north–south oriented Caroline Arc was formed at the collision zone with the Greater Pacific Plate. Due to backarc spreading during the Oligocene creating the Caroline Sea Plate, this island arc, consisting of fragments now part of northern New Guinea, started a nearly 90° clockwise movement. A third island arc, the Melanesian Arc, was created at the southern margin of the Pacific Plate at the subduction zone with the Australian plate. This process intensified during the Oligocene due to backarc spreading, creating the Solomon Sea Plate. Around 25 Ma, the Philippine Arc and the Caroline Arc were more or less in line at the northern margin of the Australian and Solomon Sea Plates, while still rapidly rotating clockwise. From the Miocene onwards, the Melanesian Arc formed a continuation of the Caroline Arc in eastern direction. These island arcs or island groups are considered relevant in biogeographical analysis. At *c.* 30 Ma the South Caroline Arc consisted of (from west to east) the Tosem Block (now northern Vogelkop), northern Papua (Irian Jaya), the Gauttier terrane, the Bewani–Torricelli Mountains, the Adelbert ranges, and the Finisterre ranges (Hill and Hall 2003), and was situated northeast of the Australian continent (Fig. 4). The Melanesian Arc consisted of New Britain, New Ireland, and then to the south, the Solomon Islands, Vanuatu, Fiji, and Tonga (Hall 2002; Hill and Hall 2003). In a previous reconstruction, based on Hall (2002), Beuk (2002a) included central New Guinea, the Papuan Peninsula, northern New Guinea, Finisterre, and Bismarck/New Britain in the Caroline Arc, while the Melanesian Arc started south of New Britain with New Ireland.

Polhemus (1995) and Polhemus (1998) mentioned additional hypotheses on island arc systems in analysing the distribution patterns of aquatic insects with sister-group relationships between the Philippines and New Guinea, while not occurring in the Moluccas and Sulawesi. The reconstruction of this ‘Inner Melanesian Arc system’ is partly visible in Yan and Kroenke (1993). This must have been a pre-Eocene, presumably Cretaceous, ‘arc’ extending from Mindanao, a section of northern Australia that later became New Guinea, the Solomon Islands, and New Caledonia to New Zealand. Parts of this arc now may have a position in the highlands of New Guinea. The ‘arc’ collided with the northern Australian continental plate during the Mesozoicum. Technically, the Inner Melanesian Arc cannot be considered an arc system, but a series of slivers of continental crust that became isolated during the process of rifting along the northern Australian margin (Polhemus 1998). Recently, the name ‘Inner Melanesian Arc’ was used by Quarles van

Ufford and Cloos (2005) for an Eocene–Oligocene Arc including the Bewani–Torricelli Arc, the Papuan ophiolite belt, and (much further to the south) New Caledonia. In a more recent publication, Polhemus and Polhemus (2002) relied more on Hall (1998) for their palaeogeographic interpretations, but their terminology is different from Beuk (2002a).

3.4. **Geological area cladogram**

A geological area cladogram was first presented for the West Pacific by de Boer (1995), and further elaborated by de Boer and Duffels (1997) and Beuk (2002a, b) (Fig. 5). The area cladograms were based on the geological reconstructions of southeast Asia by Daly et al. (1991), Pigram and Davies (1987), and Rangin et al. (1990), and several papers describing the history of smaller parts of the area.

Three island arcs were distinguished, namely the West Pacific Arc (from west to east consisting of central Philippines, northern/eastern Sulawesi, central New Guinea, Papuan Peninsula, northern New Guinea, Finisterrre, Bismarck archipelago, northeastern Solomons), the eastern Philippine–Halmahera Arc (from north to south consisting of eastern Philippines and the Halmahera Arc, and possibly also the Marianas and Yap), and the Southwest Pacific Arc (from north to south consisting of Solomon Islands, Vanuatu, Fiji, and Tonga). Most areas in the island arcs coincide with areas of endemism for cicadas (Homoptera, Cicadidae) (Beuk 2002a: 248). Particularly the West Pacific Arc is believed to be relevant for the dispersal of many groups of animals. It should be realized that several parts of the area did not belong to any of the arcs, but were a group of microcontinents with a history more connected with Australia. Beuk (2002a) presented an update of this view. He considered the eastern Philippines and Halmahera not related to an arc system. His South Caroline (as Carolina) Arc system (at *c*. 30 Ma, late Oligocene) consisted from west to east of central New Guinea, Papuan Peninsula, northern New Guinea, Finisterre, Bismarck, and New Britain, while the north–south oriented Melanesian Arc consisted of Bismarck/New Ireland, Solomon Islands, Vanuatu, Fiji, and Tonga. The timing of the fragmentation sequence is also given in Fig. 5.

According to the reconstructions by Hall (1998, 2001, 2002) and Hill and Hall (2003) the geological history of the Philippines and Sulawesi is more complex than that presented by Daly et al. (1991). Especially the position of Luzon is distinctly different, since it was formed at the northern margin of the Philippine plate by southward subduction of the Pacific plate at 45 Ma. The southwestern peninsula of Sulawesi is supposed to have the same position in relation to Borneo since at least the Middle Eocene (45 Ma). The northern peninsula was part of an island arc at the southern margin of the West Philippine Basin, while the eastern peninsula had a position on the westernmost part of the Australian plate (see Fig. 3).

The present reconstructions (Hill and Hall 2003) differ in various ways relevant to biogeographical analysis.

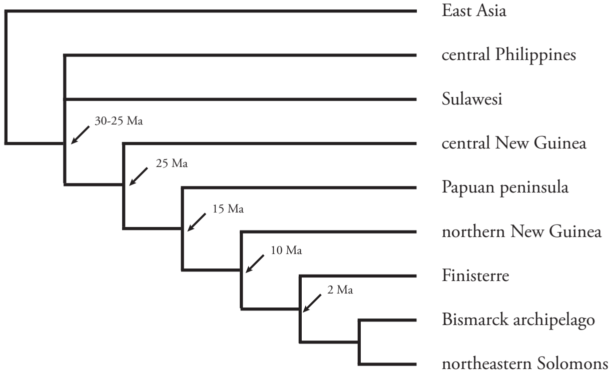


Figure 5. Geological area cladogram of southeastern Asia (from Beuk, 2002).

First, the Philippine Arc (Mindanao, Halmahera) continued to the west with peninsular northeastern Sulawesi at least during the Oligocene (35 Ma). This island arc continued to the east in the Melanesian Arc, where the Moluccas and New Britain seem to have had a position rather close to each other during the Oligocene. The Caroline Arc formed the continuation of the Philippine Arc to the north at the subduction zone of the Great Pacific Plate. Due to backarc spreading creating the Caroline Sea Plate, mentioned above, the Philippine Arc and the Caroline Arc more or less formed one arc system during the Late Oligocene (25 Ma). The Melanesian Arc began to form one line with the Caroline Arc during the Miocene. The counterclockwise rotation of New Britain and New Ireland was induced by the spreading of the Solomon Plate during the Pliocene only.

4. **Distribution patterns**

4.1. **Introduction**

Very few revisions with an extensive cladistic reconstruction of the phylogeny of aquatic groups are available for southeast Asian taxa, and such examples are uncommon even if all terrestrial biotas are considered (see Turner et al. 2001 for an overview). It is, therefore, not feasible to construct a generalized area cladogram based on aquatic taxa. We even doubt whether the construction of a generalized area cladogram as presently used is methodologically sound for an area as southeast Asia with reticulate relationships of areas of endemism. It is necessary to estimate the timing of splitting events in the original cladograms based on independent data. Geological evidence of minimum ages of areas of endemism may reveal molecular clock data for splitting events in various taxonomic groups. Such data are needed, since effects of random dispersal, local extinctions, vicariance events without splitting of lineages, apart from the usual incertainties in phylogenetic trees based on misinterpretations of homologies, will disturb the process of construction of a generalized area cladogram. As has been noticed before in other words, a taxon can only belong to one historical entity, but an area may be part of more than one entity. This may be due to amalgamation, splitting, or displacement of the area under study as compared to another area.

For an area for which so few cladograms are available, not all of them are equally useful. To resolve area relationships, it is minimally needed to study the taxonomy and phylogeny of a group of predominantly parapatric taxa. So, even when well-founded phylogenies have been published, some studies are hardly useful in the reconstruction of area relationships. Up to now, more extensive phylogenies have been published for several groups of aquatic Hemiptera of southeast Asia (Andersen 1991, 1998, Damgaard et al. 2000, Damgaard and Zettel 2003, Polhemus, 1994, 1996, Polhemus and Polhemus, 1987, 1988, 1990, 1994, 2002). For some insect orders, e.g., the Plecoptera, the phylogenetic relationships of the families seem to be intimately connected with the break-up of Pangaea, and various examples have been included below.

The methodology of direct comparison between palaeogeography and phylogenetic relationships is not uncontroversial. Eskov (2002) discussed the ‘Gondwanan’ ranges of recent taxa. He mentioned several examples of presumably Gondwanan groups, which appeared to have representatives in the fossil record of Eurasia or North America. Consequently, such present-day ‘Gondwanan’ groups are only relics of a wider, possibly even global distribution, which may or may not have included Gondwana during its break-up. In conclusion, reconstructions in zoogeography have to be based on all available evidence (total evidence tree).

The main order of this chapter is taxonomical, but papers with special attention for the Sulawesi fauna will be discussed in section 4.4.

4.2. **Odonata**

4.2.1. *Odonata: Ancient families as ‘Gondwanan’ elements in Australia and South America*

As the oldest extant group of pterygote insects, it may not be surprising that Gondwanan distributions are still recognizable in Odonata at the family level. According to Watson (1982), possibly up to 40% of the Australian fauna should be considered of Gondwana origin, i.e., that there are sister-group relationships between the fauna of Australia and South America. This problem was extensively discussed by Carle (1995), when he re-analysed the phylogeny of the ancient Anisoptera. The extant dragonfly superfamilies were all well established before the break-up of Pangaea, and dispersal of the groups was made possible by the so-called trans-pangaeian mountain system. Carle (1995: 394–395) concluded that 'repeated north-south congruences with early anisopteran phylogeny indicate that the trans-pangaeian montane dispersal route was persistent yet tenuous'. Such a route during the Mesozoicum is probably the cause of the occurrence of several primitive genera of anisopteran superfamilies in the eastern USA.

Carle (1995) presented a new phylogenetic hypothesis based on morphological characters of ancient families of Odonata. Several of these families were redefined based on his new analysis of characters, and the distributions of the new groups further discussed.

The Gomphoidea has been mentioned several times as an example of a Gondwanan element in the Australian fauna. It is an ancient group indeed and has a fossil record extending as early as the Jurassic. The Petaluridae are represented in the southern hemisphere with the subfamily Petalurinae in Australia (*Petalura* Leach), New Zealand (*Uropetala* Selys), and Chile (*Phenes* Rambur). One fossil petalurid species is known from the Jurassic of Europe.

The next monophyletic group is formed by the Aeshnoidea and Libelluloidea, of which the Austropetaliidae are the most plesiomorphic. The Austropetaliidae are known from Tasmania and eastern Australia (*Austropetalia* Tillyard), and two genera in Chile, another example of Gondwanan distribution. All species of this family are confined to seepages or small streams; the larvae of most, if not all, species are semiterrestrial.

Carle (1995) also re-evaluated the status of the genus *Neopetalia* Cowley (one species, confined to Chile), and concluded that it represents a family on its own, and forms the sister-group of the non-cordulegastrid Libelluloidea. All other genera formerly included in the Neopetaliidae were placed in the Austropetaliidae (see above). The non-cordulegastrid Libelluloidea are the most speciose group of all extant dragonflies. According to Carle, this adaptive radiation started *c.* 140 Ma in Antarctica.

4.2.2. *Odonata: Calicnemiinae*

Recently, taxonomy and phylogeny of the calicnemiine Platycnemididae of southeast Asia have been studied extensively (Gassmann 1999, 2000; Gassmann and Hämäläinen 2002; Dijkstra, unpublished). A reconstruction of the phylogeny of this subfamily was published by Gassmann (2005). The characters used in the analysis, and details how the results were obtained will not further be discussed here.

Both subfamilies of the Platycnemididae, namely the Platycnemidinae and Calicnemiinae, are found in the Afrotropical, Palaearctic, Oriental, and Papuan regions. The family is absent from Australia and the New World, and, remarkably, from Sulawesi. The subfamily Calicnemiinae is widespread in India and Indochina, especially in the mountainous regions around the Himalayas. Its distribution in Malesia is illustrated in Fig. 6. On some islands, several genera show significant radiation at the species level. For example, the rather widespread genus *Coeliccia* Kirby of southeast Asia is very speciose in Borneo. Many other well-defined genera have restricted ranges within Malesia, e.g., *Idiocnemis* Selys is confined to New Guinea and the adjacent islands, *Risiocnemis* Cowley is restricted to the Philippines, and *Lieftinckia* Kimmins is confined to the Solomon Islands. Several smaller, but distinctly different, genera have even smaller ranges, e.g., *Asthenocnemis* Lieftinck (Palawan), *Arrhenocnemis* Lieftinck, *Lochmaeocnemis* Lieftinck, *Cyanocnemis* Lieftinck, and *Torrenticnemis* Lieftinck (all New Guinea).

The simplified version of the cladogram (Fig. 7) will be discussed here in relation to the present distributions of the taxa, mainly genera. The substitution of taxa for areas of endemism will also present a basis for a

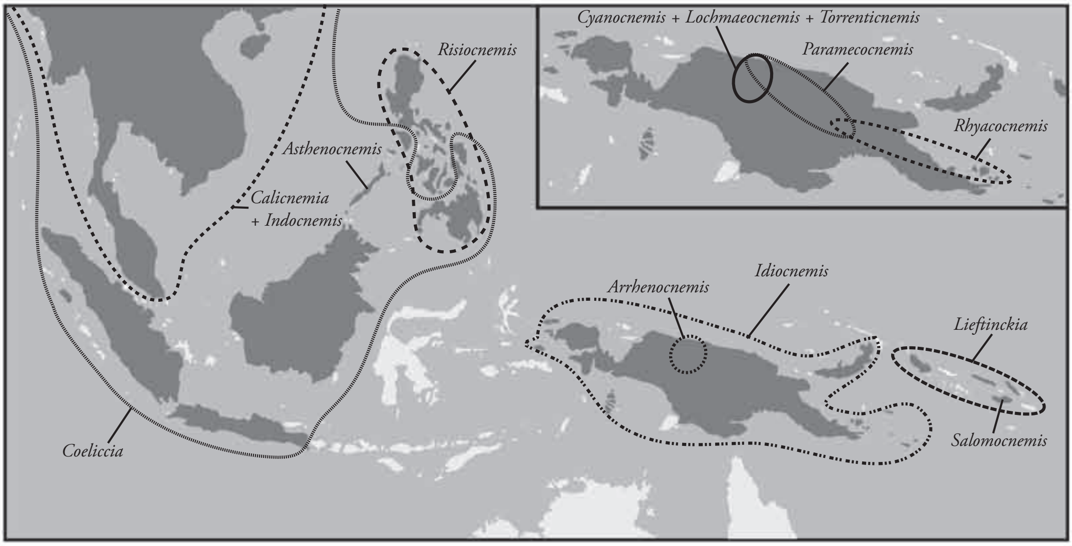


Figure 6. Distribution of the Calicnemiinae (Odonata, Platycnemididae).

hypothesis on the history of the distributional patterns. Two genera of Platycnemidinae, *Copera* Kirby, and *Platycnemis* Burmeister, were used as outgroup.

At the base of the cladogram we find various Afrotropical genera (*Arabicnemis* Waterston, *Allocnemis* Selys, *Stenocnemis* Karsch, *Mesocnemis* Karsch). The sister-group of all species found in southeast Asia is *Leptocnemis cyanops* Selys, a species confined to the Seychelles. According to the present analysis, partly based on selected species of various genera, the ancestor of the genera *Calicnemia*, and *Indocnemis* Laidlaw plus *Coeliccia* is sister to all other Calicnemiinae. All taxa of this group are represented in the mainland of southeast Asia, but *Coeliccia* is also widespread in Sundaland and parts of the Philippines. Remarkably, the sistergroup of this clade consists of the genus *Paracnemis* Martin, which is restricted to Madagascar, plus, as a sister to *Paracnemis*, all other taxa of southeast Asia. However, the position of *Paracnemis* in the cladogram is still somewhat uncertain. In analyses based on recoding of some characters, *Paracnemis* is more basal in the tree, but such trees show more instability in the other branches (cf. Gassmann 2005, for a further discussion). Here we will not take the genus *Paracnemis* further into consideration.

If the present position of *Paracnemis* in the cladogram is confirmed, the taxa from *Idiocnemis* to *Asthenocnemis* in Fig. 7 are to be considered the descendants of a second dispersal event from Africa for the Calicnemiinae, the first being the group of *Coeliccia* to *Calicnemia*. If *Paracnemis* is removed from the discussion, all Asian Calicnemiinae form a monophyletic group. In one branch of the sistergroup of *Asthenocnemis* a large number of small genera endemic to New Guinea, plus the New Guinean genus *Idiocnemis* are found. The other branch is a cluster of *Risiocnemis* (including *Igneocnemis*), *Lieftinckia*, and *Arrhenocnemis*. The last genus is found on New Guinea, *Lieftinckia*, including *Salomocnemis*, is restricted to the Solomon Islands, while *Risiocnemis* is endemic to the Philippines.

The following biogeographical scenario arises from the cladogram. The Calicnemiinae of southeast Asia are derived from African Platycnemididae. Two distinct lineages can be recognized. One clade, with *Calicnemia* and *Coeliccia*, is widespread and speciose in the Oriental region including the Philippines, but does not occur east of Borneo in the Malay Archipelago.

At the base of the sister-clade, we find *Asthenocnemis stephanodera* Lieftinck, a species confined to Palawan. The sister-group of *Asthenocnemis* are all remaining

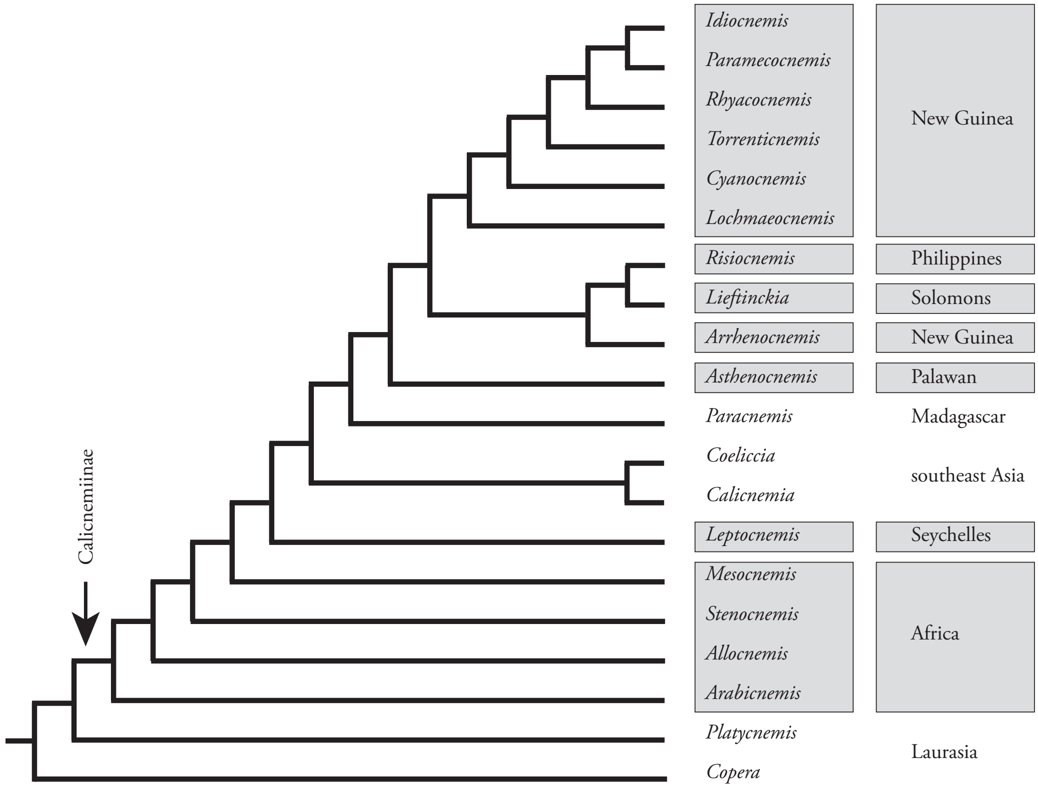


Figure 7. Simplified cladogram of the Calicnemiinae (Odonata: Platycnemididae). The distribution of the clades (area cladogram) is given as shaded areas to the right.

Calicnemiinae. In this group, two monophyletic clades can be distinguished. One, including the genus *Idiocnemis*, is completely confined to the Papuan region, while the other represents a Papuan and Philippine clade. In this clade, the genus *Arrhenocnemis* Lieftinck from New Guinea is the sister-group of an eastern Papuan and Philippine group, namely the eastern Papuan genus *Lieftinckia* Kimmins (including *Salomocnemis* Lieftinck, all from Solomon Islands) as one monophyletic group and the Philippine genus *Risiocnemis* Cowley (including *Igneocnemis* Hämäläinen).

In this scenario Malesian Calicnemiinae derived from ancestors on the mainland of Asia, including Palawan. This group may have dispersed along the eastern margin of the Philippine plate, along an arc that was formed by subduction of the Pacific plate. This so-called Izu-Bonin Arc, which was formed 40-50 Ma, is the basis of the 'northern dispersal scenario' of Beuk (2002a: 279). The Izu-Bonin Arc must be considered the northern continuation of the Caroline Arc during the Eocene. Alternatively, Polhemus (1995) and Polhemus and Polhemus (1998) hypothesized a Late Cretaceous island arc (Inner Melanesian Arc) (Mindanao to New Zealand) as a means for the dispersal route of Papuan groups of aquatic Heteroptera with distinct Asian mainland affinities. As described above, this island arc collided with the northern margin of the Australian terrane during or even before the Eocene. Taxa that reached this corner of the Pacific, later may have used the (South) Caroline Arc while still situated far north from its present position, and much later its continuation to the south, the Melanesian Arc. The taxa that evolved during that time all have remarkable autapomorphies and are presently recognized as separate genera. They have evolved on the terranes or microcontinents of the 'Inner Melanesian Arc' at the northern margin of the Australian plate; some of these terranes have a subaerial history since the Late Cretaceous.

The clade of *Lieftinckia* and *Risiocnemis* then presumably represents a westward dispersal of *Risiocnemis* from the Solomon Islands into the Philippines. As already mentioned above, the subfamily is absent from Sulawesi and the Moluccas. This may contribute to our understanding of the dating the dispersal of this group. It may be hypothesized that the Philippine Arc has played an important role in the evolution of this group. This arc collided with the Australian plate at *c*. 25 Ma (Late Oligocene). The spreading of the Philippine genus *Risiocnemis* can then be dated at *c*. 15-20 Ma (Early Miocene). The clade with the small genera distinctly represents a reflection of the tectonic history of the Caroline Arc at the subduction zone of the (Great) Pacific Plate.

The mechanism of dispersal via the Caroline Arc has already been discussed various times. Beuk (2002b) showed that the (South) Caroline Arc had a westward extension (here named Philippine Arc) via Halmahera and the eastern Philippines to southeast Asia, a southern route via northern Sulawesi, or a northern route via the northwestern Philippines at *c*. 30 Ma. This scenario is based on reconstructions by Hall (2002: 405). In that case, the absence of Platycnemididae in Halmahera can only be understood in this model if this group became locally extinct, or if we have to presume that no freshwater was available at a certain period of time. A similar pattern of distribution has been found in several groups of aquatic Heteroptera, including sagorine Naucoridae (Nepomorpha), and the *Rhagovelia novacaledonica* group (Fig. 12), gerromorph heteropterans with poor dispersal power (Polhemus 1995). According to Polhemus, however, such patterns resulted from the long, pre-Eocene northwest-southeast trending arc system. Such a system extended from New Zealand through the Solomons to Mindanao, but not including Halmahera nor Sangihe. Unfortunately, very little is known from the history of this arc system. It is also not clear from the description in Polhemus whether an arc movement in western or eastern direction is hypothesized, also since the text includes at least one evident mistake 'and has apparently transported continental fragments from the Vogelkop Peninsula *eastward* [recte: westward] to near Celebes'. Based on Hill and Hall (2003), we suppose that such sister-group relationships could also have evolved during the Oligocene, when parts of the Philippine and Caroline arc systems were relatively close to each other. More information on the tectonic history of the Moluccas seems to be crucial for a further understanding of the dispersal opportunities.

The colonization of the mainland of southeast Asia should be linked with the presence of *Leptocnemis* of the Seychelles at the basis of all southeast Asian species. As described above, the non-African lineages then split off *c*. 88 Ma (early Late Cretaceous), while the separation of India from the Seychelles is dated *c*. 65 Ma. In this scenario, the absence of the Platycnemididae from Australia asks for a local extinction in that continent, a not uncommon phenomenon for tropical groups. It seems that Gondwanan (sub)tropical groups have more rarely survived in Australia than groups confined to temperate habitats.

4.2.3. *Odonata: Platystictidae*

The Platystictidae, or forest damselflies, represents a distinct group of the suborder Zygoptera of the Odonata. The presumed monophyly of the group is based on the presence of the so-called post-cubital vein, a character not present in any other recent species of dragonfly (e.g., Bechly 1996). Presently, three subfamilies are recognized, the speciose and widely distributed Platystictinae of southeast Asia, the recently established Sinostictinae of southern China (Wilson 1997), and the Palaemnematinae of Middle and South America (e.g., Calvert 1931, 1934; Kennedy 1938) (Fig. 8). Four genera are recognized in the Platystictinae, *Platysticta* Selys, *Protosticta* Selys, *Drepanosticta* Laidlaw, and *Sulcosticta* van Tol (see van

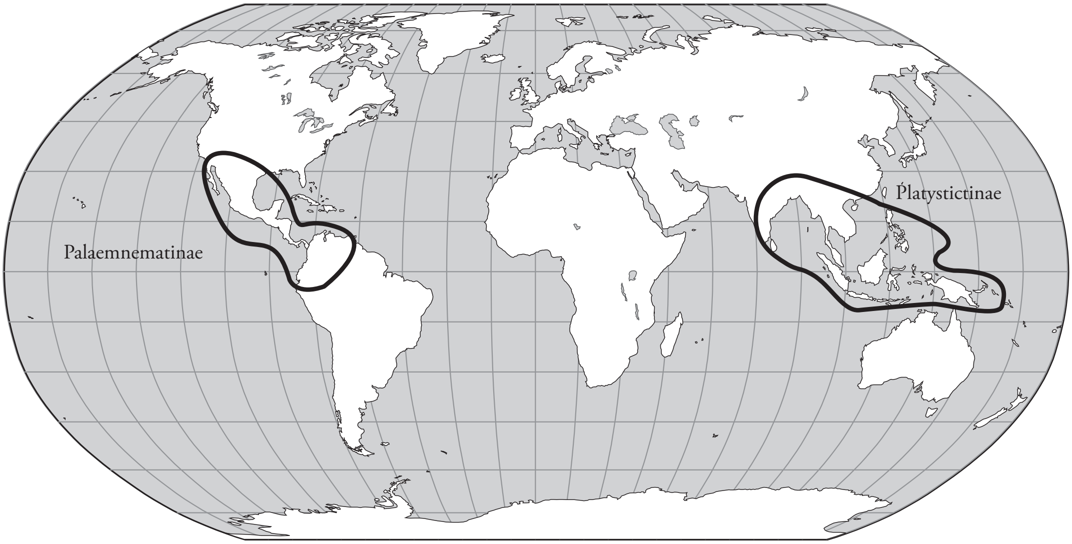
Tol 2005), one in the Sinostictinae, *Sinosticta* Wilson, and one in the Palaemnematinae, *Palaemnema* Selys. The total number of species described per subfamily is presently (van Tol unpublished) 124 in Platystictinae, two in Sinostictinae and 42 in Palaemnematinae.

The present global distribution seems to go back to at least the Cretaceous (van Tol and Müller 2003). The family was presumably distributed across Laurasia. The climate of that time was tropical, and Europe and America were still connected. After their separation, the climate became less favourable for tropical biotas, and the ancestors of the present Platystictidae were forced to move southward in both America and Eurasia. The presence of *Palaemnema* in South America possibly dates back only 3 My, following the emergence of the Panama Isthmus (Coates 1999). Comparable distribution patterns of southeast Asia and Central America have been found in some other groups as well, e.g., the plant genus *Spathiphyllum* (Araceae). If further, e.g., molecular, studies will confirm such an early separation of both subfamilies, the morphology of both groups has remained remarkably stable over the last 60 My. The structure of the male appendages, for instance, hardly differs between species of *Palaemnema* and of *Drepanosticta*.

The phylogeny of the southeast Asian Platystictinae is poorly understood. The generic characters of wing venation seem to be rather useless. Since presumed sister-species are presently assigned to two different genera, the generic diagnoses ask for rigorous redefinition. Nevertheless, some distinct groups characterized by one or more unique autapomorphies can be distinguished, providing a first base for zoogeographic analysis. Such a group is the *Drepanosticta lymetta* group, which is characterized by the unique structure of the hind margin of the posterior lobe of the pronotum (Fig. 9). The group is distributed from Luzon to eastern New Guinea, with (partly undescribed) species known from Luzon, Siquijor, Mindanao, Halmahera, and New Guinea, and one species on Java. This pattern shows a largely congruent relationship with the Philippine–Caroline Arc and its continuation to the northwest.

The subfamily Platystictinae shows its highest structural diversity in the mainland of southeast Asia, in some sense extending over the Greater Sunda islands, but a few groups show extreme radiation on various islands, such as the genus *Protosticta* Selys on Sulawesi (van Tol 2000) and the genus *Drepanosticta* Laidlaw on the Philippine islands (van Tol 2005).

Figure 8. Global distribution of Platystictidae (Odonata) (after van Tol & Müller, 2003).



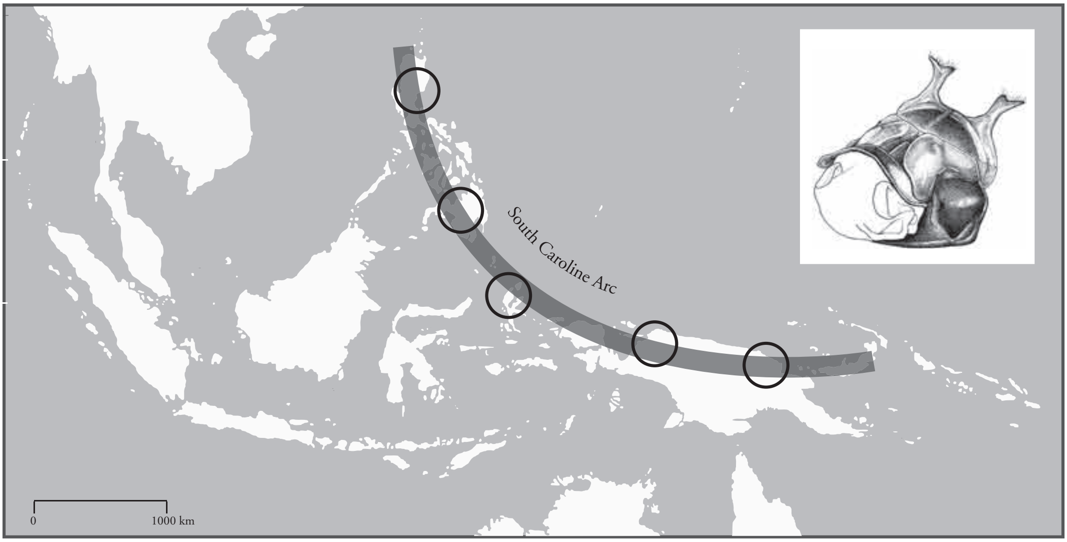


Figure 9. Distribution of the *Drepanosticta lymetta* group.

Structural differentiation seems to decrease in eastern direction towards New Guinea.

4.2.4. *Odonata:* Rhinocypha tincta *complex (Chlorocyphidae)*

'The geographical distribution of this subspecies [i.e., *Rhinocypha tincta semitincta* Selys] is puzzling, but I am still unable to differentiate between the various populations from remote localities. Some of the specimens from the Solomon Islands seem absolutely inseparable from topotypical *semitincta* of Halmahera, with which I have actually compared them' (Lieftinck 1949a: 27). The distribution of this subspecies of chlorocyphid damselfly (Fig. 10) also includes the easternmost part of New Guinea (Papuan Peninsula), the Baliem valley (central New Guinea), the Kai and Aru islands, the Sula islands and a very restricted part of central Sulawesi (Lieftinck 1938, 1949a, own observations). Records from Cape York have not been confirmed in the 20th century (Watson, Theischinger and Abbey 1991: 173).

What most puzzled Lieftinck was, of course, the distance between populations of this taxon that were morphologically inseparable. Apart from *R. t. semitincta*, many more taxa in this complex are distinguished, of which several inhabit the areas between the populations assigned to *R. tincta semitincta*. The *R. tincta*-group is distributed (Fig. 10) from the Philippines to New Britain and the Solomon Islands with the following taxa: *Rhinocypha colorata* (Hagen) widespread in the Philippines and considered the sister-species of *R. tincta* or a subspecies of *R. tincta*, *R. frontalis* Selys and *R. monochroa* Selys, and possibly also *R. phantasma* Lieftinck, from Sulawesi, the typical *R. tincta*, which is only known from Waigeo, subspecies *R. tincta sagitta* Lieftinck occurring on Salawati and in the southern part of the Bird's Head of New Guinea. Further east, in the northern parts of the Berau Peninsula, and in the isthmus of western New Guinea, we find *R. tincta retrograda* Lieftinck, along the north coast of New Guinea occurs *R. tincta amanda* Lieftinck, except for the Finisterre range and adjacent areas, where *R. tincta dentiplaga* Lieftinck is found. Further eastward, specimens from Bougainville and the Shortland islands are assigned to *R. tincta adusta* Lieftinck. Finally *R. liberata* Lieftinck inhabits Ugi and Guadalcanal. According to Lieftinck (1949b), *R. liberata* is the sister-group to the Moluccan *R. ustulata*.

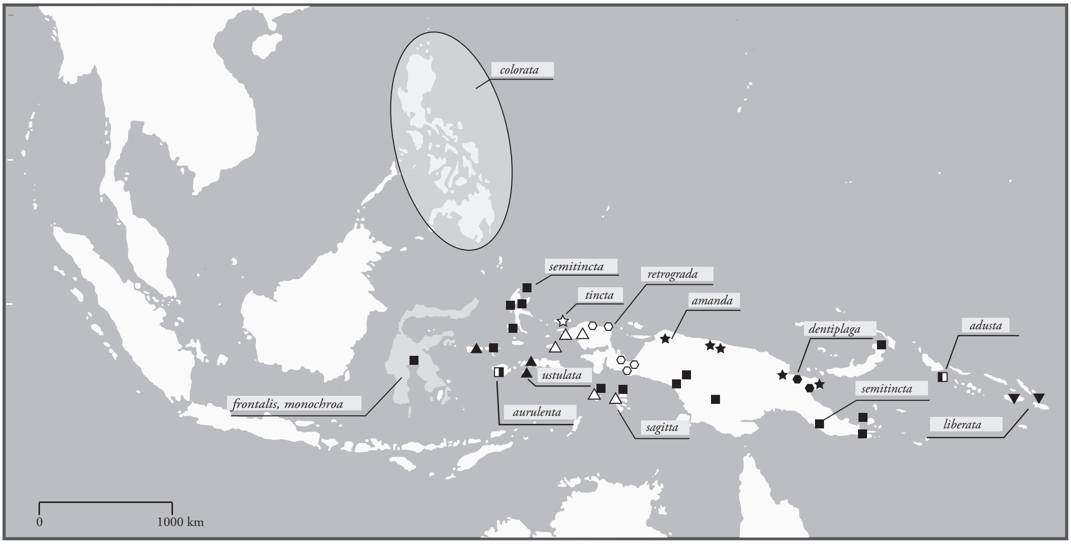


Figure 10. Distribution of the *Rhinocypha tincta* group.

Although the phylogenetic relationships of these taxa are poorly understood, their distributions are congruent with a series of tectonic events also found in patterns of other taxa. The series of subspecies (at least *retrograda*, *amanda*, *dentiplaga* and *adusta*) along the northern coastal margin of New Guinea reflects the pattern of the Caroline island arc north of New Guinea that partly accreted with New Guinea during the Late Miocene and Pliocene. If tectonic events and present distributions have to be related, the Caroline Arc is the most likely pathway for this complex to reach the area. The distribution of many taxa particularly reflects the palaeogeography during the Oligocene. The distribution of the widespread *R. tincta semitincta,* occurring on the Moluccas and the Solomon Islands, but absent from the area in between, seem to indicate an evolution since the Oligocene (35 Ma). The occurrence of this taxon in a very limited area in central Sulawesi may be an indication that a fragment of this area also formed part this island arc, but no palaeogeographical reconstruction confirms this observation. It could, however, explain the occurrence of Papuan elements in the Sulawesi fauna, and should be subject to further studies. The series of related species, such as those from the Philippines and Sulawesi, may have evolved on the Philippine island arc during the late Oligocene (25 Ma).

4.2.5. *Odonata: the genus* Macromia *Rambur (Corduliidae)*

Macromia Rambur is a virtually cosmopolitan genus of rheophilic dragonflies. With more than 120 species, *Macromia* is one of the largest genera of the Anisoptera. The Sulawesi species of this genus were studied by van Tol (1994), who also provided a reconstruction of phylogenetic relationships between species in southeast Asia.

The Papuasian representatives of this genus share at least four characters, including a small discoidal triangle in the hind wing and a minute pterostigma (Lieftinck 1952, 1971). Lieftinck (1971) distinguished three groups among the Papuan species, which are all but one confined to New Guinea, the Bismarck archipelago, Waigeu, and Misool, while one species, *M. chalciope* Lieftinck, is known from Schouten Island, Halmahera and Bacan. The genus *Macromia* is not further known from the Moluccas. About 15 species are known from the Malay Peninsula and the Greater Sunda islands. A preliminary grouping by Lieftinck was apparently not based on natural affinities. The Philippines are inhabited by three species, including at least one endemic.

Van Tol (1994) presented a phylogenetic tree of the Indo-Australian species groups of *Macromia* (also Fig. 11). It appeared that the groups as defined by Lieftinck were not corroborated by the analysis. The tree, rooted with the species of the mainland of southeast Asia, showed that the species of Sulawesi are the sister-group of the Papuan species. Secondly, *M. chalciope* Lieftinck from Halmahera appeared to be the sister-species of *M. terpsichore* Förster from northeast New Guinea, while these two species together formed the sister-group of *M. melpomene* Ris.

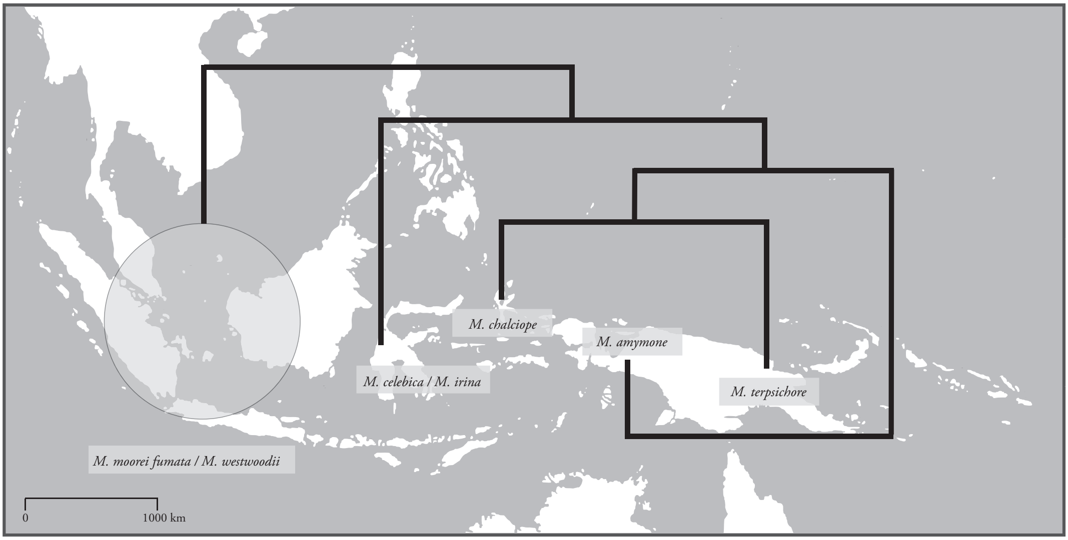
When the distributions of the species are used to define areas of endemism and are plotted on a map, the area cladogram (Fig. 11) is congruent with the geological area cladogram of Beuk (2002b).

4.3. **Other groups**

4.3.1. *Mollusca*

Although several species of Malesian freshwater molluscs were described as early as the late 19th century, they have remained poorly known up to now. Molluscs are rarely considered in biogeographical studies (Davis 1982, Glaubrecht et al. 2003). Glaubrecht et al. (2003) analysed the *Corbicula* freshwater bivalves (Corbiculidae) of southeast Asia, especially Sulawesi. The genus *Corbicula* Megerle von Mühlfeld is a monophyletic taxon, in which all Old World species are the sister-group of the Japanese *C. japonica* Prime. Two species are widely distributed in Asia and introduced in Europe and North America, *C. fluminalis* O.F. Müller and *C. fluminea* O.F. Müller; some authors have lumped all described taxa under these two names. The first species is salt-tolerant and occurs in estuaries and similar habitats; it releases a veliger larva. The second species is more restricted to the lacustrine environment, and incubates embryos in the gills. More careful studies, e.g., in Japan, have revealed that the taxonomy is more complicated. For instance, some forms reproduce by androgenesis (using only the genome of spermatozoa). The genetic variation in the *Corbicula* species of Sulawesi has proved to be much more complicated, and these taxa cannot be assigned to only one or two species. Based on an analysis of morphological and molecular characters,

Figure 11. Relationships of *Macromia* species in the Malay archipelago, the distributions plotted on a map (after van Tol, 1994).



at least five additional species were recognized, one on Sumatra and four on Sulawesi, all endemic to one of the large lakes of Sulawesi (Matana, Poso, Lindu). These lakes are presumably not older than 2 My. All these Sulawesi taxa reproduce sexually. This pattern of endemic taxa has also been found in the pachychilid gastropod genus *Tylomelania* Sarasin and Sarasin, and in ancylid molluscs (von Rintelen and Glaubrecht 2003). The data on the timing of the evolution of these taxa was discussed by Glaubrecht et al. Molecular studies revealed a shallow polytomy based on mitochondrial COI sequences for *Corbicula* species from Japan to Australia, which suggests a relatively recent origin of these taxa, and such data were confirmed when the Indonesian taxa were included. Even a Pleistocene age is not unlikely, which would indicate that dispersal over larger distances should have played a major role in the evolution of the present distribution of the extant species. Long range dispersal by birds may have played a role. On the other hand, a phylogenetic analysis of the pachychilid gastropods of the genus *Brotia* H. Adams of southeast Asia showed that they reflected palaeogeographical events of the Cretaceous rather than of recent geological periods. In this case vicariance events rather than dispersal seem to have played the dominant role in distributional evolution.

4.3.2. *Plecoptera*

Stoneflies, or Plecoptera, are most diverse in the temperate regions, and not common in tropical areas. Their poor flying capacities and specialized ecology make dispersal unlikely. The zoogeography of the groups was discussed by Zwick (2000), who did not follow previous conclusions by Illies (1965).

The suborder Antarctoperlaria is presumably an old group occurring in South America, New Zealand, and Australia, but absent from Africa, Madagascar, and India. The Permian *Euxenoperla* Riek is assigned to the Gripopterygidae, a family of the Antarctoperlaria, but the assignment is considered doubtful. Nevertheless, if the group is Cretaceous or older, an extinction in Africa and India is needed to explain the pattern, or dispersal is more likely in this group than presently presumed. The genera that are known from the Greater Sunda islands and the Philippines are all representatives of the suborder Arctoperlaria, which is typically holarctic. The Neoperlini originated in the Oriental region, and have even reached New Guinea to the east (one species of *Neoperla* Needham), and North America via the northwest. The genus *Neoperla* is also widespread in the Afrotropical region.

According to Zwick (2000) it is still uncertain whether Plecoptera patterns are old (pre-Cretaceous). In the case of old patterns, massive extinctions in the Arctoperlaria have to be postulated in Gondwana. However, if the patterns are more recent, extensive dispersal across seas must be hypothesized. A further study of the phylogeny of at least the *Neoperla* of southeast Asia would provide a valuable contribution to zoogeography of aquatic biotas.

4.3.3. *Ephemeroptera*

Mayflies represent probably one of the best groups of aquatic insects for biogeographic studies. The larval stages are usually stenotopic, and imaginal and subimaginal stages are short-lived and weak flyers, which make them poor dispersers. Unfortunately, little information of the phylogeny of this group of insects is available. Soldán (2001) recently summarized systematic knowledge of the Oriental (including Malesian) Ephemeroptera fauna. Not more than 535 species of mayflies have been described from the Oriental region and its transition zones (Afghanistan, Himalayas, China and Papua New Guinea). About 35% of the nominal taxa are only known from the larval stage, and 39% only from the adult stage. The total number of species will probably be three to four times higher. For the species of southeast Asia, only very few taxonomic revisions are available, and Ulmer's (1939, 1940) treatment of the fauna of the Sunda islands needs both extension and updating. Zoogeography has been discussed by Edmunds (1979) for the Oriental fauna, and Edmunds and Polhemus (1990) for the Malay Archipelago, with special attention to Sulawesi.

The fauna of the Malay Archipelago, as far east as New Guinea, is nearly fully of Oriental origin, while Australian elements are rare. Many Oriental elements known from the Sunda islands (33 genera) do not reach Sulawesi (Edmunds and Polhemus 1990). The fauna of New Guinea is relatively poor, and based on radiations of only seven clades, of which six are Oriental. Only the genus *Tasmanocaenis* is shared between Australia and New Guinea, and no other species of Australian mayfly occurs in New Guinea. The genus *Sulawesia* Peters and Edmunds is considered the only Australian element in the fauna of Sulawesi.

4.3.4. *Hemiptera*

Systematics, phylogeny and zoogeography of the aquatic and semiaquatic Heteroptera of southeast Asia have intensively been studied by N.M. Andersen, P. Chen, N. Nieser, D.A. Polhemus, J.T. Polhemus, and H. Zettel. The results of the study of the Sulawesi fauna will be discussed below.

Andersen (1991, 1998) described the cladistic biogeography of the marine water striders of the families Hermatobatidae, Veliidae, and Gerridae of the Indo-Pacific region. *Hermatobates* Carpenter is the only genus of Hermatobatidae, and species occur along continental coasts and islands in the Indo-Pacific, including the Red Sea, East Africa, Seychelles, Maldives, Ryukyu islands, Philippines, Indonesia, Australia, and Hawaii. One species is known from the Caribbean. Species of other families with similar ecological preferences usually have smaller distributional ranges (see Andersen 1998, for details). For an analysis of the distributions, the Indo-Pacific region was divided in eight areas of endemism: Australia, East Asia, Indian Ocean, Malayan, Papuasia, Philippines, Sulawesi, and West Pacific. The analysis for the various groups revealed cladograms that were not necessarily congruent. The combination of all groups studied yielded two completely resolved area cladograms, which only differed in the position of the Indian Ocean, but a strict consensus of both is completely unresolved. One of the two trees is (Aus (W Pac (Papu (Sula (Phil (Ind-O (Mala and East Asia))))))). This area relationship distinctly indicates a trend in a western direction from Australia. Andersen (1998) remarks that, for instance, the *Halovelia* Bergroth species of East Africa, Madagascar and the islands of the Indian Ocean belong to the southeast Asian *H. malaya* group, and possibly have to be considered a late dispersal. The archipelago of volcanic islands and microcontinents between Australia and Asia during the Cenozoic must have been a perfect place for allopatric speciation. Fossils, however, show that *Halovelia* and *Halobates* have occupied a much wider area than at present, indicating that (local) extinction must have played a major role in shaping present distribution patterns.

D.A. Polhemus, frequently with J.T. Polhemus (e.g., Polhemus and Polhemus 1998) discussed regional distribution patterns in more detail (Fig. 12).

They surveyed and analysed the Nepomorpha and Gerromorpha fauna of New Guinea in detail, and have linked that to the palaeogeography of the region, although many early papers lack a cladistic analysis. Polhemus and Polhemus (2002) includes an analysis of the biogeography of the small waterstriders of the subfamily Trepobatinae based on a careful phylogeny of this taxon. This group is very speciose in New Guinea and the ranges show strong correlations with past tectonic events, such as the accretion of island arcs, although the various tribes appeared to have all differing biogeographic histories. All Metrobatini of New Guinea and Australia are the sister-group of the Neotropical *Metrobates* Uhler. This pattern indicates to a Gondwanan origin, the vicariance presumably due to separation of Australia and Antarctica at *c*. 85 Ma. Many taxa of New Guinea have distributions congruent with the geological entities as defined by Pigram and Davies (1987). The genus *Metrobatopsis* Esaki (Fig. 13) is confined to the Solomons, the Bismarck archipelago and along the northern coast of New Guinea, portions of the Miocene-Pliocene Solomons Island Arc (cf. Kroenke 1996). The genus *Andersenella* J.T. Polhemus and D.A. Polhemus only occurs on the Papuan Peninsula, which is, according to Polhemus and Polhemus (2002), an indication of the relatively recent accretion of this complex terrane

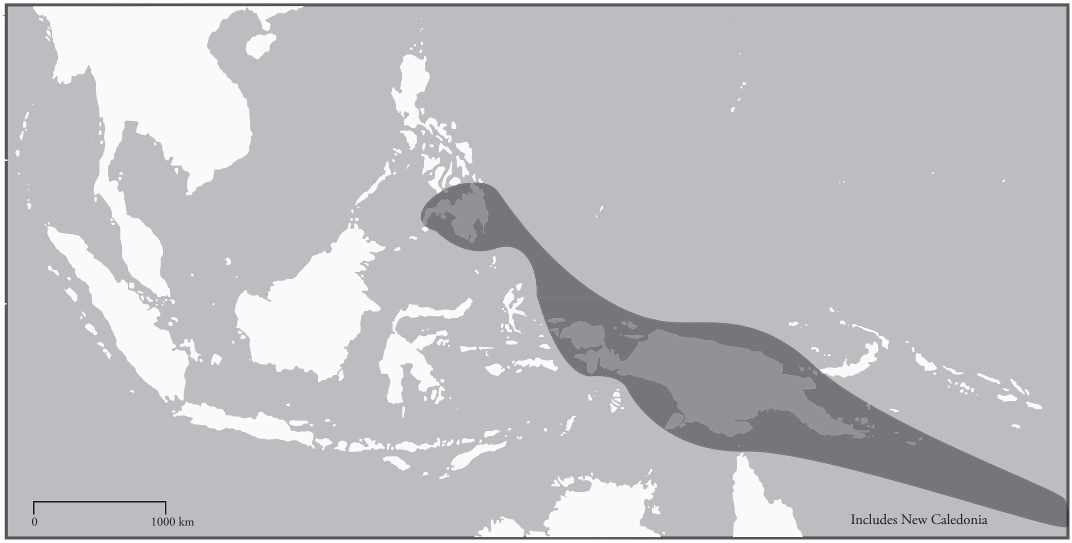


Figure 12. Distribution of the *Rhagovelia novacaledonica* group (from Polhemus, 1995).

with the rest of New Guinea. The genus *Metrobatoides* Polhemus and Polhemus is only known from the Torricelli mountains of northern New Guinea and the northern part of the central mountain ranges in the Mamberamo River Basin, which are both portions of accreted terranes. Three other genera of Metrobatini are extending over those parts of New Guinea that once formed part of the Australian continental craton. Such groups may have evolved on the Vogelkop microcontinent, which fused with the rest of New Guinea during the Late Miocene or Early Pliocene, or on the Halmahera Arc (considered part of the Philippine Arc in the present paper), which lay north of New Guinea from the Oligocene through the Miocene.

The genus *Calyptobates* Polhemus and Polhemus of the tribe Naboandelini is distributed over Australia, New Guinea, the Moluccas, Borneo, the Andaman Islands, and Sri Lanka, but not east of New Guinea. All other species occur in Africa. Since all three species of New Guinea occur south of the central mountain ranges, Polhemus and Polhemus presumed that the genus reached New Guinea via Australia, being a Gondwanan element. The Stenobatini, the third tribe of this group of waterstriders, includes one genus, *Thetibates* Polhemus and Polhemus, with a distribution pattern congruent with the Solomons Arc terranes.

It is hypothesized that most groups that evolved in Asia reached the New Guinea region via the so-called Papuan Arc. This arc collided with the northern margin of Australia in the Late Eocene to Early Oligocene. Species that evolved in this arc can now be expected in central New Guinea and mountains of the Vogelkop Peninsula, and have outgroup relationships with groups to the west. Polhemus and Polhemus were able to identify various taxa with distribution patterns that reflect the Papuan Arc distribution, including Microveliinae, Gerridae (genus *Ptilomera* Amyot and Serville), and Naucoridae (genera *Nesocricos* and *Tanycricos*). Finally, some groups evolved in the Caroline Arc during the Oligocene. This island arc accreted to northeast New Guinea until the Early Pliocene. The distribution of *Rhagovelia biroi* Lundblad is considered to be an example of a Solomon Arc distribution of Miocene age.

Polhemus and Polhemus (1994) analysed the phylogenetic position of the Timorese endemic waterstrider *Aquarius lili* Polhemus and Polhemus (Gerridae). The genus *Aquarius* Schellenberg is widespread in the Palaearctic, Afrotropical, Oriental and Australian regions, but it is absent from Sulawesi, the Moluccas or the Lesser Sunda islands (see Andersen

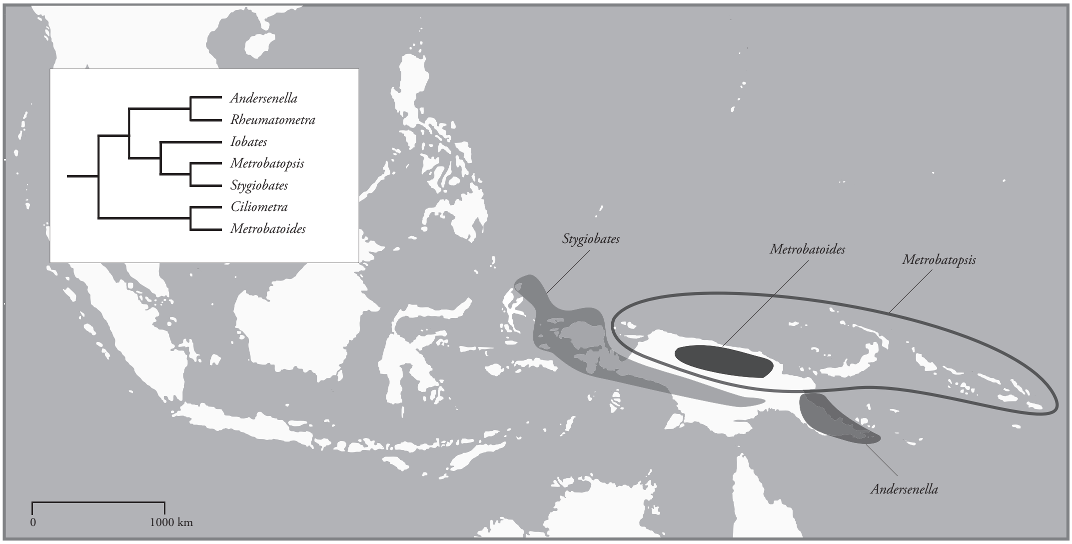


Figure 13. Distribution of genera of Metrobatini (after Polhemus and Polhemus, 2002).

1990). In a cladistic analysis, confirmed by Damgaard et al. (2000) and Damgaard and Zettel (2003), *Aquarius lili* appeared to be the sister-species of *A. adelaidis* (Dohrn), a species widespread in the mainland southeast Asia, the Philippines and the Greater Sunda islands, rather than of the Australian species. This result supports the geological fore-arc ridge hypothesis of Hamilton (1979), in which Timor is part of the Banda Arc fore-crest, rather than the deformed northwestern edge of the Australian continental plate. If Timor is part of the Banda arc system, rafting of Asian elements, such as *A. lili*, during the eastward migration of this island during the Miocene from a position near Celebes and Borneo to its present position is hypothesized. As stressed by Polhemus and Polhemus, such a scenario seems to be supported by records of a full-size Eocene anthracothere with southeast Asian affinities on Timor. A further zoogeographical analysis of Timor has to await further detailed cladistic analyses of groups including Timorese endemics. Polhemus and Polhemus (1994) mention a sistergroup relationship of *Ptilomera timorensis* Hungerford and Matsuda (Heteroptera: Gerridae) with species occurring on the mainland of southeast Asia.

4.3.5. *Trichoptera*

Distribution patterns of Australasian caddisflies Trichoptera were reviewed by Mey (2001), mainly at the family level. The origin of the families of the Trichoptera precedes the break-up of Pangaea for the Spicipalpia and Annulipalpia, but (most) families of the Integripalpia evolved after the break-up. The Asian and Australian faunas made contact when the Australian plate collided with island arcs in the 'midwestern Pacific' from the Late Oligocene. Some of the arcs or island chains provided dispersal routes for some elements of the Trichoptera fauna. The dispersal capacity of various groups of caddisflies may, however, differ considerably.

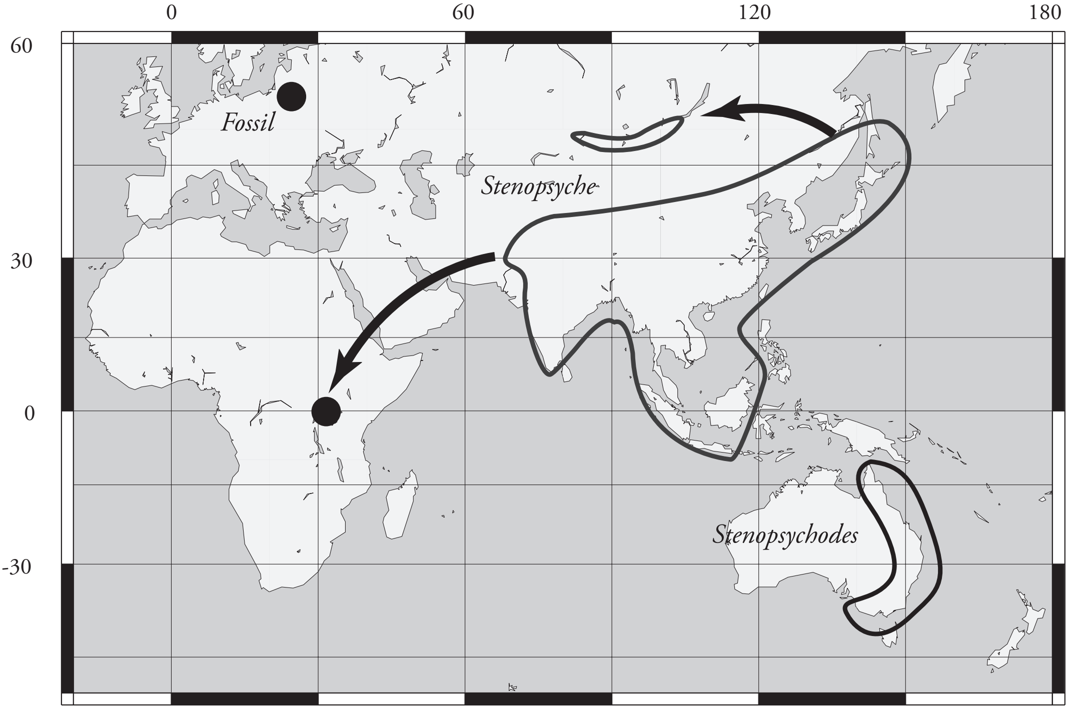
The Gondwanan influence on the Oriental fauna after the docking of India has not been studied yet, but the distribution of the genus *Apsilochorema* Ulmer has been attributed to the accretion of terranes in southeast Asia before India reached the southern margin of Laurasia (Mey 1998, 1999). *Apsilochorema* is a genus of the Hydrobiosidae (Spicipalpia), which contains 20 genera in South America, of which only one has dispersed northward up to southern North America. Twentyfive genera of Hydrobiosidae are known from Australia.

The genus *Apsilochorema* itself is widespread (with two subgenera) in Australia, Indonesia, the southeastern part of Asia, along the Pacific coast northward up to Japan, and westward through the Himalayas. There are disjunct populations in southern India and Sri Lanka, and the southern part of the Caspian Sea. Families like Goeridae, Lepidostomatidae, and Dipsodopsidae extend into the northern part of the Australian region, but are 'clearly of Asian origin' (Mey 2001: 263). The distribution of the Stenopsychidae (Annulipalpia) (Fig. 14) shows distinct disjunctions, presumably due to poor dispersal capacities. Three genera are known of this family, *Pseudostenopsyche* Döhler in the southern Andes, *Stenopsychodes* in eastern Australia, and *Stenopsyche* MacLachlan in the mainland of southeast Asia including India and northward to Japan, and in the Greater Sunda islands in the Malay archipelago. The genus occurs disjunctly in southern Siberia, and central Africa, while it is known from Baltic amber in Europe. Mey (2001) suggests that this genus has had a much larger distribution in the past.

4.4. **Sulawesi**

The biogeography of Sulawesi has been the subject of studies since the 19th century. The remarkable mixture of Oriental and Australian elements, with endemics of isolated phylogenetic origin, has attracted attention since Wallace (e.g., 1860, 1863) travelled and studied the Malay archipelago. The study and analysis of the flora and fauna continues up to today (e.g., Knight and Holloway 1990, Whitmore 1981, Whitten et al. 1987, Holloway 1997, van Oosterzee 1997), while much new information on the geological history of the region has provided a basis for the understanding of the processes that presumably gave rise to the evolution of so many species. The details of the geological history have been summarized above. In summary, the southwestern arm may have a subaerial history for the last 60 My, while the other arms derive from the margin of the Australian plate (eastern arms) or the southern margin of the Philippine plate. The northern arm may have had a position not far from the SW arm

Figure 14. Example of the distribution of Stenopsychidae (Trichoptera) (after Mey, 2001).



since the Eocene (Wilson and Moss 1999), or much later (Hall), the microcontinents of Banggai-Sula and Buton-Tukang Besi only accreted during the Pliocene. It is still uncertain to what extend they have a history above sea level. Some geological reconstructions include conclusions of floral or faunal analyses, so that the use of such data for biogeographical analyses requires caution. It is worthwhile to mention that western Sulawesi remained in or near tropical latitudes throughout the Cenozoicum (Wilson and Moss 1999).

As in many other groups, the composition of the aquatic invertebrates of Sulawesi is characterized by a high percentage of island endemism, and the absence of groups that are common and speciose elsewhere in the Malay archipelago. All these phenomena are clearly related to the long isolation of Sulawesi. Also, many species are restricted to parts of Sulawesi, and the species distributions within the island frequently show distinct congruence with the geological history of the island. The present knowledge of the aquatic biotas is summarized here.

Absence of widespread taxa. Although absence is methodologically difficult in zoogeographical analyses, for several groups data are sufficiently abundant and reliable as a basis for discussion.

In Odonata there is a remarkable absence of some families that occur widely west of Sulawesi in the Greater Sunda islands, namely Amphipterygidae, Euphaeidae, Platycnemididae, and Cordulegastridae, while other families are poorly represented, e.g., Calopterygidae, Protoneuridae, and Gomphidae. The ranges of many Australian/Papuan taxa above the species level reach their western limits in Sulawesi (see below), but the families Isostictidae and Synthemistidae are not known west of Halmahera (Moluccas). As compared to the Philippines, the same families of odonates are absent as compared to the Greater Sunda islands.

Affinities. The affinities of the fauna of Sulawesi are predominantly Oriental. The analysis of the Ephemeroptera (Edmunds and Polhemus 1990) showed that 20 genera of mayflies are known from Sulawesi, of which at least 3 genera are endemic. The other genera mainly have an Oriental distribution (14 genera shared with the Greater Sunda islands, 8 with the Philippines). Only six genera occurring on Sulawesi are shared with the Moluccas. In addition, Peters and Edmunds (1990) noted the depauperate nature of the Sulawesi Ephemeroptera fauna, since many genera found in Borneo, Java, Sumatra, and the southeast Asian mainland are lacking. The interpretation of all these figures is, however, severely hampered by incomplete data sets.

Among the exceptions of Oriental affinity are the genus *Echinobaetis* Mol of the Baetidae (Mol 1989) and genus *Sulawesia* Peters and Edmunds of the atalophlebiine Leptophlebiidae (Peters and Edmunds 1990). *Echinobaetis* is considered most closely related to *Jubabaetis* Müller-Liebenau from Luzon (Philippines). According to Edmunds and Polhemus (1990), *Sulawesia* is a member of an ancient Gondwanan lineage and the only genus of mayflies in the region that has southern (Australian) affinities, with its relatives known from Australia, New Zealand, southern South America, Madagascar, Sri Lanka, and southern India, but not from the Papuan region. *Sulawesia* seems to belong to a group of genera restricted to South America, Australia, and New Zealand, rather than to a group distributed in Madagascar, Sri Lanka, and India.

The Odonata of Sulawesi are also primarily of Oriental origin (van Tol 1987a). Several elements of the Papuan fauna reach the western limit of their ranges in Sulawesi, including the genus *Nososticta* Hagen in Selys (Protoneuridae, one species in Sulawesi and 28 in the Papuan region), *Nannophlebia* Selys (Libellulidae, one species in Sulawesi, at least 8 in the Papuan region), and *Diplacina* Brauer (Libellulidae, 3 species in Sulawesi, at least 7 in the Papuan region) (cf. Lieftinck 1949a). Although the sister-groups of some Sulawesi taxa are found in the Philippines, e.g., in *Drepanosticta* Laidlaw (Platystictidae) and *Diplacina,* both faunas further share only common and widespread species (cf. Hämäläinen and Müller 1997). According to Vane-Wright (1990: 19) ‘Sulawesi shares by far the greatest portion of its genera [of butterflies] with the Philippines (…), but at the species level its strongest unique link is with the Moluccas.’ This observation cannot be confirmed for the Odonata, nor for other aquatic insects. Among the aquatic Heteroptera, Sulawesi has 41 out of 42 genera in common with the Greater Sunda islands or continental Asia. Polhemus and Polhemus (1990) hypothesized that most elements have crossed the Makassar Strait from Borneo.

Island endemism. Island endemism at the species level is extremely high for many groups in Sulawesi, e.g., 98% of the mammals (excluding bats) (Whitten et al., 1987), 95% in cicadas (Cicadidae) (Duffels 1990), 76% in amphibians, and 29% in swallowtail butterflies (Whitten et al. 1987). Not many data are available for aquatic invertebrates, but Polhemus and Polhemus (1990) estimated 65% endemicity at the species level; no endemic genera are known from Sulawesi. Edmunds and Polhemus (1990) provide some data for Ephemeroptera, including two out of six genera of Baetidae endemic to Sulawesi. In the Odonata, nearly all species in various families with poor dispersal power are island endemics. Examples are the Platystictidae and Chlorocyphidae, both with 100% island endemics (although recent data confirm the occurrence of the Papuan *R. tincta semitincta* of the Moluccas in Central Sulawesi). Van Tol (1987a, b) noticed that Odonata species confined to streams in primary forest are nearly all endemics, while the secondary habitats are inhabited by widely distributed, dispersive species. Similarly, the percentage of endemicity at the species level in the aquatic Heteroptera is nearly 100% (instead of 65%) if species confined to rice paddies and similar habitats are excluded from the analysis (Polhemus and Polhemus 1990).

Isolated phylogenetic position. Quite some species endemic to Sulawesi are distinctly different from other known species and have been attributed to separate genera. The occurrence of such taxa with isolated taxonomic position can be related to infrequent contact with the source area, usually a continental mainland, but in the case of Sulawesi presumably the Greater Sunda islands. Well-known examples on Sulawesi include mammal species such as anoa, *Bubalus depressicornis* (H. Smith), and babirusa *Babyrousa babyrussa* (L.). Babirusa has no common ancestor since the Oligocene (30 Ma) (Whitten *et al.* 1987).

Among the Odonata, three endemic genera of Chlorocyphidae are recognized, namely *Disparocypha* Ris, *Sclerocypha* Fraser, and *Watuwila* van Tol. Apart from these genera, representatives of two more widespread genera also inhabit the island. An analysis of the genera of the Chlorocyphidae of southeast Asia (Fig. 15) (cf. van Tol 1998 for details) shows that the Sulawesi genera belong to at least three monophyletic clades, which are all widespread in southeast Asia. The Sulawesi endemics *Sclerocypha* and *Watuwila* both split off early in a clade that also includes the widespread genus *Libellago* Selys. The aberrant genus *Disparocypha*, placed in a separate subfamily by Munz (1919), appears to be the sister-group of *Cyrano* Needham and Gyger, a genus confined to the Philippines. Although *Disparocypha* is characterized by many autapomorphies, it appears to be a relative recent clade in the Chlorocyphidae. Genera endemic to Sulawesi are also recognized in the Megapodagrionidae (*Celebargiolestes* Kennedy), and Libellulidae (*Celebophlebia* Lieftinck, *Celebothemis* Ris), but no phylogenetic analyses are available for these families.

Areas of endemism within Sulawesi. Species in many groups have small distributional ranges within Sulawesi, making the island extremely suitable for detailed biogeographical analysis. Examples include such diverse groups as macaques, carpenter bees (cf. Whitten et al. 1987), and cicadas (Duffels 1990). Distribution data of freshwater invertebrates are available for some groups of Nepomorpha, Gerromorpha, Trichoptera, and Odonata. For aquatic and semiaquatic Heteroptera, Polhemus and Polhemus (1990) provided a first overview and analysis, of which the distribution patterns of the veliid genus *Rhagovelia* Mayr are of particular interest. New species and distributional records of *Rhagovelia* species have been published since then by Nieser and Chen (1993, 1997) (Fig. 16). Based on congruent patterns of speciation, Polhemus and Polhemus identified five 'centres of endemism', namely one in the Minahasa (northern arm), one around Kendari (Southeast arm), one near Makassar/Maros (southwestern arm), and two in central Sulawesi, the Toraja, and Poso centres. These areas are also recognized as separate entities in tectonic reconstructions.

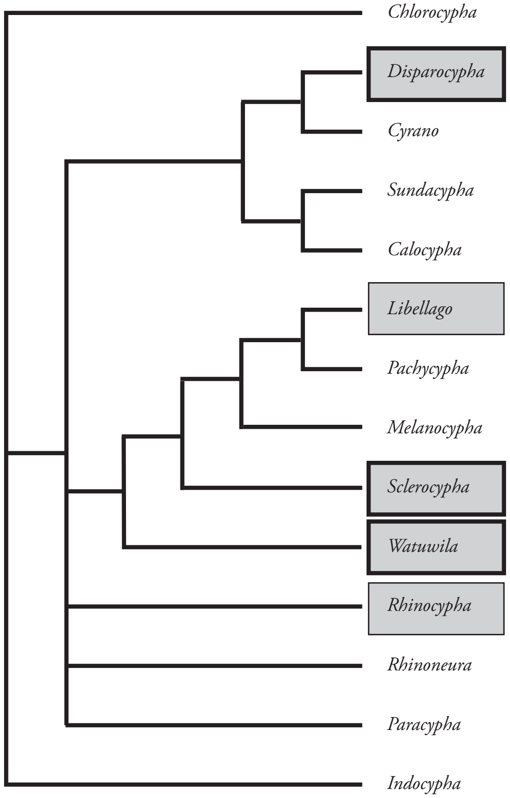


Figure 15. Cladogram of genera of Chlorocyphidae (Odonata) (after van Tol, 1998). Genera occurring in Sulawesi in grey box, genera endemic to Sulawesi in bold border. Chlorocyphidae are very diverse on Sulawesi, even at generic level.

Similar patterns were found when relationships of Odonata were used. Distribution maps or distributional data for Odonata taxa were published by van Tol (1987b, 1994, 2000). An example is given in Fig. 17 for the red-coloured and superficially similar chlorocyphids *Watuwila*, *Libellago*, and *Sclerocypha*. *Watuwila* is only known from the southeastern peninsula, possibly an artefact. *Sclerocypha* is confined to the northern arm of Sulawesi, while the *Libellago*-complex inhabits the rest of Sulawesi. Within the last clade, the southwestern arm is sister to central and eastern Sulawesi. As an example of a distribution pattern of two closely related species (or parapatric subspecies) one may use the distribution of *Diplacina m. militaris* Ris, and *D. militaris dumogae* van Tol (Fig. 18). The genus *Diplacina* is of particular interest since it represents a distinct Philippine or Papuan relationship. The sister-species of *D. militaris s. l.* is *D. bolivarii* Selys, which is widespread in the Philippines (Luzon, Mindoro, Visayan regions). According to Hämäläinen and Müller (1997), the populations of *D. bolivarii* of Palawan and the Sulu islands are distinct and presumably represent another subspecies. Other species of *Diplacina* Brauer occur in the Moluccas and New Guinea, while three more species are known from the Philippines, including *D. braueri* Selys and *D. nana* Brauer, which are both closely related to *D. bolivarii*. Two more species of *Diplacina* are also known from Sulawesi, of which *D. torrenticola* van Tol belongs to the *D. militaris* species group. The affinities of *D. sanguinolenta* van Tol are uncertain, and cannot further be discussed. The common ancestor of the Philippine and Sulawesi *Diplacina* species presumably lived on one of the terranes in the Philippine Arc. Whether the occurrence on Sulawesi should be attributed to a dispersal event from a Philippine element of this arc to Sulawesi, or to a subaerial history of the northern Sulawesi Peninsula itself, is unknown. The dispersal power of *Diplacina* is presumably low. In particular, the absence of this genus from Borneo, even though it is known from Palawan, is remarkable. The subaerial history of the northern Sulawesi arm is still very uncertain, but Wilson and Moss (1999: 329) explicitly mention the existence of dispersal routes from the Philippines to Sulawesi 'along vulcanic arcs, such as the long-lived arc along the North arm of Sulawesi'.

5. Discussion

The number of groups for which a well-founded phylogenetic reconstruction of the southeast Asian taxa at the species level has been published is still low. The best studied groups are plants, and some groups of insects. Invertebrate taxa, including insects, of freshwaters remain particularly poorly studied. Actually, not only the phylogeny is poorly known, but even the basic data such as inventories, taxonomic revisions, and distributional data are insufficiently available as a backbone for zoogeographical studies.

Figure 16. Distribution of the *Rhagovelia orientalis* group on Sulawesi.

The cladistic biogeographical analysis of the Calicnemiinae, as described in this paper, is the first example of such an analysis of a widespread aquatic group comprising many taxa with restricted ranges. Based on available, but mostly more limited, zoogeographical analyses in various taxonomic groups, it appears that general patterns in the zoogeography of aquatic invertebrates are not significantly different from strictly terrestrial groups for analyses that go back as far as the break-up of Pangaea. At least two scenarios emerge for the historical biogeography of aquatic groups during the break-up of Pangaea, and later Gondwana. These scenarios are presumably related to habitat requirements rather then to the age of the groups. Families with species confined to small streams and seepages of mountainous regions frequently show a wide distribution in southern latitudes. Such patterns may have evolved as early as the Jurassic.

The distributions of families or genus-groups with species of the (sub)tropical region have presumably evolved during the Cretaceous. Presently, no data are available for the timing of speciation in tropical groups of freshwater invertebrates from South America, but several groups may have dispersed from Middle America into South America only after the closing of the Panama Isthmus.

India has played a significant role in the history of the freshwater fauna of southeast Asia, although a dispersal along the northern margin of the Meso-Tethys cannot be excluded in some cases. The occurrence of the sister-group of most southeast Asian Calicnemiinae on the Seychelles corroborated, however, the ‘Out–of–India’ hypothesis for this group of odonates, as was recently also confirmed for amphibians (Bossuyt and Milinkovitch 2001).

Much uncertainty remains for the dispersal route or routes of the taxa of Oriental origin from the mainland of southeast Asia or the Greater Sunda islands eastward to New Guinea. Insufficient details are available for the composition and position of a presumably Cretaceous island arc that accreted to the northern margin of New Guinea during the Eocene. One or more island arcs along the southwestern margin of the Pacific plate during the Eocene may have played a role in some groups, for many other taxa this remains highly improbable. At least in the Calicnemiinae several ancient taxa are found in northern New Guinea, suggesting a history related to the Caroline arc system along the western margin of the Great Pacific Plate. Dating of the time of splitting of clades, for instance based on molecular data, is not yet possible. In several orders of aquatic insects monophyletic groups show a pattern of distribution from the Philippines eastward to eastern New Guinea or even further into the Pacific, excluding Sulawesi and the Moluccas. Since such patterns cannot be explained by ecological or climatological conditions, the geological history of the area is presumed to be the causal factor. Although new information on the palaeogeography of southeast Asia has become available since the 1990s, the history of the island arcs and series of microcontinents along the southern and western margins of the Pacific plate (and partly also the Philippine plate) is still insufficiently known. A pre-Eocene, presumably Cretaceous, arc running from Mindanao to the Pacific, but excluding Sulawesi and the Moluccas, has been hypothesized

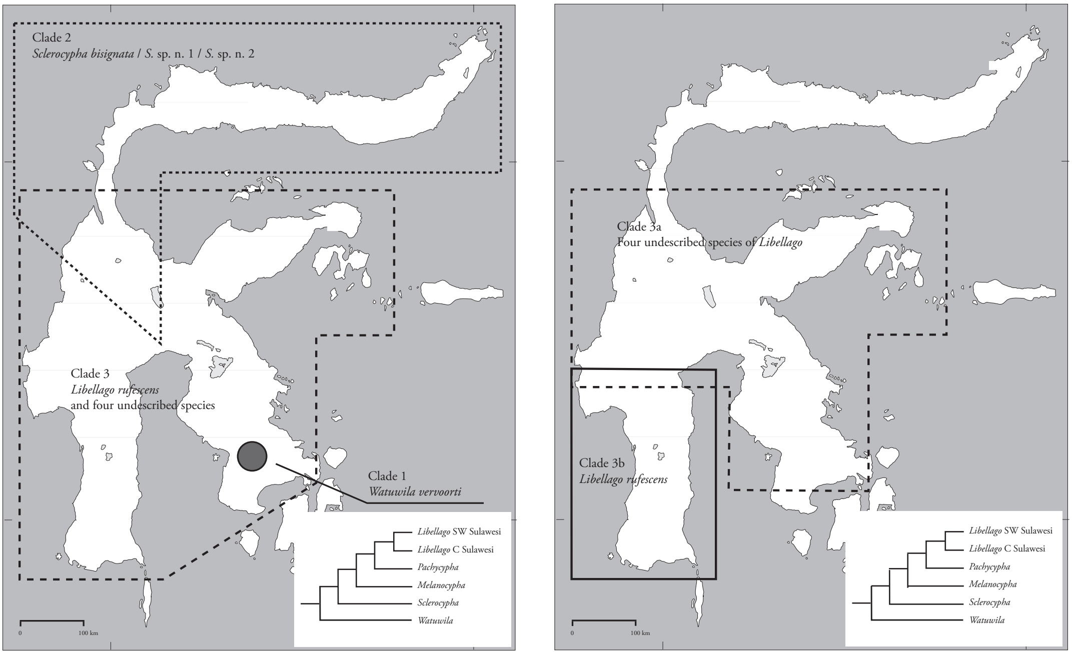


Figure 17. Area relationships in Sulawesi based on phylogenetic relationships of *Libellago*, including *Sclerocypha*, in Sulawesi. – Left: First division in cladogram. – Right. Second division in cladogram.

(Polhemus 1995), but not much geological information is available.

The special, 'unbalanced' composition of the biota of Sulawesi is also confirmed for aquatic invertebrates. Most groups are of Oriental origin, but examples are available of monophyletic groups with Papuan affinities which do not occur west of Sulawesi. These patterns presumably go back as far as the early Mesozoicum, since when the southwestern arm of Sulawesi has remained in the same geographic position compared to Borneo as today. Endemicity at the species level is more than 50% for most groups, and is usually between 90% and 100% when only taxa confined to primary habitats are considered. Phylogenetically isolated taxa are also known among the Sulawesi freshwater invertebrates, e.g., in odonates, and such groups also have Oriental sister-group relationships. Although the geological origin of the other arms of Sulawesi is fairly well known now, the uncertainties of the subaerial history of these islands and their position in relation to New Guinea and parts of the Philippines are a serious handicap in understanding the distributional history of some remarkable taxa with Papuan affinities, e.g., in the genus *Rhinocypha* (Odonata). Area cladistic analyses based on taxa with restricted distributions within Sulawesi, defining areas of endemism, are congruent with the sequence of events in geological reconstructions.

The Malay archipelago is an area in which the distribution of land and sea has proved to be the primary driving force in the composition of the biotas. Many aquatic invertebrates, especially those confined to rain forests, are poor dispersers. Their distribution is the result of splitting, movement, and amalgamation of the areas they inhabit, plus the more improbable oversea dispersal of the biotas themselves. The origin and disappearance, and also the significant movements, of terranes and island arcs in southeast Asia for at least the last 60 My, have provided the stage for the evolution of its highly diverse flora and fauna. A pattern caused by dispersal events by whole biotas may be difficult to distinguish from a pattern evolved by splitting of areas. Some authors simply state that dispersal should be considered the driving force,

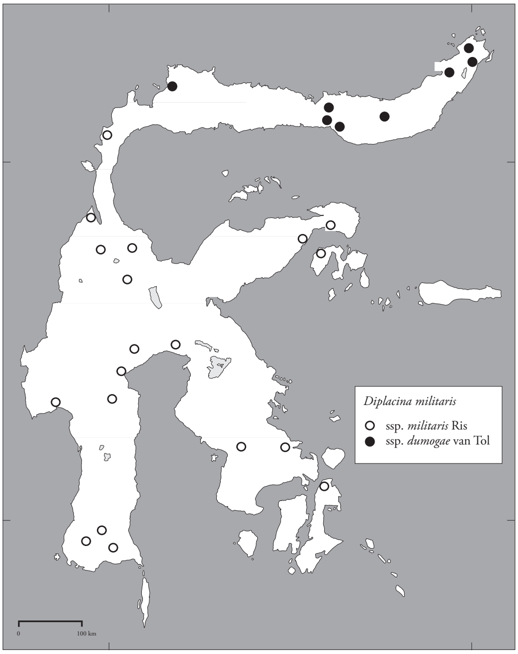


Figure 18. Distribution of subspecies of *Diplacina militaris* Ris on Sulawesi.

e.g., De Jong (2001: 135) ‘Whatever the land–sea distribution may have been since the mid Oligocene, animals and plants did disperse from Asia to Australia and *vice versa*.’ The question in zoogeography then will be how a certain monophyletic group has evolved, given the distribution of land and sea, and the biological characters of the species. While we are still searching for generalized patterns of area relationships, an analysis of the evolution of a particular group remains problematic.

The study of area relationships is hampered by phenomena as poorly corroborated phylogenetic reconstructions, no insight into the timing of speciation, insufficient data of land–water distributions in the past, and *random* dispersal of taxa. In the case of the Malay archipelago and the West Pacific, it is likely that at least the *effect* of dispersal has not been random, since survival after dispersal is strongly constrained by the seas surrounding the islands. It is methodologically still unexplored how patterns derived from rifting of terranes or island arcs, amalgamation of such land masses, or active directional dispersal of the biotas should be distinguished. Also, not much effort has been made up to now to estimate the scale of dispersal. The distribution pattern of any species is, of course, generally due to small-step active or passive dispersal, depending on the life strategy of the species. Such dispersal can best be called *spreading* or *dispersion* over suitable habitat. Dispersal events over *unsuitable* habitat theoretically have another character. Specific characters, such as preferred habitat or ecological plasticity or adaptivity, rather than dispersal capacity per se, seem to determine the result of long-distance dispersal over geological times. For some groups of animals and plants, the drifting over sea of rafts of up to a few square kilometers might be one of the most likely methods of dispersal, as has especially been established for pieces of riverine forest. Based on these suppositions, species with very specific habitat requirements have little chance to establish populations on remote islands, since even successful active or passive transport to such a place does not guarantee survival of transported specimens. Even such an analysis meets many difficulties. Many species occurring on islands are extreme habitat specialists, but such a specialization may apparently evolve rather rapidly after a dispersal event, as has been shown for several groups of large and flightless insects of the Chatham islands (Trewick 2000), but actually already for the Darwin finches of the Galapagos islands.

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Part 2

Taxonomy

3. Notes on some species of the genus *Protosticta* from Vietnam (Odonata, Platystictidae)

Jan van Tol

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Key words: Odonata; Platystictidae; *Protosticta*; new species; new records; Vietnam.

Based on a study of various recent collections of *Protosticta* Selys from Vietnam, the dragonfly species *P. grandis* Asahina and *P. khaosoidaoensis* Asahina (sensu stricto) are reported from Vietnam for the first time. New records are provided for *P. satoi* Asahina (new status), and the affinities of *P. satoi* and *P. beaumonti* Wilson are discussed. The status of a very dark form of *Protosticta satoi* found in Tam Dao (northern Vietnam) is also discussed. Two species from Chu Yang Sin National Park (southern Vietnam, Dak Lak province) are described as new to science, viz. *P. caroli* spec. nov. and *P. linnaei* spec. nov.

Introduction

Recent studies in the odonate family Platystictidae have revealed an astonishing diversity at the species level. The diversity of the fauna of Latin America was comprehensively described as early as the first half of the 20th century (*e.g.* Calvert, 1931; Kennedy, 1938, 1942), and less than ten new species have been described during the last 25 years (*e.g.* Brooks, 1989; Donnelly, 1992; De Marmels, 1989).

The diversity of the fauna of Southeast Asia, however, appeared to be far more diverse than expected until recently, with forty species described as new to science in the genus *Drepanosticta* Laidlaw alone since 1990 (van Tol, 2007a). Although most species were described from the Philippines (*e.g.* van Tol, 2005), Sulawesi (van Tol, 2007c), the Moluccas (van Tol, 2007b) and New Guinea (Theischinger & Richards, 2005), the family appeared to be also much more speciose in the mainland of Southeast Asia. New species were discovered in Thailand (Asahina, 1984; Hämäläinen, 1999), Hong Kong and southern China (Zhou, 1986; Wilson, 1997; Wilson & Reels, 2001, 2003; Wilson & Xu, 2007).

Most species of Oriental Platystictidae are assigned to *Drepanosticta* and more than one hundred species are presently known. The genus *Platysticta* Selys is restricted to Sri Lanka and southern India, the recently described genera *Sinosticta* Wilson and *Sulcosticta* van Tol are confined to southern China and the Philippines, respectively. Finally, the genus *Protosticta* Selys as presently defined takes an intermediate position. It is rather widespread in the mainland of Southeast Asia (Table 1) and occurs in the Philippines, Borneo and Sulawesi with 38 species. However, its monophyly is uncertain (van Tol, 2005), since the genus is based on the reduction of the anal crossing in the wing venation, a character susceptible to homoplasy. A phylogenetic study based on a wide variety of morphological and molecular characters is in progress (van Tol, in prep.). It seems unlikely that the species of the mainland form a monophyletic group with the type species of the genus *Protosticta*,

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Table 1. Distribution of the species of *Protosticta* in mainland Southeast Asia. References to all original descriptions are included in the references section.

Species of *Protosticta*	Distribution
P. antelopoides Fraser, 1931a	India (Travancore)
P. beaumonti Wilson, 1997	Hong Kong; China (Guangdong)
P. caroli spec. nov.	Vietnam
P. curiosa Fraser, 1934	Lower Burma (East Mergui); Thailand (widespread in western part)
P. damacornu Terzani & Carletti, 1998	NE India (Meghalaya)
P. davenporti Fraser, 1931b	South India (Mudis Hills)
P. foersteri Laidlaw, 1902	Peninsular Malaysia
P. fraseri Kennedy, 1936	India (Assam)
P. grandis Asahina, 1985 syn. *P. robusta* Asahina, 1984 [nec Fraser]	Thailand (Chang Mai), Vietnam
P. gravelyi Laidlaw, 1915 syn. *P. mortoni* Fraser, 1924 syn. *P. stevensi* Fraser, 1922	India (Cochin State; Coorg; Nilgiris)
P. hearsayi Fraser, 1922	India (Nilgiris)
P. himalaiaca Laidlaw, 1917 syn. *P. lindgreni* Fraser, 1920	India (Pashok, Darjeeling)
P. khaosoidaoensis Asahina, 1984	Thailand (Chantaburi and Chiang Mai), Vietnam
P. kiautai Zhou, 1986	China (Zhejiang)
P. medusa Fraser, 1934	Lower Burma (East Mergui), western Thailand (Kanchanaburi and Tak)
P. robusta Fraser, 1933	Laos (Taweing)
P. rufostigma Kimmins, 1958	South India (Tinnevelly Dt.)
P. sanguinostigma Fraser, 1922 forma *cerinostigma* Fraser, 1924	South India (Nilgiris) South India (Nilgiris)
P. satoi Asahina, 1997	northern Vietnam
P. taipokauensis Asahina & Dudgeon, 1987	Hong Kong; ? China (Fujian)
P. trilobata Fraser, 1933	Laos (Muang Cha)
P. uncata Fraser, 1931b	Upper Burma (North Shan States)

P. simplicinervis Selys, and with other species from Sulawesi.

Only one species of *Protosticta*, *P. khaosoidaoensis satoi* Asahina has been reported from Vietnam up to now (Asahina, 1997; Tsuda, 2000; Cuong & Hoa, 2007). More intensive collecting of Odonata in Vietnam during the last decades provided the opportunity to study new material of *Protosticta* from Vietnam. The present paper gives descriptions of two new species of *Protosticta* and enumerates new records of previously described species. This paper does not report on all specimens of *Protosticta* I have seen from Vietnam; some collections are incomplete or only consist of females and need further study.

This paper is part of a series of papers prepared by staff of the National Museum of Natural History Naturalis on the occasion of the 250th anniversary of zoological nomenclature on 1 January 2008. Zoological nomenclature starts with the tenth edition of Linnaeus's Systema Naturae, which is 'deemed to be published on 1 January 1758' (International Commission on Zoological Nomenclature, 1999). The damselfly family Platystictidae was unknown to Linnaeus. This may be not surprising for a group with mainly small and inconspicuous species virtually confined to the tropics, but the first species was described and illustrated only fifteen years after 1758 (Drury, 1773). Although the type of *Libellula paulina*, now *Palaemnema paulina* (Drury) is lost, the name is still valid, since Calvert (1931) inferred the identity of the nominal taxon, which was generally accepted.

Material and methods

I have examined specimens available in the National Museum of Natural History Naturalis (Leiden, The Netherlands) (RMNH), which includes collections brought together by M.A. Lieftinck (specimens from India and Burma from the F.C. Fraser collection), M. Hämäläinen (Espoo, Finland) (specimens from Thailand, Laos) and myself (Thailand, Vietnam). H. Karube, via M. Hämäläinen, made material preserved in the Kanagawa Prefectural Museum, Odawara, Japan available for this study. K.D.P. Wilson donated specimens of *P. beaumonti* for comparison with the Vietnamese species.
The specimens were studied and photographed with a Leica MZ16A equipped with a Leica DFC500 camera, motor focusing and LAS auto-imaging software. Terminology, also of wing venation, follows Watson & O'Farrell (1991).

Platystictidae of Vietnam

Protosticta grandis Asahina

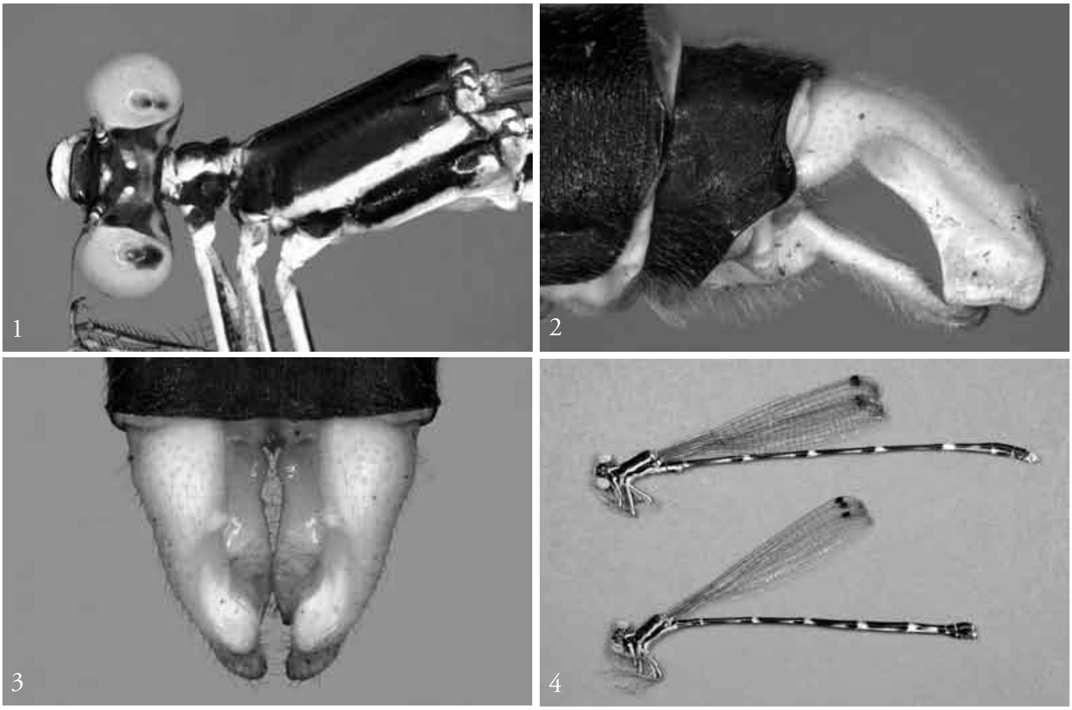
(Figs 1-4)

Protosticta robusta Asahina, 1984 [nec Fraser]: 590-591, 595, figs 16-20 (original description) [preoccupied].

Protosticta grandis Asahina, 1985: 334 (new name for *Protosticta robusta* Asahina, 1984). – Hämäläinen & Pinratana, 1999: 60 (distribution Thailand: Chiang Mai and Kanchanaburi); Tsuda, 2000: 326 (catalogued Thailand).

Material examined. – **Thailand**: Chiang Mai, Doi Suthep, 600 m, 29 March 2003, leg. M. Hämäläinen, 1 male, 1 female, in RMNH. – **Vietnam**: Vinh Phu province, Tam Dao, 1993, leg. H. Karube and collaborators, 3 females, in KPMO; same site, 16-17 May 1997, leg. H. Karube and collaborators, 1 female, in KPMO; Ninh Binh province, Cuc Phuong NP, 6 Jan. 1998, leg. H. Karube, 1 male, in KPMO; Dak Lak province, Chu Yang Sin National Park, small streams and seepages around confluence of Krong K'mar river and Ea Kchur river, ca. 12°28'N 108°20'E, 750 m asl, June 2007, leg. J. van Tol, 9 males 1 female, in RMNH and IEBR; Lam Dong province, Bao Loc, various dates 1996-1998, leg. H. Karube and collaborators, 4 males 4 females, in KPMO.

Protosticta grandis was extensively described by Asahina (1984), based on specimens from Chiang Mai, northern Thailand. It is also known from the Thai province of Kanchanaburi (Hämäläinen & Pinratana, 1999). Topotypical material from Thailand was compared with specimens collected in Burma, Laos and Vietnam. Although specimens from different sites show some variation, I consider the specimens from Vietnam mentioned above conspecific with the topotypical *Protosticta grandis*. Specimens from Tam Dao (females only) are larger than those of other sites (e.g. JvT 27971 from Tam Dao, abdomen 48 mm, hind wing 35 mm, as compared to JvT 26155, topotypical female from Chiang Mai, abdomen 41 mm, hind wing 30 mm). A specimen collected near Hue superficially resembles *P. grandis*, but presumably represents an undescribed species.
Based on morphological characters (see Figs 1-3), *P. grandis* represents a clade only distantly related to the other species of Vietnam, which all belong to the *P. curiosa* or *P. beaumonti* groups. This observation was confirmed by a molecular study of about 490 base pairs of the 16S gene, revealing a difference of tens of base pairs between *P. grandis* and other species described in this paper.
Remark. – The status of the specimens from Burma and Lao P.D.R. has not been ascertained; *P. grandis* has



Figures 1-4. *Protosticta grandis* Asahina, male [JvT 28493, Vietnam, Chu Yang Sin National Park]. – 1, head and synthorax, left lateral view. – 2, anal appendages, left lateral view. – 3, anal appendages, dorsal view. – 4, habitus, male (above) and female (below).

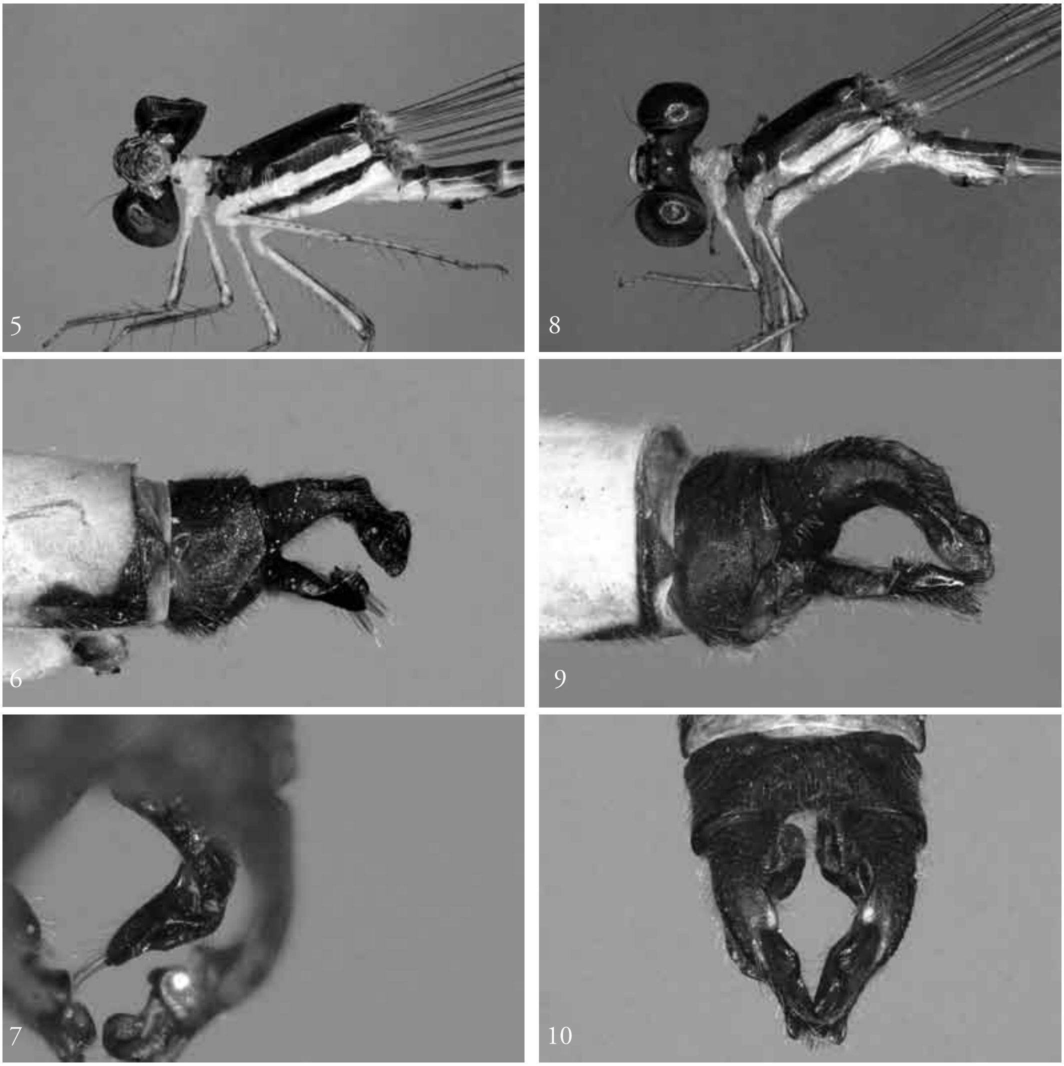
not been recorded from Burma and Lao P.D.R. before (Tsuda 2000).

Protosticta khaosoidaoensis Asahina
(Figs 5-10)

Protosticta khaosoidaoensis Asahina, 1984: 588-590, figs 8-15 (original description, type locality Thailand, Khao Soi Dao mountains). – Hämäläinen & Pinratana, 1999: 60 (distribution Thailand: Chiang Mai and Chanthaburi).

Material examined. – **Vietnam**. Nghe Tinh province. Huong Son district, west of Rao Qua: logging road along tributary of river An Bun. Rivulets, rocky stream and pools, dense logged forest and secondary growth. 100-150 m, 18°20'N 105°15'E, 2 July 1990, F.G. Rozendaal, 2 males [JvT 1144-5], in RMNH; Nghe Tinh province, Ky Son district. Forest stream Khe Thuong, a tributary of river Song Ca. Primary forest. Altitude ca. 500 m, ca. 19°15'N 104°23'E. 8 July 1990. Leg. F.G. Rozendaal, 1 male [JvT 1146], in RMNH; Nghe Tinh province, Thang Chuong district. Doi Khe Lao. Several streams through logged forest. ca. 100 m, 18°40'N 105°15'E, 11-12 July 1990, F.G. Rozendaal, 2 males [JvT 1147-8], in RMNH.

Specimens from the Huong Son district of the Nghe Tinh province (now province of Ha Tinh) structurally resemble *P. curiosa* Fraser, but show characters of *Protosticta khaosoidaoensis* sensu stricto as defined by Asahina, especially in the coloration of the pronotum. A male from Thailand (Chiang Mai) is illustrated in Figs 5-7, a male from Vietnam in Figs 8-10. The inferior appendages lack the cup-like structures of *Protosticta linnaei* spec. nov., as described below. It is uncertain whether *P. curiosa* and *P. khaosoidaoensis* indeed represent two different taxa, since structural differences seem to be small. For a better judgment, more material from Burma, Laos and Cambodia should be studied.



Figures 5-10. *Protosticta khaosoidaoensis* Asahina, male [figs 5-7, Northern Thailand, Chiang Mai, Doi Suthep (JvT 19422). – 8-10, Vietnam, Nghe Tinh province, Huong Son district, 1990 (JvT 1145)]. – 5 and 8, head and synthorax, left lateral view. – 6 and 9, anal appendages, left lateral view. – 7 and 10, right inferior appendage, dorsal view (detail).

Protosticta satoi Asahina, **new status**

(Fig. 16)

Protosticta khaosoidaoensis satoi Asahina, 1997 [June]: 108-109, figs 3-4 (original description, type locality [Vietnam], Tam Dao, 960 m, 21 May 1995). – Tsuda, 2000: 326 (catalogued Vietnam)

Protosticta khaosoidaoensis nec Asahina; Cuong & Hoa, 1997: 65 (distribution map).

? *Protosticta beaumonti* Wilson, 1997 [March]: 57-59, figs 11-16 (original description, type locality Hong Kong, Lantau, 22 May 1994, in BMNH). – Tsuda, 2000: 305 (catalogued China).

Material examined. – **Vietnam**: Ninh Binh province, Cuc Phuong National Park, 1994-1998, leg. H. Karube and collaborators, 12 males 3 females (in KPMO).

Description. – Male [Vietnam, Ninh Binh province, Cuc Phuong NP, 30 Apr 1994, H. Karube, JvT 27950, in KPMO] (colours of preserved specimen).

Head. – Labium, including lateral lobes, dirty white, distal half of lateral lobes with setae nearly as long as lobe itself; labrum bluish-white, anterior one-fifth black; mandibles black with triangular bluish-white spot adjoining labrum, anterior black stripe of mandibles much wider than stripe on labrum; anteclypeus bluish-white, postclypeus brown, rest of head black with some metallic sheen, fine coriaceous around ocelli, but area around eyes shining; scapus brown, pedicellus with basal three-quarters ivory white, rest of pedicellus brown, flagellum brown; transverse occipital carina just discernable, without lateral extremities.

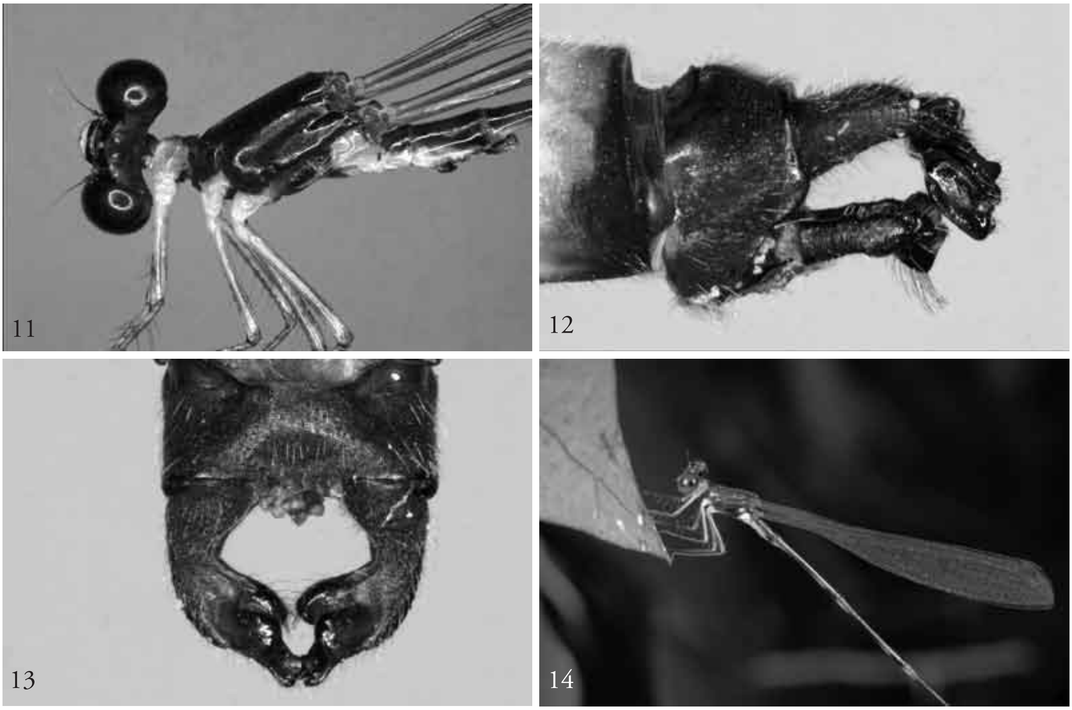
Thorax. – Pronotum with anterior and posterior lobes simple, without distinct lateral or posterior processes; yellowish white, but medially on posterior lobe a trapezoid dark marking. Synthorax with mesepisternum brownish-black with metallic sheen; mesepimeron pale brown; metepisternum largely dirty yellow; upper side of mesokatepisternum brown, lower side dirty yellow, central part brownish black; metepimeron and metakatepisternum pale; venter yellowish-white. Legs yellowish-white, but outer surface of all femora and basal half of tibiae with narrow black lines. Wings clear with venation brown; Px 15 in fore wing, Px 14 in hind wing; R4+5 arising distinctly distal to Ax2; Ab vein missing; CuP meeting hind margin of fore wing at Px3, of hind wing at Px 4; number of cells between Arculus and place where CuP meets hind margin of fore wing 6, of hind wing 7; R3 arising in hind wing at level of Px 6; pterostima trapezoid.

Abdomen. – First six segments relatively pale, base colour dirty yellow, rest of abdomen darker, except segment 9; segment 1 pale with inconspicuous dorsal trapezoid brown marking, segment 2 also with dorsal brown marking and oblong ivory white markings in latero-anterior corners; segments 3-6 brownish, each segment anteriorly with short and narrow yellow marking, ca. one-fifth of each segment; segment 7 anteriorly pale brown, posterior three-quarters dark brown; segment 8 brownish black; segment 9 ivory white with narrow black line anteriorly adjoining intersegmental ring; segment 10 brownish-black. Anal appendages (Fig. 16) brownish black, superiors ca. 2 times length of segment 10 of abdomen; basal half stout, cylindrical and tapering; distal half compressed with short dorsal tooth; inferiors basally diverging, distal half with oblong triangular shape, terminally pointed and provided with tuft of setae, dorsal surface with of terminal part with cup-shaped structure, with terminal spine bent abaxiad.

Measurements. – Abdomen, including appendages, 44 mm, hind wing 21 mm.

Remarks. – The rather incomplete description of *P. khaosoidaoensis satoi* Asahina is based on one female from Tam Dao. The collections of *Protosticta* from Tam Dao before me (KPMO, RMNH / IEBR), however, do not contain further specimens comparable to the description of this nominal taxon. Presuming that the measurements of ‘subspecies’ *satoi* are comparable to the nominate *P. khaosoidaoensis*, the abdomen of the male should be about 37-38 mm and the hind wing 19-20 mm. The coloration of the synthorax of *P. satoi* (pale brown mesepimeron, dirty yellow metepisternum and metepimeron with a fine stripe over metapleural suture), as well as the pale blue marking meso-posteriorly on segment 9 of the abdomen, are markedly different from the same structures in *P. khaosoidaoensis* sensu stricto.

However, I consider female *Protosticta* specimens from Cuc Phuong National Park (see material section) to be *P. satoi* (new status), since they agree with the description and illustrations of this taxon (Asahina, 1997). Males from the same locality, with similar synthorax as the females, are structurally similar to topotypical *P. beaumonti* Wilson (RMNH, ex coll. Wilson) (see description above, and Figs 16 and 17). The abdomen, including anal appendages, of males of *P. beaumonti* measure 44-45 mm, the hind wings 22-22.5 mm. The abdomen of males from Cuc Phuong measure ca. 44-45 mm, the hind wings 20-22 mm. Further studies (see also below) should reveal whether *P. satoi* is a senior synonym of *P. beaumonti*, or whether both represent distinct species.



Figures 11-14. *Protosticta satoi* dark form, male [JvT 28748 (figs. 11-13, Vietnam, Tam Dao, 2007]. – 11, head and synthorax, left lateral view. – 12, anal appendages, left lateral view. – 13, anal appendages, dorsal view. – 14, living male, northern Vietnam, Tam Dao, 2007.

Protosticta satoi dark form

(Figs 11-15)

? *Protosticta beaumonti*. – Wilson & Reels 2003: 273-275, figs 114-120 (dark form from W Guangxi, Diding).

Material examined. – Vietnam, Vinh Phu province, Tam Dao: 1993-1994, leg. H. Karube, 3 males, 2 females, in KPMO; idem, 30 May 1997, leg. H. Karube, 1 male, in KPMO; idem, various streams around village, including crossing road to Tamdao 2, 13-15 May 2007, leg. J. van Tol 10 males 1 female, in RMNH and IEBR.

Description. – Male [based on JvT 28703] (see also Fig. 14).

Head. – Labium dirty yellow, lateral lobes distal half pale brown with setae nearly as long as lateral lobe itself; labrum bluish-white, anterior two-fifths black; mandibles black with triangular bluish-white spot in inner basal corner; anteclypeus bluish-white, rest of head dark black, fine coriaceous with longitudinal striae, but area around eyes shining; scapus dark brown, pedicellus basal half dirty white, distal half brown, flagellum broken off in type [brownish black in other specimens]; transverse occipital carina just discernable, without lateral extremities.

Thorax. – Pronotum with anterior and posterior lobes simple, without distinct lateral or posterior processes; base colour yellowish-white, with black markings as follows: anterior lobe black, median lobe with paired protuberance brownish black, medially darker; lateral lobes yellowish white; posterior lobe black, but lateral corners dirty yellow. Synthorax (Fig. 11) very dark brownish black with some metallic sheen, but lower posterior corners of mesokatepisternum and metakatepisternum, and posterior half of metepimeron, yellowish-white; venter distinctly bicolorous, anteriorly brownish black, posteriorly yellowish white as continuation of pale markings of metepimeron. Legs

Figures 15-17. Anal appendages male, postero-lateral view. – 15, *P. satoi* dark form, Tam Dao. – 16. *P. satoi*, northern Vietnam, Cuc Phuong. – 17, *P. beaumonti*, Hong Kong.

yellowish-white, but rims on outer surface of all femora dark. Wings clear with dark brown venation, basally middle brown; Px 16 in fore wing, Px 15 in hind wing; R4+5 arising at subnodus; Arculus arising just distal to Ax2; Ab vein missing; CuP meeting hind margin of fore wing at level of Px3, of hind wing at Px4; number of cells between Arculus and place where CuP meets hind margin of fore wing 6, of hind wing 8; R3 arising in hind wing at level of Px7; pterostigma trapezoid, the proximal and basal veins convex, 1.0 mm wide, 0.6 mm high; dark brown, but bordered with narrow white line against veins; cells between Costa and R1 distal to pterostigma undivided.

Abdomen. – Brownish black and middle brown; segment 1 dorsally with brown marking covering ca. three-fifths of segment width, rest of segment pale; segment 2 nearly fully brown, somewhat darker along posterior margin, with oblong triangular pale marking in latero-anterior corner, ca. three times as long as high; segments 3-5 brown, but paler anterior markings of ca. one-eighth of segment length just behind anterior margin, and other pale markings of ca. one-sixth of segment-length ca. one-sixth of segment-length from posterior margin; segments 6-7 as 3-5, but without posterior pale markings; segment 8 dorsally brownish black, with small triangular markings in latero-anterior corners, ca. three-fifths length of segment; segment 9 pale ivory-white with narrow incomplete dark anterior margin and complete, dark posterior margin, laterally somewhat widening; segment 10 brownish black.

Anal appendages (Figs 12-13, 15) black; superiors ca. 2.0 times length of abdominal segment 10, basal half stout, cylindrical and tapering, distal half somewhat compressed, with stout dorsal tooth at base of compressed part, and a short protuberance ventrally at base of compressed part; distal half ventrally somewhat emarginate, distally rounded; inferiors in ventral view with bases ca. 60° diverging, and distal half bent axiad; terminal part more than two times as wide as base, club-shaped, ventrally with row of setae, terminally denser than at base, but not forming a distinct tuft; in posterior view a long and stout terminal spine, which is bent abaxiad, visible; dorsal side of inferiors cup-shaped, the cup placed fully terminally.

Measurements. – Abdomen, including appendages, 44 mm, hind wing 22 mm.

Figure 18. Small stream at crossing road between Tamdao and Tamdao 2, June 2007. *Protosticta satoi* dark form can be found in dense vegetation immediately above the road, together with, e.g., *Devadatta ducatrix* Lieftinck, *Agriomorpha fusca* May, *Indocnemis ambigua* Asahina and *Coeliccia onoi* Asahina, while *Calicnemia* sp. is most common at the most sunny sites near the road.

Female [JvT 28715]. – As male, except for the following characters: median lobe of pronotum ivory-white without dark coloration; abdominal segment 4-6 anteriorly with ivory-white triangular markings, with base anteriorly adjoining intersegmental annulae, lateral to these markings in latero-anterior corner subrectangular pale markings, larger on each following segment, segment 7 anterior third bluish pale white with irregular margin with dark posterior two-thirds, segment 8 brownish-black with triangular pale marking in latero-anterior corner, segments 9-10 brownish-black, valve brownish-black, terebra ivory-white.
Measurements. – Abdomen 46 mm, hind wing 23 mm.

Variation. – The coloration of the pronotum of the males shows significant variation; the median lobe may be either fully pale coloured, or heavily smudged dark. Measurements: male abdomen, including appendages, 43-48 mm, hind wing 22-26 mm.

Remarks. – Medium-sized *Protosticta* (Fig. 14) with long abdomen and short wings; inferior appendages of males ending in cup-shaped structure, as in *P. satoi* Asahina, *P. beaumonti* Wilson (Fig. 17) and *P. caroli* spec. nov., but can immediately be distinguished from other species by fully brownish-black synthorax without pale stripes and only a triangular posterior marking on the metepimeron. This may be the same taxon as recorded by Wilson & Reels (2003: 273-275) from western Guangxi, a province of China bordering Vietnam. As already stressed by Wilson & Reels (2003), the structural differences of the anal appendages and other diagnostic characters of these specimens with *P. beaumonti* are subtle. Apart from the remarkably unusual coloration, I only found significantly longer wings as a diagnostic character of the dark form of *P. beaumonti* or *P. satoi*. The hind wings of the dark form (Tam Dao) virtually reach to the posterior margin of segment 5 of the abdomen, and are 52-56% of the length of the abdomen (including anal appendages). The two males from Guangxi (*P. beaumonti*) agree with these figures (53-56%). The hind wing of specimens from Cuc Phuong, here identified as *P. satoi*, only reach to halfway segment 5 and are 47-48% of the length of the abdomen. Hind wings of topotypical specimens of *P. beaumonti* are also short, reach to halfway segment 5 and are 47-49% of the length of the abdomen.

A final judgment of the status of the populations from Tam Dao has to be postponed until more material is available, or results of a molecular study of at least *Protosticta beaumonti* can be compared with the specimens from Tam Dao, Cuc Phuong ('*satoi*') and southern Vietnam ('*linnaei*'). A preliminary study of the 16 rDNA region (about 490 base pairs) revealed that specimens from Tam Dao differ in at least 18 base pairs from both *P. caroli* spec. nov. and *P. linnaei* spec. nov., indicating a larger difference than the difference between the last two mentioned species (about 9 base pairs), which differ considerably in structural characters.

Distribution. – Vietnam (Vinh Phu province): Tam Dao. Rather uncommon on small, steep rocky streams around the village (Fig. 18). This mountain ridge is a national park, but at least the fauna of the streams in the immediate surroundings of the village is under threat, since all water sources are used for drinking water supply under the rapid development of the tourist sector in the park.

Descriptions of new species

Protosticta caroli spec. nov.

(Figs 19-22)

Type material. – Holotype male [JvT 28496] in RMNH: 'Vietnam (Dak Lak province). Chu Yang Sin NP: stream with small brooklet and seepage in forested area. 12°31'03"N 108°17'41"E. Alt. 500 m. 7 Jun 2007. Leg. J. van Tol.' – Paratypes (9 specimens, in RMNH and IEBR): Bao Lok, 3-5 May 1997, leg. H. Karube, 2 males, in KPMO; Chu Yang Sin NP: small sandy forest stream (left bank just above dam in Krong K'mar river). 12°26'48"N 108°20'10"E. Alt. 760 m. 3, 8 and 10 Jun 2007, leg. J. van Tol, 5 males; same data as holotype, 1 male; same site, but 9 June 2007, 2 males.

Diagnosis. – Medium-sized, rather dark *Protosticta* of the *P. curiosa*-complex, but most closely related to *P. satoi* and *P. beaumonti* as defined above; males differ from *P. satoi* by the dark coloration of the prothorax (most specimens) and synthorax, a much smaller pale marking on segment 9 of the abdomen, and a larger cup-like structure of the appendix inferior; the terminal spine is smaller, although also distinctly curved axiad; distinct subterminal tuft of setae ventrally on appendix inferior.

Male [holotype, JvT 28496]. – Head. Labium dirty yellow, lateral lobes distal half pale brown with setae nearly as long as lateral lobe itself; labrum bluish-white, anterior two-fifths black; mandibles black with triangular bluish-white spot in inner basal corner; anteclypeus bluish-white, rest of head black, fine coriaceous with longitudinal striae, but area around eyes shining; scapus dark brown, pedicellus basal half dirty white, distal half brown, flagellum (broken in holotype) brownish-black; transverse occipital carina just discernable, without lateral extremities.

Thorax (Fig. 19). – Pronotum with anterior and posterior lobes simple, without distinct lateral or posterior processes; base colour dirty yellowish-white, with black markings as follows: anterior lobe with median trapezoid spot, posterior side ca. one-third of posterior width of anterior lobe, median lobe with variegated brownish-black markings, but latero-anterior corner pale; lateral lobes yellowish-white with narrow black stripe along dorsal and posterior margin; posterior lobe black. Synthorax dark brownish-black; mesepisternum and mesepimeron black; metepisternum dorsally with pale stripe, ca. three-fifths the height of metepisternum, more or less parallel-sided, continuing over mesokatepisternum; metepimeron dorsal half brownish-black, but pale ventral marking continuing along posterior margin; metakatepisternum dorsally black, ventral half pale. Legs yellowish-white, but outer surface of all femora, and tibiae of fore and hind legs with narrow black lines. Wings clear with dark brown venation, basally middle brown; Px 14 in fore wing, Px 13 in hind wing; R4+5 arising distinctly distal to subnodus; Arculus just distal to Ax2; Ab vein missing; CuP meeting hind margin of fore wing at level of Px2, of hind wing at Px3; number of cells between Arculus and place where CuP meets hind margin of fore wing 5, of hind wing 6; R3 arising in hind wing at level of Px5; pterostigma subrectangular, 0.8 mm wide, 0.6 mm high; reddish-brown, but bordered with narrow white line against veins; cells between Costa and R1 distal to pterostigma undivided.

Abdomen. – Dark brown and yellowish-white; segment 1 dorsally with brown marking which is medially constricted, rest of segment pale; segment 2 nearly fully brown, with oblong pale marking in latero-anterior corner, ca. three times as long as high; segment 3 brown, with somewhat paler anterior ring against segment 2, posterior one-fifth distinctly darker; segments 4-6 brown, with oblong pale marking in latero-anterior corner against preceding segment, ca. four times longer than high (median part of each segment also paler brown), and distal one-fifth of each

Figures 19-22. *Protosticta caroli* spec. nov., male [JvT 28519 (figs 19-21), Vietnam, Chu Yang Sin National Park, and JvT 28351 (fig. 22), same locality]. – 19, head and synthorax, left lateral view. – 20, anal appendages, left lateral view. – 21, anal appendages, dorsal view. – 22, ligula, oblique view.

segment darker brown; segment 7 brown, gradually darker posteriorly, and a paler crescent-shaped spot in latero-anterior corner, ca. one-third length of segment; segment 8 dorsally dark brown, with large triangular markings in latero-anterior corners, ca. three-fifths length of segment; segment 9 dirty brownish-yellow, with triangular medio-anterior marking, ca. three-fifths length of segment, posterior one-sixth of segment dark brown, stripe somewhat widening towards corners; segment 10 brown. Anal appendages black (Figs 20-21); superiors ca. 2.0 times length of abdominal segment 10, basal half stout, cylindrical and tapering, distal half compressed, with short dorsal tooth at base of compressed part, and a short protuberance ventrally at base of compressed part; distal half ventrally somewhat emarginate, distally rounded; inferiors in ventral view forming a heart-shaped figure, bases ca. 60˚ diverging, and distal half again 60˚ bent axiad; terminal part more than two times as wide as base, club-shaped with distinct terminal tuft of setae; in posterior view a long and stout terminal spine, which is bent abaxiad, visible; dorsal side of inferiors cup-shaped, the cup placed fully terminally.

Measurements. – Abdomen, including anal appendages, 39 mm; hind wing 20.5 mm.

Female. – Unknown.

Variation. – Males from Chu Yang Sin National Park: abdomen, including anal appendages, in all specimens from *ca.* 45 mm; hind wing 22-23 mm.

Etymology. – Named for Carolus Linnaeus, founder of biological nomenclature, on the occasion of the 250th anniversary of zoological nomenclature (Linnaeus, 1758). *Caroli*, a noun in the genitive case.

Biology. – At small streams and seepages (see also Fig. 12).

Distribution. – Southern Vietnam: Dak Lak province (Chu Yang Sin National Park), Lam Dong province (Bao Loc).

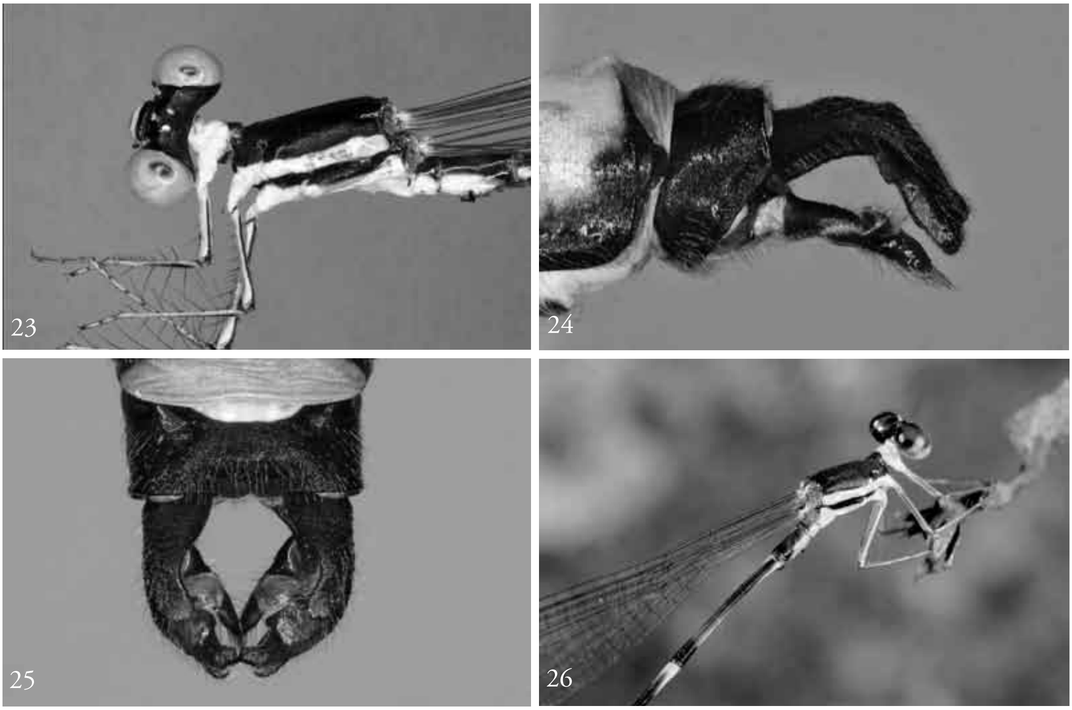
Protosticta linnaei spec. nov.

(Figs 23-26)

Type material. – Holotype male [JvT 28352]: 'Vietnam (Dak Lak province). Chu Yang Sin NP: small sandy forest stream (left bank just above dam in Krong K'mar river). 12°26'48"N 108°20'10"E. Alt. 760 m. 3 Jun 2007. Leg. J. van Tol', in RMNH. – Paratypes (9 males, in RMNH and IEBR) (all Vietnam, Dak Lak province, Chu Yang Sin National Park): Da K'mla river (left bank of Krong K'mar river just above hydro-electric dam under construction), small river in rather steep valley, rocks, boulders, pebbles and coarse sand, secondary forest, 12°26'51"N 108°20'09"E. Alt. 760 m. 2 Jun 2007. Leg. J. van Tol, 3 males; Same data as holotype, 2 males; Ea Kchur river near Thon 3. Small river, c. 8 m wide, steep valley, rocks, some pebbles and coarse sand (including a small muddy tributary); secondary vegetation, gardens, 12°28'32"N 108°17'33"E. Alt. 570 m. 6 Jun 2007. Leg. J. van Tol, 1 male; Stream with small brooklet and seepage in forested area, 12°31'03"N 108°17'41"E, Alt. 500 m, 7 Jun 2007, Leg. J. van Tol, 1 male; Sandy forest stream. 12°26'48"N 108°20'10"E. Alt. 760 m. 8 Jun 2007. Leg. J. van Tol, 2 males.

Diagnosis. – A slender *Protosticta* of the *P. curiosa* group (Fig. 26) with short wings, dark base colour of head and thorax strongly contrasting with bluish-white markings; pale markings in comparison to *P. caroli* more extensive and distinct, also in live specimens; males with tip of inferior appendage elongate and tapering, with a subterminal cup-like structure on dorsal surface of inferiors. Differs from *P. curiosa* by the presence of a distinct cup-like structure on the dorsal side of the inferior appendage (see remarks below).
Male [holotype, JvT 28352]. – Head. Labium dirty white, median lobe very pale brown, lateral lobes dirty white, distal half with setae nearly as long as lateral lobe itself; labrum bluish-white, anterior two-fifths black; mandibles black with triangular bluish white spot adjoining labrum, the anterior black stripe as a continuation of the stripe over labrum; anteclypeus bluish-white, rest of head black with some metallic sheen, fine coriaceous with longitudinal striae, but area around eyes shining; scapus pale with some black markings, pedicellus basal half ivory-white, distal half brown, flagellum brown; transverse occipital carina just discernable, without lateral extremities. Eyes green in living individuals (Fig. 26).

Thorax. – Pronotum with anterior and posterior lobes simple, without distinct lateral or posterior processes; base colour ivory-white, with markings as follows: anterior lobe with narrow brown stripe over anterior ridge, posterior lobe brownish-black but with narrow anterior and wider lateral pale stripes. Synthorax (Fig. 23) brownish-black; mesepisternum and mesepimeron black; metepisternum dorsally with pale stripe, ca. four-fifths the height of metepisternum, more or less parallel-sided, continuing over mesokatepisternum and lower side over metastigma; metepimeron dorsal half brownish black, but pale ventral marking continuing along posterior margin; metakatepisternum dorsally black, ventral two-thirds pale; venter ivory-white. Legs yellowish-white but outer surface of all femora and basal half of tibiae with narrow black lines. Wings clear with brown venation; Px 13 in fore wing, Px 13 in hind wing; R4+5 arising at subnodus; Arculus just distal to Ax2; Ab vein missing; CuP meeting hind margin of fore wing at level of Px2, of hind wing at Px3; number of cells between Arculus and place where CuP meets hind margin of fore wing 5, of hind wing 6; R3 arising in hind wing at level of Px5; pterostigma subrectangular, 0.8 mm wide, 0.6 mm high; brown, but bordered with narrow white lines against veins; cells between Costa and R1 distal to pterostigma undivided.
Abdomen. – Dark brown and bluish-white markings with high contrast; segment 1 dorsally with brown marking, laterally concave, posterior side wider than anteriorly, rest of segment ivory-white; segment 2 nearly fully brown, medially somewhat paler, with oblong ivory-white marking in latero-anterior corner, ca. three times as long as high; segment 3 brown, anteriorly with short and narrow bluish-white marking sharply pointed posteriorly, brown marking paler posteriorly until reaching dark posterior ring adjoining posterior margin of segment; segments 4-7 brown, with somewhat irregular bluish-white basal markings, laterally covering anterior one-sixth, one-fifth, one-quarter and one-third of respective segments, posterior part of each segment somewhat darker than median part; segment 8 dorsally brownish-black, with large triangular markings in latero-anterior corners, ca. three-fifths length of segment; segment 9 bluish-white



Figures 23-26. *Protosticta linnaei* spec. nov., male [JvT 28302 (figs. 23-25), Vietnam, Chu Yang Sin National Park, 2007]. – 23, head and synthorax, left lateral view. – 24, anal appendages, left lateral view. – 25, anal appendages, dorsal view. – 26, living male, southern Vietnam, Chu Yang Sin National Park, 2007.

or ivory-white, with narrow stripe adjoining anterior intersegmental ring, latero-posterior corners black; segment 10 brownish black. Anal appendages (Figs 24-25) black; superiors ca. 2.0 times length of abdominal segment 10, basal half stout, cylindrical and tapering, distal half compressed, with short dorsal tooth at base of compressed part, and a short protuberance ventrally at base of compressed part; distal half ventrally somewhat emarginate, distally distinctly bilobed; inferiors basally diverging, the distal half club-shaped and curved inwards, dorso-basally and subterminally on distal half a cup-shaped structure.

Measurements. – Abdomen, including appendages, 42 mm; hind wing 20 mm.

Variation. – Paratypes: abdomen, including appendages, 40-42 mm; hind wing 21-22 mm.

Female. – Unknown.

Remarks. – The relationship of this species with *P. curiosa* and *P. khaosoidaoensis* needs further study. Fraser (1934) does not mention a cup-like structure dorsally on the inferior appendage of the type specimen of *P. curiosa* (Lower Burma, East Mergui). Such a structure was not illustrated nor described by Asahina (1984) for *P. curiosa* or *P. khaosoidaoensis*. It is not present in a specimen from Thailand (Kanchanaburi, 1-3 Oct 1986, leg. M. Hämäläinen, ex coll. M. Hämäläinen, now in RMNH, JvT 19432), nor in specimens from Vietnam mentioned under *P. khaosoidaoensis* (see above). All specimens are also characterized by extremely short hind wings (type 18 mm, Asahina specimens 18-21 mm, and the RMNH specimen 17 mm). The cup-like structure was, however, described and illustrated by Wilson & Reels (2003: Fig. 113) based on a male *Protosticta* from Phuket (Thailand) identified as *P. curiosa*, which may indicate that *P. linnaei* occurs in Thailand as well.

Etymology. – Named for Carolus Linnaeus, founder of biological nomenclature, on the occasion of the 250th

anniversary of zoological nomenclature (Linnaeus, 1758). *Linnaei*, a noun in the genitive case.
Biological notes. – Generally on larger streams than *P. caroli* spec. nov.
Distribution. – Southern Vietnam: Dak Lak province.

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4. Forest damselflies of the Philippines, their evolution and present status, with the description of *Drepanosticta moorei* spec. nov. from Luzon (Zygoptera: Platystictidae)

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Abstract. *D. moorei* sp. n. (holotype male: Philippines, Luzon, Nueva Viscaya, Sta Fe, Atbo River, 550-800 m, 10-VI-1991, in RMNH) is described, and illustrated. It is closely related to *D. belyshevi* Hämäläinen from the Philippines. Some general remarks on the historical biogeography and the present status of the family are made. The current distribution of the family (SE Asia, Middle and northern South America) presumably dates back to the Upper Cretaceous.

Introduction

The family Platystictidae seems to be a well-established monophyletic taxon (e.g. Jarzembowski et al., 1998), based on the presence of a 'basal post-cubital vein' (Fraser, 1957). Bechly (1995) doubts the homology of the latter with the post-cubital vein in the 'ancient zygopteroid stock' (e.g. *Kennedya* Tillyard), and considered it the genuine CuP. The presence of this vein is a character that easily distinguishes this family from other Zygoptera, and is an apomorphy rather than a plesiomorphy in the Platystictidae (Jarzembowski et al., 1998). The family can also be identified by some other structural features, such as the groundplan of the anal appendages and the structure of the so-called gomphine-shaped lateral appendages of the labium. However, the diagnostic characters of, and the relationships between the genera are at present still unclear.

In the field, almost all SE Asian species are inconspicuous, brown and brownish black, confined to seepages and smaller streams. Most species move very little during the day. With their cryptic coloration they are difficult to find among dense vegetation. The males of some species have a bright blue spot at the tip of the abdomen, which perfectly mimics the water drops at the tip of thin branches in the forest, the very sites where *Drepanosticta* Laidlaw and *Protosticta* Selys rest during the day.

The family occurs in southeastern Asia, from Sri Lanka over India, southern China and Malaysia, into Indonesia up to the Solomon Islands. *Drepanosticta palauensis* Lieftinck is known from Palau (Lieftinck, 1962). Most species of SE Asia are assigned to the Platystictinae, but recently Matsuko & Saito (1996) and

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Previously published in: Odonatologica 32 [2003]: 39-45, figs. 1-5.

Wilson & Reels (2001) found two species for which the subfamily Sinostictinae was erected by Wilson (1997). Another subfamily, the Palaemnematinae, occurs in Middle America and in the northwestern part of South America. All New World species are assigned to the genus *Palaemnema* Selys. Several of these are remarkably similar to those of SE Asia, both in general appearance and in structural details, such as the anal appendages. Although the historical biogeography of the family should be investigated in more detail based on phylogenetic and preferably also molecular studies, our hypothesis is that its present geographic pattern goes back to the Late Cretaceous (ca 65 Ma). The family was at the time presumably distributed over Laurasia and northern North America. The climate was tropical, and Europe and America were still connected. After their separation, the climate became less favourable for tropical biota. Apparently, ancestors of the present Platystictidae moved southward, following tropical conditions, in both North America and Laurasia. The presence of *Palaemnema* in South America is presumably rather recent in geological terms, following the emergence of the Isthmus of Panama, the connection of North and South America about 3 Ma (Coates, 1999).

Most of the Philippine *Drepanosticta* species are structurally more similar to those of the Moluccas (undescribed species) and New Guinea than to the mainland species. The characteristic structures include large processes posteriorly on the posterior lobe of the pronotum and relatively simple male anal appendages. They are also particularly dull in coloration. We hypothesize that this pattern is due to the presence of an island arc along the Pacific plate during the Oligocene and Miocene (20-30 Ma) (Hall, 1998).

Drepanosticta of the Philippines

Diversity. – *Drepanosticta* is a very large genus, with presently 87 valid species described and more than 20 awaiting description in the collection of the Leiden Museum alone, mostly from the Philippines, the Moluccas and New Guinea. Most species have small distributional ranges. The situation may prove even more complex, since many species show significant geographical variation (cf. e.g. van Tol, 1999, for Sulawesi *Protosticta*). Although the morphological differences between such populations may be rather small, it is not unlikely that these populations are separated for millions of years. Molecular studies by the first author to address this problem are in preparation. A significant number of the undescribed species from the Philippines were collected by the second author and his collaborators in the 1980's and 1990's. General information of this collection, which is now housed in the National Museum of Natural History Naturalis, at Leiden, was published by Hämäläinen & Müller (1997), where also the history of the study of Odonata in the Philippines is adequately outlined. The first *Drepanosticta* species were described by Brauer (1868), viz. *D. halterata* and *D. lestoides*. It is remarkable that

Table 1. – Nominal taxa of *Drepanosticta* from the Philippines (in chronological order)

Species-group	Original genus	Author(s)
halterata	*Platysticta*	Brauer, 1868: 551
lestoides	*Platysticta*	Brauer, 1868: 552
annulata	*Platysticta*	Selys, 1886: 156
mylitta	*Drepanosticta*	Cowley, 1936: 160
lymetta	*Drepanosticta*	Cowley, 1936: 161
megametta	*Drepanosticta*	Cowley, 1936: 163
trimaculata	*Drepanosticta*	Lieftinck, 1939: 149
aries	*Drepanosticta*	Needham & Gyger, 1941: 144
taurus	*Drepanosticta*	Needham & Gyger, 1941: 145
philippa	*Drepanosticta*	Lieftinck, 1961: 132
ceratophora	*Drepanosticta*	Lieftinck, 1974: 117
belyshevi	*Drepanosticta*	Hämäläinen, 1991: 65

Semper also collected such inconspicuous insects, which suggests that these must have been very common. The first species is still common indeed in the area studied by Semper, but *D. lestoides* is not common at all now. See also Table 1 for a list of the 13 nominal taxa, representing 12 species, described from the Philippines up to date. *D. septima* Needham & Gyger was considered by Hämäläinen & Müller (1997) a possible synonym of *D. mylitta* Cowley.

Apart from the species described hereunder, more than ten new species will be described in a revision of the Philippine Platystictidae (van Tol, 2003).

Conservation. – Like all biota confined to tropical forests and characterized by small distributional ranges, most Platystictidae are under serious threat. The Philippine forests rank high among the tropical forests of southeastern Asia, and they are under severe pressure of degradation and destruction. The total surface of the 7100 islands of the Philippines amounts to just over 300,000 km^2. The total forest cover is ca 20%, of which less than 3% primary forest. An FAO report suggests that less than one million hectares of 'old growth' dipterocarp forest remain.

The human population amounts to ca 62 million, while the total surface of the archipelago is similar to Italy in Europe, or to New Mexico in the USA. According to a rough estimate, nearly 500 ha of secondary forest disappear daily. At present more than 90% of the forest is already destroyed; on some islands hardly any forest is left (e.g. less than 3% on the island of Negros). The best forest remnants can be found on Palawan, which is inhabited by a completely different flora and fauna and, biogeographically, does not form a part of the Philippines.

Conservation International described the Philippines as 'the hottest of hotspots'. Approximately 50% of the 8000 native plant species are endemic. The number of named dragonfly species of the Philippines is ca 250 (Hämäläinen & Müller, 1997), of which more than 50% are endemic, including all *Drepanosticta* species. It is fortunate that none of the *Drepanosticta* species is under such an immediate threat as is, for example, the platycnemidid *Risiocnemis seidenschwarzi* Hämäläinen (Hämäläinen, 2000), confined to a stretch of 30 m of stream in the Tabunan forest of Cebu. On this island, with a total surface area of 1707 square mi (4400 km^2) , not more than 145 ha of primary forest are left (pers. comm. Dr Hämäläinen, 2002).

We are honoured to be able to contribute this short paper to the *Festschrift* on the occasion of Dr. Norman W. Moore's 80th birthday. Through Dr. Moore's efforts, Odonata are high on the international agenda of invertebrate conservation and protection (e.g. Moore, 1997). Naming one of the Philippine forest damselflies after him is more than appropriate.

Drepanosticta moorei sp. n.

Figs 1-5

Platysticta annulata Selys, 1886: 156 (pro parte)

Drepanosticta sp. – Lieftinck, 1961: 136 (specimen '588' in Selys collection, IRSN Brussels, a paralectotype of *Drepanosticta annulata* [Selys], not conspecific with lectotype).

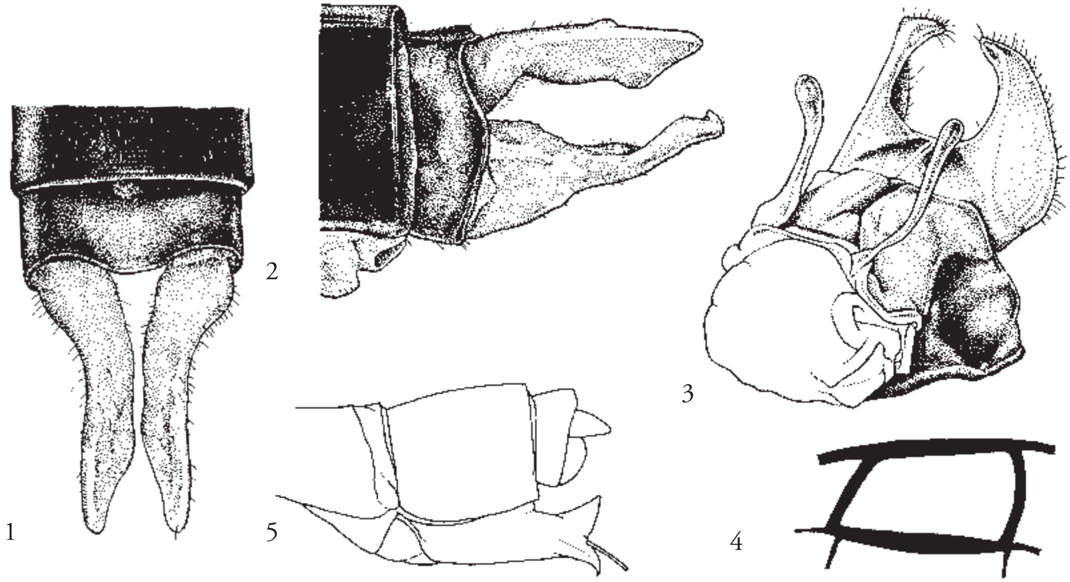
Drepanosticta sp. n. note 7. – Hämäläinen & Müller, 1997: 276-277.

Material. – **Holotype** male, Philippines, Luzon, Nueva Viscaya, Ste Fe, Atbo River, 550-800 m, 10-VI-1991 / R.A. Müller leg. / coll. R.A. Müller [JvT 22225], coll. RMNH. – **Paratypes** (all ex coll. R.A. Müller, now in RMNH): Luzon, Nueva Viscaya, Dalton Pass, 850-900 m, 8/9-VI-1991, R.A. Müller, 1 male; same site as holotype, 11 males 10 females; Luzon, Nueva Ecija, Caranglan, Batching River, 700-850 m, 11-VI-1991, R.A. Müller leg., 2 males; Luzon, Aurora Prov., Dilalongam, Sitio Biyak, Dibaray bay, 3/15-VII-1996, 300-500 m, Celso M. Nazareno leg.; Luzon, Zambales Prov., Masinloc, Mt Coto, Tal-tal, 400-700 m, 1/8-IV-1997, C.M. Nazareno leg.

Etymology. – Named after Dr Norman W. Moore, for his contributions to the conservation of Odonata.

A remarkable and unmistakable species by the pronotum structure; the coloration of the synthorax is also different from that in most other Philippine congeners.

Male [JvT 22225, Luzon, Nueva Viscaya]. – Head. Labrum and anteclypeus very clear blue, anterior border of labrum with narrow black line; mandibles



Figures 1-5. *Drepanosticta moorei* sp. n. – 1, male anal appendages, dorsal view. – 2, same, left lateral view. – 3, male promotum, oblique view. – 4, pterostigma, right hind wing. – 5, female last abdominal segments.

brown, but inner basal corner blue; rest of head bronze-black; parorbital carina distinct; postoccipital carina indistinct and lacking conspicuous extremities. Thorax. Pronotum (Fig. 3) with anterior and median lobe yellowing, lateral lobe brown, posterior lobe dirty yellow; anterior lobe approximately halfway each side with very long subcylindrical process, touching median lobe, and reaching virtually hind margin of central portion of posterior lobe; median and lateral lobes simple; hind lobe laterally with enormous collar, half round, nearly twice as long as basal part of posterior lobe; lateral margin with long and thin setae. Synthorax bronze-black, but metepisternum nearly fully greenish yellow. Legs dirty yellow. Wings with 13 Px in fore wing, 13 Px in hind wing; origin of R4+5 just distal to nodus, R3 arises 6 cells distal to nodus in fore wing, 5 cells in hind wing; Arculus just distal to Ax2, distinctly stalked; Ac and Ab forming a Y, hardly stalked; number of cells between distal end of quadrangle and place where CuP meets hind margin of wing in fore wing 5, in hind wing 7; pterostigma (Fig. 4) brown, with a narrow pale line against veins; ca. 1.6 times longer than high, the proximal side oblique, the distal side rounded; veins distal to pterostigma undivided.
Abdomen. Brown, but basal one-tenth of segment 3, basal one-sixth of segments 4-6, basal one-third of segment 7 dirty yellow; segments 8-10 tergites brown. Appendages (Figs 1-2) greyish brown, top of inferiors castaneous; superiors with basal one-fourth stout, rest narrow in dorsal view, actually strongly flattened dorso-ventrally, and broadly triangular in lateral view; inferiors in ventral view subparallel, the top bent outward, then inward in a semicircle, in lateral view the top bends in 90°.
Measurements (in mm). – Abdomen including appendages ca 37, hind wing 22.

Female. – Very similar to male, including coloration, and structure of pronotum; segments 8-10 brown, anal appendage lightbrown, genital valves surpassing apex of appendages (Fig. 5).

Differential diagnosis. – This species differs from other species of the Philippine islands by the long processes on the anterior lobe of the pronotum. This character is present in both males and females. The only other Philippine species with long processes on the anterior lobe of the pronotum is *D. belyshevi* Hämäläinen (type locality Panaon Is.), characterized by the strongly curved, slender processes of the posterior lobe of the pronotum, and pale markings in the posterior thirds of metepisternum and metepimeron (in some specimens also of mesepimeron).

Distribution. – Central Luzon (provinces Nueva Viscaya, Nueva Ecija, Aurora and Zambales). Apparently it occurs in low densities over a relatively large area. In larger numbers found at the type locality only.

Relationships. – Based on the highly characteristic processes of the anterior lobe of the pronotum, *D. moorei* sp. n. seems to be most closely related to *D. belyshevi* Hämäläinen. Although a direct link of these two species to most of the other Philippine congeners is not apparent, a close relationship to the mainland species is also unlikely.

Acknowledgements

We are grateful to Dr Matti Hämäläinen (Espoo, Finland), who sorted out the R.A. Müller collection from the Philippines, and was helpful with expert advise. Figures 1 and 2 were made by B. Blankevoort and Figure 3 by E.J. Bosch (both Museum Naturalis, Leiden).

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5. Revision of the Platystictidae of the Philippines (Odonata), excluding the *Drepanosticta halterata*-group, with descriptions of twenty-one new species

J. van Tol

Tol, J. van. Revision of the Platystictidae of the Philippines (Odonata), excluding the *Drepanosticta halterata* group, with descriptions of twenty-one new species.
Zool. Meded. Leiden 79-2 (10), 22.vii.2005: 195-282, figs 1-109, 1 table. – ISSN 0024-0672.

Key words: Odonata; Platystictidae; *Drepanosticta*; *Protosticta*; *Sulcosticta*; Philippines; new species; new genus.

Thirty-one species of the family Platystictidae of the Philippines are revised, i.e. all species recognised, excluding the species of the *Drepanosticta halterata*-group. The following new taxa are described: 16 species in *Drepanosticta* Laidlaw: *D. acuta* sp.n., *D. aurita* sp. n., *D. centrosaurus* sp. n., *D. clados* sp. n., *D. flavomaculata* sp. n., *D. furcata* sp. n., *D. hermes* sp. n., *D. krios* sp. n., *D. luzonica* sp. n., *D. malleus* sp. n., *D. myzouris* sp. n., *D. paruatia* sp. n., *D. pistor* sp. n., *D. quadricornu* sp. n., *D. rhamphis* sp. n., *D. trachelocele* sp. n., two in *Protosticta* Selys, viz. *P. lepteca* sp. n. and *P. plicata* sp.n., and three in *Sulcosticta* gen. n., viz. *S. striata* sp. n., *S. pallida* sp. n. and *S. viticula* sp. n. The status of eleven previously discribed nominal taxa is established. One, *D. septima* Needham & Gyger, is doubtfully considered a synonym of *D. mylitta* Cowley.
Based on a preliminary phylogenetic analysis, the species of *Drepanosticta* are divided into informal species groups. Most species of the Philippines have affinities to species of Sulawesi, the Moluccas and New Guinea. Several species confined to Palawan have sister-group relationships with species from Borneo. The affinities of various other species confined to the Sulu archipelago, are unsettled as yet. The species of Platystictidae here assigned to *Protosticta* Selys are presumably not closely related to the type species, *P. simplicinervis* Selys from Sulawesi. However, a better placement has to await a more detailed phylogenetic study of the family. For three species the new genus *Sulcosticta* gen. n. is erected. These species are closely allied based on the structure of the appendages, but should have been assigned to different genera if based on the present generic definitions.
Many species here described have small distributional ranges, a common phenomenon in Platystictidae. Since most forests in the Philippines are heavily under threat or have already disappeared in the last fifty years, several taxa described in this paper should be considered under threat of immediate extinction.

Introduction

Forest damselflies, Platystictidae, are among the most characteristic elements of seepage areas, trickles and small streams of virgin forests in Southeast Asia. Both the mainland and many of the islands of this region are inhabited by great variety of species of the genera *Protosticta* Selys and *Drepanosticta* Laidlaw (Fig. 1). Most platystictid species of Southeast Asia were described by Lieftinck (e.g. 1937, 1939, 1961,

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Previously published in: Zoölogische Mededelingen 79-2 [2005]: 195-282, figs. 1-109, table 1.

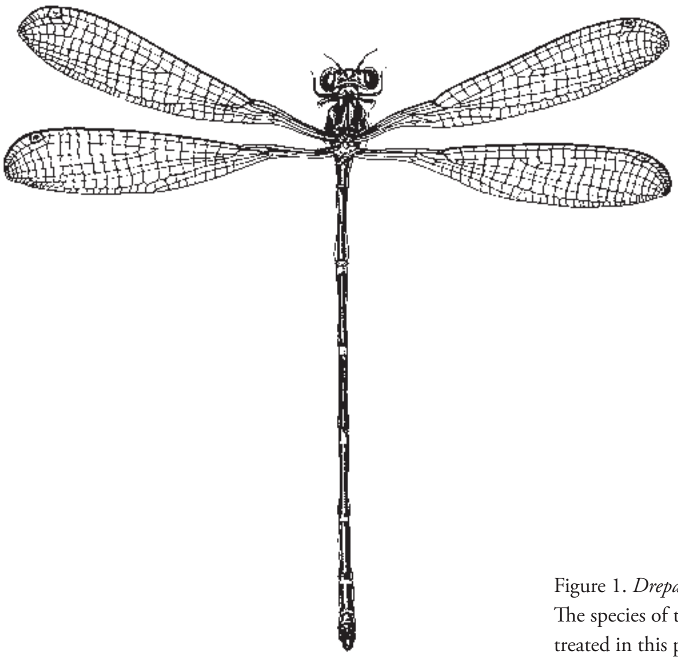


Figure 1. *Drepanosticta halterata* complex. Habitus of male. The species of the *D. halterata* species group are not fully treated in this paper.

1965), while more recently mainly Asahina (e.g. 1984), Hämäläinen (1991, 1999), Wilson (1997), Wilson & Reels (2001) and Van Tol (2000) have contributed to the regional knowledge of this family. For the Philippines, especially the publications by Needham & Gyger (1939, 1941) are relevant, although the first Philippine species were already described by Brauer (1868).

Drepanosticta and *Protosticta* species generally have small distributional ranges, and island endemicity at the species level is high, e.g. on Sulawesi for the genus *Protosticta* it is hundred percent (Van Tol, 2000).

The same picture of small ranges and high island endemicity is apparent for platystictids of many other islands of Indonesia, and is also true for species of this damselfly family of the Philippines as well. Hämäläinen & Müller (1997) mentioned the high number of species, especially in the genus *Drepanosticta*. They enumerated 35 species in the family, 32 species of *Drepanosticta* and three species of *Protosticta*.

Only twelve valid Philippine species in the genus *Drepanosticta* have been described so far, and one other nominal taxon is considered a synonym. So, twenty species in *Drepanosticta* and three species in *Protosticta* awaited description.

The paper by Hämäläinen & Müller (1997) was based on a careful study of the specimens available in museums, but focussed on the collection brought together by Mr. Roland A. Müller (St. Gallen, Switzerland) and his collaborators between 1985 and 1997 (Fig. 2). The Müller collection is the first collection of Philippine Odonata representative of all parts of the country. It is also outstanding in the documentation of localities. The National Museum of Natural History Naturalis at Leiden and Mr. Roland A. Müller were able to reach an agreement on the deposition of this collection in Leiden in 1998. The collection is rich in species of previously neglected families as Platycnemididae and Platystictidae. Some presently still undescribed species are represented with more than 200 specimens. Nearly all material of the Müller collection was identified by Dr Matti Hämäläinen (Espoo, Finland). His pioneering work has revealed the value of this collection in many ways. Hämäläinen himself published a series of papers describing taxa new to science (see Hämäläinen

& Müller, 1997 for an overview; and Hämäläinen 1997, 2000; Gassmann & Hämäläinen 2002, Van Tol & Müller, 2003 for results published since that time).

This paper is part of a series of papers in which I hope to revise the Platystictidae of the Oriental and Papuan regions, and to reconstruct the phylogeny of this family, including the *Palaemnema* species of the New World. New species of *Drepanosticta* from various parts of the mainland of Southeast Asia, and from several islands in Indonesia, await description. Also, the generic division of the Oriental species is far from satisfactory, as it is mainly based on one wing venational character, which seems to contradict a grouping of species based on an analysis including various other characters (see also Orr, 2003: 69-72).

The present papers includes all Philippine species of Platystictidae, except the species of the *Drepanosticta halterata* group. The latter group is widespread in Luzon (incl. Batan), the West Visayas (Panay, Negros, Cebu, Sibuyan) and East Visayas (Samar, Bohol). Although material is available in sufficient numbers, and clearly recognisable variation in characters exists between populations, the distinction of species needs further study of the material, including some type specimens. Three obviously closely related species are assigned here to a new genus, as a first step to define monophyletic groups within this family.

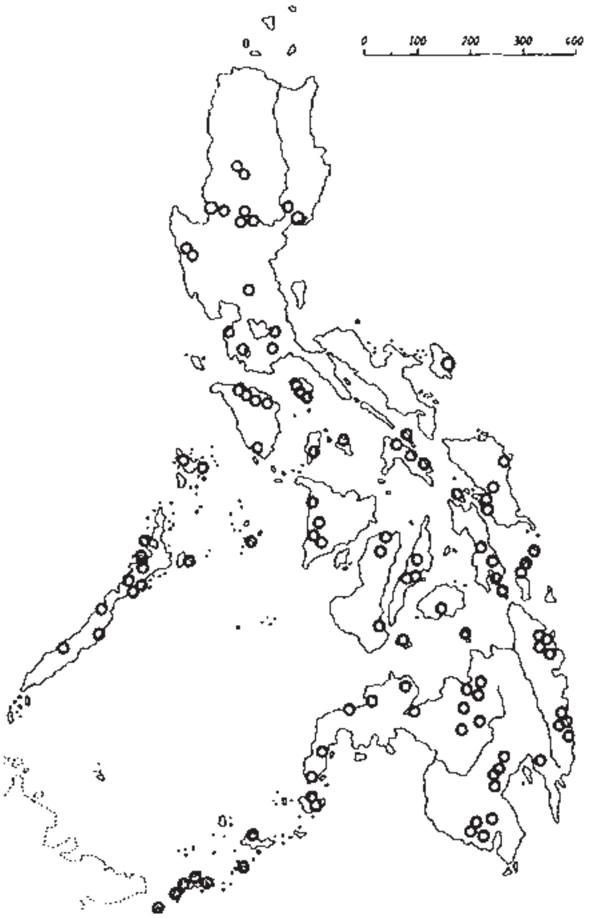


Figure 2. Approximate position of localities of the specimens in the Roland Müller collection (from: Hämäläinen & Müller 1997: 250). Scale bar in kilometers.

The studies of the forest damselflies of Southeast Asia by others and myself, partly still unpublished, slowly unravel a fascinating image of diversity as a result of millions of years of evolution. Most species are dull-coloured, small and inconspicuous insects, superficially looking very similar. The variation in small details of the male anal appendages is remarkable in the species of the mainland. Most species of the Philippines have structurally similar anal appendages in the male, but they show the most exuberant structures in projections of the pronotum. The information of these features to reconstruct the phylogenetic relationships have only just started.

The uneasy observation must be made that many of the spectacular life forms described in this paper are on the verge of extinction. Several species are described here from only one or very few specimens collected from a forest reserve of one hectare of less. Since several of such precious sites already got lost since the collections were made, we must fear for their survival. One may only be hopeful that the present paper may contribute to the awareness in the Philippines of the huge, unique and irreplaceable diversity of insect life of this country.

Material and methods

This paper is based on the material in the National Museum of Natural History (Leiden), including the former collections of Roland A. Müller (St. Gallen, Switzerland) (see above) and Dr. Matti Hämäläinen (Espoo, Finland). The latter collection, although much smaller than the Müller collection, was also valuable since it includes both duplicates from the Müller collection retained after his identifications, as well as specimens collected by Hämäläinen himself. Types were examined, if necessary, for several previously described species. The study of the types of species described by Needham and Gyger had to be postponed. I have relied on the descriptions, or material in the Leiden museum identified by M. A. Lieftinck after comparison with types.

Deposition of other material is documented, with collections identified by codens as follows: BMNH, Natural History Museum, London, UK [= British Museum (Natural History)]; CASC, California Academy of Sciences, San Francisco, USA; CUIC, Cornell University, Ithaca, New York, USA; FMNH, Field Museum Natural History, Chicago, Illinois, USA; IRSN, Institut royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; MCZC, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN, Museum National d'Histoire Naturelle, Paris, France; RMNH, National Museum of Natural History, Leiden, The Netherlands [formerly Rijksmuseum van Natuurlijke Historie]; SMFD, Senckenberg Museum, Frankfurt a. M.; ZMUC, Zoological Museum University of Copenhagen.

Descriptions of all species start with a diagnosis, enumerating the most distinct characters as compared to other Philippine species, especially in the species groups distinguished. Terminology generally follows Watson & O'Farrell (1991), and Cowley (1936) for specialised terminology of the head structure. For most species the description of the male is based on the holotype. Measurements are also for the holotype, with variation of the paratypes in brackets. The descriptions of the females are concise, typically comparing the female with the male. Measurements for the females are presented separately. Illustrations are based on specimens in the RMNH collection (except for the holotype of *Drepanosticta megametta* Cowley); the references to the actual specimens are given in the captions. The distributions are summarized at the end of each description. A series of distribution maps is presented at the end of the paper (Figs 99-109).

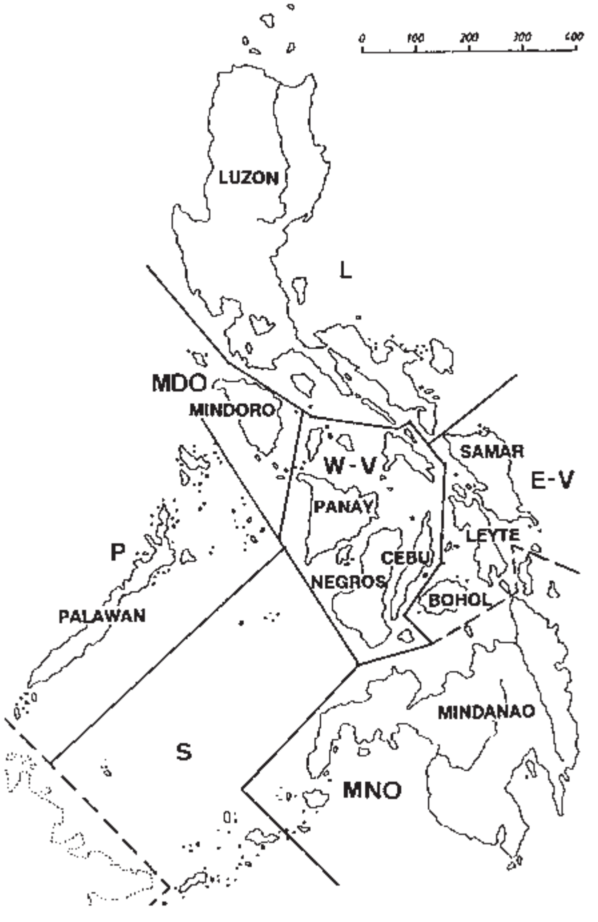
Phylogenetic relationships

Although a more elaborate analysis of the phylogeny of the Philippine Platystictidae has to await the analysis of all species of this family for Southeast Asia, a few remarks can be made.

Firstly, various species of Palawan and Busuanga have little in common with most other species of the Philippines. Species such as *D. ceratophora* Lieftinck and *D. paruatia* sp. n. have sister-group affinities with species of Borneo. The relationship of another species of the Palawan area, *D. quadricornu* sp. n., is uncertain. Based on the remarkably similar structure of the male anal appendages of almost all other species of Philippine *Drepanosticta*, these species are presumably derived from one common ancestor. Based on the structure of both anal appendages and pronotum, the closest affinities of this group are definitely with species as *D. ephippiata* Lieftinck from Sulawesi, or *D. clavata* Lieftinck from New Guinea (see also Lieftinck 1937: 72-74). The males of the Philippine species, although also showing subtle differences in the structure of the anal appendages, are most easily distinguished by the structure of the pronotum. Both the anterior and the posterior lobe of the pronotum can be furnished with the most exuberant projections, sometimes even exceeding in length the size of the pronotum itself. The characters of the pronotum as mentioned here are those of the male. In some species male and female have very similar projections on the pronotum, while seemingly closely related species male and female are structurally different in this respect.

Within this group of closely related species, various species groups could be identified based on a preliminary analysis of the characters. These groups have been used in this publication to provide a first structuring of the variation. Some more widespread species show clinal variation in the structure of e.g. the projections of the pronotum. Also, some islands forms were recognisable. Decisions whether such forms had to be considered as separate species, were difficult and are debatable. For instance, the 'form' of *D. belyshevi* Hämäläinen from Samar was considered so distinct that it is raised here to species level. On the other hand, the group of 'geographically recognizable forms' of *D. mylitta* Cowley was not split, but kept under the name *D. mylitta*. Further studies, including molecular studies, are needed to provide an understanding of the relationships of these complexes, thus also providing a better basis for such taxonomic decisions.

Figure 3. Faunal regions in the Philippines, with names of islands mentioned in the text. Abbreviations for regions as follows: L: Luzon region, MDO: Mindoro region, WV: West-Visayan region, EV: East Visayan subregion, MNO: Mindanao subregion (EV plus MNO together form Mindanao region), P: Palawan group (part of Greater Sunda region), S: Sulu rgion. Luzon, Mindoro, West-Visayan and Mindanao regions comprise the Philippine biogeographic region proper (from: Hämäläinen & Müller 1997: 251). Scale bar in kilometers.



Various species in this paper are assigned to the genus *Protosticta* Selys, based on the absence of the anal bridge vein (Ab) at the base of the wing. However, it is unlikely that these species are closely related to the type species of *Protosticta*, *P. simplicinervis* Selys from Sulawesi. It is certain that the venational character distinguishing *Protosticta* and *Drepanosticta* will prove to be of little phylogenetic significance. It has to remain open for further research whether all Philippine '*Protosticta*' belong to the *Drepanosticta*-complex of the Philippines, or should be regarded as a distinct genus. Unfortunately, all species of this group of species are rare in the collection, and presently no material is available for molecular analysis. Such an analysis may also provide further insight in the relationships of the species here assigned to the new genus *Sulcosticta*.

The generic placement of most species in the genus *Drepanosticta* in the present sense seems rather unproblematic. However, the genus is based on a synplesiomorphy, and its monophyly is both unestablished as well as unlikely. A further division into monophyletic groups has to await the revision of the species of the mainland of South-East Asia. The assignment of other species to *Protosticta* is, as explained above, preliminary. The character presently defining the genus *Protosticta*, viz. the absence of the Ab vein, is clearly not a unique apomorphy in the family, and will prove unsuitable for the definition of a monophyletic group. For example, one of the species here included in *Protosticta* on the characters of the male would have to be included in *Drepanosticta* if

Table 1
Distribution of Platystictidae described in this paper, per faunal region. The East Visayan and Mindanao regions are usually considered subregions of one single region.
× Present. — o Absent. — (×) Status uncertain. — ? Locality uncertain.

	Luzon	Mindoro	West Visayan	East Visayan	Mindanao	Sulu	Palawan
Drepanosticta acuta sp. n.	×	o	o	o	o	o	o
Drepanosticta aries Needham & Gyger	o	o	o	o	×	o	o
D. krios sp. n.	o	o	o	?	×	×	o
D. rhamphis sp. n.	×	o	o	o	o	o	o
D. belyshevi Hämäläinen	o	o	o	×	o	o	o
D. flavomaculata sp. n.	o	o	o	o	×	o	o
D. trachelocele sp. n.	o	o	o	×	o	o	o
D. luzonica sp. n.	×	o	o	o	o	o	o
D. moorei Van Tol & Müller	×	o	o	o	o	o	o
D. clados sp. n.	o	o	o	o	×	o	o
D. furcata sp. n.	o	o	×	o	o	o	o
D. hermes sp. n.	o	o	o	o	×	o	o
D. lymetta Cowley	o	o	o	o	×	o	o
D. taurus Needham & Gyger	o	o	o	o	×	o	o
D. centrosaurus sp. n.	o	o	o	o	×	o	o
D. megametta Cowley	o	o	o	o	×	o	o
D. aurita sp. n.	o	×	o	o	o	o	o
D. ceratophora Lieftinck	o	o	o	o	o	o	×
D. malleus sp. n.	o	o	o	o	×	o	o
D. mylitta Cowley	(×)	o	o	×	(×)	o	o
D. myzouris sp. n.	×	o	o	o	o	o	o
D. paruatia sp. n.	o	o	o	o	o	o	×
D. pistor sp. n.	×	o	×	o	o	o	o
D. quadricornu sp. n.	o	o	o	o	o	o	×
Protosticta annulata Selys	×	o	o	o	o	o	o
P. lepteca sp. n.	×	o	o	o	o	o	o
P. plicata sp. n.	o	o	×	o	o	o	o
Sulcosticta pallida sp. n.	×	o	o	o	o	o	o
S. striata sp. n.	×	o	o	o	o	o	o
Total	11	1	3	3-4	10-11	1	3

based on the wing venation of the female.

Three species with different wing venation, but otherwise evidently closely related, are placed in a new genus based on the similar structure of the male genitalia. It is expected that a further phylogenetic analysis may reveal that more species will have to be placed in this genus.

Distributional patterns

This is not the place to provide a profound zoogeographical analysis based on the Platystictidae, since the prerequisites for such an analysis are not fulfilled. Nevertheless, some brief remarks on the distributions of presumed monophyletic groups, or sister-group relationships with other areas in South-East Asia, may contribute to the definition of a more detailed zoogeographical study. The platystictids will be discussed based their occurrence in the faunal regions as defined by e.g. Vane-Wright (1990) (see Fig. 3).
The biogeography of the Philippines has been discussed several times the last decades, also in relation to the palaeogeography of the region. A relevant discussion is De Jong & Treadaway (1993: 81-111). Their study was hampered by insufficient knowledge of the phylogeny of the Hesperiidae, making a cladistic biogeographical analysis impossible as well. Instead, they compared hypothesized distribution patterns derived from geological events with actual patterns found. If such patterns cannot be traced, dispersal rather than a geological event was supposed to be the cause of such a pattern. Mainly based on terrestrial vertebrates, the Philippines were subdivided in faunal regions. Interestingly, this subdivision is similar to the regions as defined by Semper (1892) based on butterflies around hundred years earlier.

The palaeogeography of the region is very complicated indeed. Continental fragments are restricted to the western part of the Philippines, while most islands were formed along the Philippine plate during the last 40 million years. These islands were formed along the westside of the Philippine Sea Plate by closewise rotation of the plate from the late Eocene (42 Ma). Further to the west, not far from the mainland, parts of Palawan, Panay and Mindoro (Calamian block) were situated. The Calamian block rifted eastward by seafloor spreading during the Oligocene. Even during the Miocene, the islands arc along the westside of the Philippine Sea Plate still existed, including (parts of) Luzon, Zambales, East Mindanao, North Sulawesi and (more to the east) Halmahera. The Zamboanga peninsula of Mindanao had a more western position at the northern part of the Celebes Sea. In the late Miocene, the island of Luzon arc still moved northward, and partly collided with northern Palawan. Also the during the Pliocene the clockwise rotation of the plate continued. As a result, for instance, the island of Halmahera was still north of the Vogelkop peninsula in the Pliocene, 500 km east of its present position. The island of Luzon, in its present shape, was only formed during the late Pliocene (2 Ma).
Another important, and geologically recent, phenomenon is the lowering of the sea level during the ice ages of the Quaternary. Many of the island were connected when sea level was c. 150 m lower than today. The channel between Borneo and the Philippines is not deeper than 145 m and Borneo and Palawan formed one island, while also many of the Sulu islands were connected at the time.
As discussed above, the Palawan group of species seems to be most closely related to the species of Borneo, and not to the other species of the Philippines. This phenomenon is well known in other groups as well, and can be understood with present knowledge of recent geology. It should, however, be realised that various lineages with many autapomorphies living in Palawan have not reached Borneo, or have become extinct in Borneo.
The area of highest diversity in the Platystictidae (table 1) is the eastern part of the island of Mindanao. Many species widespread in Mindanao, and in some cases also in other islands, occur in this area together with many species with extremely small distributional ranges and endemic to this area. This is best shown in the *D. lymetta* group.
The fauna of Luzon is most diverse on the level of species-groups. The *belyshevi* group, the *halterata* group, the *moorei* group, the *Protosticta* group and several unplaced species are all confined to, or strongly represented in, Luzon. From most other islands only one or very few species are known. Although this observation may partly be an artifact due to insufficient collecting, or massive deforestation in some parts of the Philippines in recent times, it is in agreement with the generally recognized biogeographical pattern. The small

number of species on Mindoro, however, is remarkable and should be studied further.

Systematic part

Key to the males of Platystictidae of the Philippine Islands

1. Inferior appendages (ventral view) broad and short, the top bifid or with top shining brown sclerotized and flattened (Fig. 95); synthorax with variegated pattern of longitudinal stripes (*Sulcosticta* gen. n.) 2

– Inferior appendages much broader at base than at top, usually base stout, the distal half much more slender, without shining brown sclerotization at distal margin; synthorax usually uniform brown or with one longitudinal stripe; if synthorax with variegated pattern , then inferiors long and slender 5

2. Inferior appendage undivided, the top flattened and sclerotized, directed dorsad, the margin with a row of teeth (Polillo) . . . . . *Sulcosticta* sp. n. [unnamed]

– Inferior appendage bifid, or with distinct inward directed projection 3

3. Inferior appendage subterminally with distinct, inward directed projection ending as flat sclerotized surface . . . . *S. viticula* sp. n.

– Inferior appendage bifid, both parts subequal, inner part sclerotized, but not ending in a flat surface 4

4. Synthorax very pale, mesepisternum greyish yellow, except along dorsal carina; anterior lobe of prothorax simple without processes; Anal bridge present but not connected with Anal crossing . . . . *S. pallida* sp. n.

– Synthorax with a complex pattern of dark and pale markings, mesepisternum predominantly black with a narrow pale stripe against humeral suture; anterior lobe of prothorax with a paired of long processes, curved anteriad, twice as long as length of anterior lobe itself . . . . *S. striata* sp. n.

5 (1). Anal bridge (Ab) present and connected with Anal crossing as Y-shaped vein (*Drepanosticta* Laidlaw) 6

– Anal bridge absent (*Protosticta* Selys) 31

6 (5) Posterior margin of posterior lobe of pronotum with a single, median process, curved anteriad (Fig. 55) . . . . *D. ceratophora* Lieftinck

– Posterior margin of posterior lobe of pronotum simple without processes, or with a pair of shorter or longer processes 7

7. Anterior *and* posterior lobes with conspicuous, paired processes on hind margin, the processes distinctly longer than length of lobes themselves 8

– Anterior *or* posterior lobes (not both) with conspicuous processes longer than length of lobes themselves, or processes lacking on both anterior and posterior lobes 11

8. Transverse occipital carina poorly developed, at least without conspicuous angulate lateral extremities 9

– Transverse occipital carina well developed with distinct, angulate lateral extremities 10

9 (8). Paired processes of anterior lobe of pronotum filiform, much more slender than the processes of posterior lobe (Fig. 28); hind wing c. 22 mm (Luzon) . . . . *D. moorei* Van Tol & Müller

– Paired processes of anterior lobe of pronotum flat and triangular; paired processes of posterior lobe hornlike (Figs 77-78); hind wing c. 18 mm (Palawan, Busuanga) . . . . *D. quadricornu* sp. n.

10 (8) Base of posterior processes of posterior lobe of pronotum (dorsal view) very close together, distance between both processes c. two times the width of process; processes smoothly curved abaxiad (Fig. 16) . . . . *D. belyshevi* Hämäläinen

– Base of posterior processes wide apart, distance between both processes more than five times the width of process; processes curved somewhat dorsad, the distal three-quarters ventrad (Fig. 22) . . . . *D. trachelocele* sp. n.

11 (7) Transverse occipital carina poorly developed, at least without conspicuous angulate lateral extremities; hind wing 25 mm or more 12

– Transverse occipital carina with distinct lateral extremities; hind wing shorter than 25 mm 15

12 (11) Hind margin of posterior lobe of pronotum

with a pair of processes, longer than the median length of the posterior lobe 13

– Hind margin of posterior lobe of pronotum with smoothly rounded, or somewhat lifted, but without a process longer than median line of posterior lobe 14

13. Tip of inferior appendage with a long subterminal, medially directed tooth (Figs 69-70); processes of posterior lobe with top widening as a funnel, top flat as a sucker (Fig. 68) . . . .*D. myzouris* sp. n.

– Tip of inferior appendage on innerside smooth or somewhat projected, but without a distinct tooth; processes of posterior lobe tapering or club-shaped, but tip not flat . . . . *D. halterata* group

The following described species are included in this group: *D. halterata* Brauer, *D. philippa* Lieftinck, and *D. trimaculata* Lieftinck; several undescribed species are available in collections. The status of various nominal taxa in uncertain. This group is common and widespread in Luzon. A special publication on this group is in preparation.

14 (12) Superior appendages with distinct dorsal tooth (Figs 59-60); lateral sides of hind lobe of pronotum flat and sharp (Fig. 58); head very smooth and shining, without microsculpture (c. 30 times magnification) . . . . *D. lestoides* Brauer

– Superior appendages without distinct ventral tooth (Figs 26-27); lateral sides of hind lobe of pronotum somewhat uplifted and broadly rounded (Fig. 25); head coriaceous . . . . *D. luzonica* sp. n.

15 (11) Metepisternum and metepimeron predominantly creamish white; mesepisternum with a bluish antehumeral stripe . . . .*Drepanosticta paruatia* sp. n.

– Metepisternum and metepimeron brown; pale coloration, if present, a squarish, creamish white marking against posterior margin of synthorax; no antehumeral stripe. 16

16. Synthorax with a complex coloration of brownish black and pale markings; superior appendages in lateral view strongly curved (Figs 75-76) . . . . *D. pistor* sp. n.

– Synthorax concolorous; superior appendages in lateral view nearly straight 17

17. Synthorax castaneous; lateral corners of posterior lobe of pronotum sharply projected (Fig. 64). . . . . *D. mylitta* Cowley

– Synthorax brownish black; lateral corners of posterior lobe of pronotum rounded, or distinct processes longer than median length of posterior lobe itself on hind margin 18

18. Posterior lobe of pronotum with lateral corners broadly rounded (‘ears’), the projections densely set with long setae (Fig. 52) . . . .*D. aurita* sp. n.

– Posterior lobe of pronotum with distinct processes, longer than the median line of the lobe 19

19. Posterior lobe of pronotum with paired collar-like processes, broadly rounded at top, constricted at base and broadly connected with the lobe 20

– Posterior lobe of pronotum with paired processes, usually slender, the top in some species split into branches or hammer-like structure 21

20. Paired processes of posterior lobe of pronotum approximately as long as wide, only somewhat constricted in the middle (Figs 49-50) . . . . *D. megametta* Cowley

– Paired processes of posterior lobe of pronotum much wider than long, the middle distinctly constricted, thus the top with long projections (Fig. 46) . . . . *D. centrosaurus* sp. n.

21 (19). Paired processes of posterior lobe of pronotum curved, undivided, usually approximately as long as the length of posterior lobe itself (*D. aries* group) 22

– Paired processes of posterior lobe of pronotum erect, not distinctly curved, but tip frequently split and developed as a knob, or a fork, or a disk . . . 24

22. Posterior part of metepisternum and metepimeron with creamish yellow squarish markings; abdominal segment 10 and appendages pale (Figs 20-21) . . . .*D. flavomaculata* sp. n.

– Posterior part of metepisternum and metepimeron dark brown, concolorous with other parts of synthorax; at least segment 10 brown, colour not not different from segment 9 23

23. Px 16-17 in fore wing, 15-16 in hind wing (Mindanao, Mt Apo) . *D. aries* Needham & Gyger

– Px 14-15 in fore wing, 13-14 in hind wing

(Mindanao, but not in Mt. Apo region) . . . . *D. krios* sp. n.

24 (21). Superior appendages in lateral view curved, the inferiors distinctly surpassing the level of the superiors (Figs 32-33) . . . . *D. clados* sp. n.

– Superior appendages in lateral view more or less straight, the inferiors and superiors in lateral view approximately of equal length 25

25. Top of paired processes of posterior lobe of pronotum ending abruptly in a smaller or larger hook 26

– Top of paired processes straight or split, but branches of splitting not forming an angulate hook with main stem of process 28

26. Paired processes of posterior lobe of pronotum very long and heavy, length more than twice the median line of the posterior lobe itself; branches of T-splitting also strongly built (Fig. 61); Y-vein at base of wing distinctly stalked . . . .*D. malleus* sp. n.

– Paired processes of posterior lobe of pronotum approximately as long as median line of posterior lobe itself; Y-vein (sub)-sessile 27

27. Superior appendage (dorsal view) with a very short, mediad tooth near appendage base, and a hardly discernable tubercle at base of club-shaped part of appendage; paired posterior processes of posterior lobe of pronotum with distinct stem (Fig. 13) (Catanduanes Id.) . . . . *D. rhamphis* sp. n.

– Superior appendage with a long and acute, ventro-mediad tooth at base of club-shaped top; paired posterior processes of posterior lobe of pronotum club-shaped part with short stem (Fig. 4) (Luzon) . . . . *D. acuta* sp. n.

28 (25). Paired processes of posterior lobe of pronotum straight and erect (perpendicular to body axis), the top somewhat thicker (Fig. 43) . . . . *D. taurus* Needham & Gyger

– Paired processes of posterior lobe of pronotum split in branches, usual of unequal length, the process not 90˚ erect, but more directed posteriad 29

29. Synthorax castaneous; paired processes of posterior lobe of pronotum divided in two short branches similar to the stem (Fig. 34) (Siquijor Id) . . . . *D. furcata* sp. n.

– Synthorax brownish black; paired processes of posterior lobe of pronotum divided into two longer, usually asymmetrical branches which are more slender than the stem (Mindanao Id). 30

30. Distal half of inferior appendage curved like as clasper; outer branch of paired processes of posterior lobe of pronotum distinctly longer than inner branch (Fig. 37). . . . . *D. hermes* sp. n.

– Distal half of inferior appendage straight; inner branch of paired processes of posterior lobe of pronotum typically longer than outer branch, but in some specimens difference indistinct (Fig. 40) . . . . *D. lymetta* Cowley

31 (5). Anterior lobe of pronotum with paired processes, approximately as long as median line of anterior lobe itself; hind lobe of pronotum with a pair of longer processes, which are curved anteriad (Fig. 84) . . . . *Protosticta lepteca* sp. n.

– Anterior lobe of pronotum simple, without processes; hind lobe with short processes never bent anteriad 32

32. Paired processes of hind lobe of pronotum erect, the top sharp (Fig. 81). . . . . *P. annulata* (Selys)

– Paired processes of hind lobe of pronotum with rounded top, formed since the process is halfway recurved distad the fully 180˚ (Fig. 87) . . . . *P. plicata* sp. n.

List of Platystictidae of the Philippines

The species are arranged by species-group. The sequences of the species-groups, and the species within the species-groups, are alphabetical.

Drepanosticta Laidlaw, 1917
  D. aries group
    1. *D. acuta* sp. n. 141
    2. *D. aries* Needham & Gyger, 1941 143
    3. *D. krios* sp. n. 144
    4. *D. rhamphis* sp. n. 146
  D. belyshevi group
    5. *D. belyshevi* Hämäläinen, 1991 147
    6. *D. flavomaculata* sp. n. 149
    7. *D. trachelocele* sp. n. 151

[*D. halterata* group]
[not reviewed in this paper]
D. halterata Brauer, 1868
D. philippa Lieftinck, 1961
D. trimaculata Lieftinck, 1939

D. moorei group

D. lymetta group

D. megametta group

Drepanosticta: other species

Protosticta Selys, 1885

Sulcosticta gen. n.

Drepanosticta Laidlaw

Drepanosticta Laidlaw, 1917: 339.

Drepanosticta Laidlaw is traditionally distinguished within the Platystictidae by the combination of a straight, rather than fractured, IR3 vein, and the presence of an Anal bridge, joining the Anal crossing or the hinder margin of the wings. Here, a new genus is erected for three Philippine species based on the shape of the superior appendages. One of these species does have an Anal bridge, which does not join the Ac before or at the wing margin ('sessile Y-vein'), but meets the hinder margin of the wing far from the Ab.
The Philippine species of *Drepanosticta* are placed here in various informal groups based on preliminary phylogenetic studies, as explained above. The following groups have been defined (in alphabetical order): *D. aries* group, *D. belyshevi* group, *D. moorei* group, *D. lymetta* group, *D. megametta* group. The groups are named after the species of the group that was first described.

***Drepanosticta aries* group**

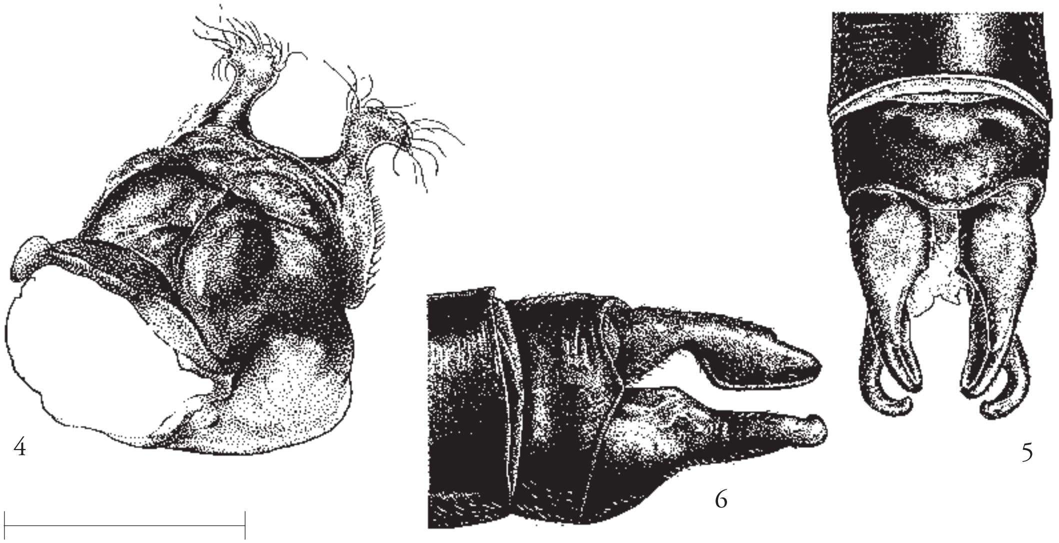
Transverse occipital carina well developed, with distinct lateral extremities; anterior lobe of pronotum smooth and flat; posterior lobe of pronotum with flat and curved processes, approximately the median length of the posterior lobe; synthorax brown; pterostigma wider than high; superior appendages with dorsal tooth; inferior appendages straight, the tip curved medio-dorsad.
Included species: *D. acuta* sp. n., *D. aries* Needham & Gyger, *D. krios* sp. n., *D. rhamphis* sp. n.
Distribution: Luzon, Catanduanes, Mindanao, Sulu archipelago; Samar doubtful.

Drepanosticta acuta van Tol, **sp. n.**

(Figs 4-6, 99)

Drepanosticta sp. n. 10. – Hämäläinen & Müller 1997: 257, 277 (Luzon).

Type material . – Holotype male [JvT 18985] in RMNH: 'Philippines. Luzon Id. Camarines Sur. Pili. Bungcao Curry. Mt. Isarog. Caririca river. 200-400 m. 4-15 Aug 1997, Celso Nazareno'. – Paratypes (all Philippine Islands). **Luzon**: Mt. Isarog, 8.iv.1916 (G. Boettcher) 1 female (in SMFD); P. I., M.T. Iriga / Camarines Sur, 6.iv.1962 (H.M. Torrevillos) 1 male; Camarines Sur. Pili. Bungcao Curry. Mt. Isarog. Caririca river. 200-400 m, 4-15.viii.1997 (Celso Nazareno) 8 males 4 females.



Figures 4-6. *Drepanosticta acuta* sp. n., male [JvT 18981, Luzon, Camarines Sur, Pili, Bungcao Curry, Mt Isarog, 200-400 m, 4-15 Aug 1997]. – 4, pronotum, oblique view. – 5, anal appendages, dorsal view. – 6, idem, left lateral view. Scale bar 1 mm.

Diagnosis. – Medium-sized; very broad superior appendages in lateral view, which also have a remarkably long and sharp ventro-mediad tooth at the base of the widened part. The three other species in this group with short to very short, inconspicuous tooth at base of widened part. Females without projections on posterior margin of posterior lobe of pronotum; the same structure in *D. rhamphis* sp. n. with distinct projections.

Male [holotype, JvT 18985]. – Head. Labrum, mandibles and anteclypeus bluish white; anterior border of labrum with narrow black line; rest of head bronze-black, postclypeus and frons shining brownish black, dorsal side of head coriaceous, with many elongate striae lateral to ocelli; transverse occipital carina with distinct acutely angulate extremities; antenna with scapus brownish black, pedicellus yellowish white, tip of pedicellus and flagellum lightbrown.

Thorax. Pronotum (Fig. 4) with central part of anterior and posterior lobe, median and lateral lobes (except ventralmost part) brownish black, rest of anterior and posterior lobes castaneous; posterior lobe with caudal processes rather wide apart, base solid, tapering, the top directed 90° abaxiad, as head of woodpecker, distal part with long setae. Synthorax unicolorous bronze-black, especially metepisternum and metepimeron shining black, rest coriaceous. Legs dirty yellow, femora near joints of tibiae with brownish black ring. Wings hyaline; venation brown, somewhat darker in posterior part; Px 17 in fore wing, Px 16 in hind wing; R4+5 arising just distal to subnodus, IR3 just distal to that level; Arculus arising just distal to Ax2; quadrangle somewhat widening posteriorly in fore wing; pterostigma castaneous, c. two times as wide as high, proximal side acutely angulate; cells between Costa and R1 distal to pterostigma undivided.

Abdomen. Segments 1-7 brown to brownish black, with distinct pale yellow basal annulae covering 1/8 to 1/5 of length of each segment; segments 8-10 brownish black. Appendages (Figs 5-6) with superiors stout at base, distal three-fifths tapering, a distinct ventro-mediad triangular tooth at base of distal club-shaped part, distal part in inner-lateral view club-shaped with a short dorsal tubercle at half of the length; inferiors in ventral view with triangular basal part one-third of length; caudal part with basal half straight and cylindrical, top constricted, bent in semicircle 90° dorso-axiad.

Measurements. Abdomen including appendages 29 (29-30) mm, hind wing 19 (19-20) mm.
Female. – As the male, but posterior margin of posterior lobe of pronotum without projections.
Measurements. Abdomen 27-28 mm, hind wing 20 mm.
Etymology. – *Acutus* (Latin), sharp; for the acute tooth on superior appendage. An adjective.
Distribution (Fig. 99). – Philippine Islands: Luzon (Camarines Sur).

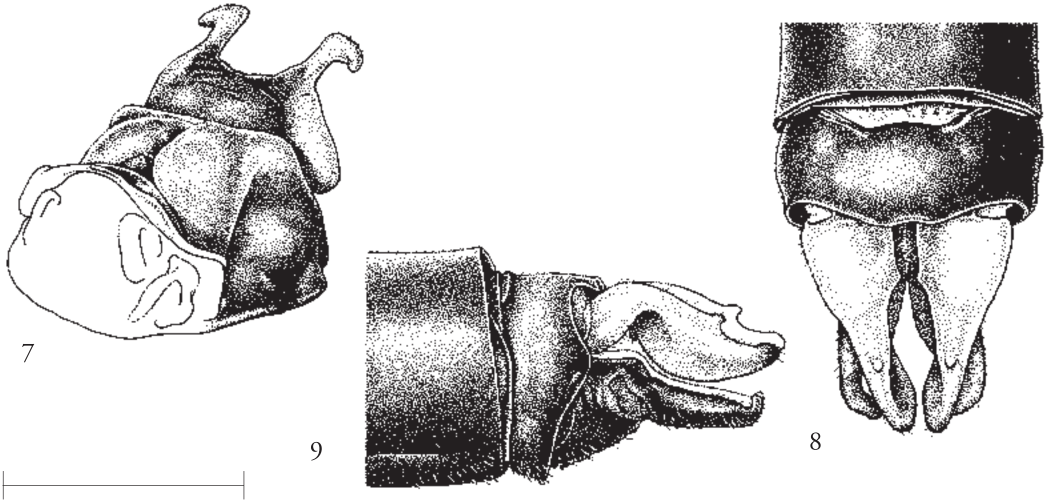
Drepanosticta aries Needham & Gyger
(Figs 7-9, 99)

Drepanosticta aries Needham & Gyger, 1941: 144-145, figs 3, 4, 8, 9 (original description, type locality Mindanao, Mnt Apo, Galog river, in MCZC) [type MCZN 23831, not examined]. – Hämäläinen & Müller 1997: 257, 276 (distribution Mindanao).

Material examined (all specimens Philippines, in RMNH). – **Mindanao**. Tra'ankina. Lake Sebu. 21-23.xi.1991 (J. de los Reyes) 1 male; Tra'ankina. Lake Sebu. 3-5.i.1992 (J. de los Reyes) 1 female; Lake Sebu, Lamlahak, Talubek. 26.i. - 1.ii.1994 (L. Vinciguerra & E. Horn) 3 females; North Cotabato, Mt. Apo, Philipp. National Oil Comp. forest area, 1600-1800 m, 12-25.iii.1994 (Alex Buenafe) 1 female; North Cotabato, Mt. Apo, Marbel river, 700-900 m, 12-25.ix.1994 (Alex Buenafe) 1 male; Davao del Sur, Mt Talomo, Malagos, Baguio, Eagle Camp, Kal-lay Creek, 700-1000 m, x.1994 (Alex Buenafe) 1 female; North Cotabato. Mt. Apo. Lake Agko. 1200-1300 m, 29.iii. -2.iv.1995 (R. A. Müller) 5 males 4 females; North Cotabato, Mt. Apo, Ilomavis, Lake Agko, Dum Creek. 1100-1200 m, ix.1995 (Alex Buenafe) 7 males 1 female; North Cotabato, Mt. Apo, Ilomavis, Kal-ay Creek, Sitio Sayaban. 1200-1300 m, ix.1995 (A. Buenafe) 3 males; North Cotabato, Mt. Apo, Ilomavis, Lake Agko, Babang Creek. 1600-1700 m, ix.1995 (A. Buenafe) 1 female.

Diagnosis. – Dark and medium-sized *Drepanosticta*; differs from other species in the *aries* group by the robust superior appendages, i.e. approximately two times as long as wide in dorsal view (appr. three times in *D. krios* sp. n.), and the complete dark segment 8 of the abdomen. Superior appendages robust in lateral view, but those of *D. acuta* sp. n. (from Luzon) are significantly wider. Confined to Mt. Apo and Lake Sebu on Mindanao.

Male. – Head. Labrum, mandibles, anteclypeus dirty white, narrow brownish black line along anterior border of labrum and mandibles; rest of head bronze-



Figures 7-9. *Drepanosticta aries* Needham & Gyger, male [JvT 20089, Mindanao, North Cotabato, Mt Apo, Ilomavis, Lake Agko, 1100-1200 m, ix.1995]. – 7, pronotum, oblique view. – 8, anal appendages, dorsal view. – 9, idem, left lateral view. Scale bar 1 mm.

black; antenna with scapus and pedicellus yellowish white, tip of pedicellus and flagellum brown; transverse occipital carina well developed with lateral extremities apiculate.

Thorax. Pronotum (Fig. 7) medium brown, but middle of posterior lobe, and lateral lobe dark brown; anterior lobe simple, but anterior ridge distinct; median and lateral lobes without distinct features; posterior lobe with both sides approximately halfway a caudally directed, flat and not erect process, approximately as long as median length of posterior lobe of pronotum, process ending in a 90° outward directed tip, somewhat more robust than base, ca. one-fourth the length of base. Synthorax dark brown, except for a paler spot around spiracle. Legs pale, except for darker rings on femora near tibiae. Wings hyaline, venation dark brown; Px 16-17 in fore wing, 15-16 in hind wing; origin of R4+5 at subnodus, IR3 just distal to that level; Arculus arising just distal to Ax2, quadrangle in forewing widening distally, anal veins shortly stalked; pterostigma castaneous, subquadrangular and oblique, proximal corner acute, distal side distinctly convex, cells between Costa and R1 distal to pterostigma rarely divided.

Abdomen. Dark brown, but paler basal annulae on segments 3-7. Appendages (Figs 8-9) middle brown, superiors base stout, in dorsal view tapering towards the tip, length ca. 2.5 times largest width, superiors actually fully flattened, thus hollow underside at base, dorsally at three-fifths from base a very short dorsal triangular tooth; inferiors in ventral view somewhat shorter than superiors, somewhat diverging, but tips directed inwards at c. 70°.

Measurements. Hind wing 24-25 mm, abdomen including appendages 35-36 mm, one specimen very small with hind wing 20 mm, abdomen including appendages 30 mm.

Female. – Very similar to the male, but posterior lobe of pronotum with lateral processes distinctly shorter, without terminal knob, approximately the length of hind lobe and semi-erect; wings with anal veins sessile, 17 Px in fore wing and hind wing. Some females presumably conspecific with males of *D. aries* (collected on same sites) with lateral extremities of postorbital carina acute rather than apiculate; pronotum with posterior lobe indistinct, the erect lateral processes absent, only with short erect collar.

Measurements. Hind wing 22-24 mm, abdomen 31-32 mm.

Status. – The name *Drepanosticta aries* Needham & Gyger is used here exclusively for specimens from Mount Apo, the type locality, and Lake Sebu, which is situated c. 120 km south of Mt. Apo. Other specimens with similar pronotum and appendages are known from other places in Mindanao, from Eastern Samar, Tawi Tawi and Sanga Sanga. They are assigned to *Drepanosticta krios* sp. n. The other two species of this group occur in Luzon.

Distribution (Fig. 99). – Philippine Islands: Mindanao (Mt. Apo, Lake Sebu)

Drepanosticta krios van Tol, **sp. n.**

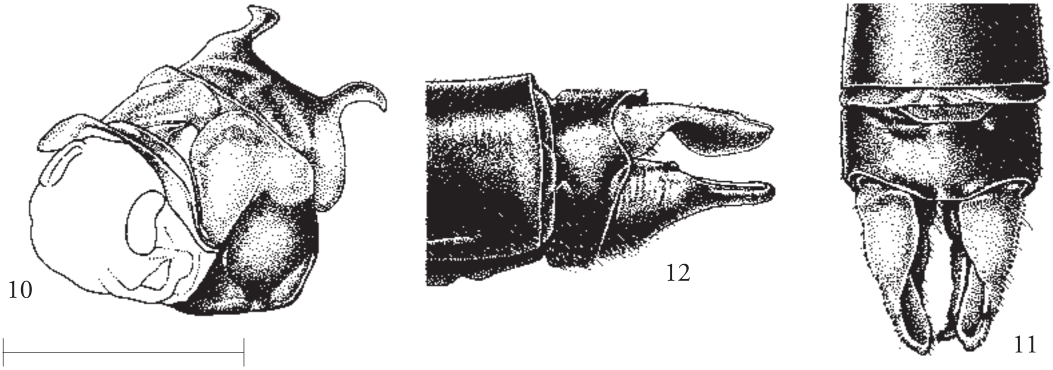
(Figs 10-12, 99)

Drepanosticta sp. n. 3. – Hämäläinen & Müller 1997: 257, 276.

Type material. – Holotype male [JvT 18867] in RMNH: 'Philippines, Tawi Tawi / Languyan, 80-100 m / June 8, 1990 / Roland A. Müller legit'. – Paratypes (all Philippine Islands, in RMNH, 112 males 22 females): **Mindanao**. Lanao del Norte, Kapatagan, Mt. Puting, Bato Sapad, 250 ft., x.1988 (W. Catal) 10 males 1 female; Lanao del Norte, Sitio Tinago, 10-16.viii.1997 (A. Buenafe) 37 males 11 females; Lanao del Norte, Iligan. Mimbalot Falls. 8°10'50"N 124°10'10"E. 29 m asl. 25.iii.2004 (V. Kalkman & J. van Tol) 14 males; Zamboanga del Norte Prov., 20 km S of Manucan, Labauan Mts, 680 m, 15.x.1959 (Quate) 1 male; Zamboanga del Norte Prov., Tampilisan, Gampoy river, 5-9.i.1991 (Th. Borromeo Jr) 3 males 1 female; Idem, Zamboanga del Sur, Tigbao, Mt Timolan, Tigbao Creek, 12-21.viii.1994 (Th. Borromeo) 28 males 4 females. – **Sulu archipelago**, Tawi Tawi Id. Languyan, 80-100 m. 6-9.vi.1990 (R. A. Mueller) 15 males 3 females; Batu Batu, 14-16.iii.1991 (Th. Borromeo) 2 males; Sanga Sanga Id. 2.vi.1992 (Th. Borromeo) 1 male; Tawi Tawi Id., Tarawakan. 100 m. 22-26.vi.1992 (Treadaway) 1 male 2 females.

Excluded from type series. – **Samar**. Eastern Samar, Oras, 10-22.viii.1994 (Th. Borromeo leg) 1 male (locality doubtful).

Diagnosis. – A rather small *Drepanosticta*, similar in structural details to *D. aries* Needham & Gyger, but



Figures 10-12. *Drepanosticta krios* sp. n., male [JvT 22092, Tawi Tawi, Languyan, 80-100 m, 9.vi.1990]. – 10, pronotum, oblique view. – 11, anal appendages, dorsal view. – 12, idem, left lateral view. Scale bar 1 mm.

of smaller size, with flatter processes of the posterior lobe of the prothorax, the superior appendages much more slender (especially visible in dorsal view), a lower number of postnodal crossveins in both fore and hind wings, and a conspicuous oblong bluish spot on abdominal segment 8; differs from both *D. acuta* sp. n. and *D. rhamphis* sp. n. in the smaller projections of the posterior lobe of the pronotum, and from the former in the straight rather than curved and tapered inferior appendages, and from the latter in the dorsal tooth of the superior appendage.

Male (JvT 18867, holotype). – Head. Labrum, mandibles, anteclypeus bluish white with a brownish black line along anterior border of labrum and mandibles, line on labrum in middle approximately one-fifth the height of labrum, and tapering towards the corners; rest of head bronze-black, coriaceous, with light-brown oval spots somewhat smaller than ocelli, anterior to anterior ocellus and lateral to lateral ocelli; antenna with scapus and pedicellus yellowish white, tip of pedicellus and flagellum brown; transverse occipital carina well developed with lateral extremities apiculate. Thorax. Pronotum (Fig. 10) pale brown or dirty yellow, but middle of posterior lobe, and lateral lobe brown; anterior lobe simple, with anterior ridge distinct; median and lateral lobe without distinct features; posterior lobe with both sides approximately halfway a caudally directed, flat and not erect process, somewhat shorter than median length of posterior lobe of pronotum, both ending in smoothly recurved, tapering tip. Synthorax vivid brown, except for a paler spot around spiracle and a narrow, oblong spot along lower margin of metepimeron. Legs pale, except for darker rings on femora near tibiae. Wings hyaline, venation brown; Px 14-15 in fore wing, 13-14 in hind wing; origin of R4+5 at subnodus, IR3 halfway first cell distal to that level; Arculus arising at Ax2, quadrangle in forewing hardly widening posteriorly, anal veins shortly stalked; pterostigma castaneous, width 1.6 times the height, oblique, proximal corner acute, distal side distinctly convex, cells between Costa and R1 distal to pterostigma rarely divided.
Abdomen brown, but paler basal annulae on segments 3-7, segment 8 anteriorly with an oblong, bluish white spot, approximately two-fifths the length of segment, and posteriorly rounded. Appendages (Figs 11-12) middle brown, superiors base stout, in dorsal view tapering towards the tip, length ca. 3.5 times largest width, superiors flattened and curved, thus hollow underside at base, dorsally at five-sevenths from base a very short dorsal triangular tooth; inferiors in ventral view somewhat longer than superiors, parallel-sided, but tips directed inwards at c. 70°.
Measurements. Hind wing 18.5 mm (18-19 mm); abdomen, including appendages 29 mm (29-30 mm).

Female. – Similar in coloration as male; structure of hind margin of posterior lobe more simple, straight, lateral parts ending sharp, below that level a broadly rounded lobe; Px fore wing 16, hind wing 15; anal appendages brown, valves pointed and surpassing tip of cercus.

Measurements. Hind wing 19-20 mm; abdomen 28-29 mm.

Note. – Dr. M. Hämäläinen confirms that the specimen from Samar may be a case of mislabelling. Most specimens collected by Mr Borromeo are reliably labelled, but there are some other clear cases of mislabelling in the collection. Usually, mislabelling is much higher in collections of commercial collectors. This is an opportunity to emphasize the professionalism of the collectors working for Roland A. Müller.

Etymology. – *Krios* (Greek), ram; for its resemblance to *D. aries* Needham & Gyger. A noun in apposition.

Distribution (Fig. 99). – Philippine Islands: Mindanao, Tawi Tawi, Sanga Sanga. The locality of the specimen from Samar is considered doubtful, and not on the map.

Drepanosticta rhamphis van Tol, **sp. n.**

(Figs 13-15, 99)

Drepanosticta sp. n. 11. – Hämäläinen 1997: 257, 277 (distribution Catantuanes I.).

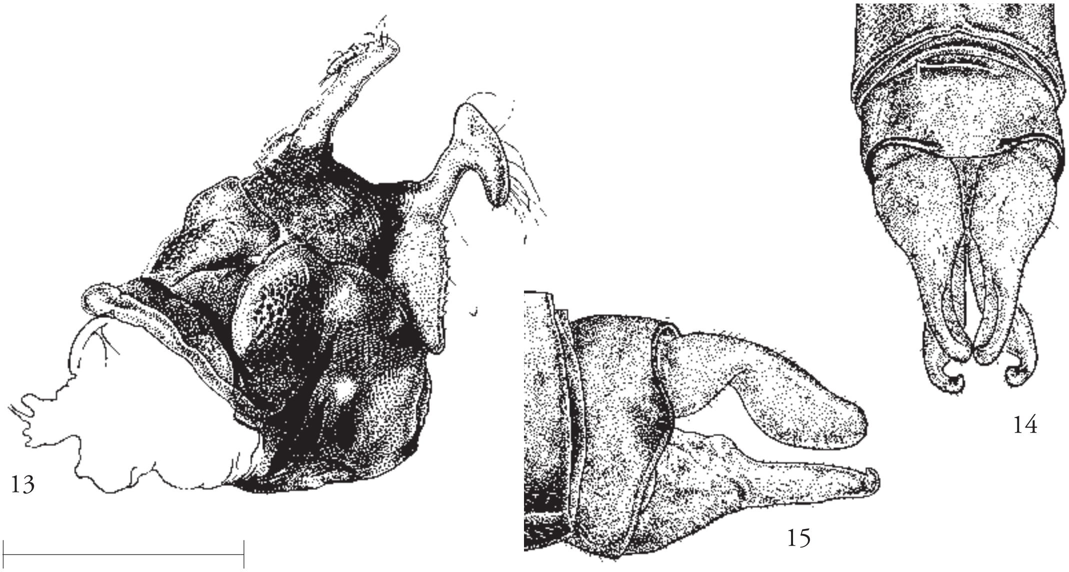
Type material. – Holotype male [JvT 18991] in RMNH: 'Philippines, Catanduannes [sic!] Id / Gigmoto, San Pedro / Egwang Tapayas Creeks / June 20.-30. 1996, 300-500 m / Alex Buenafe legit / Coll. Roland A. Müller'. – Paratypes (all Philippine Islands, in RMNH): **Catanduanes Id**, Gigmoto, San Pedro, Simohe Creeks, 300-500 m, 20-30.vi.1996 (A. Buenafe) 4 males; same, Tongao Creeks, 400-500 m, 20-30.vi.1996 (A. Buenafe) 1 female.

Non-type material. – **Luzon Id**, Camarines Norte, Sn Lorenzo Ruiz, San Isidro, Sitio Bakalid, Patag river, 300-500 m, 26-27.ix.1997 (C.M. Nazareno) 1 female.

Diagnosis. – A medium-sized species with dark synthorax and paler brown abdomen with distinct small bluish markings anteriorly on abdominal segments 3-6; hind margin of hind lobe of pronotum with a pair of hammer-like projections. The female of *D. rhamphis* sp. n. has similar projections on the posterior lobe of the pronotum as the male, while the female of *D. acuta* sp. n. is distinctly different from the male; for differences with *D. aries* Needham & Gyger and *D. krios* sp. n., see under these species.

Male [JvT 18991, holotype]. – Head. Labium brown; labrum bluish white, anteriorly with narrow brown line, fading towards pale coloured part of labrum; mandibles bluish white with narrow brown anterior line; anteclypeus bluish white, rest of head coriaceous, black with metallic shine; transverse occipital carina well-developed, the lateral extremities acutely angulate. Thorax. Pronotum (Fig. 13) multi-coloured, with middle part of anterior lobe, central parts of both halfs of median lobe, posterior part of lateral lobe, and central part of posterior lobe brownish black, rest much paler; structure of anterior, median and lateral lobes simple, posterior lobe relatively long, with a paired posterior process, long, ending abruptly in an antero-laterally directed part, turned 110-120° backward, the tip with long and stout setae. Synthorax completely brownish black, legs fully yellowish white. Wings hyaline, venation brown, lighter in basal half; Px 16 in fore wing, Px 16 in hind wing; R4+5 at or even just proximal to Ax2; IR3 arising halfway first cell distal to that level; Arculus just distal to Ax2; quadrangle somewhat widening distally in fore wing; anal veins asymmetrical, sessile or very shortly stalked; pterostigma oblique, width c. 1.7 times the height, proximal side acutely angulate, distal side convex; cells beyond pterostigma between Costa and R1 undivided. Abdomen. Middle brown with pale, bluish white, anterior markings on each segment as follows: segment 2 narrow, covering anterior 2/5th of segment, segments 3-6 with dorso-anterior spot of 1/10th of segment length, segment 7 pale in anterior 1/6th of segment, rest of anterior half of this segment lightbrown, segment 9 with small bluish anterior spot, segment 10 pale bluish (?). Appendages (Figs 14-15) creamish; superiors in dorsal view with stout base, approximately 2/3 of segment length ending in small dorsal tooth, distal part scoop-like and vertically oriented; inferiors rather slender, distal half bent outwards, the tip strongly tapered and first bent axiad, then dorsad.

Measurements. Hind wing 19 mm, abdomen including appendages 28.5 mm.



Figures 13-15. *Drepanosticta rhamphis* sp. n., male [JvT 18858, Catanduannes, Gigmoto, San Pedro, Simohe Creeks, 20-30. vi.1996]. – 13, pronotum, oblique view. – 14, anal appendages, dorsal view. – 15, idem, left lateral view. Scale bar 1 mm.

Female. – As the male, but posterior processes of posterior lobe of pronotum somewhat shorter, of similar shape as in the male.
Measurements. Hind wing 19 mm, abdomen 28 mm.

Etymology. – *Rhamphis* (Greek): hook; after the structure of the processes at hind margin of posterior lobe of pronotum. A noun in apposition.
Distribution (Fig. 99). – Philippine Islands (Luzon region): Catanduanes, Luzon.

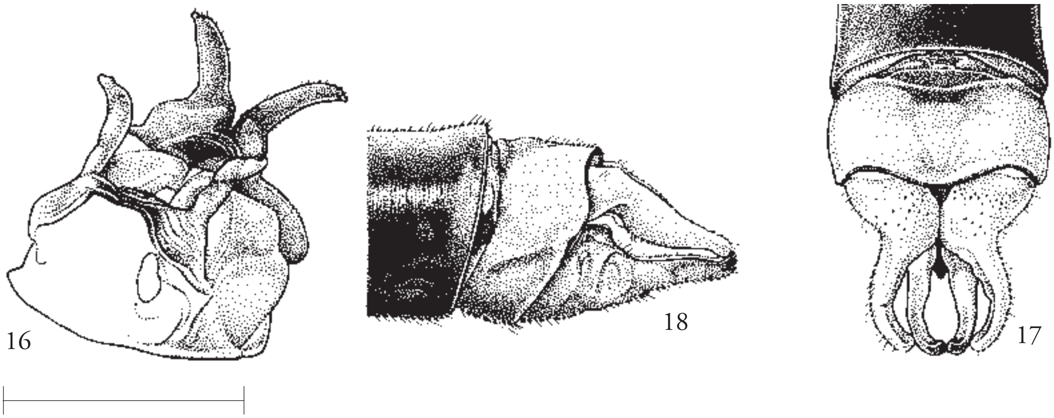
Drepanosticta belyshevi group

Transverse occipital carina distinct, with lateral extremities sharp, but not apiculate; lateral corners of anterior lobe or pronotum distinctly widened or even with a long process; posterior lobe with a pair of rather short, flat, curved or folded processes; synthorax with characteristic pale markings in posterior corner of metepisternum and metepimeron; pterostigma somewhat wider than high; superior appendages with ventral side of base (lateral view) curved sharp dorsad, a sharp ventral tooth near base, but size variable between species; inferiors in ventral view more or less clasper-like, the tip curved medio-dorsad.
Presumably the sister-group of the *D. lymetta* + *D. megametta* group.
Included species: *D. belyshevi* Hämäläinen, *D. flavomaculata* sp. n. , *D. trachelocele* sp. n.
Distribution: Bohol, Leyte, Panaon, Samar, Mindanao, Camiguin Id.

Drepanosticta belyshevi Hämäläinen
(Figs 16-18, 100)

Drepanosticta belyshevi Hämäläinen, 1991: 65-68, figs 1-4 (original description, holotype male Philippines, Panaon Id., San Francisco, Anislagon Gamay (200 ft), Aug 1988, W. Catal leg. [in Müller collection, now in RMNH] [examined], distribution Panaon Id). – Hämäläinen & Müller 1997: 257, 276 (distribution East Visayan subregion: Leyte, Panaon, Bohol).

Material examined (all Philippine Islands, in RMNH). – **Bohol**, Sierra Bullones, Pilar, 10-11.iv.1989 (W. Catal) 4 males. – **Samar**, Samar Prov., Hinubangan, San Isidro, San Isidro river, 90-200 m, 31.iii. - 5iv.1997 (R.A. Müller) 1 female. – **Leyte**, S. Leyte, Mahaplag, Hilusag, Mt Balocaue,



Figures 16-18. *Drepanosticta belyshevi* Hämäläinen, male [JvT 22216, Bohol, Sierra Bullones, Pilar, 10-11.iv.1989]. – 16, pronotum, oblique view. – 17, anal appendages, dorsal view. – 18, idem, left lateral view. Scale bar 1 mm.

700 m, 30.xi. - 2.xii.1989 (Th. Borromeo jr) 2 males 1 female; idem, Magsuganao river, 18-30.ix.1990 (Th. Borromeo jr) 2 males. – **Panaon**, Southern Leyte prov., San Francisco. Mt Kaneo, 400 ft, viii.1988 (W. Catal) 2 males 1 female; idem, San Francisco, Anislagon Gamay, 200 ft, viii.1988 (W. Catal) 1 male (holotype) 1 female; idem, San Francisco, Panan-awan Creek, viii.1988 (W. Catal) 1 male; idem, San Francisco, Batong Lapad, viii.1988 (W. Catal) 1 male; idem, San Francisco, Gabing Gamay, big river, x.1988 (W. Catal) 1 male; idem, San Francisco, Tabon river Lilo-an, x.1988 (W. Catal) 1 male; idem, San Francisco, Mt Anislagon, 350 ft, viii.1988 (W. Catal) 2 male; idem, Anislagon river, 10-12.x.1990 (Th. Borromeo jr) 3 males 3 females.

Diagnosis. – A relatively slender and pale brown coloured *Drepanosticta*, with conspicuous processes on the sides of both the anterior and the posterior lobe of the pronotum, and posterior one-third of metasternum and metepimeron bluish or yellowish white. Shares remarkable structure of anterior lobe of pronotum with *D. trachelocele* sp. n., *D. moorei* Van Tol & Müller, *D. quadricornu* sp. n. and *Protosticta lepteca* sp. n. The projected corners of the anterior lobe of the pronotum, although only known for species in the Philippines, is considered a parallel evolution, and not a synapomorphy. Its closest relative is *Drepanosticta trachelocele* sp. n. from Samar (for differences see under that species); *D. moorei* can immediately be distinguished on the presence of a broad pale band over metepisternum and dorso-posterior third of metepimeron; *D. quadricornu* from Palawan has an extensive pale stripe over posterior three-quarters of metepisternum and very distinct superior appendages; *Protosticta lepteca* sp. n. can be distinguished by the absence of the Ab vein, and the structure of dorsal appendages, which are not clasper-like. *D. flavomaculata* sp. n. is considered to be closely allied, but lacks the projections of the anterior lobe of the pronotum.

Male. – Head. Labium brown, labrum and anteclypeus bluish white, labrum with apical third brown, mandibles pale, bluish, but somewhat darker than labrum; rest of head brownish black, frons and vertex coriaceous; transverse occipital carina distinct, lateral extremities sharp, but not apiculate. Antenna with scapus and pedicellus yellowish white, flagellum brown. Thorax. Pronotum (Fig. 16) pale brown, the median lobe pale yellowish, anterior lobe laterally with a pair of dorsally erect cylindrical processes, the tip directed outward, length in lateral view nearly as high as lateral lobe; median and lateral lobes simple; hind margin of posterior lobe medially acute, laterally with a paired flat process, in lateral view approximately as long as median lobe, directed posteriad, curved outward, with a short triangular spine as base. Synthorax medium brown, but the following parts yellowish: small marking of mesepimeron, approximately one-third of metepisternum posterior to metastigma, and approximately one-third of metepimeron. Wings hyaline, venation brown, Px 15-16 in fore wing, Px 14-15 in hind wing; R4+5 arises well distal to subnodus, IR3 approximately halfway first cell distal to that level; Arculus arises distal to Ax2; quadrangle somewhat widening in fore wing, scarcely so in hind wing; anal veins asymmetrical and shortly stalked, pterostigma width c. 1.9 times the height, brown with narrow pale line against veins; some cells distal to pterostigma between Costa and R1 divided.

Abdomen. First segments medium brown, more caudal segments darker, especially segment 3-6 with yellow basal annulae. Appendages (Figs 17-18) with superiors in dorsal view basal half very stout, the caudal half slender and dorso-ventrally flattened, bent as a forceps, the tip squarish; inferiors in ventral view somewhat longer than superiors, nearly straight, the tip bent 90° dorsad.

Measurements. Hind wing 18-20 mm, abdomen including appendages 27-32 mm.

Female. – As the male, but abdomen distinctly stouter; structure of prothorax as male, but processes of anterior and posterior lobe of prothorax shorter and more slender; last abdominal segments stout, brown, the valve relatively slender, the stylus not surpassing the cercus.

Mesurements. – Hind wing 20-22 mm, abdomen 28-32 mm.

Occurrence. – Apparently occurring only in low densities on most sites, since only short series are available. Rather widespread, but specimens from Samar are here considered specifically distinct, *Drepanosticta trachelocele* sp. n.

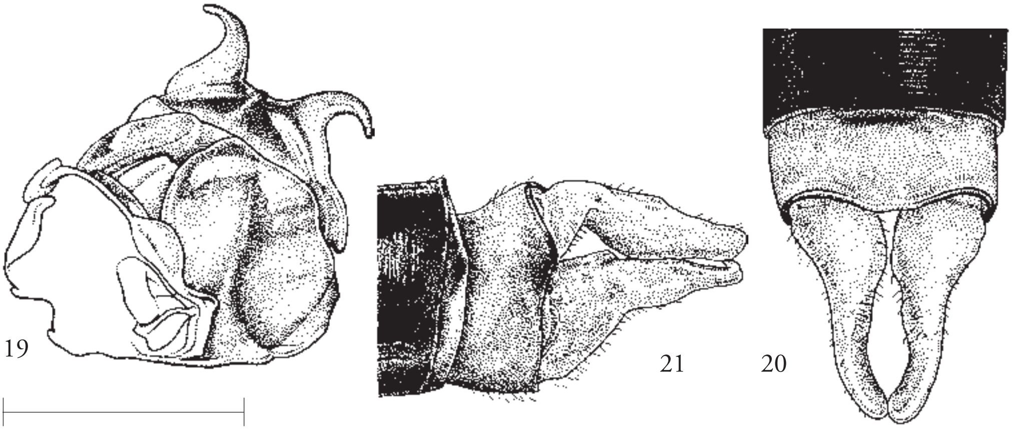
Distribution (Fig. 100). – Philippine Islands (East Visayan subregion): Leyte, Panaon and Bohol.

Drepanosticta flavomaculata van Tol, **sp. n.**

(Figs 19-21, 100)

Drepanosticta sp. n. 18. – Hämäläinen & Müller 1997: 258, 277 [Mindanao, Camiguin].

Type material. – Holotype male [JvT 20359] in RMNH: ‘Philippines. Mindanao Id / Bukidnon, Kalatungan Mts / Pangantocan, Brgy Mendes / Mikaramagan Creek, Mandom / June 1995. 900-1200 m / Alex Buenafe legit’ . – Paratypes (all Philippine Islands, in RMNH, total 160 specimens) (by island in chronological order): **Camiguin Id**. Mambajao. Brgy Pandan, Mt Timpo-ong, Katibawasan Falls, 500-700 m, 22.v.1995 (A. Buenafe) 6 males 1 female; Catarman, Tuasan Falls, 29.x.2003 (R.J. Villanueva) 2 males. – **Mindanao**. Zambo[a]nga d. Norte. Manucan, 20 km So. Labauan Mts, 680 m, primary forest, 15.x.[19]59 (Quate) 1 male; South Cotabato, Salacafe, El Milil, 1250 m, 7.iv.1985 (R.A. Müller) 2 males; [South Cotabato, Koronadal], Barrio 8, 13.iv.1985 (R.A. Müller) 2 males; South Cotabato, Koronadal, Barrio 8, 100-200 m, 12-14.vii.1986 (R.A. Müller) 11 males 5 females; South Cotabato, Koronadal, Barrio 8, 19.vii.1987 (J. de los Reyes) 1 male; South Cotabato, Koronadal, Barrio 8, 30.vi.1991 (J. de los Reyes) 1 male 1 female; North Cotabato,



Figures 19-21. *Drepanosticta flavomaculata* sp. n., male [JvT 20225, Mindanao, Koronadal, Barrio 8, 4.ii.1994]. – 19, pronotum, oblique view. – 20, anal appendages, dorsal view. – 21, idem, left lateral view. Scale bar 1 mm.

Alamada, Mt Makatoring, 700-900 m, 1000 m, 1.ii.1992 (Th. Borromeo) 10 males; South Cotabato, Koronadal, Barrio 8, 29.viii.1993 (J. de los Reyes) 5 males; South Cotabato, Mt Matutum, 500-700 m, 16-19.ix.1993 (Th. Borromeo) 2 males; South Cotabato, Koronadal, Barrio 8, 4.ii.1994 (L. Vinciguerra & E. Horn) 2 males; Davao del Sur, Malagos, Baguio, Eagle Camp, 500-600 m, 28.iii.1995 (R.A. Müller) 1 male; Davao Oriental, Baganga, Brgy Upper Mikit, Mangoy Falls, 300-350 m, 6.iv.1995 (A. Buenafe & A. Gorostiza) 1 female; Davao Oriental, Cateel, Aliwagwag Falls, 200-300 m, 10.iv.1995 (A. Buenafe & A. Gorostiza) 1 male 1 female; Data as holotype, 5 males 1 female; Bukidnon, Mt Kalatungan, Talakag, Brgy Mebadiang, Magamanason Creek, Sitio Olayan, 1000-1100 m, 5-18.viii.1995 (A. Buenafe) 4 males 6 females; Bukidnon, Mt Kalatungan, Pangantocan, Sitio Mandon, Mekaramagan Creek, 1800 m, 12-15.viii.1995 (A. Buenafe) 4 males; Bukidnon, Mt Katanglad, Impasugong, Brgy Impulatao, Gantongan Creek, 800-900 m, 19-29.viii.1995 (A. Buenafe) 9 males; Bukidnon, Mebadiang, Dumatap, Mt Kalatungan, Mansabilan Creek, 1000-1300 m, 24.xi.1995 (A. Buenafe) 3 males 1 female; Bukidnon, Mebadiang, Dumatap, Mt Kalatungan, Muntian Creek, 1200-1400 m, 24-25.xi.1995 (A. Buenafe) 6 males 2 females; Surigao del Sur, Tabon, Tabon Falls, 100-200 m, 26.v.-8.vi.1996 (A. Gorostiza & A. Buenafe) 9 males 3 females; Davao Oriental, Boston, Mt Agtuuganon, Camp 55, 1020 m, 29.v. -7.vi.1996 (R.A. Müller et al.) 4 males 4 females; Davao Oriental, Sigaboy, Tandang Sora, Yakal, Tabamban River, Lakahan Creek, 400-800 m, 5-14.x.1996 (A. Buenafe) 7 males 3 females; Davao Oriental, Sigaboy, Tandang Sora, Yakal, Tabamban River, Buyo Creek / Tubonol Creek / Langanisan Creek, 400-800 m, 5-14.x.1996 (A. Buenafe) 3 males; Lanao del Norte, Linamon, Sitio Tinago, 200-400 m, 10-16.viii.1997 (A. Buenafe) 15 males 6 females; Bukidnon, Katanglad Mts, Impasugong, Impalutao, Gantongan Creek, 1200-1400 m, 17-28.viii.1997 (A. Buenafe) 4 males; Davao City, Datu Salumay, 25 Feb 2004 (R.J. Villanueva) 1 males; Iligan, Tinago Falls, 8°09'33"N 124°11'11"E, 160 m, 25.iii.2004 (V. Kalkman & J. van Tol) 4 males.

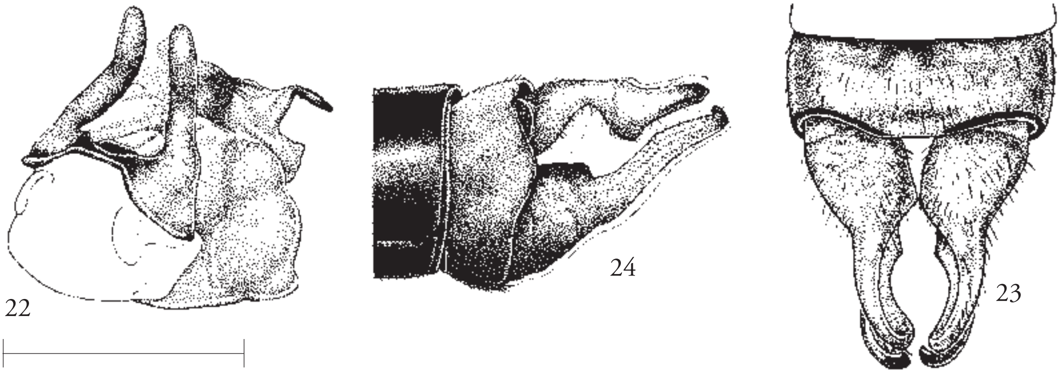
Diagnosis. – Based on the structure of the anal appendages, and the coloration of the synthorax, in one group with *D. belyshevi* Hämäläinen. Distinguishable from other species in this group by the absence of a conspicuous, paired process on the anterior lobe of the pronotum, the curved and flat processes on the posterior margin of the posterior lobe of the pronotum, and a poorly developed ventro-medial tooth on the superior appendage of the male.

Male [JvT 20359, holotype]. – Head. Labrum, mandibles, and anteclypeus ivory white, anterior one-fifth of labrum and mandibles brownish black; rest of head bronze-black, frons and vertex coriaceous; transverse occipital carina distinct, lateral extremities sharp, not apiculate. Antenna with scapus and pedicellus dirty yellow, flagellum brown, somewhat paler at base.

Thorax. Pronotum (Fig. 19) with anterior lobe castaneous, dull, median and lateral lobes dirty yellow, only dorsal parts somewhat obscured; posterior lobe brown; anterior lobe erect, lateral sides broad and flat, median and lateral lobes simple; posterior lobe with lateral portion on innerside with flat, short, recurved process, just somewhat longer than length of median portion of posterior lobe. Synthorax castaneous, coriaceous except for metepimeron and metepisternum, with a squarish pale marking just before posterior margin of metepisternum, and a similar marking in posterior corner of metepimeron. Wings hyaline, venation brown; Px 16 in fore wing, PX 15 in hind wing; R4+5 arising at or just distal to subnodus; IR3 circa halfway first cell distal to that level; Arculus arising distinctly distal to Ax2 in fore wing, c. distance between R+M and CuP; quadrangle widening in fore wing; anal vein long and symmetrical; pterostigma width c. 1.5 times the height, a narrow pale border against veins; many cells between Costa and R1 distal to pterostigma divided.

Abdomen. Segment 1 brown, each more caudal segment darker, except for segment 10, which is completely blue dorsally; segments 3-7 with basal one-sixth to one-eighth with yellow marking. Appendages (Figs 20-21) dirty yellow, superiors with stout base, distal three-fifths in dorsal view clasper-like, tip squarish, in lateral view distal half distinctly flat, a sharp, but rather inconspicuous, ventro-mediad tooth near base; inferiors approximately as long as superiors, stout at base, distal three-fifths approximately cylindrical, bent 80° inward, innerside emarginate, tip directed dorsad (caudal view).

Measurements. Hind wing 24 (20-24) mm, abdomen (including appendages) 34 (30-34) mm.



Figures 22-24. *Drepanosticta trachelocele* sp. n., male [JvT 20331, Samar, Hinabangan, San Isidro, 100-200 m, 29.viii-20.ix.1996]. – 22, pronotum, oblique view. – 23, anal appendages, dorsal view. – 24, idem, left lateral view. Scale bar 1 mm.

Female. – Coloration as the male, but structure of pronotum distinctly different, with processes on posterior lobe short and erect, flat, although with much variation in length and shape between specimens. Innerside of these processes rounded, outerside sharply projected in some specimens, broadly rounded in others, but process may even be shaped as a small triangular, erect projection.
Measurements. Hind wing 22-23 mm, abdomen 30-32 mm.

Etymology. – *Flavomaculatus* (Latin), with yellow markings; for the coloration of the synthorax. An adjective.
Distribution (Fig. 100). – Philippine Islands (Mindanao subregion): Camiguin Island, Mindanao. Rather widespread in Eastern Mindanao region.

Drepanostocta trachelocele van Tol, **sp. n.**

(Figs 22-24, 100)

Type material. – Holotype male [JvT 20323] in RMNH: ‘Philippines, Samar Id / Samar Prov., Hinubangan / Arizona, 100-280 m / March 29.-April 6. 1997 / R.A. Müller leg. et coll.’, ‘*Drepanostocta belyshevi* Hämäl. (ssp. ?) M. Hämäläinen det.’. – Paratypes (all Philippine Islands, in RMNH, 18 specimens): **Samar Id**, Hinabangan, Bagakay, Arisona, 100-200 m, 29.viii-20.ix.1996 (A. Buenafe) 4 males 1 female; same site, but San Isidro, 100-200 m, 100-200 m, 29.viii-20.ix.1996 (A. Buenafe) 1 male 3 females; same site as holotype, 3 males 1 female; same site, but San Isidro, San Isidro river, 90-200 m, 31.iii.-5.iv.1997 (R.A. Müller) 1 male 2 females; Western Samar province, San Jose de Buan, Mt Hurao, San Andres. 14-20.v.1997 (A. Buenafe) 2 males.

Diagnosis. – One of the very few species of *Drepanosticta* with paired processes on hind margin of both the anterior and the posterior lobe of the pronotum; most closely related to *D. belyshevi* Hämäläinen, from which it differs particularly by the structure of the processes of the posterior lobe of the pronotum: the processes in *D. belyshevi* are placed close to the median line and curved over the abdomen, whereas the processes in *D. trachelocele* are placed near the lateral corners, with a short erect base and the rest recurved ventrad. For differences with other Philippine *Drepanosticta* species with projections on anterior lobe of pronotum, see *D. belyshevi* Hämäläinen.

Male [JvT 20323, holotype]. – Head. Labium, mandibles and anteclypeus bluish white, a brownish black margin on anterior one-fifth of labium and one-eighth of mandibles; rest of head brownish black with bronze metallic shine, frons and vertex coriaceous; transverse occipital carina well developed, with acute lateral extremities, more angulate that in *D. belyshevi*; antenna with scapus and pedicellus dirty yellow; flagellum castaneous.
Thorax. Pronotum (Fig. 22) with anterior lobe castaneous, somewhat darker at hind margin, middle and lateral lobes dirty yellow, posterior lobe pale brown with a rounded or sub-triangularly shaped marking in

middle, hind margin of posterior lobe also somewhat darker; anterior lobe with a paired process, laterally on lobe, rounded and directed anterio-dorsad, total length surpassing median length of pronotum; hind margin of posterior lobe with a paired process, distance between bases of processes more than five times the width of process at base, process halfway curved backward (ventrad) and inconspicuous in many specimens (much variation), but not a long, flat and curved process as in *D. belyshevi*. Synthorax castaneous, but meso- and metakatepisternum somewhat paler, a subsquarish bluish white spot posteriorly on metepisternum, and a similar spot on metepimeron, the latter one with a ventro-lateral projection. Legs dirty yellow, obscure brown rings on two-thirds the length of femora. Wings hyaline, venation brown; Px 16 in fore wing 16, Px 15 in hind wing; R4+5 distal to subnodus, IR3 halfway first cell distal to subnodus; Arculus distal to Ax2; Ab vein joining Ac just before wing margin (Y-veins subsessile); pterostigma castaneous, oblong, c. two times wider than high; veins distal to pterostigma numerous, but undivided.

Abdomen castaneous, with creamish or bluish white markings as follows: segments 3-6 with a narrow ring against anterior border of segment, the white marking projecting posteriorly on both sides of median line of tergites against borders; segment 8 with yellowish white anterior ring, c. one-fourth of length of segment. Appendages (Figs 23-24) very pale brown, superiors dorsally stoutly built, distal half as a clasper in dorsal view, and club-shaped on innerside; inferiors in ventral view very slender, straight, the top bent medio-dorsad.

Measurements. Hind wing 19 (18-19) mm; abdomen including appendages 30 (28-32) mm.

Female. – Similar to male, including structural details of the processes of the anterior and posterior lobes of the pronotum, although both pairs of processes are somewhat smaller, especially the ones on the anterior lobe.

Measurements. Hind wing 18-20 mm, abdomen 27-29 mm.

Affinities. – Based on the structure of the pronotum, this species is considered the sister-species of *D. belyshevi* Hämäläinen.

Etymology. – *Trachelocele*: a genus of antelopes; for the shape of the processes on the pronotum. A noun in apposition.

Distribution (Fig. 100). – Philippine Islands: Samar.

D. moorei group

Transverse occipital carina poorly developed, lateral extremities absent or just discernable; pronotum with processes on anterior and posterior lobe distinctly different between species; synthorax with long and distinct stripes over mesepisternum and mesepimeron; pterostigma slightly wider than high; superiors strongly flattened dorso-ventrally, and broadly triangular in lateral view; base of inferiors in ventral view subparallel, the top as a clasper, with a more or less distinct ridge on inner margin; tip sharp.

Based on structure of male anal appendages and the coloration of the synthorax, the species of this group are not members of the group of 'typical Philippine *Drepanosticta*' species. Their affinities are presently unsettled.

Included species: *D. luzonica* sp. n., *D. moorei* Van Tol & Müller.

Distribution: Luzon.

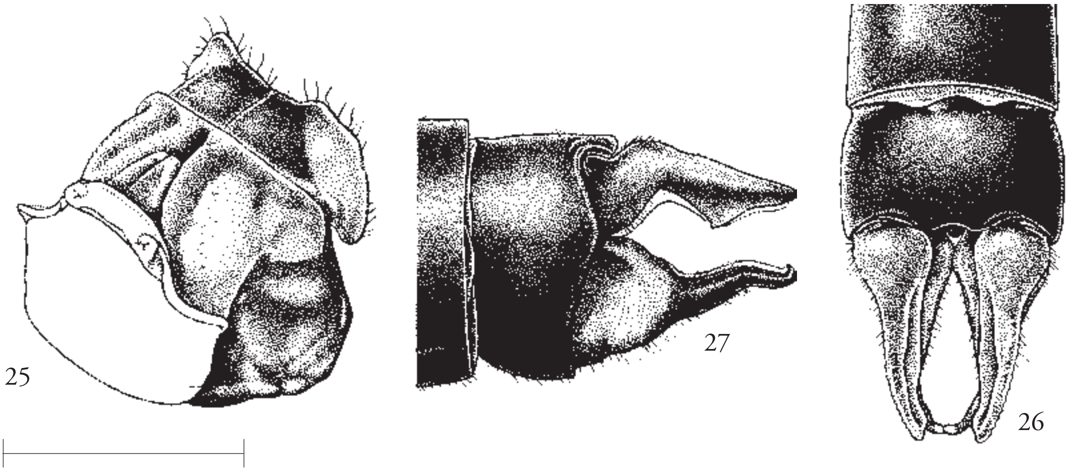
Drepanosticta luzonica van Tol, **sp. n.**

(Figs 25-27, 101)

Drepanosticta sp. n. 9. – Hämäläinen & Müller 1997: 257, 277.

Type material. – Holotype male [JvT 9451] in RMNH: 'Philippines / [Luzon] Ifugao Province / Jacmal Bunhian / 24 km E Mayoyao 800- / 1000m 7-8.iv.1967'.

Diagnosis. – A relatively large species, with conspicuous yellow markings on synthorax. Based on synthoracic pattern, superficially resembling *Drepanosticta lestoides* Brauer, but superior anal appendages distinctly different, lacking the superior tooth, and the tip squarish rather than smoothly rounded. Differs from *D. moorei* Van Tol & Müller by



Figures 25-27. *Drepanosticta luzonica* sp. n., male [JvT 9451, holotype]. – 25, pronotum, oblique view. – 26, anal appendages, dorsal view. – 27, idem, left lateral view. Scale bar 1mm.

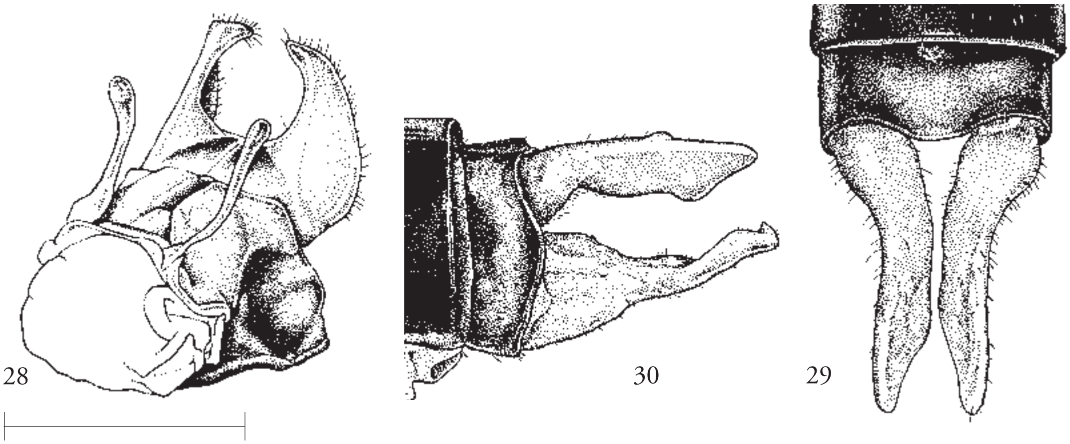
the absence of conspicuous processes on anterior and posterior lobes of pronotum.

Male [JvT 9451]. – Labrum, anteclypeus and mandibles bluish white, partly yellowish white; anterior one-fourth of mandibles brownish black; rest of head bronze-black, frons and vertex coriaceous; postoccipital carina without extremities; antenna with scapus brownish black, pedicellus brown, flagellum broken in type.
Thorax. Pronotum (Fig. 25) dark with distinct, pale yellowish white markings; anterior and median lobe yellowish white with higher parts of median lobe brown; posterior lobe with median portion brownish black, lateral portions greyish brown, lateral lobes brownish black, but central parts with pale spots; anterior, median and lateral lobes simple; posterior lobe with lateral portions semi-erect, somewhat extended ventrad, broadly rounded caudally. Synthorax bronze-black with pale yellow markings as follows: dorsal carina, a small and narrow line dorso-posteriorly on mesepisternum; metepisternum nearly fully pale, except for posteriormost part, anteriorly extending over lower part of mesepimeron and mesokatepisternum; lower half of metepimeron, pale marking extending posteriad and covering the full width in posterior quarter of metepimeron.
Wings hyaline, venation brown, basal half paler; Px 13 in fore wing, Px 12 in hind wing; Arculus arising at Ax2; R4+5 arising at subnodus; IR3 halfway cell distal to R4+5; quadrangle oblong and quadrangular, not widening posteriorly; pterostigma rhomboid, ca 1.5 times as wide as high; cells between Costa and R1 beyond pterostigma undivided.
Abdomen. Brown, lower parts of segments 1-2 yellowish white, anterio-basal part of segments 3-7 pale (partly discoloured in type), but dark line extending over full length; lower half of segments 8-9 pale; appendages (Figs 26-27) brown, superior club-shaped distal part with tip squarish, the ventral margin forming a broad triangular tooth; superiors without dorsal tooth; inferiors in distal half very slender, curved inward, the very tip dorsad, lacking an inward directed tooth.
Measurements. Hind wing 23 mm, abdomen including appendages 38 mm.

Female. – Unknown.

Etymology. – *Luzonicus* (Latin), from Luzon, for the type locality. An adjective.

Distribution (Fig. 101). – Philippine Islands: Luzon



Figures 28-30. *Drepanosticta moorei* Van Tol & Müller, male [JvT 18624, Luzon, Nueva Viscaya, Sta Fe, Atbo river, 550-800 m, 10.vi.1991]. – 28, pronotum, oblique view. – 29, anal appendages, dorsal view. – 30, idem, left lateral view. Scale bar 1 mm.

(central northern part). Apparently a local or rare species; not represented in the Müller collection.

Drepanosticta moorei Van Tol & Müller
(Figs 28-30, 101)

Drepanosticta moorei Van Tol & Müller, 2003: 42 [original description, holotype male Luzon, Nueva Viscaya, Sta Fe, Atbo River, 550-800 m, 10 Jun 1991, R.A. Müller] [examined].
Platysticta annulata Selys, 1886: 156 [partim].
Drepanosticta sp. – Lieftinck 1961: 136 [specimen '588' in Selys collection, IRSN Brussels, a paralectotype of *D. annulata* (Selys), not conspecific with lectotype].
Drepanosticta sp. n. 7. – Hämäläinen & Müller 1997: 257, 276-277 [distribution Luzon].

Material examined [all Philippine Islands, in RMNH]. – **Luzon**. Nueva Viscaya, Dalton Pass, 850-900 m, 8-9.vi.1991 (R.A. Müller) 1 male; Nueva Viscaya, Sta Fe, Atbo river, 550-800 m, 10.vi.1991 (R.A. Müller) 12 males 10 females [including holotype]; Nueva Ecija, Caranglab, Batching river, 700-850 m, 11.vi.1991 (R.A. Müller) 2 males; Aurora Prov., Dilalongan, Sitio Biyak, Dibaraybay, 300-500 m, 3-15.vii.1996 (C.M. Nazareno) 1 female; Zambales Prov., Masinloc, Mt Coto, Tal-tal, 400-700 m, 1-8.iv.1997 (C.M. Nazareno) 1 female.

Diagnosis. – Unmistakable species by the combination of long processes on the anterior lobe of the pronotum, and the conspicuous greenish yellow stripe over synthorax. For a comparison of species with long projections of the anterior lobe, see *D. belyshevi* Hämäläinen; for a comparison with other species with pale stripe over synthorax, see *D. luzonica* sp. n.

Male [holotype, JvT 22225]. – Head. Labrum and anteclypeus very clear blue, anterior border of labrum with narrow black line; mandibles brown, but inner basal corner blue; rest of head bronze-black; antenna with scapus and pedicellus dirty yellow, the tip of pedicellus somewhat darker, flagellum brown; transverse occipital carina indistinct and lacking conspicuous extremities.
Thorax. – Pronotum (Fig. 28) with anterior and median lobe yellowish, lateral lobe brown, posterior lobe dirty yellow; anterior lobe approximately halfway each side with very long subcylindrical process, touching median lobe, and reaching virtually hind margin of central portion of posterior lobe; median and lateral lobes simple; hind lobe laterally with enormous collar, half-round, nearly twice as long as basal part of posterior lobe; lateral margin with long and thin setae. Synthorax bronze-black, but metepisternum nearly fully greenish yellow, and dorso-posterior third of metepimeron greenish yellow. Legs dirty yellow. Wings hyaline, venation brown; Px 13 in fore wing, Px 13 in hind wing; origin of R4+5 just distal to subnodus,

IR3 arises six cells distal to nodus in fore wing, five cells in hind wing; Arculus just distal to Ax2, distinctly stalked; Ac and Ab forming a Y, subsessile; number of cells between distal end of quadrangle and place where CuP meets hind margin in fore wing 5, in hind wing 7; pterostigma brown, with a narrow line against veins; ca. 1.6 times longer than high, the proximal side oblique, the distal side convex; cells between Costa and R1 posterior to pterostigma undivided.
Abdomen brown, but basal one-tenth of segment 3, basal one-sixth of segments 4-6, basal one-third of segment 7 dirty yellow; segments 8-10 tergites brown. Appendages (Figs 29-30) greyish brown, top of inferiors castaneous; superiors with basal one-fourth stout, rest narrow in dorsal view, actually strongly flattened dorso-ventrally, and broadly triangular in lateral view; inferiors in ventral view subparallel, the top bent outward, then inward in a semicircle, in lateral view the top bends in 90°.
Measurements. Hind wing 22 (20-22) mm; abdomen including appendages 37 (31-37) mm.

Female. – Very similar to male, including coloration and structure of pronotum; segments 8-10 brown, anal appendage light brown, genital valves surpassing apex of appendages.
Measurements. Hind wing 21-22 mm, abdomen 30-31 mm.

Affinities. – Van Tol & Müller (2003: 44) assumed a close relationship of this species with *D. belyshevi* Hämäläinen, particularly based on the structure of the processes of the anterior lobe of the pronotum. A more recent analysis revealed that the structure of the pronotum of both species is distinctly different, and the projections cannot be considered homologous. Based on the coloration of the synthorax and the structure of the anal appendages of the male, *D. moorei* must be considered the sister-species of *D. luzonica* sp. n.
Distribution (Fig. 101). – Philippine Islands: Central Luzon (provinces Nueva Viscaya, Nueva Ecija, Aurora and Zambales). Apparently occurring in low densities over a relatively large area; in larger numbers on type locality only.

***D. lymetta* group**

Transverse occipital carina distinct, with acutely angulate lateral extremities; anterior lobe of pronotum simple, without projections or processes; posterior lobe of pronotum with a pair of processes on hind margin, typically divided or hooked at top; synthorax castaneous; pterostigma distinctly wider than high; superior appendages with a blunt dorsal tooth and a sharp medially directed one on inner surface; inferior appendages slender and straight, the tip emarginate, curved 90° medio-dorsad, undivided. Based on the structure of the anal appendages, presumably the sister-group of the *D. megametta* group.
Included species: *D. clados* sp. n., *D. furcata* sp. n., *D. hermes* sp. n., *D. lymetta* Cowley, *D. taurus* Needham & Gyger.
Distribution: Mindanao and Siquijor.

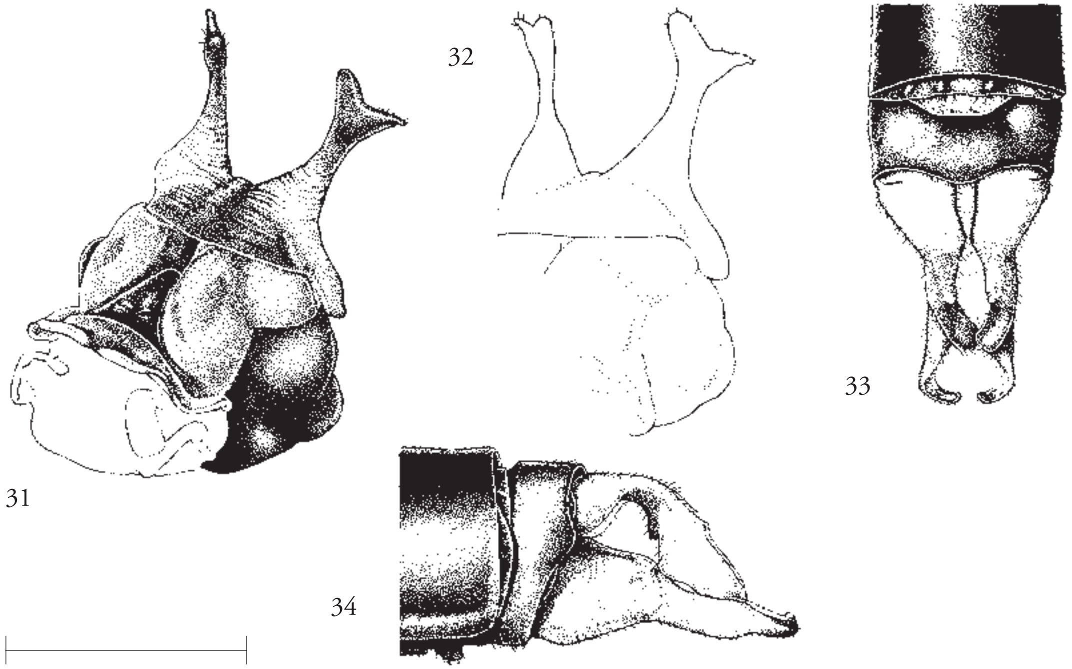
Drepanosticta clados van Tol, **sp. n.**

(Figs 31-34, 102)

Type material. – Holotype male [JvT 26817] in RMNH: '[Philippine Islands, Mindanao] 002-XII-7-2003 / Spring -Malabog, Pakibato Dist., Davao City / R.J. [Villanueva]'. – Paratype: 1 male, same data [in RMNH].

Diagnosis. – An inconspicuous brown species; posterior processes of hind lobe of pronotum extremely long, c. 80% of median length of pronotum, the tip bifid, both branches of equal length; also characterised in the *lymetta*-group by its long inferior appendages, distinctly surpassing the hooked superiors in lateral view (Fig. 33).

Male [holotype, JvT 26817]. – Head. Labrum, anteclypeus and mandibles ivory or bluish white, anterior one-third of labrum and mandibles brown; rest of head bronze-black; transverse occipital carina distinct, with distinctly angulate lateral extremities; antenna with scapus brownish-black, pedicellus brown, flagellum unknown (missing).
Thorax. Pronotum (Figs 31-32) rather dark, with anterior lobe wide, but relatively simple with only anterior margin distinctly erect, brown in median part,



Figures 31-34. *Drepanosticta clados* sp. n., male [JvT 26816, Mindanao, Davao City, Pakibato District, Malabog, 7.xii.2003]. – 31, pronotum, oblique view. – 32, pronotum, frontal view of projection of hind lobe. – 33, anal appendages, dorsal view. – 34, idem, left lateral view. Scale bar 1 mm.

paler in lateral corners; median lobe with a paired, convex, brownish black protuberance, better defined than in *D. lymetta*; posterior lobe castaneous, medially somewhat darker, posteriorly with a paired long process, c. 80% of length of pronotum itself, apically V-shaped, the branch of equal length and stoutly built. Synthorax castaneous, but mesokatepisternum, metakatepisternum, metepimeron and anterior part of metepisternum darker, no pale markings. Legs with fore coxa and upper part of middle coxa dark brown, rest of legs yellowish or reddish brown. Wings hyaline, veins brown; Px 15-16 in fore wing, Px 15 in hind wing; R4+5 arising from subnodus, IR3 arising half a cell distal to that level; Arculus just distal to Ax2; Y-shaped anal veins virtually sessile, distinctly asymmetrical; pterostigma 1.8 times as wide as high, innerside angulate; cells between Costa and R1 distal to pterostigma undivided.

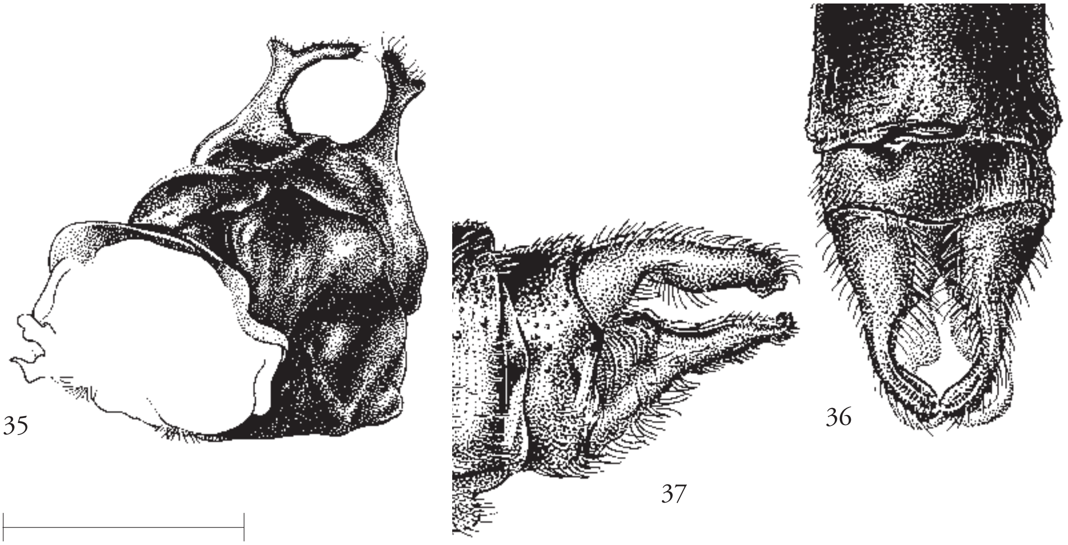
Abdomen. Brown, with pale hastate markings dorsally on segment bases as follows: segment 2 very small, one-sixth of segment length, one-seventh on segments 3-4, one-eighth on segments 5-6, and one-seventh on segment 7; segments 8-10 brown, but segment 10 presumably paler in life. Appendages (Figs 33-34) yellow; superiors in lateral view distinctly hooked, basal third directed dorsad, distal two-thirds slightly ventrad; base of terminal part with short, triangular tooth, and just distal to that a similar distal tooth; terminal two-thirds flattened, the tip squarish; inferiors in ventral view straight, the terminal one-sixth more slender, tapering and curved dorso-mediad.

Measurements. Hind wing 21.5 mm; abdomen including appendages 33 mm.

Female. – Unknown.

Etymology. – *Clados*: branch (Greek), for the structure of the processes of the posterior lobe of the pronotum. A noun in apposition.

Distribution (Fig. 102). – Philippine Islands: Eastern Mindanao, around Davao City.



Figures 35-37. *Drepanosticta furcata* sp. n., male [JvT 18862, Siquijor, Barrio Bandilaan, 28-23.iv.1993]. – 35, pronotum, oblique view. – 36, anal appendages, dorsal view. – 37, idem, left lateral view. Scale bar 1 mm.

Drepanosticta furcata van Tol, **sp. n.**

(Figs 35-37, 102)

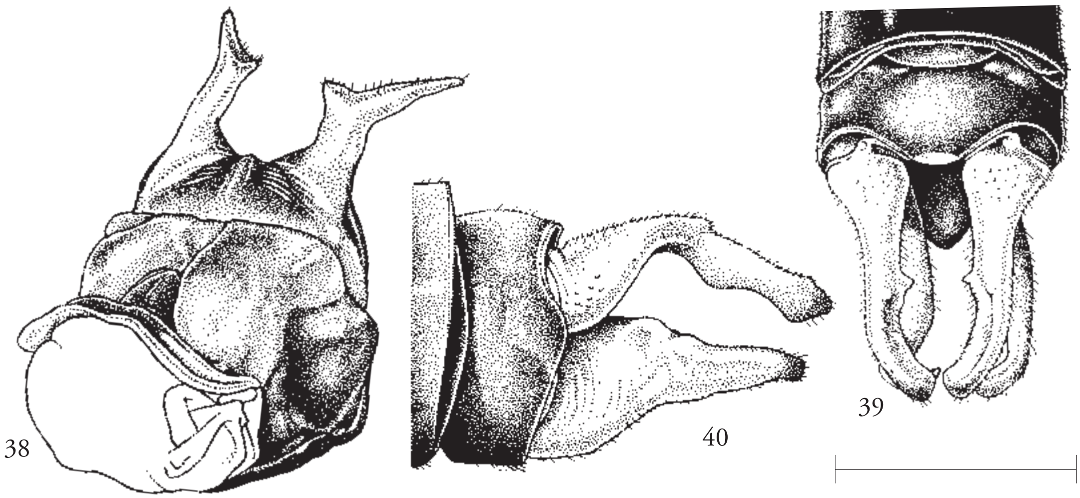
Drepanosticta sp. n. 4 (cf. *lymetta*). – Hämäläinen & Müller 1997: 257, 276 [Siquijor, 7 males in collection].

Type material. – Holotype male [JvT 18860] in RMNH: ‘Philippines. Siquijor Id / Barrio Bandilaan / April 18.-23. 1993. / Th. Borromeo legit / Coll. Roland A. Müller’. – Paratypes. Same data as holotype, 6 males (in RMNH).

Diagnosis. – Medium-sized species with brown pronotum; pronotum with a paired and forked process; distinguishable from other species in the *D. lymetta* group by the long inner branch of the forked process; the superior appendage with a subbasal, very sharp, medio-ventrad tooth, a second and more distal tooth as present in *D. lymetta* is only discernable as a knob-like structure; confined to Siquijor Id. See also remarks under *D. lymetta*.

Male [holotype, JvT 18860]. – Head. Labium brown; labrum yellowish white, but anterior two-fifths pale brown; mandibles yellowish white, with anterior one-sixth brown; anteclypeus bluish white, rest of head bronze-black, especially on dorsum of head with coppery shine; transverse occipital carina well developed with sharp lateral extremities; antennae yellowish, flagellum brown (right flagellum missing in holotype).

Thorax. Pronotum (Fig. 35) with anterior lobe pale brown, darker in centre, well-developed, with anterior margin erect; middle lobe flat, yellowish brown; lateral lobe brown as lower part of synthorax; posterior lobe brown, narrow, hind margin with paired process approximately twice as long as median length of posterior lobe, more or less erect or lying flat over synthorax, ending in a bifurcation of which inner branch is distinctly longer than outer brach (virtually symmetrical bifurcation in one specimen). Synthorax castaneous. Legs dirty yellow, only somewhat darker at joints of femora (right fore leg missing in holotype). Wings hyaline, Px 14 in fore wing (left wing with two additional cross-veins), Px 14 in hind wing; origin of R4+5 at subnodus, IR3 halfway first cell distal to that level; Arculus arising distinctly distal to Ax2; quadrangle of fore wing somewhat widening posteriorly; anal veins shortly stalked, slightly asymmetrical; pterostigma castaneous, c. 2.4 times as



Figures 38-40. *Drepanosticta hermes* sp. n., male [JvT 18824, Mindanao, Davao Oriental, Boston, Mt Agtuuganon, 1020 m, 29.v-7.vi.1996]. – 38, pronotum, oblique view. – 39, anal appendages, dorsal view. – 40, idem, left lateral view. Scale bar 1 mm.

long as high; proximally obtusely angulate, distal side somewhat convex; cells between Costa and R1 distal to pterostigma rather frequently divided.

Abdomen. Brown, but with paler yellowish white markings as follows: ventro-anterior part of segment 2, anterior one-fifth of segment 3, anterior one-fourth of segment 4-6 (segment 6 somewhat darker yellow), segment 10 pale brown. Appendages (Figs 36-37) yellowish brown; superiors in dorsal view stout in basal half, on innerside ending in sharp tooth directed ventro-axiad; distal half of superiors scope-like, ending subacute; inferiors in ventral view with stout base, distal half straight, cylindrical, the tip strongly constricted and outer margin curved 80° inward.

Measurements. Hind wing 21.5 (21-22) mm, abdomen including appendages 33 (31-33) mm; one theratological specimen with abdomen of 24 mm.

Female. – Unknown.

Etymology. – *Furcatus* (Latin), forked; for the shape of the processes of the hind margin of the posterior lobe of the pronotum. An adjective.

Distribution (Fig. 102). – Philippines Islands (West Visayan region): Siquijor Island.

Drepanosticta hermes van Tol, **sp. n.**

(Figs 38-40, 102)

Drepanosticta sp. n. 16. – Hämäläinen & Müller 1997: 258, 277 (distribution Mindanao, Davao Oriental).

Type material. – Holotype male [JvT 18850] in RMNH: 'Philippines, Mindanao Id / Davao Oriental, Boston / Mt Agtuuganon, Camp 55 / May 29. - Juni 7, 1996, 1020 m / Müller/Buenafe/Gorostiza leg. / Coll. Roland A. Müller'. – Paratypes (43 specimens, all in RMNH): same data als holotype, 42 males ; same, Boston, Caatijan, 500-550 m, 28.v.1996 (Müller, Buenafe & Gorostiza), 1 male.

Diagnosis. – Relatively small, dark, castaneous brown species, closely allied to *D. lymetta* Cowley; the processes of the hind lobe of the prothorax long, bifurcate at top with a short inner branch and a longer outer branch; the very slender superior appendages (dorsal view) diagnostic; base of superiors in lateral view distinctly directed dorsad; ventral teeth of superiors with basalmost one approximately in middle of appendage, the other tooth poorly developed. See also under *D. lymetta* Cowley.

Male [JvT 18819]. – Head. Labium brown; labrum, mandibles and anteclypeus creamish white; anterior one-third of labrum pale brown, mandibles with

narrow anterior dark line; rest of head brownish black; parorbital carina and postocular carina well developed with distinct, acutely angulate lateral extremities; antennae dirty yellow, flagellum brown.
Thorax. Pronotum (Fig. 38) laterally and medially brownish black; rest dirty yellow to pale brown; anterior lobe short, with anterior margin distinctly erect; posterior lobe with a paired process on hind margin, process as long as middle lobe, lying more or less flat over synthorax; bifurcate at top, with a short tooth directed mediad, and a long tooth directed abaxiad, this tooth approximately as long as base of fork. Synthorax castaneous; some parts slightly paler, but no significant creamish white stripes; legs dark yellow. Wings hyaline, venation brown; Px 17 in fore wing and Px 15 in hind wing; R4+5 arising from subnodus; IR3 halfway first cell distal to that level; Arculus just distal to Ax2; quadrangle widening distally in forewing; anal veins subequal, stalked; pterostigma width 1.5 times the height; several cells between Costa and R1 beyond pterostigma divided.
Abdomen. Brown, but anterior one-sixth to one-fifth of segment 3-7 somewhat paler; appendages (Figs 39-40) dark yellow; superior appendages slender, base short, distal part forcipate with very short dorsal tooth, and short and sharp ventral tooth in middle and a broader process distal to the sharp tooth, top of appendage blunt; inferiors with slender base, distal half of inferior subcylindrical, somewhat bent outward, the top slender and directed inward, the tip curved dorsad.
Measurements. Hind wing 21.5 (21-23) mm, abdomen including anal appendages 34 (33-34) mm.

Female. – Unknown (but see below under remarks).

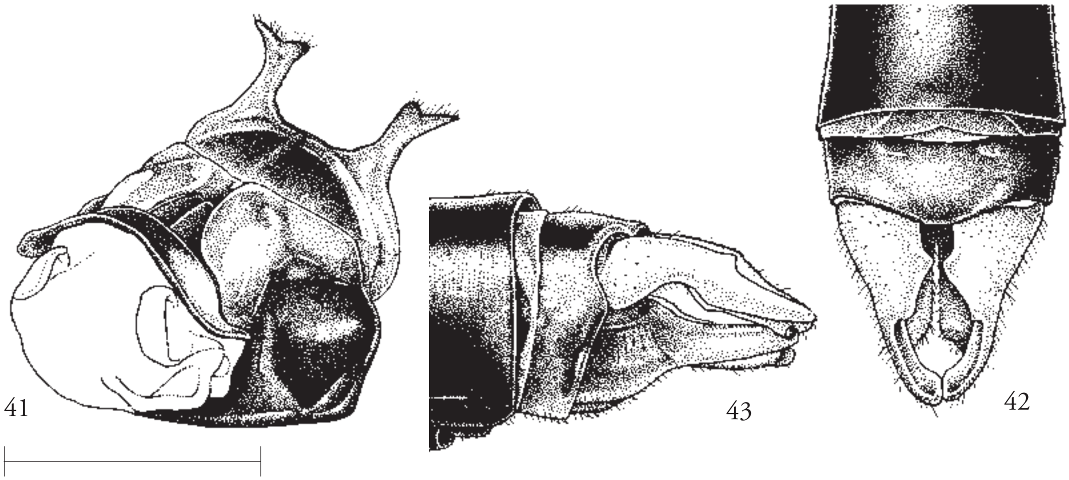
Remark. – The female of this species is almost certainly among the specimens collected by Müller and collaborators in Davao Oriental. However, *Drepanosticta taurus,* a species with similar coloration as the present species, is syntopic. Females (8 specimens) collected on Mt Agtuuganon with coloration as *D. hermes* sp. n. or *D. taurus* Needham & Gyger have a very different hind margin of the hind lobe of the pronotum. Consequently, the status of these females will remain uncertain until pairs are found in copula. Hämäläinen & Müller (1997: 277) mention 45 males. One specimen (JvT 18825) was identified as the present species, but is in my view not conspecific, and concerns *Drepanosticta flavomaculata* sp. n.
Etymology. – *Hermes* (Greek), herald of the Olympian gods, usually depicted with a winged hat; for the structure of the paired processes of the posterior lobe of the pronotum. A noun in apposition.
Distribution (Fig. 102). – Philippine Islands: Mindanao (Davao Oriental).

Drepanosticta lymetta Cowley
(Figs 41-43, 102)

Drepanosticta lymetta Cowley, 1936: 161-163, figs 13-14 (original description, holotype male, Philippine Islands, Surigao, Mindanao, C. F. Baker [BMNH] [examined]). – Needham & Gyger 1939: 263-264, figs 197-198, 200, 202, 205, 310 (description, material from type locality); Hämäläinen & Müller 1997: 257 (distribution Mindanao subregion: Mindanao).

Material examined (all Philippines, in coll. RMNH, except given otherwise). – **Mindanao**. Surigao, 21.v.1915 (G. Boettcher) 1 female (ex SMFD); Surigao, 12.xi.1915 (G. Boettcher) 1 female in SMFD; Surigao, 23.viii.1916 (G. Boettcher) 1 male (ex SMFD) and 2 males 2 females in SMFD; Surigao, before 1920 (C.F. Baker) 1 male (in BMNH) [holotype of *Drepanosticta lymetta* Cowley]; Agusan [del Sur], San Fran[cisco] (Quate) 1 female; Davao del Norte, Maco, Mainit, Mait Creek, 500-700 m, 14-17.ix.1995 (A. Buenafe) 6 males; Davao del Norte, Maco, Mainit, Masara Mine, 500-700 m, 27-28.xi.1995 (A. Buenafe) 1 male.

Diagnosis. – A rather inconspicuous brown species, the males characterized (but see below under remarks) by a pair of shortly branched processes on the hind margin of the hind lobe of the pronotum, and rather straight superior anal appendages with halfway a dorsal tooth and two medially directed teeth at innerside, of which the basalmost one is sharp. This species is closely related to *D. hermes* sp. n. from northern Davao Oriental (Boston region), which differs by the much longer outer branch of the pronotal process, a more slender base of the superior appendage (dorsal view),



Figures 41-43. *Drepanosticta lymetta* Cowley, male [JvT 18613, Mindanao, Davao del Norte, Maco, Mainit, 500-700 m, 14-17. ix.1995]. – 41, pronotum, oblique view. – 42, anal appendages, dorsal view. – 43, idem, left lateral view. Scale bar 1 mm.

and by the inferior appendages, which are curved rather than straight in the distal half. It is also close to *D. furcata* sp. n. from Siquijor, which differs by a significantly longer inner branch of the pronotal process, also by the absence of the dorsal tooth on the superior appendages, and a poorly developed second ventral tooth on superior appendage.

Male. – Head. Labrum, anteclypeus, mandibles ivory white; anterior one-fourth of labrum brown; rest of head bronze-black; transverse occipital carina distinct, with distinctly angulate lateral extremities. Antenna with scapus brown; pedicellus and flagellum yellowish brown.
Thorax. Pronotum (Fig. 41) predominantly brown, but sides of anterior and median lobe white; central part of posterior lobe and lateral lobes brownish black; anterior, median and lateral lobes simple; posterior lobe with lateral portions narrow, with elongate stout process on posterior border, process ending in a terminal tooth at outer surface, approximately as long as width of process; synthorax bronze-black, a paler marking over humeral suture; legs yellow. Wings hyaline, venation middle brown, but Costa somewhat darker; Px 15 in fore wing, 13 in hind wing; R4+5 arising from subnodus, IR3 arising half a cell distal to that level, Arculus distinctly distal to Ax2, anal veins shortly stalked, distinctly asymmetrical; pterostigma c. 1.8 times as wide as high, rhomboid; cells between Costa and R1 posterior to pterostigma undivided.
Abdomen. Brown, anterior one-tenth of segment 3-6 yellow, dorsally bluish white; appendages (Figs 42-43) yellow; superiors in dorsal view very stout, converging into a short, blunt dorsal tooth at circa three-fifths from base, distal two-fifths laterally compressed, semicircular; at base of club-shaped top a pair of characteristic ventral teeth, the basal one sharp; inferiors in ventral view basal one-third rather stout, distal two-thirds straight, subterminally constricted at innerside, the tip curved nearly 90° mediad, hardly directed dorsad.
Measurements. Abdomen incl. appendages 30-33 mm, hind wing 20-21 mm.

Female. – As the male, but hind margin of posterior lobe of pronotum without projections.
Measurements. Abdomen 27 mm, hind wing 19 mm.

Status. – The holotype of *Drepanostigma lymetta* Cowley is incomplete (abdominal segments 6-10 missing), while the only paratype, also a male, lacks head and abdominal segments 3-10. The incomplete status of both types was already so when this species was described, so that the structure of the abdominal segments and the anal appendages has remained unknown. Material available for comparison was collected in Surigao by G. Boettcher in 1915/1916, but unfortunately, *Drepanosticta* material from this area is not well represented in the R.A. Müller collection. The structure of the pronotum of a male collected by Boettcher, now in the RMNH collection [JvT 19767], is rather close to the holotype (see also Cowley 1936, Fig. 13) and was identified as *D. lymetta* by Lieftinck. The structure of the anal appendages of the specimens from Davao del Norte: Maco agrees rather well with JvT 19767, but the structure of the rather characteristic processes of the hind lobe of the pronotum is distinctly different. The divided processes are better developed axiad than abaxiad in the type, but in the specimens from Maco (e.g. JvT 18613) the outer branch is distinctly larger than the inner branch. Also, the appendages of JvT 19767 are brown and concolorous with the abdomen, while the appendages of all Davao specimens are dirty white, and clearly distinct from the abdomen, including segments 9-10. The differences may prove sufficient to distinguish more than one taxon in due time. For the present, I have refrained from naming these forms, awaiting further material from Surigao, and also from the region between San Francisco (Agusan) and Maco.

Distribution (Fig. 102). – Philippine Islands: Mindanao region (Eastern Mindanao).

Drepanosticta taurus Needham & Gyger

(Figs 44-46, 102)

Drepanosticta taurus Needham & Gyger, 1941: 145-146, figs 1, 2, 5-7, 10 (original description, holotype male, type locality Mindanao, Davao Province, La Lun river (in MCZC).

Drepanosticta taurus Needham & Gyger. – Hämäläinen & Müller 1997: 258 [distribution Mindanao subregion: Mindanao).

Drepanosticta sp. n. 17. – Hämäläinen & Müller 1997: 258, 277 [distribution Mindanao].

Material examined. – Philippines, Mindanao Id., Davao Oriental, Boston, Mt. Agtuuganon, Camp 55, 1020 m, 29.v. - 7.vi.1996, Muller, Buenafe & Gorostiza, 42 males 1 female.

Diagnosis. – Medium-sized dark species; long and erect posterior projections of posterior lobe pronotum in the male diagnostic; superior appendages of male in dorsal view with stout base, the distal half slender.

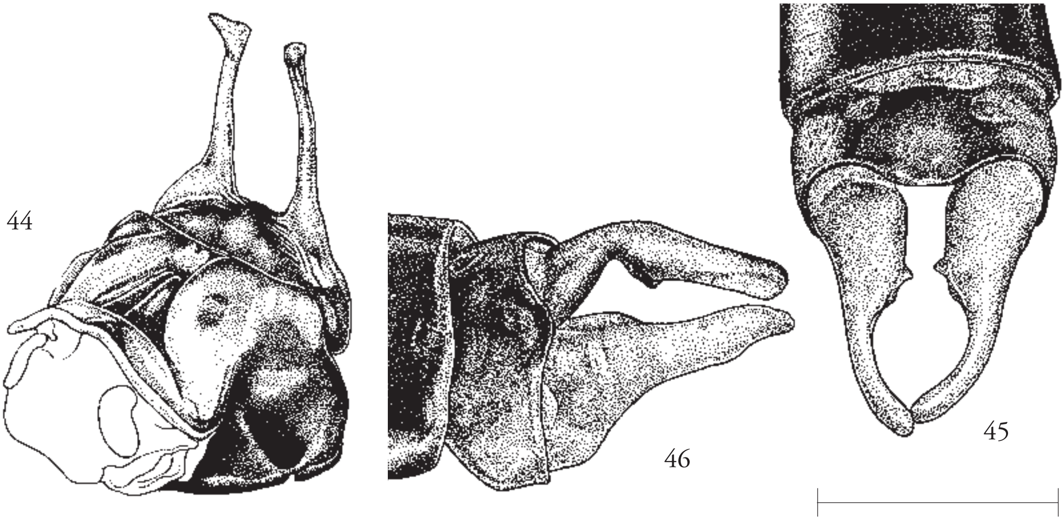
Male. – Head. Labrum, mandibles and anteclypeus white or bluish white, anterior fourth of labrum with brown line; rest of head bronze-black, frons and vertex coriaceous; antenna with scapus brownish black, pedicellus dirty yellow, flagellum brown; transverse occipital carina distinct, with sharp triangular extremities.

Thorax. Pronotum (Fig. 44) with anterior and median lobe, and lateral portions of posterior lobe brown, rest brownish black. Anterior lobe large, erect at 45º; lateral parts of median lobe somewhat protuberant; posterior lobe short, with lateral portions with very sharp and long processes, directed dorsad, length of process of same length as median lobe of pronotum, both processes running more or less parellel. Synthorax castaneous, dorsally bronze-black; legs yellow. Wings hyaline, venation brown; Px 17 in fore wing, Px 15 in hind wing; R4+5 at subnodus, IR3 approximately halfway first cell distal to that level; Arculus distal to Ax2; quadrangle fore wing distinctly widening; anal veins subequal, unstalked; pterostigma brown, with narrow pale margin against veins, oblong, c. 1.7 times as wide as high, the proximal side acutely angulate.

Abdomen. Segments 1-6 brown, segments 7-10 brownish black, anterior portions of segments indistinctly paler; appendages (Figs 45-46) dark yellow, base of superiors dark grey, somewhat conical, distal half semi-circular, bent inwards, tip sub-squarish; at base of basal portion three teeth as follows: one dorsal directed caudad, a larger, sharp tooth directed inward just basal to first, and a broad and inconspicuous tooth just distal to first; inferiors with stout base, distal part with base straight, just directed outwards, the top bent 90º inward, innerside emarginate, tip not directed dorsad.

Measurements. Hind wing 21-24 mm, abdomen including appendages 33-36 mm.

Female. – Females of this species and *D. hermes* sp. n. are indistinguishable.



Figures 44-46. *Drepanosticta taurus* Needham & Gyger, male [JvT 18765, Mindanao, Davao Oriental, Boston, Mt. Agtuuganon, 1020 m, 29.v-7.vi.1996]. – 44, pronotum, oblique view. – 45, anal appendages, dorsal view. – 46, idem, left lateral view. Scale bar 1mm.

Status. – The specimens here assigned to *D. taurus* Needham & Gyger, do not fully agree with the original description, and were identified as a new species by Hämäläinen & Müller (1997). Although the present specimens have the same characteristic projections of the posterior lobe of the pronotum, the size of the specimens is very different from the type. Needham & Gyger explicitly mention the very elongate abdomen, measuring 47 mm, and a hind wing 25 mm for the male. However, I presume that the size of the abdomen is a printing error for 37 mm, a size that would better fit the given measurements of wings, female abdomen, and the measurements of the specimens in the Müller collection. Unfortunately, I have not been able to study the type to confirm my supposition. According to Needham & Gyger, the type was deposited in MCZN. Dr. Philip D. Perkins of the Museum of Comparative Zoology informs me (e-mail 28 May 2004) that the type is not present in MCZN collection. On his suggestion, I also contacted Dr. James K. Liebherr at Cornell University, where Needham worked, who informed me that the type could not be traced in that collection as well. Awaiting the recovery of the type, and possible more material from the Davao region in Mindanao, I have decided to consider the present specimens representing *D. taurus*.

Distribution (Fig. 102). – Philippine Islands: Mindanao (Davao Oriental). The type locality of *D. taurus*, La Lun river, was not found in any atlas or gazetteer, and is not represented on the map.

Drepanosticta megametta group

Transverse occipital carina distinct, with acutely angulate lateral extremities; anterior lobe of pronotum erect, at least in *D. centrosaurus* sp. n. partly folded; posterior lobe of pronotum with a pair of processes on hind margin, very wide and broadly connected with the posterior margin of the posterior lobe; pterostigma distinctly wider than high; superior appendages slender without dorsal tooth, but a sharp tooth directed medially on innerside; inferior appendages slender and straight, the tip emarginate, curved 90° mediad. Based on the structure of the anal appendages, presumably the sister-group of the *D. lymetta* group.

Included species: *D. centrosaurus* sp. n. and *D. megametta* Cowley.

Distribution: Mindanao.

Drepanosticta centrosaurus van Tol, **sp. n.**

(Figs 47-49, 103)

Drepanosticta sp. n. (14). – Hämäläinen & Müller 1997: 258, 277 (distribution Mindanao, Surigao del Sur).

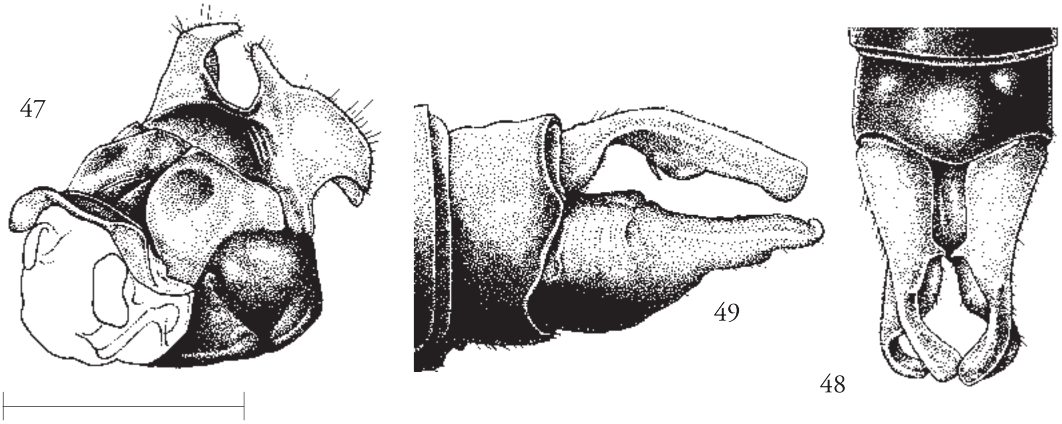
Type material. – Holotype male [JvT 18715] in RMNH: 'Philippines, Mindanao Id / Surigao del Sur, Tago / Meme River, 100-300 m / June 12.-18., 1996 / Buenafe A. / Gorostiza A. leg / Coll. Roland A. Müller'. – Paratypes (all Philippines, in RMNH, 98 males 19 females), **Mindanao**. Surigao del Sur: San Miguel, Suba River, 150-250 m, 13.iv.1995 (Müller, Buenafe & Gorostiza) 29 males 3 females; Tandag, Hitaub Creek, 500-600 m, 16-19.iv.1995 (Buenafe & Gorostiza) 26 males 2 females; Carmen, 2. Equipment Shop, km 9 and 11 Lanang Line, 500 and 600-650 m, 21-24.iv.1995 (Müller, Buenafe & Gorostiza) 1 male 2 females; Lingig, Mandus, 100 m, 27.v.1996 (Müller, Buenafe & Gorostiza) 3 males 1 female; same locality as holotype, 38 males 11 females; San Miguel, foot of Diuata Mountains, Castillo, Kagda-o Creek, 300-500m, 2-5.iv.1998 (Piamonte) 1 male.

Diagnosis. – Small and dark species, characterized by very broad processes of the posterior lobe of pronotum, the bases wider than the distance between the processes; superior appendages with a large laterally, but hardly ventrally directed tooth at base of distal, clasper-like part.

Male [JvT 18715]. – Head. Labrum, mandibles, anteclypeus ivory white, anterior one-third of labrum pale brown, rest of head bronze-black, frons and vertex coriaceous; transverse occipital carina distinct, lateral extremities apiculate; antenna with scapus and flagellum brown, pedicellus dirty yellow.

Thorax. Pronotum (Fig. 47) with central part of anterior, median and posterior lobe, and complete lateral lobe dark brown; lateral portions of anterior and median lobe bluish white, lateral portions of posterior lobe middle brown; anterior lobe large and erect; median and lateral lobes simple; posterior lobe with lateral portions large, each approximately as large as half of median lobe, base ca. one-third of hind margin of posterior lobe, distal half somewhat wider on innerside, and significantly broadened on outer surface. Synthorax concolorous castaneous, without bronze shine, dorsal part finely coriaceous. Legs yellow. Wings hyaline, venation brown; Px 15 in fore wing, Px 14 in hind wing; R4+5 arising distal to subnodus, IR3 in distal half of first cell distal to subnodus; quadrangle of fore wing slightly widening posteriorly; Arculus arising distal to Ax2; anal veins somewhat asymmetrical, sessile; pterostigma brown, with paler margin against veins, c. 1.6 times wider than high; one cell between Costa and R1 beyond pterostigma in left hind wing divided, remaining cells undivided (divided cells also rare in paratypes).

Abdomen. Castaneous brown, base of segments 3-6 dorsally with oblong ivory white spot. Appendages



Figures 47-49. *Drepanosticta centrosaurus* sp. n., male [JvT 18625, Mindanao, Surigao del Sur, Tandag, Hitaub Creek, 500-600 m, 16-19.iv.1995]. – 47, pronotum, oblique view. – 48, anal appendages, dorsal view. – 49, idem, left lateral view. Scale bar 1 mm.

(Figs 48-49) pale brown or yellow; superior appendages very slender, in dorsal view base more or less straight, a conspicuous tooth on innerside halfway of superiors (well visible in lateral view in the holotype, but inconspicuous in many other specimens), superiors in distal half bent semicircular, ending abruptly squarish; inferiors in ventral view with basal two-fifths stout, distal part narrow at base, then slightly widening, the distalmost part abruptly constricted, bent 60° inward, the tip acute.
Measurements. Hind wing 20 (19-21) mm, abdomen including appendages 31 (30-32) mm.

Female. – As the male, but posterior margin of posterior lobe of pronotum rather simple, with a paired, very short process, in shape more as a denticle with a group of setae, rather close to the middle of the lobe, hind margin laterally of processes emarginate, then rounded towards lateral corner.
Measurements. Abdomen 26-28 mm, hind wing 18-20 mm.

Etymology. – *Centrosaurus* (Latin), a genus of dinosaurs, for the similary of the 'collar'. A noun in apposition.
Distribution (Fig. 103). – Philippines: Mindanao (Surigao del Sur).

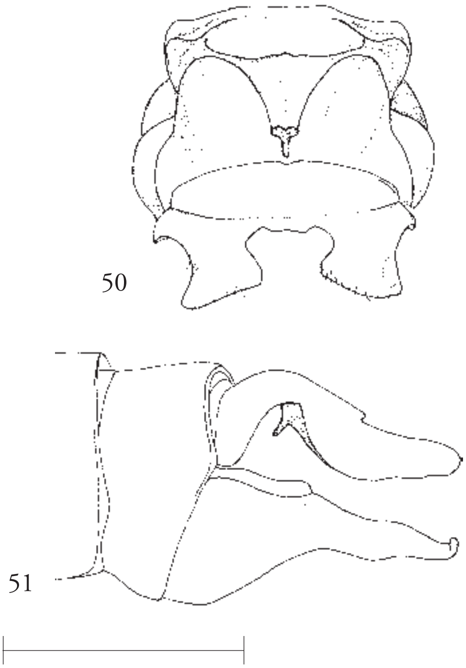
Drepanosticta megametta Cowley
(Figs 50-51, 103)

Drepanosticta megametta. – Cowley 1936: 163-167, figs 15-22 (original description, type locality Philippine Islands, Surigao, Mindanao (BMNH)).
Drepanosticta megametta Cowley. – Lieftinck, 1937: 72-74 (*D. ephippiata* from Celebes considered most closely to *D. megametta*); Needham & Gyger, 1939: 263, 264 (key, no new material); Hämäläinen & Müller 1997: 257 (distribution Mindanao subregion: Mindanao).

Material examined. – Mindanao, Surigao, 23.viii.1916 (G. Boettcher) 2 males (juv) in SMFD; Mindanao, Surigao (Baker) 1 male (holotype) in BMNH.

Diagnosis. – A medium-sized species; distinguishable from most other Philippine *Drepanosticta* by the wide posterior processes of the posterior lob of the pronotum; differs from *D. centrosaurus* sp. n. by the shape of the processes, which are subrectangular in *D. megametta* and distinctly laterally projected at the top in *D. centrosaurus*; anal appendages of males of both species very similar.

Male [based on description in Cowley 1936]. – Head. Labium pale brown, labrum and mandibles pale yellow with narrow anterior brown border; anteclypeus pale yellow; rest of head black, with small exterior brown spot against lateral ocelli; transverse occipital carina well developed, with acutely angulate lateral extremities. Antenna with scapus and pedicellus yellowish brown, flagellum darker apically.
Thorax. Pronotum (Fig. 50) brown, median lobe paler; anterior lobe erect, posterior lobe produced posteriorly as two caudally directed processes, extending over synthorax, slightly convex, apical corners rounded, only external corner slightly projecting; no specialised tufts of setae on processes. Synthorax dark brown, mesepisternum with black stripe against dorsal carina, mesepimeron paler dorsally and anteriorly, extending on to the dorso-posterior corner of mesepisternum; metepisternum with pale yellow ovoid dorso-anterior spot; about dorsal third of metepimeron pale yellow. Legs pale yellow. Wings hyaline, venation dark brown. Px 15 in fore wing, Px 13 in hind wing; R4+5 arising at subnodus, extending to beyond level of pterostigma; IR3 arising half a cell distal to subnodus; quadrilateral long, very slightly widened distally in fore wing, scarcely so in hind wing; anal veins forming a Y-shaped brace with very short stem; pterostigma brown, subquadrangular, surmounting one cell.
Abdomen brown; segments 1, 2, 8-10 without any pale markings, 3 to 7 with a complete basal yellow ring extending further apicad dorsally than laterally, occupying the basal 0.08 of segment 3, 0.10 of segment 4, 0.12 of segment 5, 0.13 of segment 6 and 0.24 of segment 7. Anal appendages (Fig. 51) brown, superior appendages about three times the length of segment 10, inferiors subequal to superiors; superiors in dorsal view basally broad with short mesal spine directed meso-ventrad at 0.22 of length, concave



Figures 50-51. *Drepanosticta megametta* Cowley, male [holotype]. – 50, pronotum, dorsal view. – 51, anal appendages, left lateral view. Scale bar 1 mm.

exteriorly, becoming narrower and concave interiorly, convex exteriorly, hollowed out mesally, apices turned meso-caudad; inferiors convex exteriorly, apices turned mesad, interiorly straight with a preapical mesal projection, thereafter strongly concave; in lateral view superiors directed dorso-caudad basally, then sharply caudad and slightly ventrad; inferiors almost straight, apices turned mesad and slightly dorsad; no specialised tufts of setae.

Female. – As the male, but the posterior projections of the posterior lobe of the pronotum shorter, subquadrangular, the top more rounded. See further Cowley (1936: 165-166).

Note. – This species is not represented in the R.A. Müller collection in RMNH.
Distribution (Fig. 103). – Philippine Islands: Mindanao (Surigao province).

Drepanosticta: other species

The following species here assigned to *Drepanosticta* do not share a unique character or character set with other species in the Philippines. Some of the species definitely have Bornean affinities, others apparently are sister to one of the species groups defined here. A more detailed phylogenetic analysis is needed to reveal their relationships. For the time, all these species are taken together in the rest-group. The species are treated in alphabetical order.
Included species: *D. aurita* sp. n. (Mindoro), *D. ceratophora* Lieftinck (Palawan, Balabac), *D. lestoides* (Brauer) (Samar, Panaon Id., Dinagat, Mindanao), *D. malleus* sp. n. (Mindanao), *D. mylitta* Cowley (Luzon, Samar, Leyte, Homonhon, Panaon), *D. myzouris* sp. n. (Luzon), *D. paruatia* sp. n. (Palawan), *D. pistor* sp. n. (Sibuyan, Negros, Panay, Luzon ?), *D. quadricornu* sp. n. (Busuanga, Palawan).

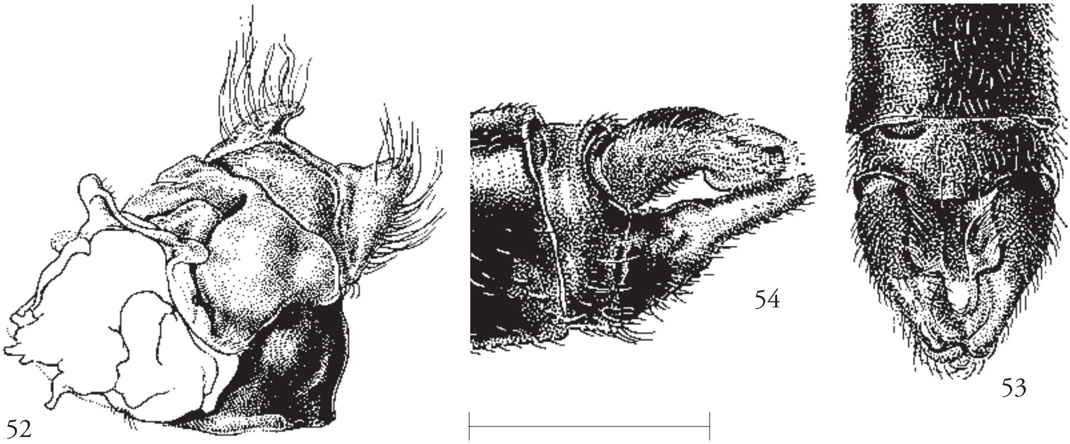
Drepanosticta aurita van Tol, **sp. n.**

(Figs 52-54, 107)

Drepanosticta sp. n. 12. – Hämäläinen & Müller 1997: 257-258, 277 (Mindoro).

Type material. – Holotype male [JvT 22190] in RMNH: 'Philippines, Mindoro Id / Mindoro Or. Prov., Calapan / Comonal, Mt Tarugin, um [= c.] 350 m / July 17./26. 1990 / Adrian Gorostiza legit / Coll. R.A. Müller'. – Paratypes (all in RMNH). **Mindoro**. As holotype, 14 males 3 females; Mt Halcon, 1000-1500 m, 2-20.v.1994 (N. Mohagan) 8 males 3 females.
Other material examined (all in RMNH). – **Lubang Island**. Mindoro Occidental, Looc, Mt. Gonting, Sitio Gonting, 300-500 m, 8-15.vii.1997 (C. Nazareno) 5 males 1 female.

Diagnosis. – Transverse occipital carina poorly developed, lateral extremities hardly discernable; processes on anterior lobe of pronotum indistinct in specimens from Mindoro, with a distinct paired anterior projection in specimens from Lubang Island; posterior lobe of pronotum with swollen lateral portions of posterior lobe with long and sturdy setae; synthorax brownish black, without pale markings;



Figures 52-54. *Drepanosticta aurita* sp. n., male [JvT 18749, Lubang Island, Mt. Gonting, Sitio Gonting, 300-500 m, 8-15. vii.1997; not a paratype]. – 52, pronotum, oblique view. – 53, anal appendages, dorsal view. – 54, idem, left lateral view. Scale bar 1 mm.

pterostigma somewhat wider than high; superior appendages without teeth or protuberances; inferior appendages in ventral view straight, only the very tip curved axiad (not dorsad).

Male [JvT 22190, holotype]. – Head. Labrum and anteclypeus bluish white, anterior border of labrum brown; mandibles pale brown, except for blue innerbasal corner, rest of head bronze-black; transverse occipital carina narrow with inconspicuous lateral extremities; antenna with scapus and flagellum brown, pedicellus dirty yellow.
Thorax. Pronotum (cf. Fig. 52) with central part of anterior, median and posterior lobe, and complete lateral lobe, brownish black; rest brown; anterior lobe simple, with anterior margin erect, but without conspicuous projections (for specimens from Lubang, see under variation); median and lateral lobes simple; posterior lobe with lateral third of both sides erect at c. 60°, stout, subrectangular, somewhat wider than high, hind margin densely covered with long and sturdy setae; synthorax fully bronze-black; legs yellowish. Wings hyaline, venation brown, pale brown in basal half; Px 16 in fore wing, Px 15 in hind wing; R4+5 distal to subnodus in forewing, at subnodus in hind wing; IR3 distinctly in distal half of first cell distal to subnodus in fore wing, a little beyond the middle in hind wing; Arculus distinctly distal to Ax2; anal veins more or less symmetrical, shortly stalked; pterostigma brown, subquadrangular, width 1.4 times the height; proximal corner angulate, the distal side somewhat convex.
Abdomen. – Brownish black, basal one-eighth of segment 3, one-sixth of segments 4-6, one-third of segment 7 yellowish; a basal spot at ventro-anterior margin of segment 8; abdominal segments 8-9 distinctly broader than other segments, brownish black. Appendages (cf. Figs 53-54) dirty yellow, base of inferiors greyish brown; superiors in dorsal view, the top dorso-ventrally flattened, the scoop-like caudal half subrectangular; inferiors with stout base, distal half slender, top rounded, the tip acute, hollow.
Measurements. Hind wing 20 (20-22) mm, abdomen including appendages 33 (33-35) mm.

Female. – As the male, but the posterior processes of the posterior lobe of the pronotum somewhat shorter than in the male, but also with long setae; last abdominal segments brownish black, with anal appendages yellowish white, valves long, surpassing the cerci.
Measurements. Hind wing 21-23 mm, abdomen 32-35 mm.

Variation. – Pterostigma is many males more squarish than holotype, width c. 1.3 times the height. Males from Lubang Island with anterior lobe of pronotum (Fig. 52) medially with a broad, unpaired process, approximately as high as the median length of anterior lobe, the upper margin of the process itself bifid, the corners laterally projected, acutely angulate. Females with the projections on anterior lobe of pronotum less distinct.

Although specimens from Mindoro and Lubang are distinct by the shape of the anterior lobe of the pronotum, the Lubang form has not been named separately, since no other structural characters seem to distinguish both populations.

Etymology. – *Auritus* (Latin), eared; for the shape of the processes of the posterior lobe of the pronotum. An adjective.

Distribution (Fig. 107). – Philippine Islands: Mindoro, Lubang Island.

Drepanosticta ceratophora Lieftinck

(Figs 55-57, 107)

Drepanosticta ceratophora Lieftinck, 1974: 117-120, figs 3-5 (original description, holotype male Palawan, Mantalingajan, Pinigisan, 600 m (in ZMUC)). – Hämäläinen & Müller 1997: 257 (distribution Palawan).

Material examined (all Philippine Islands, in RMNH). – **Palawan**. Mantalingajan, Pinigisan, 600 m, 1.ix.1961, Noona Dan Exp. 61-62, 1 female (incomplete, paratype) (ex ZMUC); Quezon, Lamakan, Magmuni Stream, 27.v. - 1.vi.1991 (Borromeo & Buenafe) 6 males 2 females; idem, Magmuni Stream, 1000 ft, 16-22.v.1992 (Borromeo T) 8 males 2 females; idem, Quezon, Malatgao, Bugon, ii.1994 (E. Vinciguerra & E. Horn) 1 female. – **Balabac**, Palawan Prov., Brgy. Dalahuan, 5-30 m, 8-14.ii.1997 (A. Buenafe) 7 males 1 female.

Diagnosis. – Small species. Transverse occipital carina and lateral extremities indistinct; anterior lobe of pronotum simple without projections; posterior lobe with a single median spine, diagnostic within the Philippine *Drepanosticta* species; synthorax castaneous; pterostigma slightly wider than high; superior appendages long, slender and straight; inferior appendages also slender, the distal half hooked laterad, the tip curved medio-dorsad, with a subterminal medially directed sharp tooth.

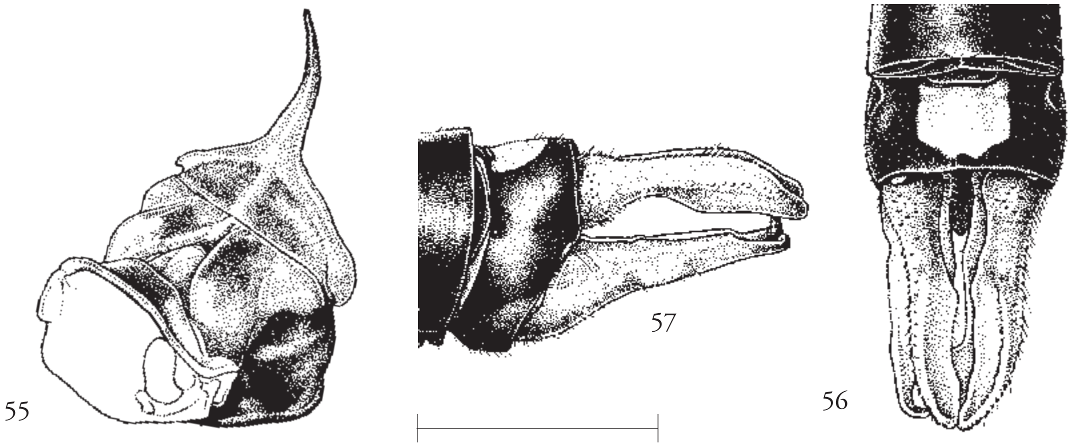
Male. – Head. Labrum and anteclypeus ivory white, anterior border of labrum brown, mandibles greyish brown, rest of head bronze-black, narrow transverse occipital carina with indistinct lateral extremities; antenna with scapus and pedicellus dirty white, flagellum pale brown.

Thorax. Pronotum (Fig. 55) dirty yellow, with lateral portion of median lobe, median portion of posterior lobe, and lateral lobes brownish black; anterior lobe large, not distinctly erect, posterior lobe with median portion diagnostic with long (unpaired) process, smoothly curved dorsad, at least as long as median length of rest of pronotum, but with much variation between specimens; lateral portion of posterior lobe simple; synthorax castaneous, lower parts brownish black; legs yellow. Wings hyaline, venation brown; Px 14-15 in fore wing, Px 13-14 in hind wing; R4+5 arising at subnodus, IR3 arising half a cell distal to that level; Arculus arising just distal to Ax2, anal veins stalked in most specimens; pterostigma subquadrangular, proximal side 80° angulate, distal side slightly more convex; cells distal to pterostigma between Costa and R1 undivided.

Abdomen. Segment 1 yellow, segment 2 brown, posteriorly somewhat paler, segments 3-6 brown, each segment with anterior and posterior one-fifth yellow, segment 7 brown with anterior third yellow, segments 8-10 brownish black, dorsum of segment 10 with irregular oval, blue marking. Appendages (Figs 56-57) yellow, slender; superiors with base far apart and gradually tapering, distal three-fifths laterally compressed, somewhat hollow; inferiors stout at base, distal half slender, more or less straight, the tip curved inward; subterminally a toothlike process on innerside, directed 90° inward.

Measurements. Hind wing 17-18 mm, abdomen including anal appendages 28-30 mm.

Female. – Coloration very similar to the male; posterior lobe of pronotum rounded without any indication of median posterior process; last abdominal segments



Figures 55-57. *Drepanosticta ceratophora* sp. n., male [JvT 20169, Balabac, Brgy Dalahuan, 5-30 m, 8-14.ii.1997]. – 55, pronotum, oblique view. – 56, anal appendages, dorsal view. – 57, idem, left lateral view. Scale bar 1 mm.

stoutly built, castaneous, but segment 10 and cerci dirty white.

Measurements. Hind wing 17-18 mm; abdomen 25-26 mm.

Affinities. – Although there is no other Philippine species of *Drepanosticta* known with an unpaired erect posterior process of the pronotum, this species resembles the Bornean *Drepanosticta monoceros* Lieftinck, only known from one male and one female specimen. The latter species, however, is very small, has distinctly different coloration, while not only the male, but also the female is provided with a conspicuous median process on the posterior lobe of the pronotum. Lieftinck considered *D. monoceros* a close relative of *D. crenitis* Lieftinck.

Distribution (Fig. 107). – Philippine Islands: Palawan, Balabac.

Drepanosticta lestoides (Brauer)

(Figs 58-60, 104)

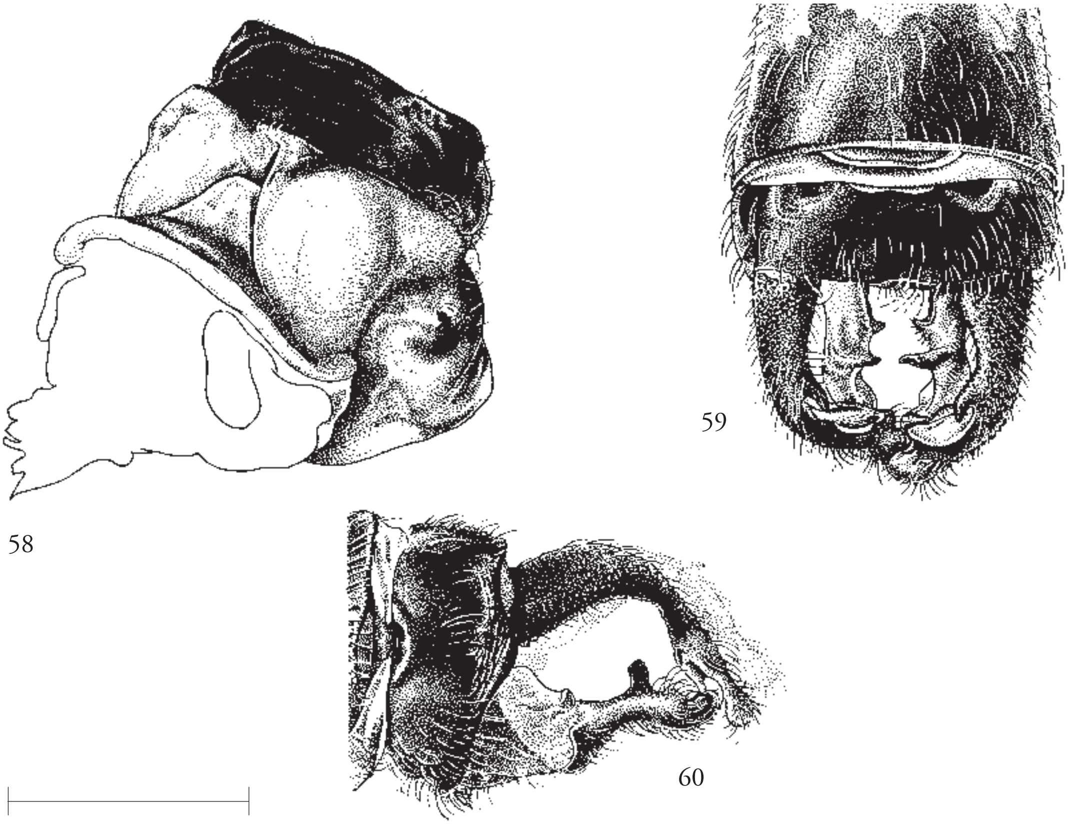
Platysticta lestoides Brauer, 1868: 552-553 (original description, type male, type locality Mindanao [in IRSN, not examined]). – Selys 1882: 30 (no new records, dates provided).

Platysticta (*Platysticta*) *lestoides*. – Selys 1886: 154-155 (description).

Drepanosticta lestoides Brauer. – Needham & Gyger 1939: 263, 264 (key, no new material); Lieftinck 1961: 133-135, fig. 47 (redescription, additional male from Surigao); Hämäläinen & Müller 1997: 257 (distribution East Visayan region: Panaon, and Mindanao subregion: Mindanao, Dinagat).

Material examined. – (All Philippine Islands, and in RMNH; arranged per island, from north to south). – **Samar**, Samar Prov., Hinubangan [=Hinabangan], Arizona, 100-280 m, 29.iii.-6.iv.1997 (R.A. Müller) 1 female, idem, San Isidro, San Isidro river, 90-200 m, 31.iii.-5.iv.1997 (R.A. Müller) 1 female. – **Panaon Id**, San Francisco (various places), viii.1988 (W. Catal) 3 males 2 females. – **Dinagat** Id., Surigao del Norte, Loreto, Mt Canbinlio, Canbinlio river, 4.vi.1988 (A. Buenafe) 1 male. – **Mindanao**, Surigao, 30.x.1915 (G. Boettcher) 1 male; South Cotabato, Mt. Matutum, 500-700 m, 16-19.ix.1993 (Th. Borromeo) 1 male; Lanao del Norte, Iligan, Tinago Falls. 8°09’33”N 124°11’11”E. 160 m, 25.iii.2004 (V. Kalkman & J. van Tol) 3 males; Davao Oriental, Boston, Mt Agtuuganon, 1020 m, Camp 55, 29.v.-7.vi.1996 (Müller, Buenafe & Gorostiza) 2 males 1 female; Mt Gantongan, Gantongan river, x.1991 (A. Buenafe) 1 male; Surigao del Sur, Tabon, Tabon Falls, 100-200 m, 26.v., 8.vi.1996 (Gorostiza & Buenafe) 1 male.

Diagnosis. – Large species with colourful thorax, pronotum with dirty white anterior, median and laterial lobes, and brownish black hind lobe, synthorax with wide yellowish white stripes over metepisternum and metepimeron. Only other Philippine species of



Figures 58-60. *Drepanosticta lestoides* (Brauer), male [JvT 18620, Mindanao, Davao Oriental, Boston, Mt Agtuuganon, 1020 m, 29.v-7.vi.1996]. – 58, pronotum, oblique view. – 59, anal appendages, dorsal view. – 60, idem, left lateral view. Scale bar 1 mm.

Drepanosticta with similar coloration are *D. moorei* Van Tol & Müller and *D. luzonica* sp. n. from Luzon; appendages of both species, however, are distinctly different, especially long tubercle directed mediad halfway on inferior appendage of *D. lestoides* diagnostic (Figs 59-60).

Male. – Head. Labrum and anteclypeus bluish white, but anterior one-sixth of labrum black, mandibles black except for bluish white inner basal corner; rest of head bronze-black and very shining, microsculpture only partly, very superficial and without conspicuous longitudinal striae between eyes; hind margin of head without transverse occipital carina, but parorbital carina present; antenna with scapus brownish black, pedicellus and flagellum brown.

Thorax. Pronotum (Fig. 58) with anterior, median and anterior portion of lateral lobe pale yellow, posterior part of lateral lobe and most of posterior lobe dark brown, lateral portion of latter slightly paler; anterior, median and lateral lobes simple; posterior lobe short, flat, only lateral corners at hind margin with triangular erect structure. Synthorax brownish black, but with conspicuous bluish yellow transversal markings on metepisternum against mesepimeron and lower half of metepimeron, apically continuing on lower hind part of metakatepisternum. Legs yellowish, femora at joints greyish brown. Wings hyaline, venation brown, but Costa brownish black in basal half and other main veins pale brown in basal half; venation rather open; R4+5 arising at or just distal to subnodus, IR3 arising just distal to that level; Arculus arising just distal to Ax2; quadrangle only slightly widening in fore and

hind wing; anal veins asymmetrical and almost sessile; pterostigma brown with broad pale lines against veins, subquadrangular, width c. 1.5 times the height, proximal lower corner acutely angulate.
Abdomen. Segments 1-7 pale brown, segments 1-2 ventrally yellowish, rest abdomen brownish black, but basal half of segment 9 with a paired irregular squarish blue marking. Appendages (Figs 59-60) with superiors semicircular, the tip distinctly wider, approximately halfway a dorsal tooth directed inward, its length approximately as diameter of appendage; inferiors straight, the tips sharply bent inward and touching, subbasally at ventral surface an inward directed triangular process, at dorsal surface a stout and long tubercle, directed inward and touching opposite tubercle.
Measurements. Hind wing 25-27 mm; abdomen including anal appendages 44-46 mm.

Female. – Generally similar in coloration to the male; structure of pronotum as male; abdominal segments with segment 1 yellowish white, dorsally a brown annule against hind margin connected with a paired brown longitudinal line; segments 2-7 brown, the first segments paler than the last, segment 2 with a narrow longitudinal line over middle of segment and a broad yellow stripe against sternite; segments 8-10 brownish black, segment 8 with a semi-circular spot against sternite; valvifer brownish black, valve pale, dirty yellow, reaching distinctly beyond cerci.
Measurements. Hind wing 25-27 mm, abdomen 37-40 mm.

Affinities. – Not closely related to any other Philippine *Drepanosticta* species. Within the Philippines, the characteristic structure of the male appendages is unique to the present species. *D. lestoides* (Brauer) seems to have closer affinities to species from Borneo, e.g. *D. actaeon* Laidlaw, or the mainland of Southeast Asia, e.g. *D. quadrata* (Selys).
Distribution (Fig. 104). – Samar, Panaon, Dinagat and Mindanao. A rather widespread but uncommon species where found.

Drepanosticta malleus van Tol, **sp. n.**

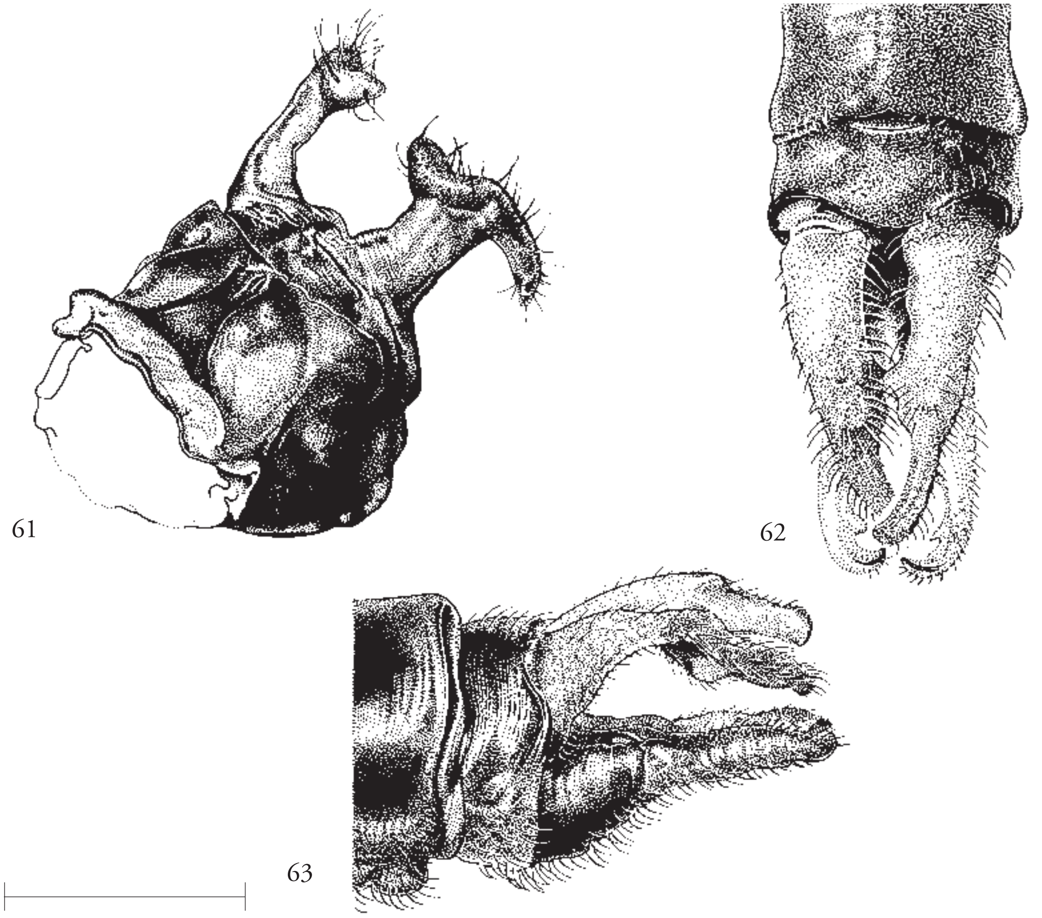
(Figs 61-63, 107)

Drepanosticta sp. n. 15. – Hämäläinen & Müller 1997: 258, 277 (Mindanao).

Type material. – Holotype male [JvT 18794] in RMNH: 'Philippines, Mindanao Id / Davao Oriental, Cateel, Aliwagwag Falls, 200-300 m / April 10, 1995 / Buenafe / Gorostiza legit / Coll. Roland A. Müller'. – Paratype: Same data [head broken to pieces], 1 male (in RMNH).

Diagnosis. – Male (female unknown) unmistakable by its huge posterior processes of posterior lobe of pronotum; appendix inferior with subterminal inward directed tooth. The last character shared with *D. myzouris* sp. n., of which the structure of posterior process is very different.

Male [JvT 18794, holotype]. – Head. Labrum and anteclypeus ivory white, labrum with anterior third light brown, mandibles greyish brown; rest of head brownish black, frons and vertex coriaceous; transverse occipital carina distinct, with acutely angulate triangular extremities; antenna with scapus brown, rest of antenna dirty yellow.
Thorax. Pronotum (Fig. 61) with anterior, median and middle part of posterior lobe middle brown, upperparts somewhat darker; median portion of posterior lobe, and lateral lobe brownish black; anterior lobe distinct and erect, middle and lateral lobes simple, posterior lobe with lateral portions distinctly developed, nearly as long as median line from anterior to posterior lobe, base broad and long, the top abruptly connected to a transversal structure, strong and relatively short on innerside, longer and more slender outside, transversal structure with sturdy setae. Synthorax castaneous. Legs yellow, femora against tibiae with a narrow brown ring. Wings hyaline, venation brown; Px 16 in fore wing, Px 15 in hindwing; R4+5 at subnodus, IR3 halfway first cell distal to that level; Arculus just distal to Ax2; quadrangle widening posteriorly in fore wing; anal veins distinctly stalked; pterostigma oblique, width c. 1.8 times the height, anterior and posterior side parallel-sided, distal side somewhat convex; several cells between Costa and R1 distal to pterostigma divided.

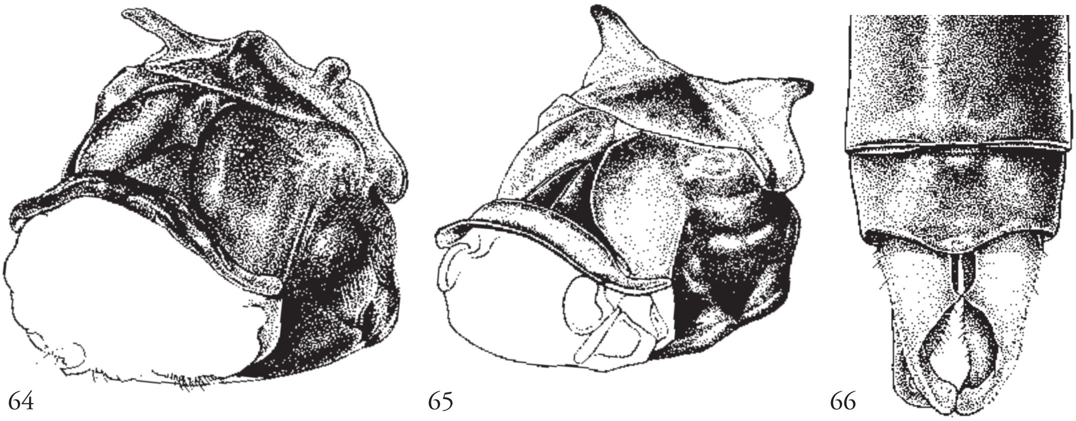


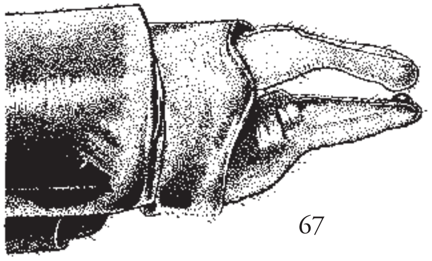
Figures 61-63. *Drepanosticta malleus* sp. n., male [JvT 18793, Mindanao, Davao Oriental, Cateel, Aliwagwag Falls, 200-300 m, 10.iv.1995]. – 61, pronotum, oblique view. – 62, anal appendages, dorsal view. – 63, idem, left lateral view. Scale bar 1 mm.

Abdomen. Castaneous, basal one-tenth of segments 3-5 paler; anal appendages (Figs 62-63) long and slender, superiors smoothly tapering from base to top, approximately halfway on innerside a sharp triangular tooth, a shorter and broader protuberance just distal to this tooth; tip of superiors rounded dorsally, acutely pointed ventrally; inferiors distinctly longer than superiors, base stout, distal half nearly straight, the top 80° bent inward, slender; subterminally a short triangular tooth directed axiad.
Measurements. Hind wing 21 mm, abdomen including appendages 32 (34) mm.

Female. – Unknown.

Affinities. – The inward directed, subterminal tooth of the inferior appendage is shared, among the Philippine taxa, with *D. myzouris* sp. n. Clustering into one group is unrealistic, since they do not share characters in the transverse occipital carina, the structure of the pronotum and the pterostigma. The subterminal tooth of the inferior appendages occurs widely in Platystictidae, including *Drepanosticta*, and has to be considered the plesiomorphic character state.
Etymology. – *Malleus* (Latin), hammer; for the structure of the paired process of the posterior lobe of the pronotum. A noun in apposition.
Distribution (Fig. 107). – Philippine Islands: Mindanao (Davao Oriental).





Figures 64-67. *Drepanosticta mylitta* Cowley, male. 64, pronotum, oblique view (‘typical *D. mylitta*’) [JvT 20141, Leyte, Mahaplag, Hilusig, Mt Balocaue, 700 m, 1.xii.1989]. – 65, pronotum, oblique view [JvT 21914]. – 66, anal appendages, dorsal view [JvT 21914]. – 67, idem, left lateral view [JvT 21914]. Scale bar 1 mm.

Drepanosticta mylitta Cowley

(Figs 64-67, 105)

Drepanosticta mylitta. – Cowley 1936: 160-161, figs 1-12 (original description, holotype Philippine Islands, Borongan, Samar [BMNH] [examined]). – Needham & Gyger, 1939: 263, 264 (key, no new material); Hämäläinen & Müller 1997: 257, 276 (distribution East Visayan subregion: Samar, Leyte, Biliran, Homonhon, Panaon; Mindanao subregion: Dinagat; *D. septima* presumably a synonym).

? *Drepanosticta septima* Needham & Gyger, 1939: 264-265, figs 201, 204 (original description, holotype female, Samar, 29 Apr 1924, R.C. McGregor [in CUIC?]).

Drepanosticta sp. n. 6 (cf. *mylitta*). – Hämäläinen & Müller 1997: 257, 276.

Material examined (all Philippine Islands, all in RMNH, except specified otherwise). – **Luzon**, [Zambales], Subic Bay, 2.vii.1907 (J. C. Thompson) 1 male [ex CASC]; [Sorsogon], Bulusan, Mt Bulusan, San Francisco, Pagjasaan river, 400-600 m, 4-5.xii.1997 (C.M. Nazareno) 2 males; Same, Obak river, 6.xii.1997 (C.M. Nazareno) 1 female; Same, Sioton river, 6-7.xii.1997 (C.M. Nazareno) 2 females; Same, San Roque, Masacrot spring, 10-11.xii.1997 (C.M. Nazareno) 1 male. – **Samar**, Borangan, date unknown, 1 male [holotype] [in BMNH]; Las Navas, Brgy San Isidro, 100-350 m, 22-28.v.1997 (A. Buenafe) 9 males 3 females. – Bilaran: Naval, Sayao Mtn, Horonan Creek, 200-400 m, 30.x.-3.xi.1992 (Th. Borromeo) 2 males; Same, Sayao Mtn, Villaconsuelo, 4-7.xi.1992 (Th. Borromeo) 1 male. – **Leyte**: Mahaplag, Hilusig, Balocaue Mtn, 600 m, 29.viii.-14.ix.1986 (Th. Borromeo) 7 males 4 females; Same, 700 m, 29.xi.1989 (Th. Borromeo) 10 males 2 females; Same, Magsuganao river, 18-30.ix.1990 (Th. Borromeo) 20 males 5 females. – **Homonhon**: Magallanes Point, 17.v.1988 (C. Treadaway) 1 male. – Dinagat: Loreto, Sinayao, June 1989 (A. Buenafe) 1 male. – **Panaon**: San Francisco, Batong Lapad, viii.1988 (W. Catal) 2 males; same, Kaneo Mtn, 400 ft (W. Catal) 1 male; Same, Gabing Gamay: big river, x.1988 (W. Catal) 2 males 2 females; San Francisco, Anislagon Mtn, 100-150 m, 2.ii.1990 (Th. Borromeo) 1 male; Same, Anislagon river, 10.x.1990 (Th. Borromeo) 3 males 2 females.

Diagnosis. – Medium-sized, nearly completely castaneous species. Pronotum typically with short and 90° erect projections on hind margin of hind lobe, but some populations on Samar with these processes flat, but otherwise structurally similar.

Male. – Head. Labrum and anteclypeus bluish white, anterior one-fourth of labrum brown; mandibles greyish white, frons middle brown, a reniform middle-brown spot posterior of lateral ocelli; rest of head bronze-black, frons and vertex coriaceous; transverse occipital carina distinct with acutely angulate lateral extremities; antenna with scapus and pedicellus very pale brown, flagellum brown, the basal part somewhat paler.

Thorax. Pronotum (Figs 64-65) with median parts of anterior, median and posterior lobes dark brown, lateral parts creamish, lateral lobes dark brown; anterior, median and lateral lobes simple; posterior lobe short, median portion with hind margin acute in the middle, lateral portions with hind margin on innerside with an erect, slender, round process, approximately as long as length of median axis of posterior lobe (see also Remarks, below). Synthorax castaneous, somewhat obscured in lower frontal part. Legs yellowish white, the coxae somewhat darker on posterior side. Wings hyaline, venation basal to nodus castaneous, rest dark brown; Px 18 in fore wing, Px 16 in hind wing; origin of R4+5 distal to or, more frequently, at subnodus; IR3 halfway first cell distal to that level; Arculus arising just distal to Ax2; quadrangle in fore wing somewhat widening posteriorly; anal veins sessile; pterostigma middle brown, subrectangular, width c. 1.8 time the height; cells between Costa and R1 undivided.

Abdomen. Middle brown, segments 3-7 with base of segments dorsally with a bluish white pale marking, subtriangular (segment 3) or panduriform (spear-like) (other segments). Appendages (Figs 66-67) dark yellow to lightbrown, superiors in dorsal view with stout basal two-fifths, distal three-fifths much more slender, curved outward, then inward, the tips not quite touching, subsquarish, base of distal portion with a short inward directed, very sharp tooth; inferiors as long as superiors, in ventral view with basal third stout, distal two-thirds in basal half straight, rest forming a heart-shaped figure with the other appendage, the top bent 90° inwards, the tip curved dorsad.

Measurements. Hind wing 18-21 mm; abdomen including appendages 28-32 mm; some specimens from Samar without spiny projections on hind margin of posterior lobe of pronotum are larger, hind wing up to 22 mm, abdomen up to 34 mm.

Female. – Similar to the male, but posterior lobe of pronotum with indistinct or even hardly discernable spiny projection just before hind margin.

Measurements. Hind wing 18-22 mm, abdomen 26-31 mm.

Variation. – A very variable species in the structure of the posterior margin of the posterior lobe of the pronotum, and the anal appendages of the male. Males ‘typically’ have a short and paired spiny projection just before the posterior margin of the posterior lobe, but some populations of Samar Id. (e.g. Hinabangan) have the corners of the hind margin of the lobe slightly projecting, but are lacking the spine. These specimens were considered a separate species by Hämäläinen & Müller (1997) (‘sp. n. 6’). The type of *D. mylitta* is also from Samar (Borongan, 11°38’N 125°27’E) and is provided with spines on the hind margin of the posterior lobe. Presently, the variation of this taxon within Samar is not understood.

Also variation in the male appendages was observed. The width of the basal part of the superior appendages (dorsal view) is very variable, but all populations are characterised by the ventro-mediad tooth at the base of the clasper-like part of the superiors; inferior appendages (ventral view) with distal part usually straight, only the tip distinctly tapering, hooked mediad, the very tip dorsad; in some specimens, however, the distal halves diverging, but otherwise similar. In some populations (e.g. Leyte Id, Mt Balocaue) the male inferiors are very robust, viz. terminal part c. two times as long as wide, as compared to c. four times in ‘typical’ specimens).

These differences may indicate that *D. mylitta* actually consists of a group of closely related species. More material is needed to map the geographical distributions of all character-states, and to re-evaluate the value of the documented variation, while also a molecular study of this species may contribute to understand the morphological variation.

Distribution (Fig. 105). – Philippines Islands (from north to south): Luzon, Samar, Biliran, Leyte, Homonhon, Dinagat, Panaon. Widespread species, including several small islands.

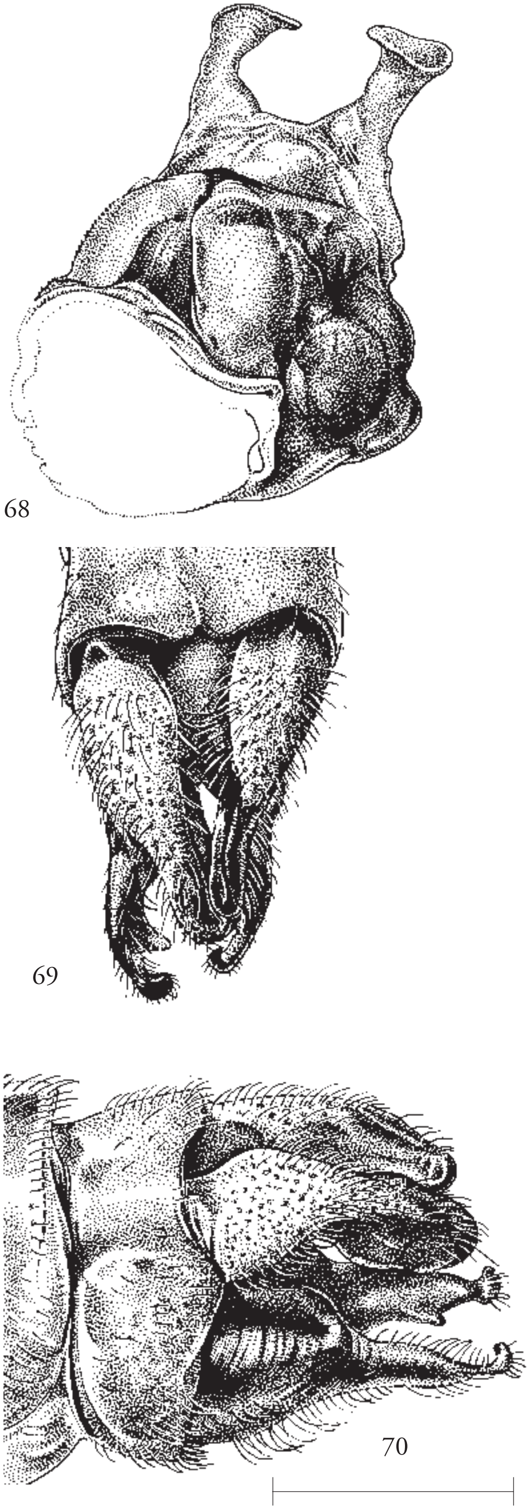
Drepanosticta myzouris Van Tol, **sp. n.**

(Figs 68-70, 107)

Type material. – Holotype male [JvT 22124] in RMNH: 'Philippines, Luzon Id / Camarines Sur, Pili / Bungcao Curry, 200-400 m / Mt Isarog, Caririca River / August 4.-15. 1997 / Celso Nazareno legit / Coll. Roland A. Müller'. – Paratypes (all in RMNH). Same data as holotype, 3 females.

Diagnosis. – Relatively large species, with distinct pale markings in posterior part of synthorax. Male unmistakable by its remarkable, sucker- or proboscis-like posterior processes of the posterior lobe of the pronotum; the same structure absent in female. Appendix inferior of male with a subterminal inward tooth (for interpretation of phylogenetic relevance, see *D. malleus* sp. n.).

Male [JvT 22124, holotype]. Head. Labrum and anteclypeus pale blue, anterior border of labrum light brown; mandibles light brown; rest of head bronze-black, small blue marking at abaxial side of lateral ocelli; transverse occipital carina without extremities. Antenna with scapus pale brown, pedicellus dirty yellow with the tip castaneous, flagellum castaneous. Thorax. Pronotum (Fig. 68) with anterior, median, upper part of lateral and posterior lobes dirty yellowish white; lower part of lateral lobes brown; anterior, median and lateral lobes simple; innerside of lateral portion of posterior lobe with a broad and flat process ending in a disc; length of process approximately median length of median lobe. Legs dirty white. Synthorax light brown, but an irregular brownish black stripe against dorsal carina, and bluish white, more or less rectangular markings in posterior quarter of mesepimeron, metisternum and metepimeron. Wings hyaline, venation rather open, brown; Px 13 in fore wing, Px 12 in hind wing; R4+5 arising at level of subnodus, IR3 arising just distal to that level; Arculus well distal to Ax2; quadrangle hardly widening



Figures 68-70. *Drepanosticta myzouris* sp. n., male [JvT 22124, holotype]. – 68, pronotum, oblique view. – 69, anal appendages, dorsal view. – 70, idem, left lateral view. Scale bar 1 mm.

posteriorly, anal veins symmetrical; pterostigma brown, with narrow paler lines against the veins, width in fore wing ca. 1.1 times the height, subtrapezoid, proximal side only somewhat shorter than distal side, in hind wing with proximal side more oblique, shorter than distal side; a few cells between Costa and R1 divided in one wing only.
Abdomen. Segments 1-6 middle brown, basal one-tenth tot one-eighth of segments 2-5 ivory white, segments 8-9 castaneous, segment 10 dorsally blue, ventral side of tergites brown. Appendages (Figs 69-70) brown, but dorsum of basal two-thirds of superiors blue; base stout, the distal half laterally compressed, high, top subsquarish, a triangular tooth at base of club-shaped distal part; inferiors as long as superiors, in ventral view with stout base, the distal half smoothly curved outward, than inward, the tip curved dorsad; subterminally a long, sharp, inward directed tooth.
Measurements. Hind wing 25 mm; abdomen including appendages 38 mm.

Female. – As the male, but process on posterior lobe of pronotum simple and relatively short, the top bent inward, approximately the length of median line of posterior lobe; abdominal segments with segments 8-9 brown, segment 10 dorsally pale blue, the anal appendages ivory white; valves long, surpassing tip of appendages.
Measurements. Hind wing 26 mm; abdomen 37 mm.

Etymology. – *Myzouris*, sucker (Gr.), for the structure of the projection of the posterior process of the pronotum. A noun in apposition.
Distribution (Fig. 107). – Philippine Islands, Luzon, Mt Isarog. Only known from the type locality.

Drepanosticta paruatia van Tol, **sp. n.**

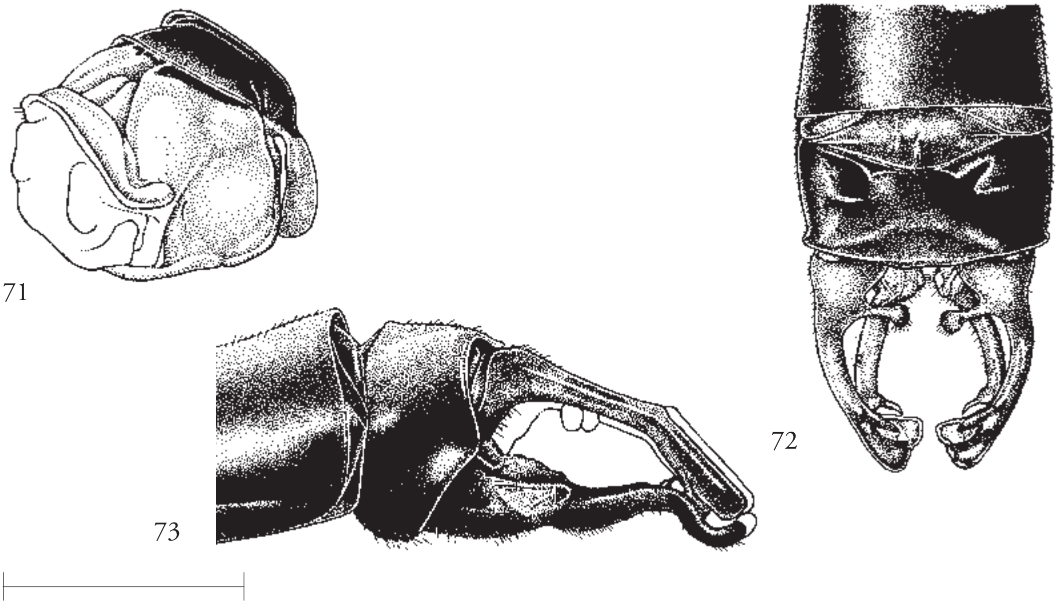
(Figs 71-73, 107)

Drepanosticta sp. n. 19. – Hämäläinen & Müller 1997: 258, 277.

Type material. – Holotype male [JvT 20337] in RMNH: ‘Philippines, Palawan Id / Port Barton, Waterfalls / May 28, 1991 / Roland A. Müller legit / Coll. R. A. Müller’.

Diagnosis. – Male unmistakable among the described *Drepanosticta* of the Philippines. Large, with conspicuous antehumeral stripe, remarkable pending appendages of the posterior lobe of the pronotum, and the structure of the appendages with a clavate mediad directed tubercle on innerside of superior appendage. Not closely related to any of the other species of *Drepanosticta* from the Philippines, but sharing several characters with Bornean species, as *Drepanosticta dupophila* Lieftinck. Only one specimen known.

Male [JvT 20337, holotype]. Head. Labrum, anteclypeus and inner basal corner of mandibles bluish white; anterior two-fifths of labrum and larger part of mandibles black; rest of head bronze-black, microsculpture very superficial, dorsal part of head very shining; transverse occipital carina distinct, with lateral extremities apiculate. Antenna with scapus and pedicellus dirty yellow, flagellum broken.
Thorax. Pronotum (Fig. 71) with anterior, median and lateral lobes ivory white, main part of posterior lobe black, the lateral portion brown; anterior, median and lateral lobes simple, posterior lobe short, the extreme lateral corners narrow based, elongate appendage directed ventrad, reaching beyond ventral side of lateral lobe, and not immediately conspicuous. Synthorax bronze-black with extensive pale markings as follows: wide antehumeral blue stripe anteriorly starting the width of stripe from anterior side of mesepisternum, length approximately three-quarters mesepisternum; lower posterior corner of mesokatepisternum ivory white, as well as complete metepisternum except for a triangular black marking in posterior corner, and complete metepimeron, except for a narrow brown line against metapleural suture; legs yellow, brown rings around joints on femora and tibiae. Wings hyaline, venation brown up to nodus, rest brownish black; Px 14 in fore wing, Px 13 in hind wing; R4+5 arising at or a trifle distal to subnodus, IR3 arising well distal to that level; Arculus arising distinctly distal to Ax2, quadrangle somewhat widening posteriorly in fore wing; anal veins somewhat asymmetrical in both fore and hind wing, shortly stalked; pterostigma short, width 1.3 times height,



Figures 71-73. *Drepanosticta paruatia* sp. n., male [JvT 20337, holotype]. – 71, pronotum, oblique view. – 72, anal appendages, dorsal view. – 73, idem, left lateral view. Scale bar 1 mm.

all sides indistinctly convex, proximal sides acutely angulate.

Abdomen. Segment 1 ivory white, segments 2 to 7 mostly brown, but segment 2 ivory white in lower part of tergite, and narrow ivory white rings anteriorly on segment 3-6; anterior three-quarters of segment 8, and anterior half of segment 9 pale, presumably blue in life, segment 10 completely brownish black, sternites of segments 8-9 blue. Appendages (Figs 72-73) brown, basal parts dark brown; both superior and inferior appendages long and slender; superiors with basal one-fifth relatively stout, ending in a bifurcation, consisting of an inward directed process approximately the length of basal part of superior; main stem of superiors curving smoothly towards each other, the distal one-fourth widening ventrally; inferiors also with stout base, distal three-quarters curved semi-circularly, the top wider and scooplike, subterminally a very slender tooth directed inward, a trifle longer than width of stem.

Measurements (type only). Abdomen including appendages 39 mm; hind wing 21 mm.

Female. – Unknown.

Etymology. – *Paruatia* (latinized version of Greek), with hanging ears; for the structure of posterior lobe of the pronotum. An adjective.

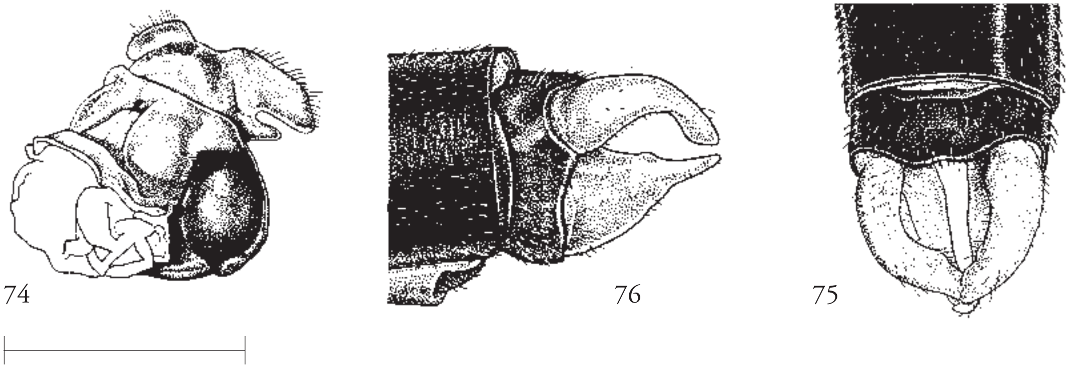
Distribution (Fig. 107). – Philippine Islands: Palawan.

Drepanosticta pistor van Tol, **sp. n.**

(Figs 74-76, 106)

Drepanosticta sp. n. 13. – Hämäläinen & Müller 1997: 258, 277 [distribution Negros, Panay, Sibuyan]

Type material. – Holotype male [JvT 20260] in RMNH: 'Philippines. Negros Id. / Negros Occ., Murcia / Mt Mawa, Brgy Canlandog / Balantak River, 400-500 m / May 4.-8. 1995 / Alex Buenafe legit / Coll. Roland A. Müller'. – Paratypes (25 specimens, all Philippine Islands, in RMNH, arranged per island in chronological order). **Sibuyan**. Romblon province, Magdiwang, Mt Guiting-Guiting, 300 m, 22-23.vi.1986 (leg. ?) 1 male 1 female; Magdiwang, Tampayan, Pawala river, 50-200 m, 19-31.vii.1986 (R.A. Müller) 2 males 1 female; Magdiwang, Silum, 5-100 m, 3.viii.1986 (R.A. Müller) 1 female; Magdiwang, Tampayan,



Figures 74-76. *Drepanosticta pistor* sp. n., male [JvT 18799, Negros Occ., Murcia, Mt. Maura, Balantak river, 4-8.v.1995]. – 74, pronotum, oblique view. – 75, anal appendages, dorsal view. – 76, idem, left lateral view. Scale bar 1 mm.

Camp Ga-ong, 80-150 m, 18-31.iii.1987 (R.A. Müller) 3 males 1 female; Magdiwang, foot of Mt Guiting Guiting, 200 m, 20-25.ii.1997 (ex coll. Treadaway) 1 male. – **Negros**. Negros Occidental Prov., Murcia, Mambucal, 2000 ft, 1-31.viii.1987 (A. Buenafe, C. Carzon) 2 females; Murcia, Mt Canlaon, Pula River, 3000 ft, 19.iv.1988 (A. Buenafe) 1 male; same, Asia River (no altitude given), 13.iv.1988 (A. Buenafe) 2 females; same, Pula River, ix.1990 (A. Buenafe) 1 male; Murcia, Mt Mawa, Brgy Canlandog, Balantak River, 400-500 m, 4-8.v.1995 (A. Buenafe) 1 male; same, Intalocan Creek, 800-900 m, 26.v.1995 (A. Buenafe) 1 male. – **Panay**. Antique province. San Remigio, Aningalam, Mt Clara, 600-850 m, 28.vii-10.viii.1996 (A. Buenafe) 1 male 3 females; idem, Mt Clara, 600-850 m, 28 Jul-10.viii.1996 (A. Buenafe) 2 females. Excluded from type series. – **Luzon**. Camarines Sur, Pili, Bungcao Curry, Mt Isarog, Caririca River, 200-400 m, 4-15.viii.1997 (C. Nazareno) 3 males 3 females; same, Himaao River, 200-400 m, 4-15.viii.1997 (C. Nazareno) 1 male 3 females.

Diagnosis. – Medium-sized, variegated species; differs from other Philippine *Drepanosticta* by the simple structure of the anal appendages of the male without any teeth or tubercles, and the cleft sides of the posterior projections of the posterior lobe of pronotum (see below for variation between populations).

Male [JvT 20260, holotype]. – Labrum, mandibles and anteclypeus bluish white; narrow black line along anterior border of labrum; rest of head bronze-black with longitudinal striae between eyes, clypeus, frons and vertex coriaceous; transverse occipital carina distinct, but without lateral extremities. Antenna with scapus and pedicellus dirty yellow, flagellum (damaged in holotype) castaneous.

Thorax. Pronotum (Fig. 74) with following coloration: anterior, median and posterior lobe dirty yellow, some parts more obscure; lateral lobes brown; anterior, median and lateral lobes simple; posterior lobe in lateral corners with bifurcate appendage, anterior portion narrow and directed abaxiad, posterior portion twice as long and wide, at base running abaxiad, distal part bent ventrad; synthorax bronze-black with dirty yellow parts as follows: dorsal carina, an oblong triangular marking in distal three-quarters of both sides of humeral suture, metastigma, and another oblong triangular marking on posterior part of metepisternum. Legs yellow. Wings hyaline, venation brown; Px 13 (13-14) in fore wing, Px 13 in hind wing; R4+5 at subnodus, IR3 halfway first cell distal to that level; Arculus distinctly distal to Ax2; anal veins symmetrical, not stalked (even divided in left fore wing of holotype); pterostigma brown, width 1.5 times the height; proximal side acutely angulate; first cell distal to pterostigma between Costa and R1 large; all cells in that area undivided.

Abdomen. Segments 1-2 and 8-10 dark brown, other segments middle brown, with narrow ivory-white markings in anterior one-tenth of segment 3-6, and

anterior two-fifths of segment 7. Appendages (Figs 75-76) yellow, base of inferiors obscured; superiors flat, in dorsal view more or less parallel-sided over full length, distal two-fifths bent c. 60° towards each other; in lateral view distal part bent ventrad; inferiors with base stout, distal two-fifths narrow, base straight, the tip bent 80° towards each other.
Measurements. Hind wing 19 (18-21) mm; abdomen including appendages 32 (26-32) mm.

Female. – Similar to the male, but more robust; structure of pronotum as in male; last abdominal segments stout, segment 9 subsquarish in lateral view; segments 8-10 brown; cerci dirty white; valves long, reaching at or beyond tip of cerci.
Measurements. Hind wing 19-21 mm, abdomen 29-31 mm.

Variation. – Specimens from Luzon are similar in most respects, but some differ from the type in the structure of the posterior process of the posterior lobe of the pronotum with the cleft dividing the lateral border of the process more equally.
Females. – Females are remarkably well represented in the collection.
Etymology. – *Pistor* (Latin): miller; named after Roland A. Müller, St. Gallen; Müller is German for miller. A noun in apposition.
Distribution (Fig. 106). – Philippine Islands: Sibuyan, Negros, Panay and Luzon. A rather widespread species, but apparently uncommon where found.

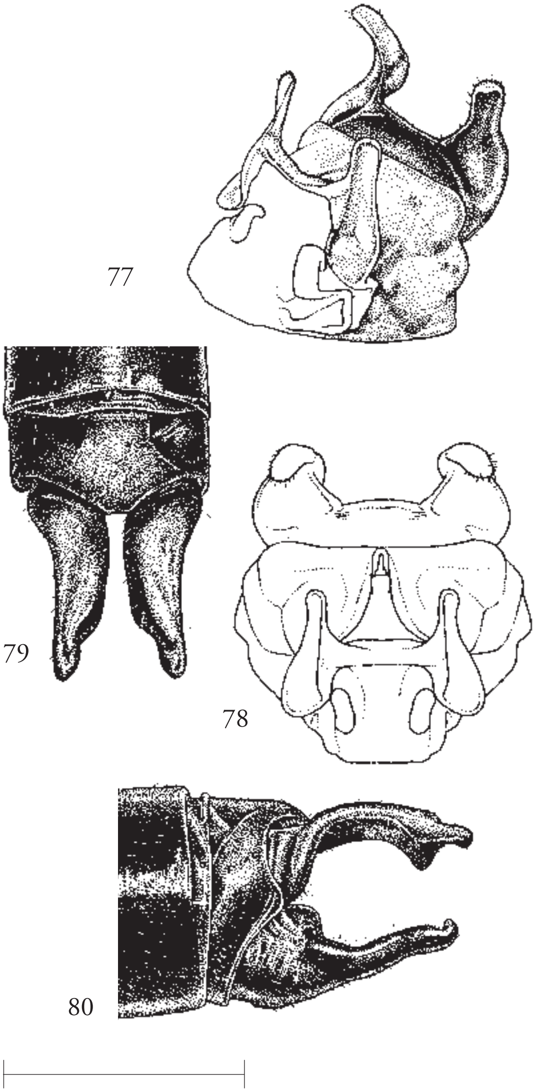
Drepanosticta quadricornu van Tol, sp. n.
(Figs 77-80, 107)

Drepanosticta sp. n. 20. – Hämäläinen & Müller 1997: 258, 277 (Palawan, Busuanga).

Type material. – Holotype male [JvT 20349] in RMNH: 'Philippines, Palawan Id / Mt Capoas, Bo Banbanan / Camp Inunugan River / 16./22. March 1992 / Vinceguerra/ Gorostiza leg.'. – Paratypes (all specimens Philippines, in RMNH) by island in chronological order. **Busuanga island**, Busuanga, 1.viii.1990 (Th. Borromeo Sr) 1 male (incomplete); Coron, 2.viii.1990 (Th. Borromeo Sr) 1 female; Coron, Mabentangen river, 4-7.v.1991 (Th. Borromeo) 2 males 1 female. – **Palawan**, Port Barton, 50-100 m, 15.vi.1985, [R.A. Müller], 1 female; Quezon district, Malatgao, Magmuni stream, 25-27.v.1991 (M. Hämäläinen) 1 male; Quezon, Lamaken [= Lamakan], Magmuni stream, 27.v.-1.vi.1991 (Borromeo / Buenafe) 1 female; Port Barton, waterfalls, 28.v.1991 (R.A. Müller) 4 males 2 females; Mt Capoas, Sitio Caoban, Camp Neutcio, ca 280 m, 11-15.iii.1992 (Vinciguerra / Gorostiza) 2 females; Mt Capoas, Bo Bandanan, Camp Inunugan River, 16-22.iii.1992 (Vinciguerra / Gorostiza) 1 male 4 females; Mt Saint Paul, Tagabinit, Babuyan River, ca 160 m, 25-30.iii.1992 (Vinciguerra / Gorostiza) 2 males; Idem, ca. 350 m, 27.iii.1992, 1 male.

Diagnosis. – Small species, with distinct projections on both the anterior and the posterior lobes of the pronotum and pale stripe over metepisternum; other species with two pairs of processes on the pronotum are *D. belyshevi* Hämäläinen, *D. trachelocele* sp. n., and *D. moorei* Van Tol & Müller. Apart from structural differences in the projections of the pronotum, both *D. belyshevi* and *D. trachelocele* have distinctly clasperlike superior appendages, while *D. moorei* can most easily be distinguished on the pale stripe over the synthorax that extends over metepisternum and metepimeron. *D. quadricornu* also differs from Philippine congenerics by the structure of the anal appendages of the male; in lateral view the superior appendage is strongly convex with a subterminal, medio-ventrally directed triangular tooth.

Male [JvT 20341]. – Head. Labrum, mandibles and anteclypeus ivory white, a narrow black anterior line on mandible; rest of head black and very shining without microsculpture; transverse occipital carina indistinct, without extremities. Antenna with scapus and pedicellus creamish white, flagellum castaneous.
Thorax. Pronotum (Figs 77-78) with anterior, median and lateral lobes dark yellow, posterior lobe brown; anterior lobe erect, large, lateral corners with sharp process, approximately twice as long as height of anterior lobe, directed dorsad; median and lateral lobes simple, posterior lobe short, but lateral portions with long process, base directed caudad, distal half curved upright, or just somewhat anteriad.



Figures 77-80. *Drepanosticta quadricornu* sp. n., male [JvT 20343, Palawan, Port Barton, 28.v.1991]. – 77, pronotum, oblique view. – 78, pronotum, dorsal view. – 79, anal appendages, dorsal view. 80, idem, left lateral view. Scale bar 1 mm.

Synthorax castaneous, but posterior three-quarters of metepisternum with wide bluish-white stripe, anteriorly sharp, posteriorly nearly touching hind margin of metepisternum, ventrally a narrow brown stripe along metapleural suture; posterior quarter of metepimeron white. Legs yellow, dark rings on femora and joints of femora and tibiae. Wings hyaline, venation brown in basal part up to nodus, rest brownish black; Px 15 in fore wing, Px 13 in hind wing; R4+5 at level of subnodus, IR3 halfway first distal to that level; Arculus just distal to Ax2; quadrangle somewhat widening posteriorly in fore wing only; anal veins sessile; pterostigma brown, with narrow pale lines against the veins, oblong, width 1.8 times the height, proximal side acutely angulate; cells between Costa and R1 undivided (rarely divided in other specimens).

Abdomen. Segment 1 ivory white; segment 2-8 with extensive ivory white rings as follows: anterior one-fifth of segment 2, anterior and posterior one-fifth of segments 3-6, segment 8 ivory-white in anterior two-fifths; segments 9 and 10 brownish black. Anal appendages (Figs 79-80) brownish black, convex; superiors in dorsal view with relatively slender base, gradually tapering towards acute tip, inner lateral view shows tip as a long process on solid base, which abruptly ends and bends ventrad; inferiors with stout base, rest nearly straight, the tips bent 50° twoards each other and nearly touching.

Measurements. Hind wing 17.5 mm, abdomen including appendages 28 mm.

Female. – Very similar to male, including structure of pronotum, and coloration; all specimens in collection with abdomen discoloured, but presumably abdominal segment 8 pale, segment 9 brown, segment 10 dark brown. Valves long and slender, surpassing level of cerci.

Measurements. Hind wing 17-18 mm; abdomen ca 25 mm.

Affinities. – The sister-species of *D. quadricornu* sp. n. is presumably to be found on Borneo; further studies are needed.

Etymology. – *Quadricornu* (Latin), four horns; for the structure of the anterior and posterior lobes of the pronotum. A noun in apposition.

Distribution (Fig. 107). – Philippines: Palawan and Busuanga.

Protosticta Selys

Protosticta Selys, 1885: cxlvi-cxlvii.

The genus *Protosticta* Selys is traditionally distinguished from other Platystictidae by combination of a straight, rather than fractured, IR3 vein, and the absence of an Anal bridge (only the anal crossing is present). Three platystictids with characteristic and similar anal appendages, but differing in the vein venation, are assigned here to the new genus *Sulcosticta*. Three other species with wing venation as the type species of *Protosticta* Selys, are described here as *Protosticta*. They are apparently nor closely related to *P. simplicinervis* Selys, nor to each other. As indicated in the introduction, a more definitive arrangement has to await a detailed phylogenetic analysis.
Included Philippine species: *P. annulata* (Selys), *P. lepteca* sp. n., *P. plicata* sp. n.
Distribution: Luzon.

Protosticta annulata (Selys)

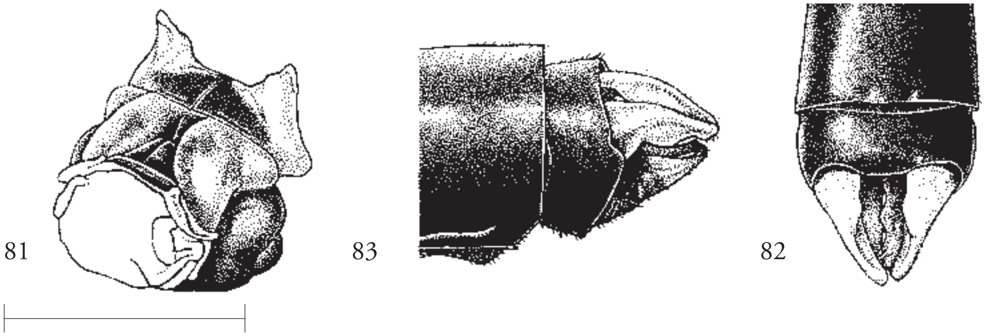
(Figs 81-83, 108)

Platysticta (*Platysticta*) *annulata* Selys, 1886: sep. 156-157 (original description, type female, type locality Luçon (in coll. Selys, IRSN).
Platysticta annulata Selys. – Selys 1891: 218 (considered close relative of *rufostigma* from Borneo).
Protosticta annulata Selys. – Needham & Gyger 1939: 263, 264 (key, no new material).
Drepanosticta annulata (Selys). – Lieftinck, 1961: 135-136 (two females left, presumably not conspecific, no 577 selected as lectotype, number 588 paralectotype; both in poor condition and status unclear); Hämäläinen & Müller 1997: 257, 276 (distribution Luzon).

Material examined. – Luzon, Nueva Viscaya, Sta Fe, Dalton Pass area, 900 m, 8-17.viii.1991 (A. Gorostiza) 1 male.

Diagnosis. – Small and delicate species, synthorax with longitudinal pale stripes as in taxa here assigned to *Sulcosticta*, last abdominal segments of male swollen; posterior margin of posterior lobe of pronotum with a paired, triangular projection.

Male [JvT 20075]. – Head. Labrum, mandibles, anteclypeus bluish white; narrow brownish black line along anterior border of labrum, approximately one-tenth of height of labrum, tapering towards corners and not quite reaching lateral corners; rest of head bronze-black, coriaceous; transverse occipital carina well developed without lateral extremities; antenna lost. Thorax. Pronotum (Fig. 81) with anterior lobe brown in median one-third, lateral to that marking a small reddish brown triangular projection from anterior border of lobe directed posteriad, lateral quarters of lobe bluish white; median lobe with anterio-median depressed part brownish black, the lateral portions vaulted, brown on mediad surface, rest bluish white, somewhat darkening posteriorly; lateral lobes brownish black, median portion somewhat paler; posterior lobe medially with triangular brownish black marking, lateral thirds dirty yellow, with erect, triangular, auriculate projections, approximately as long as median line of posterior lobe. Synthorax with dorsal carina anteriorly with a small yellow marking, mesepisternum black, a narrow dirty yellow line against humeral suture and dorsal side of mesekatepisternum; mesokatepisternum black with a dirty yellow stripe against coxa; mesepimeron black, a dirty yellow line against humeral suture, starting anteriorly the distance of dorsal side of mesokatepisternum from posterio-dorsal corner of mesokatepisternum, running along suture, posteriorly covering posterior margin of mesepimeron, continuing anteriorly along first suture almost to level of metastigma; metepisternum with longitudinal, dirty yellow stripe from anterior-ventral corner to metastigma, and another pale stripe arising just posterior to metastigma, anteriorly acute, widening posteriorly, not quite reaching posterior side of synthorax; metepimeron black with rectangular bluish white marking against posterior margin. Legs dirty white, hardly visible darker rings on femora, approximately one-quarter from joints with tibiae. Wings hyaline, venation brown, the posterior half darker; Px 12 in fore wing, Px 12 in hind wing; origin of R4+5 at subnodus, IR3 half a cell distal to that level; Arculus arising well distal to Ax2; quadrangle somewhat widening posteriorly in fore wing; Ab vein absent in all wings; pterostigma subquadrangular,



Figures 81-83. *Protosticta annulata* (Selys), male [JvT 20075, Luzon, Nueva Viscaya, Sta Fe, Dalton Pass area, 900 m, 8-17. viii.1991). – 81, pronotum, oblique view. – 82, anal appendages, dorsal view. – 83, idem, left lateral view. Scale bar 1 mm.

proximal side oblique, width 1.3 times the height; cells between Costa and R1 distal to pterostigma undivided. Abdomen brown, segments 1-2 castaneous, segments 3-6 light brown, segments 7-10 brownish black, with basal creamish white annulae as follows (lateral view): segments 2-3 one-tenth of segment, segment 4 anterior one-eleventh, segment 5 one-fifteenth, segments 6-7 one-twentieth, segment 8 half; segments 8-9 much wider than other segments. Appendages (Figs 82-83) with creamish white superiors, and inferiors with dark base and yellowish white terminal half; superiors rather slender in dorsal view, a short tooth at c. 40% from base, distal part curved inward and ventrally widened; inferiors straight, smoothly tapering towards the top, the top sharp and curved dorsad.

Measurements. Hind wing 17 mm, abdomen including appendages 27 mm.

Female. – No additional data.

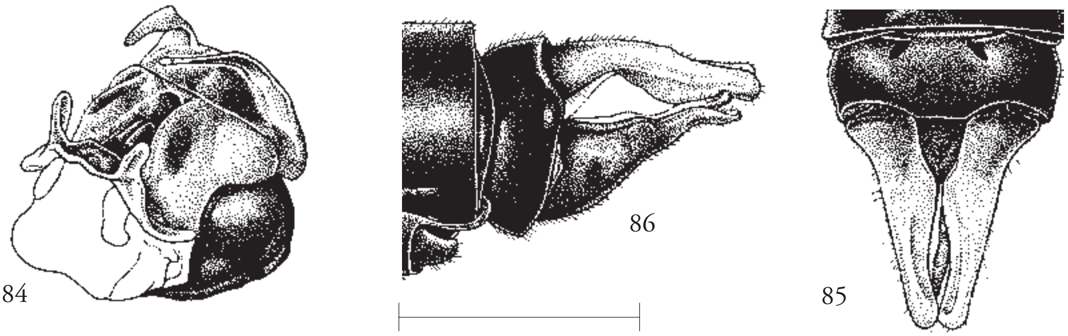
Status of *P. annulata.* – Lieftinck (1961) re-examined the type material in the Selys collection, and found that the type series consisted of two very immature females. The poor status of preservation of these specimens made it impossible to match the selected lectotype with any of the described or undescribed species known to Lieftinck. Besides, the two remaining specimens were not conspecific. The second female, a paralectotype of *D. annulata*, is a female of *Drepanosticta moorei* Van Tol & Müller (see also Hämäläinen & Müller 1997: 276-277). Thirdly, a third specimen available to Selys when describing this taxon with 'le rudiment du secteur inférieur du triangle manquant tout à fait, comme chez la *Protosticta simplicinervis*' was no longer available at all.

This information is valuable. One male platystictid in the Müller collection (data as above [JvT 20075]) was identified by M. Hämäläinen as the first male of *Drepanosticta annulata* (Selys). However, the wing venation of this male is clearly as described for *Protosticta*, i.e. with missing anal bridge. This specimen is here described as the male of *D. annulata*, but its status can only be ascertained after males and females from one site will be available, and can be compared with the lectotype.

Needham & Gyger already placed *Platysticta annulata* Selys in the genus *Protosticta*, based on the note by Selys on the state of the anal bridge. However, they clearly missed the first word of the sentence '... L'un deux présente une anomalie singulière: le rudiment .... [as above]', or: 'One of them has an aberration ...'.

Affinities. – Based on structure of the pronotum and the coloration of the synthorax, this species is considered the sister-group of the species here included in *Sulcosticta* gen. n. A further phylogenetic analysis has to reveal whether the more simple structure of the inferior appendage of *P. annulata* is plesiomorphous or apomorphous compared with the structure in *Sulcosticta* gen. n. If it will appear to be an apomorphy, *P. annulata* should be included in *Sulcosticta*.

Distribution (Fig. 108). – Philippines: Luzon (Nueva Viscaya).



Figures 84-86. *Protosticta lepteca* sp. n., male [JvT 19212, Luzon, Aurora province, Dinalungan, Mt Anaguao, Alebit river area, 600-900 m, 9-14.iii.1997]. – 84, pronotum, oblique view. – 85, anal appendages, dorsal view. – 86, idem, left lateral view. Scale bar 1 mm.

Protosticta lepteca van Tol, **sp. n.**

(Figs 84-86, 108)

Protosticta sp. n. 25. – Hämäläinen & Müller 1997: 258, 277 (1 male Quirino province).

Type material. – Holotype male [JvT 19218] in RMNH. – 'Philippines, Luzon Id / Aurora province, Dinalungan / Mt Anaguao, Alebit river / area, 600-900 m, March 9.-14. 1997 / R.A. Müller leg u. coll.' – Paratypes 7 males 1 female (all Philippine Islands, in RMNH): **Luzon**. Quirino province, Maddela, Sulong river, 500-650 m, 26-27.iv.1991 (Th. Borromeo) 1 male; Aurora province, Dinalungan, Mt Anaguao, Alebit river, 600-900 m, 9-14.iii.1997 (R.A. Müller) 1 male 1 female; same, Bungo river, 200-500 m, 15-18.iii.1997, 5 males.

Diagnosis. – Delicate species, synthorax with narrow longitudinal stripes, especially anterior to humeral suture, and over metepisternum posterior to metastigma; differs from other such species with a missing Ab vein by the following combination of characters (male): long and slender inferior appendage, pronotum with a pair of short projections on anterior lobe, and a paired, triangular, erect process directed anteriad on posterior lobe; other species have short and compact appendages and / or more rounded processes on the posterior lobe of the pronotum; the projections on the anterior corner is also present in *Sulcosticta striata* sp. n., which has distinctly different appendages.

Male [JvT 19128, holotype]. – Head. Labium bluish white, with narrow line along anterior border; mandibles bluish white in basal third, rest brownish black; remaining part of head brownish black with metallic shine, finely punctulate; transverse occipital carina poorly developed, without lateral extremities. Antenna with scapus brown, pedicellus dirty yellow, flagellum castaneous.

Thorax. Pronotum (Fig. 84) predominantly greyish yellow, with brown markings as follows: medio-posterior part of anterior lobe, anterio-median part of middle lobe, and central parts of tubercles of median lobe, central part of posterior lobe; lateral lobes fully brown; anterior lobe with a paired erect process, flat, top rounded, approximately as long as median length of anterior lobe; posterior lobe with a paired process as well, fairly close together, narrow and bent at 60° anteriad.

Synthorax brownish black with creamish markings as follows: narrow line over mesepisternum against humeral suture, widening both anteriorly and posteriorly, ending just before posterior margin of synthorax; mesepimeron with squarish marking against posterior margin of synthorax, dorso-anteriorly connected with a fine line against humeral suture, starting c. two-fifths from posterior corner of mesokatepisternum; metepisternum with oblong marking against first suture posterior ro metastigma, a longer and broader line along metapleural suture from metastigma to hind margin of metepisternum, the posteriormost part widening and bent towards middle of metepisternum; metepimeron with crescent-shaped

marking against posterior margin. Wings hyaline, venation brown; Px 13 in fore wing, Px 12 in hind wing; R4+5 arising just distal to subnodus, IR3 half a cell distal to that level; Arculus just distal to Ax2; Ab vein missing; pterostigma reddish brown, width 1.3 times the height, anterior side convex; cells between Costa and R1 posterior to pterostigma undivided.
Abdomen with segment 1 brown, segment 2 brown with a paired creamish stripe along anterior margin; segments 3-6 castaneous, anterior one-tenth of each segment creamish white; segment 7 with anterior one-third bluish white, rest of segment 7 and segments 8-10 brownish black; segments 8-10 much wider than preceding segments, shining. Appendages (Figs 85-86) with superiors creamish white, base darker, slender, the distal two-thirds ventrally projecting on innerside, inconspicuous tooth; inferiors also slender, basal three-fifths castaneous, rest pale brown, apical third nearly straight with very tip bent 90° inward.
Measurements. Hind wing 18 mm, abdomen including appendages 31 mm.

Female [JvT 19213, from Dinalungan, Alebit river]. – Structure of pronotum and coloration of synthorax differ from male of same site as follows: anterior lobe with anterior margin dilated but without projections, hind margin of posterior lobe with short and flat posterior tubercles, lateral corners tapered; synthorax distinctly paler than in male, the creamish white markings as follows: narrow line over mesepisternum against humeral suture, widening both anteriorly and posteriorly, ending just before posterior margin of synthorax; mesepimeron fully creamish white in posterior two-fifths, except for a narrow black line against humeral suture, the pale marking extending anteriorly in dorsal half, not reaching anteriormost corner, first suture with pale stripe over its full length; metepisternum with oblong marking posterior to metastigma, covering ca. half the space distal to metastigma, and a pale stripe in ventral part of metepisternum from metastigma to posterior marking; metepimeron with crescent-shaped marking against posterior margin and pale spot just in front of that.
Measurements. Hind wing 18 mm; abdomen 27 mm.

Etymology. – *Leptekes* (Greek): fine-pointed, delicate; for the structure of the projections of the posterior lobe of the pronotum. An adjective (latinized form of Greek).
Distribution (Fig. 108). – Philippine Islands: Luzon (Quirino and Aurora provinces).

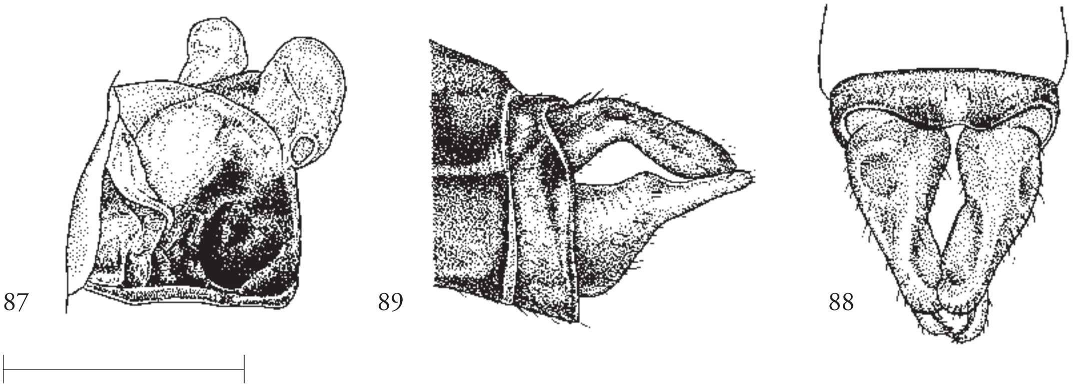
Protosticta plicata van Tol, **sp. n.**

(Figs 87-89, 108)

Type material. – Holotype male [JvT 25060] in RMNH: [Philippine Islands]: 'Kawasan Falls / Badian, Cebu / 2/13/2001 / T. Borromeo'. – Paratype (in RMNH): same data as holotype, 1 female.

Diagnosis. – Relatively large and dark species of Philippine *Protosticta*; males differs from other species by the structure of the posterior lobe of the pronotum, a distinctly folded projection with the fold globularly swollen; appendages slender as in *P. lepteca* sp. n., but posterior lobe of pronotum diagnostic. Female with wing venation as *Drepanosticta* Laidlaw (Ab vein present), but otherwise very similar to male, including structure of posterior projections of posterior lobe of pronotum.

Male [JvT 25060, holotype]. – Head. Labium, mandibles and anteclypeus bluish white, a very fine black line along anterior border of labium and mandibles, hardly visible from above; rest of head black, punctulate, with coppery metallic shine; transverse occipital carina poorly developed, no lateral extremities; antenna with scapus and pedicellus creamish white, flagellum brown.
Thorax. Pronotum (Fig. 87) with anterior, median and posterior lobes fully creamish white, lateral lobe brownish black; structure of anterior lobe simple, posterior lobe with a paired posterior process, halfway bent back nearly 180° towards pronotum, the new top bulbous and very shiny. Synthorax brownish black, with creamish white markings as follows: dorsal carina over its full length, a subulate marking in posterior fourth over humeral suture, a poorly indicated pale mark on metepisternum. Legs very pale creamish white. Wings hyaline, venation brown; Px 13 in



Figures 87-89. *Protosticta plicata* spec. nov., male [JvT 25060], holotype, Cebu, Badian, Kawasan Falls, 13.ii.2001]. – 87, pronotum, oblique view. – 88, anal appendages, dorsal view. – 89, idem, left lateral view. Scale bar 1 mm.

fore wing 13, Px 12 in hind wing; R4+5 arising at subnodus, IR3 half a cell distal to that level; Arculus distal to Ax2; Ab vein absent; pterostigma width 1.2 times the height, the proximal side somewhat convex, but distinctly acutely angulate, distal side less so; cells between Costa and R1 distal to pterostigma undivided. Abdomen with segment 1 brownish black, segment 2 dark brown, segments 3-6 dark brown with anteriorly on each segment a creamish white mark, covering approximately one-eighth, and three times one-sixth of segment-length; creamish white marking on segment 8 more extensive, c. two-fifths segment length, rest brown, the brown part anteriorly with subulate projection; segments 8-10 brownish black, much wider than preceding segments. Anal appendages (Figs 88-89) with superiors greyish brown, stoutly built, somewhat projected on innerside; inferiors surpassing length of superiors, stout at base, distal two-fifths very slender and straight, only the very tip hooked axiad (not dorsad).
Measurements. Hind wing 19 mm, abdomen, including appendages, 31 mm.

Female. – Similar to the male, but, remarkably, Ab vein present as in *Drepanosticta* Laidlaw; structure of posterior lobe of pronotum more or less as male, although the folded projection somewhat smaller. Mesurements. Hind wing 21 mm, abdomen 31 mm.

Etymology. – *Plicatus* (Latin), folded, for the structure of the paired process of the posterior lobe of the pronotum. An adjective.
Conservation status. – One of the most threatened species of damselflies in the Philippines. The type locality is one of three very small remaining patches of forest in Cebu. It has not been recorded from the other two sites by the research group of Dr. Franz Seidenschwarz. Kawasan Falls is not a conservation area, but it be may receive some protection since it is a favourite nature travel destination (M. Hämäläinen, personal communication, June 2004).
Distribution (Fig. 108). – Philippine Islands: southern Cebu (Badian). Only known from type locality.

Sulcosticta van Tol **gen. n.**

Diagnosis. – Inferior appendage short and stout, with the tip flattened and with shining brown sclerotization, or more or less bifid, and inner part with or without shining brown sclerotization; synthorax with variegated pattern of longitudinal stripes. Wing venation as in *Drepanosticta* Laidlaw or as in *Protosticta* Selys.
Remarks. – As already explained in the introductory chapter, it is presently, without extensive phylogenetic analysis, impossible to judge which other species will ultimately be placed in this genus. The similarity in the structure of the inferior appendage is such that a homoplasy is considered unlikely. Since both *Protosticta*

and *Drepanosticta* are based on characters in wing venation, a proper placement of these species in one of the present genera appeared impossible. It might appear that the variegate coloration of the synthorax will prove to be a phylogenetically informative character for a monophyletic clade, so that also all Philippine *Protosticta* can be placed here.
Type species. – *Sulcosticta pallida* sp. n.
Included species: *S. pallida* sp. n., *S. striata* sp. n. and *S. viticula* sp. n., and possibly two undescribed species (damaged male, or only female known).
Distribution: Luzon.

Sulcosticta pallida van Tol, **sp. n.**

(Figs 90-92, 109)

Drepanosticta sp. n. 8. – Hämäläinen & Müller 1997: 257, 277 (Nueva Vizcaya, Nueva Ecija and Quirino provinces).

Type material. – Holotype male [JvT 22675] in RMNH: 'Philippines, Luzon Id / Nueva Viscaya, Sta Fe / Atbo River, 550-800 m / June 10, 1991 / Roland A. Müller legit / Coll. R.A. Müller'. – Paratypes (all Philippines, in RMNH, 7 females): **Luzon Id.** Data as holotype, 2 females; Nueva Viscaya, Sta Fe, Dalton Pass area, 900 m, 8-17.viii.1991 (A. Gorostiza) 1 female; Nueva Ecija, Caraglan, Batching river, 700-850 m, 11.vi.1991 (R.A. Müller) 1 female; Quirino / Aurora boundary, Maddela, Mt Anaguao, 800-1100 m, 9-14. viii.1996 (C.M. Nazareno) 2 female; Aurora, Dinalungan, Mt Anaguao, Bungo river, Lumot creek, 1200-1400 m, 20.vi.1997 (M. Dusayen) 1 female.

Diagnosis. – The characteristic Y vein of *Drepanostocta* not closed, but separate at base, and male appendages very aberrant with inferiors short, the top bifid; the shape of the inferior appendage of the male also present in *S. striata* sp. n., which differs considerably in the shape of the hind lobe of the pronotum.

Male [JvT 22675, holotype]. – Head. Labrum, mandibles and anteclypeus pale, some parts bluish, other parts brownish; a distinct oval depression central in labrum; rest of head bronze-black; postoccipital carina with indistinct extremities; parocular suture distinct; antenna incomplete, scapus and pedicellus pale, the flagellum broken.
Thorax. – Pronotum (Fig. 90) with anterior, median and posterior lobe dirty yellow, lateral lobe brown; anterior border of anterior lobe with indistinct triangular extremity; median and lateral lobes simple; posterior lobe with lateral corners erect, triangular, with a sharp, constricted top. Synthorax dirty yellow, except for a narrow stripe against dorsal carina, the humeral line, an oblong marking over mesepimeron from just above metastigma, and posterior corner of metepimeron. Legs yellow. Wings hyaline, venation brown; Px 14 in fore wing, Px 13 in hind wing; origin of R4+5 distinctly distal to subnodus; origin of IR3 in middle of cell distal to subnodus; quadrangle parallel-sided, not widening distally; anal veins complete separated at base; pterostigma rhomboid, width c. 1.5 times the height; cells between Costa and R1 complete, undivided.
Abdomen. – Segments 1-6 pale brown, with distinct basal yellow annulae; segments 7-10 dark brown or brownish black. Appendages (Figs 91-92) grey, short and stout, superiors in dorsal view tapering, inner view shows large triangular top; inferiors very short, c. two-thirds the length of superiors, stout, the tip bifurcate.
Measurements. Hind wing 21; abdomen including appendages (approximate measurements, the abdominal segments 8-10 are broken) 31.5.
Female. – As the male, but posterior margin of posterior lobe straight without projections, lateral corners angulate; coloration of synthorax as the male.
Measurements. Hind wing 22-23 mm, abdomen 29-32 mm.

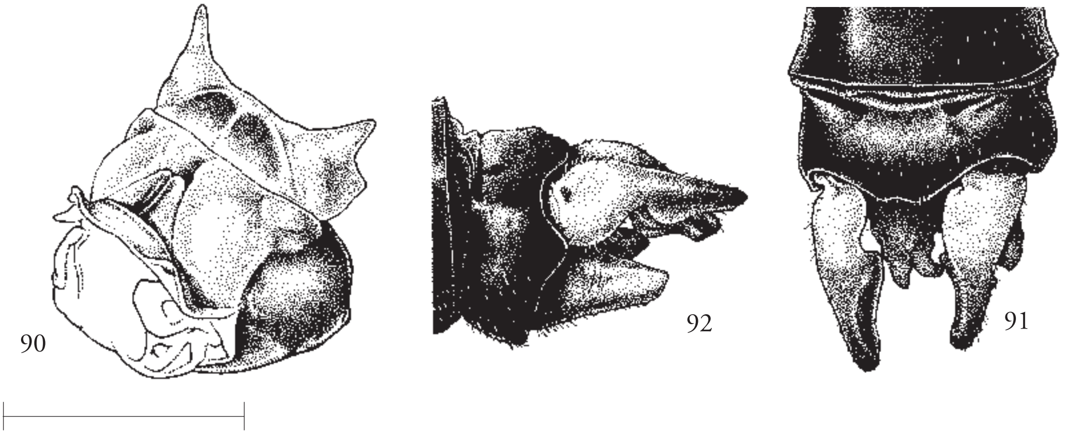
Etymology. – *Pallidus* (Latin), pale; for the coloration of the synthorax. An adjective.
Distribution (Fig. 109). – Philippines: Luzon (Nueva Vizcaya, Nueva Ecija, Quirino and Aurora provinces).

Sulcosticta striata van Tol, **sp. n.**

(Figs 93-95, 109)

Protosticta sp. n. 26. – Hämäläinen & Müller 1997: 258, 277 (Luzon).

Type material. – Holotype male [JvT 19219] in RMNH: 'Philippines, Luzon Id / Quirino/Aurora Boundary / Maddela, Mt Anaguao / 9.-14. August 1996, 800-1100 m / Celso M. Nazareno legit / Coll. Roland A. Müller'. – Paratypes (all



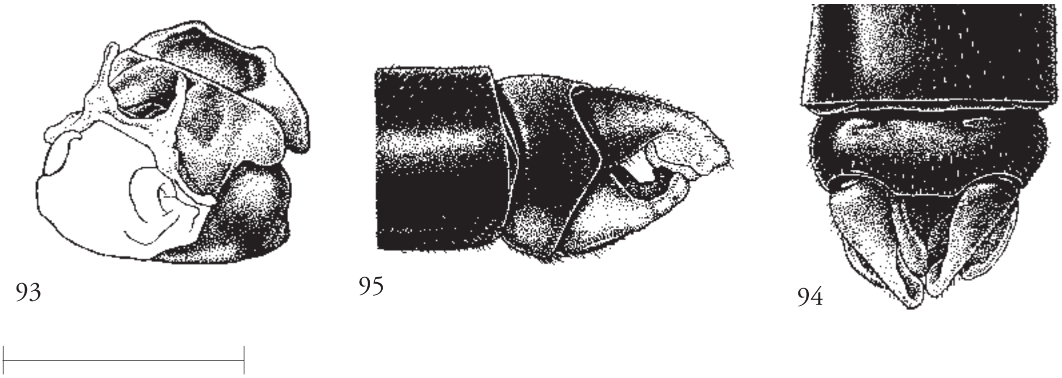
Figures 90-92. *Sulcosticta pallida* sp. n., male [JvT 22675, holotype, Luzon, Nueva Viscaya, Sta Fe, Atbo river, 550-800 m, 10.vi.1991]. – 90, pronotum, oblique view. – 91, anal appendages, dorsal view. – 92, idem, left lateral view. Scale bar 1 mm.

Philippine Islands, in RMNH, 7 males 1 female): **Luzon**. Quirino, Maddela, Sierre Madre, Mt Yadanan, Sitio Yadanan, 400-600 m, 15-30.viii.1996 (C.M. Nazareno) 1 male; Aurora province, Dinalungan, Mt Anaguao, Alebit river, 600-900 m, 9-14.iii.1997 (R.A. Müller) 1 male; Aurora Prov., Villa Maria, La-ab river, 360-500 m, 20-24.iii.1997 (R.A. Müller) 5 males 1 female.

Other material examined (Philippines, in RMNH). – Excluded from type series: Luzon, Camarines Norte, Sn Lorenzo Ruiz, Sitio Bay-Bay, Patag, 400-700 m, 24-25.ix.1997 (C.M. Nazareno) 1 female [JvT 25064].

Diagnosis. – Wing venation as in *Protosticta* Selys, male appendages distinct, with inferiors short, the top bifid; the shape of the inferior appendage of the male is also present in *S. pallida* sp. n., which differs considerably in the shape of the hind lobe of the pronotum, while that species also lacks the projections of the anterior lobe of the pronotum.

Male [JvT 19211, holotype]. – Head. Labium and mandibles bluish white, labium with a very narrow brown line along anterior border, and anterior one-fourth with brownish shade; anteclypeus bluish white, rest of head black, distinctly punctulate with bronze metallic shine; transverse occipital carina clearly defined, but without lateral extremities; antenna with scapus and pedicellus dirty yellow, flagellum brown. Thorax. Pronotum (Fig. 93) predominantly dirty yellow, with brownish black markings as follows: centre of middle lobe anterior to paired pronotal tubercles, lateral lobes in anterior and posterior quarters, median part of posterior lobe leaving a narrow pale line anterior and posterior to this marking. Anterior lobe with a paired long tapering process from anterior border of lobe, bending posteriad, the apical half curved nearly 90° from body axis; posterior lobe simple, posterior border only with sides indistinctly produced. Synthorax with complex markings of brownish black and creamish white: mesepisternum brownish black with narrow pale line along humeral suture, anteriorly above mesokatepisternum slightly widened, line not reaching posterior border of synthorax; mesokatepisternum brown with pale oblong marking near mesepisternum and against mesocoxa; mesepimeron pale, a dark stripe over humeral suture, a triangular dark marking against first suture anterior to level of metastigma, and an irregular oblong line posterior to that level; metepisternum pale, the lower half anterior to metastigma brown, a longer line over middle of metepisternum posterior to metastigma, covering approximately one-third of metepisternum, a small spot against first suture just anterior to posterior margin; metakatepisternum brown, metepimeron pale, a dark stripe over metapleural suture somewhat widening in middle, a small dark spot near anterior

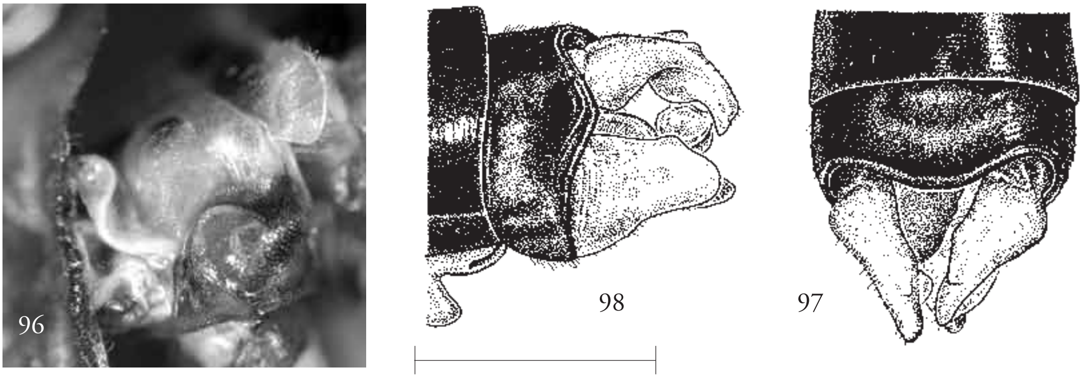


Figures 93-95. *Sulcosticta striata* sp. n., male [JvT 19220, Luzon, Aurora province, Dinalungan, Mt Anaguao, Alebit river area, 600-900 m, 9-14.iii.1997]. – 93, pronotum, oblique view. – 94, anal appendages, dorsal view. – 95, idem, left lateral view. Scale bar 1 mm.

corner, a dark oblong marking in lower posterior corner. Legs very pale. Wings hyaline, venation brown; Px 13 in fore wing, Px 12 (or 12½) in hind wing; R4+5 arising distinctly posterior to subnodus, especially in fore wing, IR3 arising at c. one-third of length of cell posterior to that level; Arculus distinctly posterior to Ax2; quadrangle not widening posteriorly, not even in fore wing; anal bridge absent (as in *Protosticta*); pterostigma approximately as wide as high, anterior and posterior sides convex in fore wing, proximal side more straight, but angulate, in hind wing; cells distal to pterostigma undivided.
Abdomen generally pale coloured with darker parts of segments 2-6 very pale brown; segment 1 dark brown, lateral parts and an annule against segment 2 creamish white; segment 2 creamish with large, crescent-shaped brown marking over full segment, enclosing medio-posteriorly a dark spot; segments 3-6 pale brown, all segments both anteriorly and posteriorly paler with annules of segments dark; segment 7 with anterior two-fifths bluish white, rest of segment 7 and segments 8-10 brownish black; segments 8-10 distinctly wider than preceding segments. Appendages (Figs 94-95) pale and short; base of superiors dorsally somewhat darker, base relatively slender and both appendages widely separate, the distal half turned 90˚ and thus dorso-ventrally oriented, the lower and distal margins sharp; inferiors wide and flattened, somewhat hollow, shorter than superiors, the tip emarginate with inner-tooth longer and curved dorsad.
Measurements. Hind wing 19 mm, abdomen including appendages c. 30 mm.

Female. – The only female assigned to this species is teneral and in rather poor condition; the processes of the anterior lobe of pronotum present, but much shorter than in male.
Measurements. Hind wing 19 mm, abdomen including appendages c. 30 mm.

Note. – The female from Quirino province mentioned in Hämäläinen & Müller (1997: 277) under note 26 [JvT 26990] is not conspecific and mentioned separately below under *Sulcosticta* sp. B. The female mentioned above and excluded from the type series [JvT 25064] is teneral and in poor condition. The projections of the posterior lobe of the pronotum are somewhat larger than in the other female assigned to this species. This specimen is preliminarily identified as *S. striata* sp. n.
Etymology. – *Striatus* (Latin), striped, for the coloration of the synthorax. An adjective.
Distribution (Fig. 109). – Philippine Islands: Luzon (Quirino, Aurora).



Figures 96-98. *Sulcosticta viticula* spec. nov., male [JvT 25062, holotype. Luzon, Zambales province, Masinloc, Mt Coto, Tal-tal, 400-700 m, 1-8.iv.1997]. – 96, pronotum, oblique view. – 97, anal appendages, dorsal view. – 98, idem, left lateral view. Scale bar 1 mm (for figures 97-98).

Sulcosticta viticula van Tol, **sp. n.**

(Figs 96-98, 109)

Type material. – Holotype male [JvT 25062]: Philippines, Luzon Id., Zambales Prov., Masinloc, Mt Coto, Tal-tal, 400-700 m, 1-8.iv.1997 (C.M. Nazareno) [in RMNH]. – Paratype (in RMNH): same data as holotype, 1 female.

Diagnosis. – Small and slender species with distinct pale longitudinal stripes over synthorax; Ab vein absent; male differs from other Philippine species with this combination of characters (*Protosticta annulata*, *P. lepteca* and *Sulcosticta striata*) by structure of inferior appendage: a subterminal process approximately diameter of appendage directed axiad, then posteriad, the tip brownish black and directed abaxiad; top of appendix rounded; combination of tips of appendage and large subterminal process superfically looking as bifid top. This combination otherwise only in the unnamed species from Polillo (*Sulcosticta* sp. A).

Male [JvT 25062, holotype]. – Head. Labium bluish white, anterior border with brownish shade only; mandibles with anterior two-thirds pale brown, rest bluish white; anteclypeus bluish white; rest of head black, distinctly coriaceous with bronze metallic shine; transverse occipital carina distinct, but without lateral extremities; antenna with scapus and pedicellus dirty yellow, flagellum brown.

Thorax. Pronotum (Fig. 96) predominantly dirty yellow, with dark brown markings as follows: centre of middle lobe anterior to paired pronotal tubercles, the lateral lobes, and median part of posterior lobe leaving a narrow pale line posterior to this marking. Anterior lobe erect with a paired projection near lateral corners, the projections short and erect; posterior lobe simple, posterior border laterally with rounded projections, approximately as long as median line of posterior lobe. Synthorax with complex markings of brownish black and creamish white: mesepisternum brownish black with narrow pale line along humeral suture, anteriorly above mesokatepisternum slightly widened, line not reaching posterior border of synthorax; mesokatepisternum brown with small pale marking above mesocoxa; mesepimeron pale, a dark stripe over humeral suture, an oblong triangular brownish black marking against first suture, anteriorly from halfway between mesocoxa and metastigma, tapering posteriorly to four-fifths of length of mesepimeron; metepisternum pale, the lower three-quarters anterior to metastigma brown, a longer line over middle of metepisternum posterior to metastigma, covering approximately one-third of metepisternum, narrow brown stripe against metapleural suture; metakatepisternum brown, metepimeron brown, a small pale spot in posterior corner. Legs very pale. Wing hyaline, venation brown; Px 11 in fore wing, Px

11 in hind wing; R4+5 arising at subnodus, IR3 arising halfway length of cell posterior to that level; Arculus distinctly posterior to Ax2; quadrangle somewhat widening posteriorly in fore wing; anal bridge absent (as in *Protosticta*); pterostigma 1.4 times as wide as high, anterior side acutely angulate; posterior side more rectangular; cells between Costa and R1 distal to pterostigma very few and undivided.
Abdomen rather pale coloured, with darker parts of segments 2-6 very pale brown; segment 1 dark brown; segment 2 brown with crescent-shaped pale markings in anterior lower corners; segments 3-6 pale brown, all segments with anterior one-tenth to one-seventh dirty white; segment 7 with anterior two-fifths white with a brown annule anteriorly, rest of segment 7 and segments 8-10 brownish black, shiny; segments 8-10 distinctly wider than preceding segments. Appendages (Figs 97-98) pale and short; base of superiors dorsally slightly darker; base relatively slender and the pair widely separate, curved inward, distal half turned 90˚, club-shaped, with inconspicuous dorsal tooth, ventral side straight; inferiors wide and flattened, top rounded, distal two-fifths with complicated curled structure: a subterminal, stoutly built process directed axiad, then posteriad, the tip brownish black and turned abaxiad.
Measurements. Hind wing 17 mm, abdomen including appendages c. 26 mm.

Female. – Generally as the male, but projections of anterior lobe of pronotum missing, lateral projections of posterior lobe of pronotum much smaller; pale markings on mesepimeron and metepisternum dististly larger in male, but generally of similar shape.
Measurements. Hind wing 18 mm; abdomen 29 mm.

Etymology. – *Viticula* (Latin), tendril; for the shape of the inward directed process of the inferior appendage. A noun in apposition.
Distribution (Fig. 109). – Philippine Islands: Luzon (Zambales).

Unplaced specimens

Drepanosticta indet. A

A female with coloration of synthorax as *D. moorei*, but without conspicuous projections on pronotum. Hind wing 24 mm, abdomen ca. 33 mm. Transverse occipital carina without lateral extremities.

Material examined (Philippines, in RMNH). – Luzon Id., Aurora Prov., Villa Maria, La-ab River, 360-500 m, 20-24. iii.1997 (R.A. Müller) 1 female [JvT 26989].

Drepanosticta indet. B

Material examined (Philippines, in RMNH). – Panaon Id., San Francisco, Batong Lapd, viii.1988 (W. Catal) 1 female [JvT 18618], and second label '*Drepanosticta lestoides* (Brauer), M. Hämäläinen det'.

A female with distinct lateral extremities of transverse occipital carina, pair of long projections on anterior lobe of pronotum and smoothly rounded posterior lobe of pronotum, synthorax with white stripe over metepisternum presumably represents a new species. Hind wing 20 mm, abdomen ca. 30 mm.

Sulcosticta sp. A

Material examined. – "Polillo, Philipp., 20.VIII.1915. G. Boettcher", 1 male (in SMFD) [JvT 26975].

Diagnosis. – Small and slender species with distinct pale longitudinal stripes over synthorax; Ab vein absent; male differs from other Philippine species with this combination of characters by structure of inferior appendages: short and tapering, distal one-fifth compressed and shining brown, the tip recurved dorso-axiad, tip ending in a comb of teeth. Apart from appendages very similar to *S. viticula* sp. n.

Male [JvT 26975]. – Head. Labium bluish white, anterior border with brownish shade only; mandibles with anterior two-thirds pale brown, rest bluish white; anteclypeus bluish white; rest of head black, distinctly coriaceous with bronze metallix shine; transverse occipital carina distinct, but without lateral extremities; antenna broken.

Thorax. Pronotum predominantly dirty yellow, with brown markings as follows: centre of middle lobe anterior to paired pronotal tubercles dark brown; lateral lobes castaneous; median part of posterior lobe brown, leaving a narrrow pale line anterior and posterior to marking. Anterior lobe erect with a paired projection near lateral corners, the projections short and erect; posterior lobe simple, posterior border laterally with rounded projections, approximately as long as median line of posterior lobe. Synthorax with complex markings of brownish black and creamish white: mesepisternum brownish black with narrow pale line along humeral suture, anteriorly above mesokatepisternum broadly widened, the line itself just reaching posterior border of synthorax; mesokatepisternum brown with small pale marking above mesocoxa; mesepimeron pale, a narrow dark stripe of humeral suture; metepisternum pale, the lower anterior three-quarters pale brown, a narrow brown stripe against metapleural suture; metakatepisternum castaneous; metepimeron castaneous, a small pale spot in anterior corner, posterior part somewhat paler than rest. Legs very pale yellowish white. Wings hyaline, venation brown; Px 12 in fore wing, Px 11 in hind wing; R4+5 arising well distal to subnodus, IR3 arising halfway length of cell posterior to that level; Arculus arising at Ax2; quadrangle hardly widening posteriorly; anal bridge absent (as in *Protosticta*); pterostigma 1.3 times as wide as high, subrectangular, anterior and posterior veins convex; cells between Costa and R1 distal to pterostigma very few and undivided.

Abdomen (broken and partly repaired). Rather pale coloured, with darker parts of segments 2-6 very pale brown; segment 1 castaneous with posterior pale yellow annule; segment 2 pale with crescent-shaped dark markings from lower latero-posterior corners to middle of segment anteriorly, a brown posterior annule; segments 3-6 pale brown, all segments with anterior one-tenth to one-seventh paler (indistinct, but this possibly due to poor preservation); segment 7 with anterior two-fifths pale brown, rest of segment 7 and segments 8-10 brownish black, shiny; segments 8-10 distinctly wider than preceding segments. Appendages (damaged and right superior appendage missing) pale and short, base relatively slender and the pair originally widely separate, curved inward, distal half turned 90° dorso-ventrad, club-shaped with inconspicuous dorsal tooth, ventral side curved, the tip distinctly angulate; inferiors wide, short, stout, and tapering, distal one-fifth compressed and shining brown, the tip recurved dorso-axiad, tip ending in a comb of short teeth.

Measurements. Hind wing 17 mm; abdomen with anal appendages ca. 26 mm.

Note. – Due to the poor state of conservation I have refrained from naming this specimen. Further studies on Polillo island may reveal new material of this phylogenetically interesting taxon.

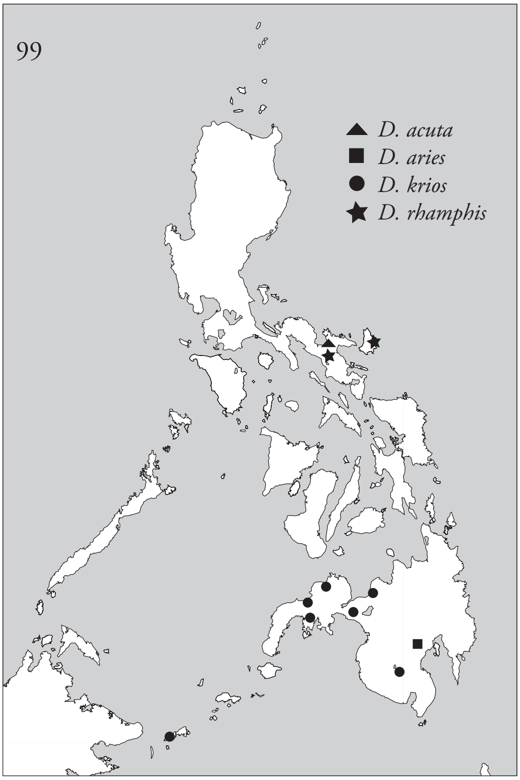
Distribution. – Polillo Island (off eastern Luzon).

Sulcosticta sp. B

Material examined. – Philippines, Luzon Id. Quirino, Maddela, Sierre Madre, Mt Yadanan, Sitio Yadanan, 400-600 m, 15-30.viii.1996 (C.M. Nazareno), 1 female [JvT 26990].

One female from Mt Yadanan in RMNH possibly belongs to the genus *Sulcosticta* as defined here, with pale thoracic markings and an Ab and Ac vein present, but separate at wing margin. Coloration of the synthorax is clearly different from *S. pallida* sp. n., while the presence of the Ab vein, plus the structure of the pronotum is distinct from *S. striata*. The latter species was also recorded from Mt. Yadanan, so a further study of this interesting complex of species is needed when more material becomes available. Hind wing 24 mm, abdomen ca. 33 mm.

Figures 99-102. Distribution of *Drepanosticta* species in the Philippines. – 99, *Drepanosticta aries* group. – 100, *Drepanosticta belyshevi* group. – 101, *Drepanosticta moorei* group. – 102, *Drepanosticta lymetta* group.



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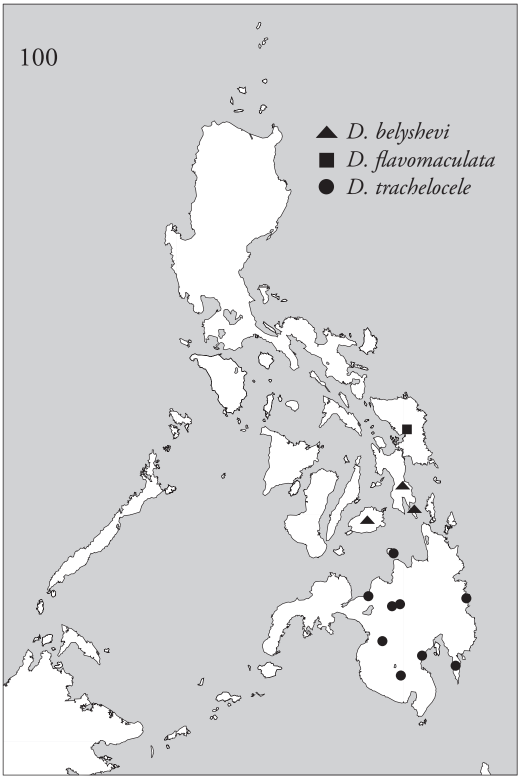

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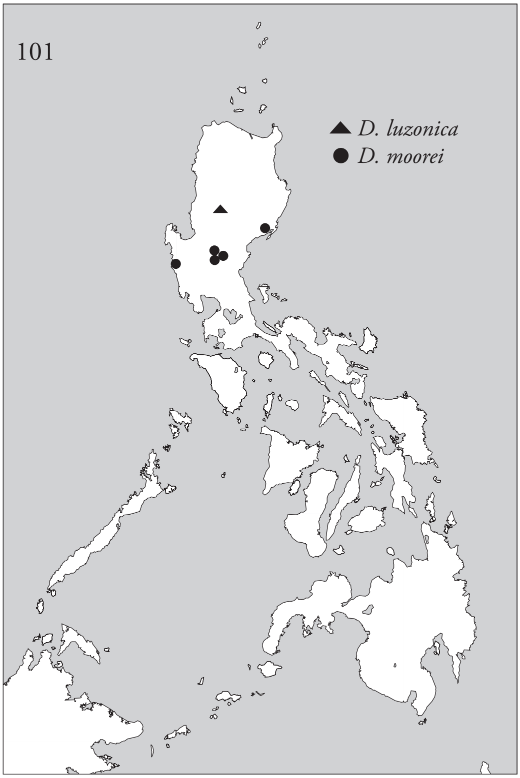

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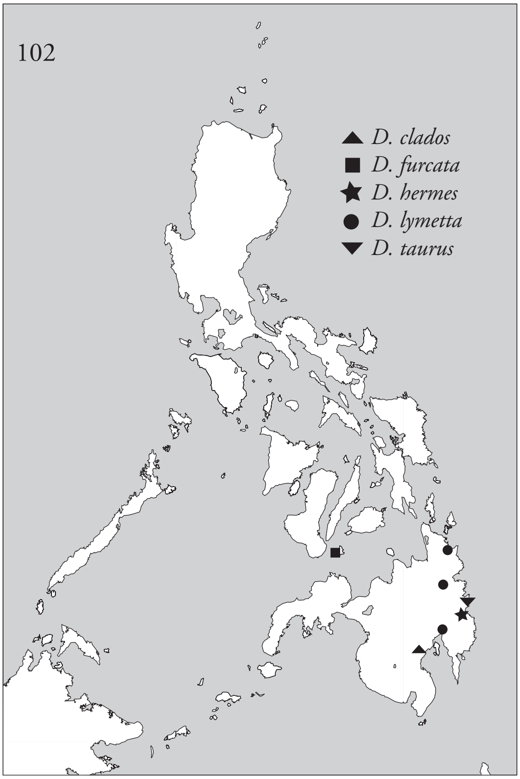

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Acknowledgements

The names of Roland A. Müller and Dr. Matti Hämäläinen will remain associated with the advancement of our knowledge of the odonates of the Philippines during the last 25 years of the 20th century. Roland A. Müller (St Gallen, Switzerland) brought together a huge and extremely rich collection between c. 1980 and 1997. Dr Matti Hämäläinen (Espoo, Finland) sorted, studied and identified all material. I am grateful to both colleagues for entrusting their collections to Museum Naturalis, and leaving the scientific study of some parts to me. Matti Hämäläinen had expertly sorted the specimens, and I have followed most, but not all, of his opinions on species delimitation; of course all decisions shall be considered mine. Dr. Hämäläinen showed me for study the specimens of SMFD he had on loan, and also kindly reviewed a draft of this paper.
Thanks are due to the staff artists of the National Museum of Natural History, Leiden, the Netherlands, Bas (S.B.) Blankevoort, Erik Jan Bosch and Inge M. van Noortwijk for preparing such attractive illustrations of this remarkable group of damselflies.
The specimens of *Protosticta plicata* sp. n. were collected by Dr. F. Seidenschwarz and Mr. Borromeo during a biodiversity survey on Cebu, and were kindly put at my disposal for this paper via Dr. M. Hämäläinen. Mr. Reagan J. Villanueva (Davao City, Philippines) presented the specimens of *Drepanosticta clados* sp. n. to the Leiden Museum, and guided me to some interesting sites in northern Mindanao in April 2004.
Finally, I am grateful to Steve Brooks (BMNH), James K. Liebherr (CUIC) and Philip D. Perkins (MCZC) for loan of material or information on material in the collections under their care.

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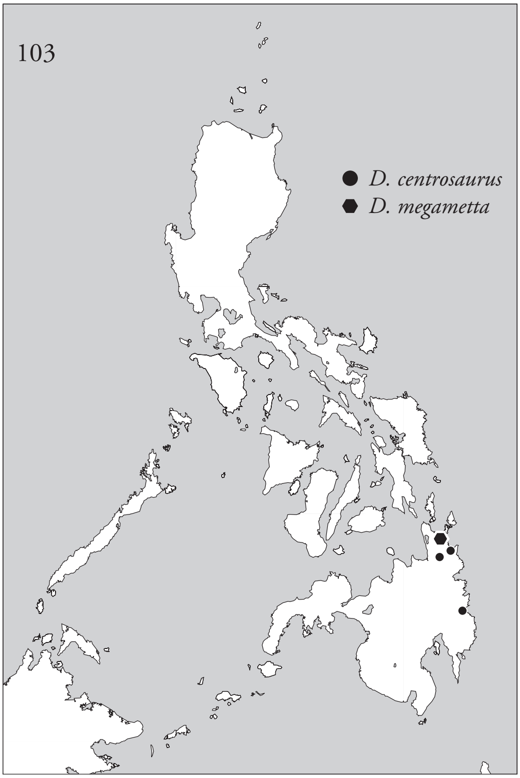
Figures 103-106. Distribution of *Drepanosticta* species in the Philippines. – 103, *Drepanosticta megametta* group. – 104, *Drepanosticta lesttoides* Brauer. – 105, *Drepanosticta mylitta* Cowley. – 102, *Drepanosticta pistor* sp. n.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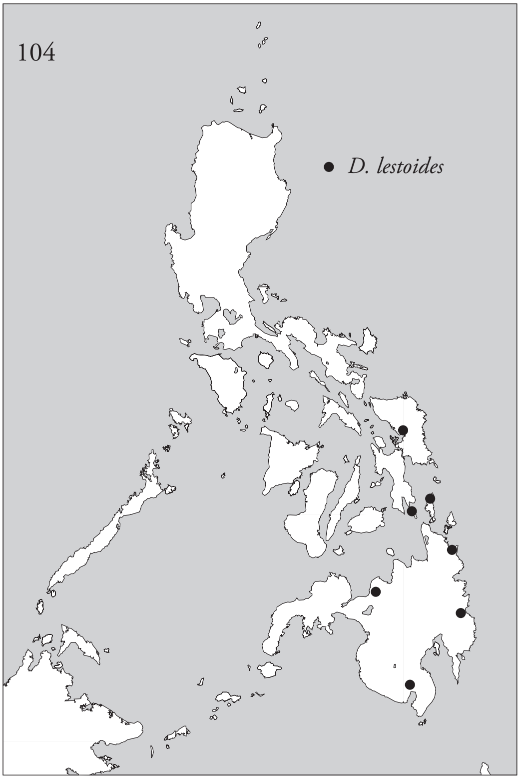
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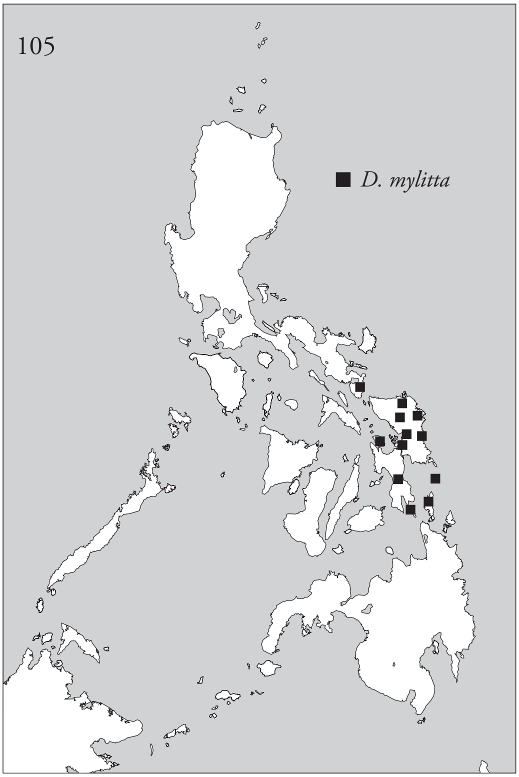
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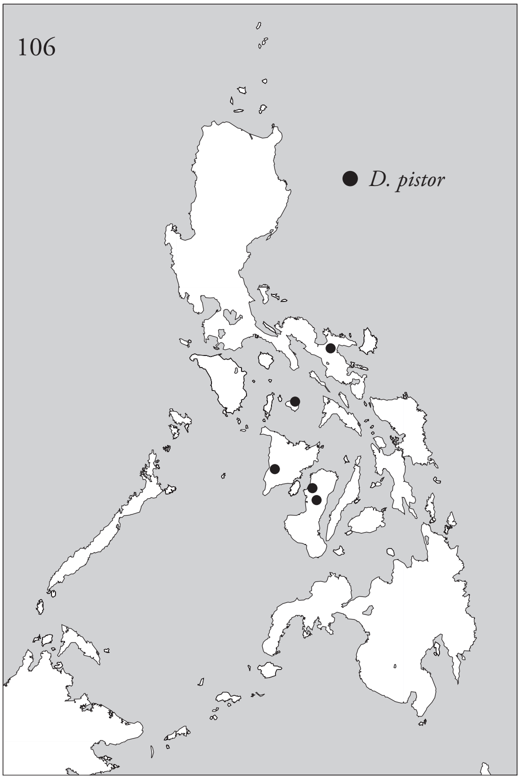
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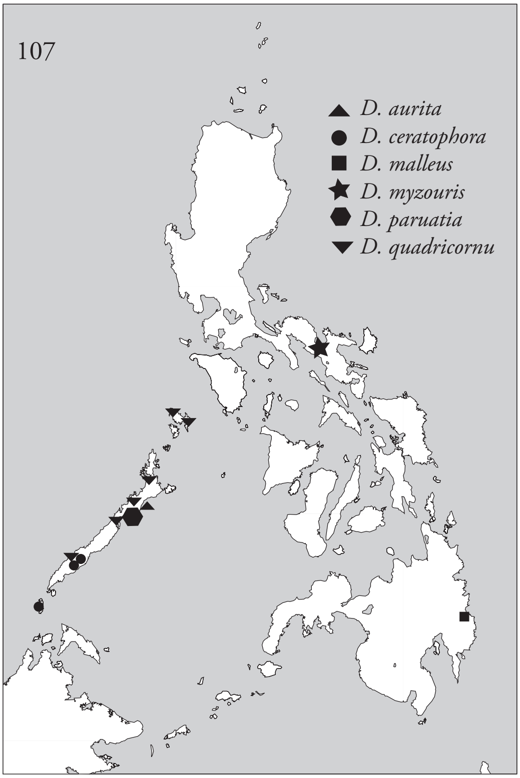

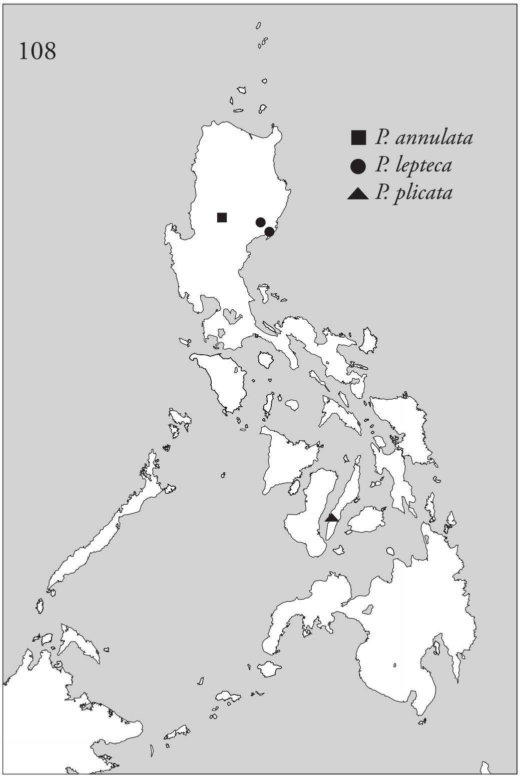

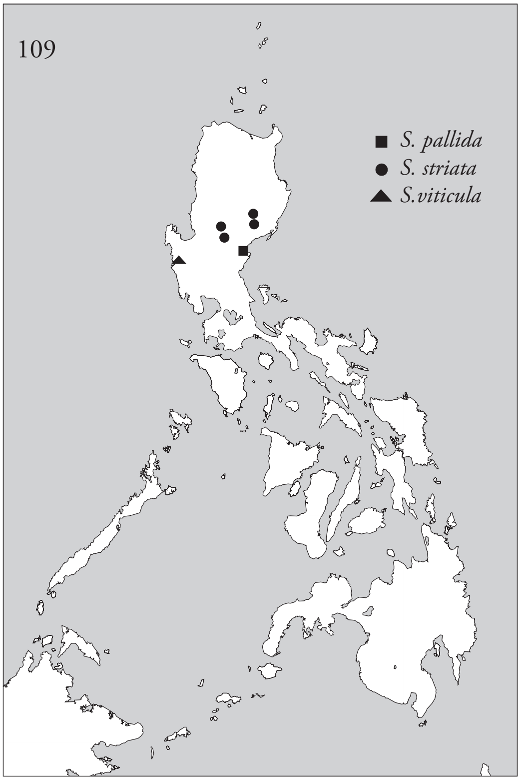

Figures 107-109. Distribution of Platystictidae in the Philippines. – 107, Distribution of *D. aurita* sp. n., *D. ceratophora* Lieftinck, *D. malleus* sp. n., *D. myzouris* sp. n., *D. paruatia* sp. n., *D. quadricornu* sp. n. – 108, Distribution of the species of *Protosticta* Selys. – 109. Distribution of the species of *Sulcosticta* gen. n.

6. The Odonata of Sulawesi and adjacent islands. Part 5. The genus *Protosticta* Selys (Platystictidae)

J. van Tol

Abstract

Tol, J. van, 2000. The Odonata of Sulawesi and adjacent islands. Part 5. The genus *Protosticta* Selys (Platystictidae). – Tijdschrift voor Entomologie 143: 221-266, figs 1-113, table 1. [ISSN 0040-7496]. Published 1 December 2000.

The type species of the genus *Protosticta* Selys, *P. simplicinervis* Selys, was described from Sulawesi (formerly Celebes, Indonesia). The present paper provides a revision of all Sulawesi species of the genus, and those of the adjacent island of Buton and the Sangihe Islands. Twelve species are recognized, three of which were previously known (*P. bivittata* Lieftinck, *P. gracilis* Kirby, and *P. simplicinervis*). One nominal species, *P. annulata* Fraser, appeared to be a synonym of *P. simplicinervis*. Consequently, nine species are described as new to science, viz. *P. coomansi* (type locality: Palu: Lindu valley), *P. geijskesi* (type locality: NNE of Malili), *P. linduensis* (type locality: Polewali), *P. marenae* (type locality: Palu: Lindu valley near Gimpu), *P. maurenbrecheri* (type locality: NW of Palopo), *P. pariwonoi* (type locality: N of Ujung Pandang: Maros), *P. reslae* (type locality: Polewali), *P. rozendalorum* (type locality: Sangihe Islands) and *P. vanderstarrei* (type locality: Polewali). Characters of importance for species recognition are the thoracal and abdominal markings, and the structure of the prothorax and anal appendages in the male. Diagnostic characters of females include the structure of prothorax and anal appendages. The females of four species are unknown. The status of the genus *Protosticta* of the family Platystictidae is preliminarily discussed. Its high diversity in Sulawesi is in contrast with the complete absence of Platycnemididae and Euphaeidae, and the virtual absence of the Protoneuridae from this island. Besides, various species as here recognized, show significant variation between populations. The morphological variation is clinal in some species (*P. coomansi*, *P. geijskesi*), presumably related to the geological history of the island.

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Key words. – Platystictidae; *Protosticta*; Sulawesi; Malesia; new species.

Introduction

The composition of the flora and fauna of Sulawesi (formerly Celebes) was the subject of various analyses in the 19th century (e.g. Wallace 1890), resulting in the hypothesis that the biotas of this island are a mixture of Oriental and Australian elements. The fauna has been extensively studied and described during the last 25 years (e.g. Whitmore 1981, 1987; Holloway 1990; Knight & Holloway 1990). The Odonata fauna of the island is no exception to the general pattern of absence of otherwise widespread groups, and remarkable radiation and high endemism in other groups. For instance, the Gomphidae are only represented by two species in Sulawesi, while this family is speciose and also very diverse at the generic level in Borneo. The damselfly families Euphaeidae

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Table 1
List of species included in *Protosticta* Selys. Species of *Protosticta* not occurring in Sulawesi have not been examined.

Name		Range
1	*antelopoides* Fraser, 1931b: 467	India: Travancore
2	*beaumonti* Wilson, 1997: 57	Hongkong, Guangdong
3	*bivittata* Lieftinck, 1939: 151	SW Sulawesi
4	*coomansi* sp. n.	Sulawesi
5	*curiosa* Fraser, 1934: 134	Lower Burma, western and southern Thailand
6	*damacornu* Terzani & Carletti, 1998: 481	NE India, East Khasi Hills
7	*davenporti* Fraser, 1931: 70	Southern India
8	*feronia* Lieftinck, 1933: 281	Borneo (NW and W)
9	*foersteri* Laidlaw, 1902: 383	Peninsular Malaysia
10	*fraseri* Kennedy, 1936: 67	Assam
11	*geijskesi* sp. n.	Sulawesi
12	*gracilis* Kirby, 1889: 302	Northern Sulawesi
13	*grandis* Asahina, 1985: 334	Northern and western Thailand
	syn. *robusta* Asahina, 1984: 590 [primary homonym of *Protosticta robusta* Fraser]	
14	*gravelyi* Laidlaw, 1915a: 389	Southern India
	syn. ? *mortoni* Fraser, 1924: 500	Southwestern India
	syn. *stevensi* Fraser, 1922: 7	
15	*hearseyi* Fraser, 1922: 5	Southern India
16	*himalaiaca* Laidlaw, 1917: 342	Northern Bengal, Assam, Sikkim
	syn. *lindgreni* Fraser, 1920: 150	
17	*khaosoidaoensis* Asahina, 1984: 588	Northern and SE Thailand
18	ssp. *satoi* Asahina, 1997: 108	Northern Vietnam
19	*kiautai* Zhou, 1986: 465	China (Zhejiang)
20	*kinabaluensis* Laidlaw, 1915b: 37	Borneo (N)
21	*linduensis* sp. n.	Sulawesi
22	*marenae* sp. n.	Sulawesi
23	*maurenbrecheri* sp. n.	Sulawesi
24	*medusa* Fraser, 1934: 135	Lower Burma, western Thailand
25	*pariwonoi* sp. n.	Sulawesi
26	*reslae* sp. n.	Sulawesi
27	*robusta* Fraser, 1933b: 111	Laos
28	*rozendalorum* sp. n.	Sangihe Islands
29	*rufostigma* Kimmins, 1958: 349	S India, Tinnevelly District
30	*sanguinostigma* Fraser, 1922: 6	Southern India
	syn. *cerinostigma* Fraser, 1924: 499	
31	*simplicinervis* (Selys, 1885): cxlv	Sulawesi
	syn. *annulata* Fraser, 1926: 492	
32	*taipokauensis* Asahina & Dudgeon, 1987: 2	Hong Kong
33	*trilobata* Fraser, 1933b: 112	Laos
34	*uncata* Fraser, 1931a: 75	Burma
35	*vanderstarrei* sp. n.	Sulawesi
36	*versicolor* Laidlaw, 1913: 78	Borneo (NW)

Note: The only species originally described in *Protosticta* and now assigned to another genus is *Protosticta carmichaeli* Laidlaw, 1915a: 390, which is the type species of *Drepanosticta* Laidlaw, 1917

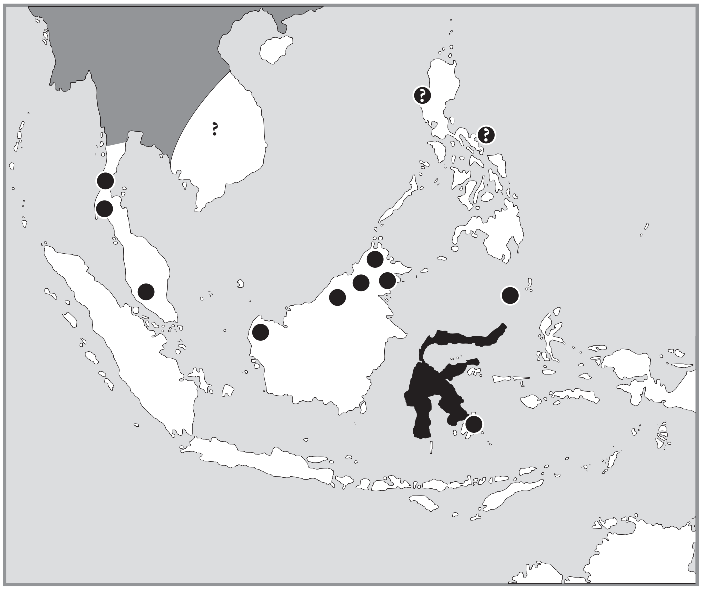


Figure 1. Distribution of the genus *Protosticta* Selys in Southeast Asia. Distribution on mainland roughly indicated only. Species from the Philippines doubtfully belonging to *Protosticta.*

and Platycnemididae are even completely absent from Sulawesi, while hardly any stream in Borneo is without at least a few species of these families. On the other hand, the family Chlorocyphidae is remarkable diverse in Sulawesi with even three endemic genera (van Tol 1998). In the genus *Libellago* Selys, 1840 (Chlorocyphidae) much variation has been noticed in various species, warranting the description of several new species (van Tol in prep.). The subject of this paper, the genus *Protosticta* Selys, 1885 of the Platystictidae, is another example of radiation in Sulawesi, a fact also noticed in such diverse groups as macaques, cicadas (Duffels 1990) and waterstriders (Polhemus & Polhemus 1988, 1990). Similar to these groups, various species in *Protosticta* show small distributional ranges, defining areas of endemism. The present paper is the fifth in a series devoted to the Odonata of Sulawesi (no. 4, see van Tol 1998). In a summarizing paper the phylogeny and biogeography of the Sulawesi Odonata will be central. No recent overview of the Sulawesi dragonflies is available. The last general list was published by Selys (1878). This publication also includes the interesting biogeographical account ‘Considérations sur la fauna de la Nouvelle Guinée, des Moluques et de Célèbes’.

Terminology. The terminology of the anatomy generally follows Watson & O’Farrell (1991); in several cases I have added alternative, frequently used terms in brackets. The abbreviations of the names of the institutions are explained in the acknowledgements; the coden RMNH is used for the National Museum of Natural History Naturalis at Leiden (formerly Rijksmuseum van Natuurlijke Historie).

The family Platystictidae

The family Platystictidae (Odonata: Zygoptera) has a transpacific distribution and contains the three subfamilies Palaemnematinae, Platystictinae and Sinostictinae. The Palaemnematinae, with *Palaemnema* Selys, 1860 as single genus included, occurs in Central America and the northern part of South America. At present 42 valid species are recognized (Garrison 1991). The Palaemnematinae are characterized by a CuP vein extending over halfway along the posterior border of the wing (Fig. 2). The speciose second subfamily, the Platystictinae, is known from the westernmost part of the Oriental region eastwards to the Papuan region. Not a single species is known from Australia. The CuP of the Platystictinae ends in the basal half of the posterior border of the wing. Recently, a third subfamily, Sinostictinae, has been proposed for *Sinosticta* Wilson, 1997, a genus of Platystictidae only known from Hong Kong (Wilson 1997), with one species included, viz. *S. ogatai* (Matsuki & Saito, 1996). As in the Palaemnematinae, *S. ogatai* has a long

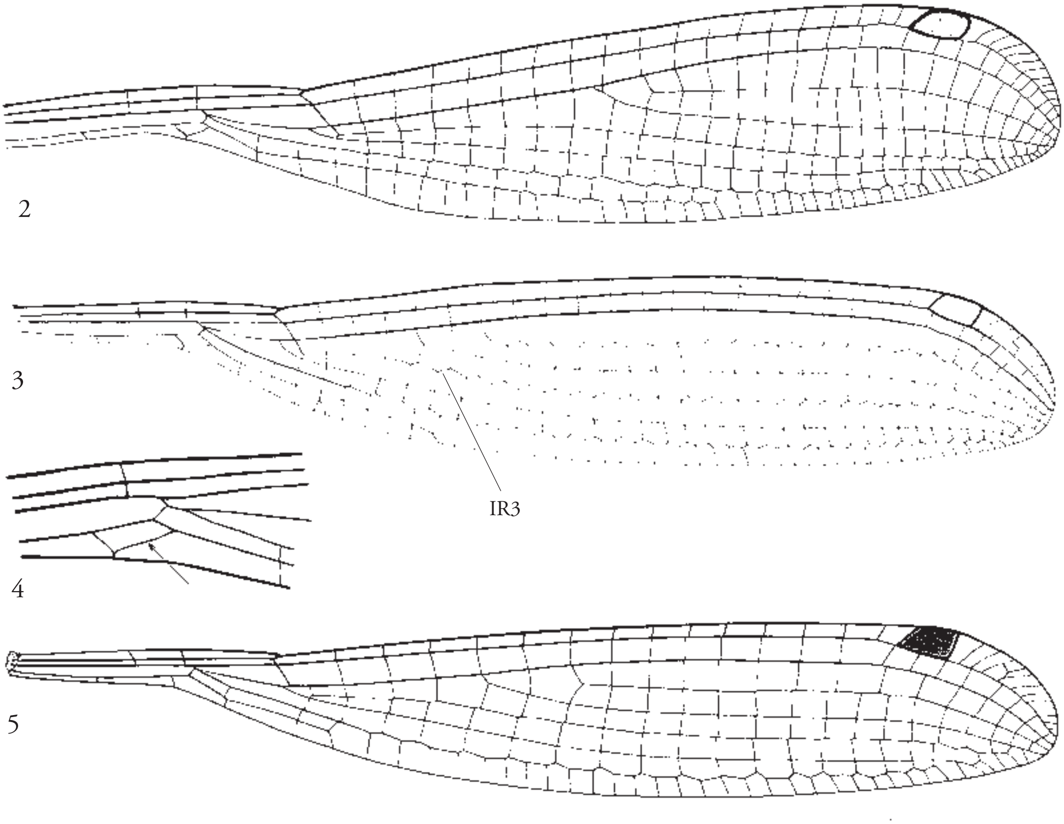
CuP vein, ending in the distal half of the wing border. Besides, it has two to four supplementary postcubital cross-veins in addition to the usual postcubital cross-vein. Unfortunately, this character is not properly illustrated in the photographs and drawings published up to now.

Three genera are recognized within the Platystictinae, *Platysticta* Selys, 1860, *Protosticta* Selys, 1885 and *Drepanosticta* Laidlaw, 1917. The last genus consists of 85 nominal species (84 valid species). *Platysticta* Selys, 1860 (syn. *Ceylonosticta* Fraser, 1931a) has only two valid species (one with two recognized subspecies). It is mainly confined to Sri Lanka (Ceylon), with only *P. maculata deccanensis* Laidlaw, 1915a also occurring in southern India (Fraser 1933a: 126). *Protosticta* presently includes 27 valid species and subspecies (table 1), to which number I add nine new species in this paper.

The most distinct diagnostic character for the Platystictidae, the presence of a supplementary crossvein in the cubito-anal space at the wing base, is, disputably, a synapomorphy for the group. At least Fraser (1957: 41-42) considers this character homologous to the cross-vein found in *Kennedya* Tillyard, 1925 (Protozygoptera: Kennedyidae), a genus described from the Lower Permian. If that hypothesis holds true, this character is a symplesiomorphy for the species of the Platystictidae, so that the monophyly of the Platystictidae has not been established as yet. Then, it is also uncertain to which extent the Platystictinae differ from the Oriental Protoneuridae, with which they share the reduced 1A and CuP veins and several other characters. For the present, I consider the Platystictinae a monophyletic group, based on admittedly weakly founded apomorphies in the shape of the pterostigma and the 'bauplan' of the male appendages. Although the general appearance of some species of *Palaemnema* and some of *Protosticta* is remarkably similar, the sister-group relationship of the Palaemnematinae to the Platystictinae (or Platystictinae+ Sinostictinae) is not soundly established as yet.

The characters traditionally used to distinguish the genera *Platysticta*, *Protosticta* and *Drepanosticta* of the Platystictinae, are given in the key below. Within the Platystictinae, no synapomorphy is known for the species now united in *Drepanosticta*, while the genus *Protosticta* is characterized by the absence of the Ab vein, a cross-vein running from the posterior side of the quadrangle to the posterior margin of the wing or the anal crossing in *Drepanosticta*. Consequently, *Drepanosticta* and *Protosticta* can not be considered valid genera based on this character. This was already foreseen by Laidlaw (1917: 340), in his original diagnosis of *Drepanosticta*, where he noticed that 'the distinction between *Drepanosticta* and *Protosticta* is not of great importance and is liable in individual cases to break down'. A comparison of the larvae of species assigned to either *Protosticta* or *Drepanosticta* (Lieftinck 1934: 468) revealed no important generic distinction. Lieftinck also remarked (p. 464) that *Drepanosticta* is 'a genus very closely allied to *Protosticta*, differing from this only in venational characters of but slight importance'. These statements are based on various observations. At the specific level, Lieftinck (1933: 285) noticed a very close similarity between a *Protosticta* and a *Drepanosticta* '... Indeed I am inclined to think that [*Protosticta*] *feronia*, although immediately distinguished from [*Drepanosticta*] *dupophila* by the generic character found in the anal veins, is closely related to that species, for I can hardly imagine that so striking a similarity can be brought forward by convergence only'. My own studies of both species confirm Lieftinck's observations. These two species share at least one strong and unique character within the Platystictinae, which was apparently overlooked by Lieftinck, making it even more likely that a phylogenetic study will result in a complete new generic subdivision of this subfamily.

However, several presumably monophyletic subgroups in *Drepanosticta* and possibly also in *Protosticta*, differ sufficiently from each other to be distinguished as different genera. Since this is also true for the species groups to which the type species of both genera are assigned, I have refrained from synonymizing *Drepanosticta* and *Protosticta*. The type species of *Protosticta*, *P. simplicinervis*, is a Sulawesi species, and all Sulawesi species lacking the Ab vein have been assigned to *Protosticta* in the present paper. However,



Figures 2-5. Hind wings. – 2, *Palaemnema domina* Calvert (Guatemala); 3, *Platysticta maculata deccanensis* Laidlaw (Travancore, 29 Sep 1932); 4, *Drepanosticta ephippiata* Lieftinck (JvT 11861, NW Sulawesi, Dumoga Bone NP); 5, *Protosticta simplicinervis* Selys (N. Sulawesi. – illustration from M.A. Lieftinck archives).

it is unlikely that this character will prove to be an autapomorphy for *Protosticta*. Based on the analysis of characters as general appearance, coloration and structure of secondary genitalia, several species of Sulawesi Platystictinae here assigned to *Protosticta* possibly make the genus concept non-monophyletic. The most prominent example is *P. vanderstarrei* sp. n., a small, slender and dark species, in general appearance more similar *Drepanosticta ephippiata* Lieftinck, than to other species of *Protosticta* described from Sulawesi in this paper. It has been incorporated in the present paper as a *Protosticta*, since it lacks the Ab vein. Platystictidae from the Philippines, as yet undescribed, possibly are more closely allied to *P. vanderstarrei.* I also have studied two new species of *Drepanosticta* in the present sense from SE Sulawesi and Kabaena (off SE Sulawesi), which are more similar in general appearance to *Protosticta* than to the other species of *Drepanosticta* of Sulawesi (RMNH Leiden). With the same arguments, I have left them for my future paper on the Sulawesi *Drepanosticta* species. After these revisions, I hope to able to present a phylogeny of the Platystictidae, resulting in at least a subdivision of the subfamily Platystictinae into monophyletic genera.

SYSTEMATIC PART

Platystictidae

Platystictinae. – Laidlaw 1924a: 360
Platystictidae. – Fraser 1957: 41; Davies & Tobin 1984: 103.

The genera included in the Platystictinae can be distinguished by the following characters (modified after Laidlaw 1917, 1924b).

1. IR3 (= radial sector) markedly fractured (Fig. 3) (anal bridge present, joining Anal crossing Ac, sectors of Arculus not stalked) . . . . *Platysticta* Selys
– IR3 straight (Fig. 5) 2
2. Anal bridge present, joining Anal crossing or hinder margin of wings, sectors of Arculus stalked (Fig. 4) . . . . *Drepanosticta* Laidlaw
– Anal bridge absent (Fig. 5) . . . . . . *Protosticta* Selys

Protosticta Selys

Protosticta Selys, 1885: cxlv (as subgenus of *Platysticta*, original diagnosis, type species *Protosticta simplicinervis*).– Laidlaw 1917: 339-343 (generic characters); Laidlaw 1924b: 306-307 (generic characters, notes on species); Bridges 1994: III.43 (catalogued).

Characters. – As mentioned above. The original diagnosis by Selys reads as follows (my translation of the French text): 'Very similar to subgenus *Platysticta* (sensu stricto) from which it only differs by the absence of the rudiment of the inferior sector of the triangle, so that it resembles (but only in this respect) the genuine *Alloneura* in which this rudiment is also lacking. But it possesses, like the other two subgenera of *Platysticta* a basal supplementary post-cubital vein between the wing base and the normal [? pcv], that is characteristic of this large genus and which I unjustly did not mention when I erected it'.

Distribution. – The genus *Protosticta* has been recorded from India (Fraser 1933a), Burma and Thailand (Asahina 1984, Hämäläinen & Pinratana 1999), Laos (Fraser 1933b), Vietnam (Asahina 1997), China (Guangdong and Zhejiang provinces) (Zhou 1986, Wilson 1997), Hong Kong (e.g. Wilson 1995), the Malaysian peninsula and Borneo (Lieftinck 1954), Celebes (Sulawesi) (Selys 1885, Lieftinck 1939), and the Philippines (see below). In India, most species have been recorded from the southern part of the country (cf. table 1), but others are confined to Assam. Although Odonata have been collected in Borneo in most parts of the island, not a single specimen of *Protosticta* is available from the southeastern part (Fig. 1). Both firstly described species of *Protosticta*, *P. simplicinervis* Selys, 1885, and *P. gracilis* Kirby, 1889, are from Celebes. Species of Platystictidae with generic characters of *Protosticta* in the present sense, have been mentioned from the Philippine islands of Luzon and Polillo (Hämäläinen & Müller 1997). Recently, RMNH Leiden purchased the collection of R.A. Müller, which enabled me to examine these specimens. Although the wing characters of these undescribed species indicate a position in *Protosticta*, I consider it more likely that a phylogenetic analysis will reveal a close relationship to other Platystictidae of the Philippines now attributed to *Drepanosticta*, rather than to *Protosticta* from Sulawesi. Therefore, I have indicated the locations of the Philippine *Protosticta* (Fig. 1) with question marks.

In the present paper, not only species found in Sulawesi proper, but also those collected on Sangihe island, located north of NE Sulawesi, are treated. One of the most common and widespread species of Sulawesi is recorded here from Buton, an island off SE Sulawesi. The distributional data, as given in table 1 and Fig. 1, indicate that no species of this genus has ever been collected on Sumatra, Java, the Lesser Sunda islands, the Moluccas and New Guinea. Almost certainly these data reflect reality, since quite intensive collecting of Odonata was executed on these islands. Moreover, many specimens of *Drepanosticta* Laidlaw are known from these places, indicating the careful search for Platystictidae in relevant habitat.

Infrageneric relationships. – Awaiting a generic revision, the Sulawesi species can be divided into the following 'species groups'. The relationships of these groups to each other, and to other species of *Protosticta*, are presently not clear, and I have refrained from using the groups in arranging the species in this paper.

The *bivitatta*-group. – With *P. bivittata* and *P. maurenbrecheri,* characterized by the presence of an antehumeral stripe.

The *geijskesi*-group. – With *P. geijskesi*, *P. linduensis*, *P.*

marenae and *P. pariwonoi*, characterized by the 'boxing glove' inferior anal appendage.

The *gracilis*-group. – With *P. coomansi*, *P. gracilis* and *P. reslae*, characterized by the sharp and long inner tooth of the inferior anal appendage, and blue coloured dorsum of abdominal segment 10.

The *rozendalorum*-group. – With *P. rozendalorum*, characterized by the shape of the appendages.

The *simplicinervis*-group. – With *P. simplicinervis*, characterized by the tubercles of the median lobe of the prothorax.

The *vanderstarrei* group. – With *P. vanderstarrei*, characterized by small size, the dark colouration, and the very short stripe over synthorax.

Key to the males of *Protosticta* species of Sulawesi

1. Dark and small species; hind wing 19-22 mm; abdominal segment 8 brownish black without pale markings; synthorax dark castaneous, with short yellowish, or somewhat bluish pale stripe over metepisternum; metepimeron and metakatepisternum brownish black, without any trace of pale coloration (Fig. 89) . . . . *P. vanderstarrei* sp. n.

– Larger species; hind wing more than 23 mm; more conspicuous pale markings on synthorax, especially pale markings on metepimeron and metakatepisternum and abdominal segment 8 . . . 2

2 (1) Dorsum of abdominal segment 10 black; all species with reduced inner-tooth of inferior appendage; species with blue coloration on abdominal segments 8-9 have mandibles with at least anterior half brownish black, usually black except for a small basal pale spot 3

– Dorsum of abdominal segment 10 blue, discoloured in poorly preserved specimens, but always recognizable; inferior appendage variable . 7

3 (2) Superior anal appendage with a ventral tooth approximately halfway, particularly well visible from innerside (Fig. 46), dorsal tooth absent; inferior appendage with stout terminal structure, the innertooth connected with the distal part by a chitinous veil (Fig. 45). Sangihe Islands . . . . *P. rozendalorum* sp. n.

– Superior anal appendage without ventral tooth, but with a more or less distinct dorsal tooth, but never with a tooth directed ventrad; top of inferior appendage a 'boxing glove' (e.g. Fig. 20) 4

4 (3) Anterior lobe of prothorax with lateral sides significantly widened, particularly well visible in lateral view (Figs 62, 64) 5

– Anterior lobe of prothorax with fore and hind margin parallel-sided; both margins may be somewhat raised, but lateral parts not a disc with raised margins 6

5 (4) Larger species, abdomen of males 26-27 mm; anterior lobe of prothorax significantly widened (Fig. 62); inferior anal appendage stoutly built (Fig. 28-29) . . . . *P. linduensis* sp. n.

– Smaller species, abdomen of male 23-24 mm; anterior lobe of prothorax less widened (Fig. 64); inferior appendages less robust (Fig. 32- 33) . . . . *P. marenae* sp. n.

6 (4) Hind margin of posterior lobe of prothorax simple without distinct characters (but in some populations with more or less erect teeth), and anterior margin of anterior lobe only with a slender ridge (Fig. 58). Variable species . . . *P. geijskesi* sp. n.

– Hind margin of posterior lobe of prothorax with more or less erect teeth, and anterior margin of anterior lobe distinctly swollen (Fig. 68) . . . . *P. pariwonoi* sp. n.

7 (2) Synthorax with distinct antehumeral stripe; dorsal spine on superior anal appendage large and approximately halfway; tip of inferior appendage stout and pointed, not curled (Figs 9, 36) 8

– Synthorax anterior to humeral suture concolorous, without antehumeral stripe; dorsal spine on superior anal appendage smaller and less distinct; extreme tip of inferior appendage with hook-like structure, which may be inconspicuous or as big as the base of the tip (e.g. Fig. 13) 9

8 (7) Large species (hind wing > 26 mm); innertooth of inferior appendage huge and shiny (Fig. 9) . . . . *P. bivittata* Lieftinck

– Smaller species (hind wing < 25 mm), innertooth of inferior appendage inconspicuous (Fig. 36) . . . . *P. maurenbrecheri* sp. n.

9 (7) Middle lobe of prothorax distinctly raised to paired cone-like protuberance (Fig. 74); hooklike tip of inferior appendage huge (Fig. 49) . . . . *P. simplicinervis* Selys

– Middle lobe of prothorax smooth, without cone-like protuberance; hook-like tip of inferior appendage usually inconspicuous to hardly visible . 10

10 (9) Protuberance (tooth) on dorsal side of superior appendage at approximately two-thirds from base of appendage; tip of superior appendage distinctly broadened in lateral view (Fig. 40) . . *P. reslae* sp. n.

– Protuberance approximately halfway or in basal half of superior appendage 11

11(10) Innertooth of inferior appendage huge and rather basal, in dorsal view its base approximately at level of dorsal spine of superior appendage, its tip nearly reaching the visible base of appendages (Fig. 23-24) . . . . *P. gracilis* Kirby

– Innertooth, although very variable, much smaller, in dorsal view the tip approximately at level of dorsal tooth of superior appendage (Figs 12-16) . . . . *P. coomansi* sp. n.

Key to the females

Species of the following species are unknown: *Protosticta gracilis*, *P. linduensis*, *P. maurenbrecheri*, and *P. reslae*.

1. Synthorax with antehumeral stripe; anterior half of dorsum of abdominal segment 9 pale (Fig. 98); abdominal segment 9 and valvae short (Fig. 90). Hind wing 42-44 mm . . . . . . *P. bivittata* Lieftinck
Note: *P. maurenbrecheri* will probably also key out here; it may at least be distinguished from *P. bivittata* by its smaller size.

– No antehumeral stripe 2

2 (1) Middle lobe of prothorax with a paired protuberance; robust species . *P. simplicinervis* Selys

– Middle lobe of prothorax flat or only somewhat convex, without a paired protuberance 3

3 (2) Small and dark species with stripe above metastigma very short (cf. Fig. 89); valve very short (Fig. 97) . . . . *P. vanderstarrei* sp. n.

– Larger species, with stripe above metastigma longer; valve longer 4

4 (3) Hind margin of prothorax with sharp and distinctly erect lateral corners 5

– Hind margin of prothorax acute, sharp or bluntly shaped, but without distinctly erect lateral corners 6

5 (4) Pale markings at sides of segment 9 of abdomen usually in lower half only, thus not or only just visible in dorsal view (Fig. 92, 100). Widespread in Sulawesi, including Southwest Sulawesi . . . . *P. geijskesi* sp. n.

– Pale markings at sides of segment 9 more extensive, and clearly visible in dorsal view (Figs 94, 102). Southwest Sulawesi only . . . . . . *P. pariwonoi* sp. n.

6 (4) Segment 9 of abdomen with two large pale (blue) spots, virtually from anterior to posterior margin, and well visible in dorsal view (Figs 91, 99); segment 8 only with a small paired pale spot in latero-anterior corners; lateral corners of hind margin of prothorax bluntly shaped; body usually stoutly built . . . . *P. coomansi* sp. n.

– Segment 9 of abdomen with pale spots smaller, covering up to c. 60% of the length of the segment; spot usually higher than long; pale spot in latero-anterior corners of segment 8 larger; lateral corners of hind margin of prothorax variable; species of diverse stature 7

7 (6) Medium-sized species (hind wing 20 mm) from Central Sulawesi; pale markings of segment 8 and 9 clearly visible in dorsal view (Figs 93, 101) . . . . *P. marenae* sp. n.

– Larger species (hind wing 24 mm) from Sangihe islands; pale markings of segment 8 invisible in dorsal view, those of segment 9 just visible in dorsal view (Figs 95, 103) . . . . *P. rozendalorum* sp. n.

Protosticta bivittata Lieftinck
(Figs 7-9, 54-55, 78, 90, 98, 106, 110)

Protosticta bivittata Lieftinck, 1939: 151-154, Fig. 5. Holotype male: 'Célèbes' (in MNHP) [examined] – Lieftinck 1971: 122 (notes on types); Davis & Tobin 1984: 107 (catalogued); Tsuda 1991: 7 (catalogued); Bridges 1994: VII.34 (catalogued).

Description

Remarkably large and robust species with very long abdomen.

Male. – Head. Labium with labial palps brownish black, median lobe with subquadrangular twinspot on both sides of mid-suture; labrum with ovoid median depression, bluish white with black anterior margin, broad in the middle and tapering towards the corners; anterior parts of mandible bluish white without any black marking; anteclypeus bluish white; postclypeus black; remaining part of head partly shining; partly velvet black; antennae concolorous brown.

Thorax. Prothorax (Figs 54-55) with anterior and median lobe creamish white, posterior lobe black; anterior lobe with erect anterior border, flattened towards lateral corners; median lobe rather smooth and simple; posterior lobe very distinct by two lateral 'inner- horns' erected in c. 100° position, i.e. pointing somewhat apicad, horns slender and approximately as high as length of posterior lobe in dorsal view. Synthorax (Fig. 78) black with bright creamish white fasciae; mesepisternum with a light coloured stripe along apical half of dorsal carina; stripe pointed anteriorly and posteriorly, but anterior side broader than posterior side; parallel-sided pale fascia above metastigma over ventral side of mesepimeron and dorsal 3/5th of metepisternum; dark stripe over metastigma continuing over metakatepisternum; remaining part of metepimeron creamish white. Legs greyish. Wings reaching to just beyond half-length of abdominal segment 5; Arculus distal to Ax2, origin of R4+5 just proximal to subnodus (Fig. 106); six cells between origin of IR3 and R3; nine cells between Cux (Ac) and place where CuP meets hind margin of wing.

Abdomen. Segments 1-2 somewhat inflated, segments 8-10 much inflated; segments 1-2 dorsally ochraceous, lateral sides creamish white; dorsum of segments 3-6 anteriorly creamish white, passing posteriorly to brown or brownish black; segment 7 brownish black except for anterior 1/6th; segments 8- 10 (Fig. 7) with distinct pale blue marking, latero-posteriorly brownish black; hind margin of segment 10 with narrow black stripe. Anal appendages ochraceous; superiors in dorsal view (Fig. 8) nearly straight, in lateral view (Fig. 10) club-shaped with a long and slender protuberance ('tooth'), longer than diameter of appendages; inferiors (Fig. 9) greatly differing from other *Protosticta* species of Sulawesi, with top in ventral view provided with strongly chitinized, shiny, hook-shaped structure, inner part strongly connected with outer part.

Female. – General appearance as male, but abdomen much shorter. Head as male. Prothorax with hind margin of posterior lobe with similar pair of erect 'inner-teeth'; synthorax and wings as male, wings reaching to anterior part of segment 6. Abdomen more robust than of male, first segments rather narrow, segments widening posteriorly; colour brown with paler markings on lateral side of segment 1, pale annulae on anterior 1/8th of segment 3, 1/6th of segment 4, 1/5th of segments 5-7; segments 8-10 as follows (Figs 90, 98): segment 8 dorsally black with antero- lateral pale markings tapering posteriorly towards fully dark posterior side, segment 9 with anterior half pale and posteriorly brown, short, segment 10 brown.

Measurements. – Male (n=4): abdomen incl. appendages 48-53 mm, hind wing 26-29 mm; female (n=2): abdomen 42-44 mm; hind wing 28-29 mm.

Comparative notes. – Males and females are easily distinguishable from most other *Protosticta* of Sulawesi by the presence of an antehumeral stripe, the presence of 'middle-horns' at the hind margin of the posterior lobe of the prothorax, and their considerable size.

P. maurenbrecheri is similar in general appearance (including size and presence of an antehumeral stripe), but it lacks the 'inner-horn' at the hind margin of the posterior lobe of the prothorax; especially, however, the inferior appendages are completely different.

The female of *P. bivittata* is immediately recognizable by the pale anterior half of segment 9, but the female

Figure 6. – Localities in Sulawesi where specimens of *Protosticta* were found.

of *P. maurenbrecheri* is unknown and presumably has similar coloration.

Material examined

Holotype, as mentioned above. – Other material: SW Celebes: Bonthain, 1884, 1 female (C. Ribbe) [paratype of *P. bivittata* Lft.] ex IRSN [JvT 1841]; Bantimurung (N. of Ujung Pandang), Pattunuang Asue, 200 m, 31 May 1982, 1 male (M.A. Lieftinck) [JvT 1842]; same site, cave near praw rock, 24 Sep 1983, 2 males 1 female (S.S. Pariwono) [JvT 1843, 1845, 1846]; Maros, Bantimurung area, Biseang Labboro, 8 Oct 1983, 1 male (S.S. Pariwono) [JvT 1844] all specimens in RMNH.

Remarks

Habitat. – Apparently an uncommon and possibly seasonal species. I have investigated the area of Pattunuang Asue and Biseang Labboro myself in 1989, where Lieftinck and Pariwono collected the species in small numbers in 1982 and 1983. Although I found numerous specimens of *P. pariwonoi* sp. n., no specimen of the present species was captured. The site is dominated by a rivulet flowing through disturbed forest on limestone hills. Water dripping from the limestone rocks gathers to several shaded trickles in the river valley.

Distribution. – Only known from SW Sulawesi; the paratype is from Bonthain (usually an indication of the Lompobatang mountain, no altitude given), all other specimens are from the Bantimurung area, north of Ujung Pandang (see Fig. 110).

Protosticta coomansi sp. n.

(Figs 10-16, 56-57, 79, 91, 99, 111)

Type material. – Holotype male: 'Celebes (Paloe) Lindoevlakte, XVIII.' 850 mbz, 8-VIII-[19]40. Coll CdR' [CdR = Coomans de Ruiter] [JvT 2016] in RMNH. – Paratypes 76 males 6 females, as follows: Paloe, Lindoevlakte, 850 m, 8 Aug 1940, 2 males 1 female (Coomans de Ruiter) [JvT 2017-2019]; Same site, 9 Nov 1940, 1 male (Felix) [JvT 2014]; Same site, 15 Jan 1941, 1 female [JvT 2015]; 50 km SE Palu, Lore Lindu NP, foothill brooks Dongi Dongi shelter, 4-9 Dec 1985, 7 males 1 female (J. van Tol) [16829-16835, 16870]; 65 km SSE Palu, Lore Lindu NP, foothill brooks nr Marena shelter, 600 m, 14-17 Dec 1985, 30 males 1 female (J. van Tol) [16836- 16865, 16871]; Gimpu, Lore Lindu NP, 450 m, 1°40'46"S 120°03'30"E, 2-3 Apr 1997, 4 males (J. van Tol) [JvT 16578, 16582, 16589, 16590]; N of Gimpu, just outside Lore Lindu NP, 450 m. 1°37'S 120°02'E, 4 Apr 1997, 20 males 2 females (J. van Tol) [JvT 16596-16617]; S of Palu, Lore Lindu NP, Kamarora, 700 m, 1°11'53"S 120°08'16"E, 7-8 Apr 1997, 12 males (J. van Tol) [JvT 16640-16643, 16646, 16648-16654] all in RMNH, except 8 males (Lore Lindu, Gimpu) in MBBJ, and 2 males in ZMAN.

Additional material (excluded from type series). – All from Sulawesi (Celebes), arranged approximately from north to south): Leok, 25 Jan 1941, 1 male (J. J. van der Starre); Sabang, Dampelas, 30 Jan 19941, 2 females (J.J. van der Starre); NE Palu, road Tawaeli-Pangi near Wentira, 800 m, 00°43'22"S 119°59'49"E, 6 Apr 1997, 1 female (J. van Tol); Donggala, 4 Jan 1941, 4 males (J.J. van der Starre); c. 40 km over road N of Wotu, brooklet on steep slope, 500 m, 91JvT20, 2°15'S 120°46'E, 29 Apr 1991, 12 males 1 female (J. van Tol); 30 km N of Wotu, Sg Anoa, waterfall, ponded sites and small tributaries, 2°20'30"S 120°47'45"E, 23, 26 October 1993, 11 males 1 female (J. van Tol);c. 15 km NNE Malili, tributary of Sg. Malili, 150 m, 2°32'S 121°12'E, 2 May 1991, 1 male (J. van Tol); Between Malili and Wasapundo, 24 Sep 1993, 1 male (M.T. Wasscher); 3 km S of Soroako, 25 Sep 1993, 1 male (M.T. Wasscher); 45 km ENE Malili, stream E side Danau Matana near Salura, 2°31'45"S 121°29'00E, 450 m, 19 Oct 1993, 3 males 1 female (J. van Tol); Tappalang, 21 Jan 1940, 1 female (J.J. van der Starre); Loewoe, Todjamboe, 1000 m, 16-17 Jul 1936, 1 male (L.J. Toxopeus); Idem, 18 Jul 1936, 2 males 1 female (L.J. Toxopeus); Tojambu, 17 Jun 1982, 1 male (M.A. Lieftinck); 10 km NW Palopo (km 15 road Palopo-Rantepao), Salo Tandung, 400 m, 91JvT15, c. 2°58'S 120°07'E, 27 Apr 1991, 7 males (J. van Tol); c. 10 km WNW Palopo, near Tojambu, river above km 23 from Palopo, 800 m, 2°56'S 120°07'E, 29 Apr 1991, 1 male (Yohan); 10 km NW Palopo: Salo Tandung and tributaries, 300-600 m, 2°57'00"S 120°07'30"E, 30 Oct 1993, 1 male (J. van Tol); Tojambu or direct surroundings, Jul / Aug 1991, 11 males (Yohan); Nanggala, Rantepao, 900 m, Sep 1937, 1 male (F.C. Drescher); 58 km N of Majene, Onan, Sg Parabaya, 19 Nov 1993, 2 males (J.P. & M.J. Duffels) [JvT 6009, 6042]; Polewali, 6 Aug 1940, 5 males 4 females (J. J. van der Starre); Polewali, 23 Oct 1940, 2 males 1 female [identified as *Protosticta* spec. E by Lieftinck]; c. 30 km E of Maros, Cakar Alam Labang, 4- 500 m, 91JvT11, 20 Apr 1991, 2 males (J. van Tol) in RMNH, partly to be deposited in MBBJ.

Description

Relatively large and stout species with significant variation between populations. An analysis based on sufficient material from all parts of the species range is needed to reveal any distinct patterns in variation. Only material from the area south of Palu, the present Lore Lindu National Park, is here considered 'typical'. See below paragraph 'Geographical variation'.

Male [holotype, JvT 2016]. – Head. Labium ochraceous to chestnut brown, the palps somewhat darker; mandibles bluish white, passing anteriorly to brown; labrum bluish white, the anterior one-fourth black (holotype with two dark spots as an artefact), boundary between black and white sharp, but somewhat irregular; anteclypeus bluish white as labrum; postclypeus and remaining part of head black, partly glossy, partly matt-black. Antenna castaneous (flagellum broken in holotype).

Thorax. Pronotum (Figs 56-57) with anterior margin brown, straight, anterior lobe rather narrow, anteriorly bordered with a distinct transversal ridge; median lobe ochraceous yellow, with flat tubercles with various brown markings; hind lobe black, relatively small, with posterior margin straight and the lateral parts inconspicuously erect. Synthorax (Fig. 79) brownish black with metallic shine; creamish yellow coloured stripe over mesepimeron and metepisternum parallel to metapleural suture and running just over metastigma; metepimeron creamish yellow, centrally with a brown marking against metapleural suture posteriorly tapering towards suture. Legs greyish to brownish yellow, the joints somewhat darker. Wings 30 mm long (almost all somewhat damaged), Arculus just distal to Ax2; origin of R4+5 well proximal to subnodus; six cells between origin of IR3 and R3; nine cells between Ac (Cux) and place where CuP meets hind margin of wing.

Abdomen. Long (including appendages 44 mm), not extremely slender, with coloration relatively inconspicuous. Segments 1-2 relatively little swollen; segments 8-10 strongly inflated; dorsum of segment 7 strongly setose with setae nearly as long as diameter of segment; segment 1 ochraceous, segments 2-6 predominantly pale brown, anteriorly with ochraceous rings and posteriorly passing to dark brown; segments

7-8 dark brown except for the dark ochraceous anterior one-fifth of each segment; dorsum of segment 8- 10 bright pale blue; tergites 8-10 laterally brown. Anal appendages (Figs 10-16) with superiors in basal part strongly built, dorsally ending in a light-coloured tooth, ventral side in innerview scythe-shaped, but ending in a knob; inferiors with stout basal part, posterior part curved subcircularly outwards, tops of inferiors approaching, but extreme tips not curved outwards; subterminally a stout tooth at innerside (Fig. 13), approximately perpendicular to body axis.

Female (Gimpu, JvT 16610). – Head and thorax not significantly different from male; abdomen with segment 1 dorsally with brown triangular marking, narrow anteriorly and widening posteriorly, remaining part creamish white; segment 2 dark brown, ventro-anteriorly against annulus with a creamish triangular marking; segments 3-7 brown with small markings anteriorly on segment 3, gradually increasing in size per segment to a larger subsquarish spot covering c. one-third the width of each side of the segment, dorsally leaving dark coloration; segment 8 (Figs 91, 99) short, brown, anteriorly with a paired pale spot, segment 9 brownish black, with a paired pale oval lateral marking, in lateral view c. half the height of the segment, anteriorly creamish white, posteriorly blue; segment 10 brownish black. Anal appendage short, dark; outer valve and terebra reaching just beyond anal appendages, stylus long and slender.

Geographical variation. – Male with significant geographical variation (variation in female largely unknown), particularly with respect to shape of the anterior margin of the prothorax, and the inner tooth of the inferior anal appendages; also the coloration of markings of segments 8-10 in the male is varying between populations and specimens, especially in the basal part of segment 8, which may be entirely blue or partly brownish black as the preceding segments. Variation is clearly demonstrated for the inferior anal appendages in Figs 14-16, for specimens from the Maros area (tip of SW Sulawesi), Gimpu (Central Sulawesi), and Leok (northern peninsula), respectively. They illustrate the general trend from south to north in the increase in size of the inner tooth of the inferior appendage. Also, in some populations (Maros, Polewali) the inner tooth is pointing not perpendicular to the body axis, but more in apical direction. The anterior ridge of the prothorax varies from bordered with two subparallel transversal ridges (Tojambu area) to the more conspicuous anterior ridge and indistinct posterior ridge, as in specimens from the Lindu valley. All these specimens are taken together here under the name *Protosticta coomansi,* since I have been unable to find distinct and discrete morphological characters between the specimens from various localities. Although some populations of *Protosticta coomansi* have characters in which they approach *P. gracilis*, it seems that (the only extant collection specimen of) *P. gracilis* is sufficiently different to separate both at the species level. However, the actually observed differential characters between both taxa may be the result of the absence of any material collected between Leok and the easternmost part of the Minahassa (Tondano), since *P. gracilis* is obviously the extreme form of this geographical trend. The status of the third taxon in this group, *Protosticta reslae*, seems to be better established.

Measurements. – Variation in measurements among populations: Leok (n=1) wing 30 mm, abdomen including appendages 45 mm; Kamarora (n=5) wing 29 (26-30), abdomen 40 (37-42); Gimpu (n=5) wing 27.5 (27-28), abdomen 40.5 (39-42); Salura (n=3) wing 29 (28-29), abdomen 42 (41-42); Polewali (n=5) wing 32 (31-33), abdomen 44.5 (42-46) mm.

Comparative notes. – *Protosticta gracilis* can immediately be distinguished from *P. coomansi* by its enormous inner tooth of the inferior appendage pointing obliquely apicad. How conspicuous this character may seem, it is easily overlooked. Several specimens of *P. coomansi* were identified as and labelled 'compared with the type' [of *P. gracilis*] by M.A. Lieftinck. Specimens here assigned to *P. coomansi* show distinct variation within and between populations, especially in size and shape of the inner tooth, although the giant size of *P. gracilis* is not reached. Besides, the tooth is pointed perpendicular to the body axis in all specimens. *Protosticta reslae* sp. n. may be distinguished from *P. coomansi* by the shape of the superior appendage in lateral view: the scythe-shaped ventral side in *P. reslae* is much broader than in *P. coomansi*; secondly the dorsal tooth is located far posterior to the base of the ventral projection in *P. reslae*, whereas the dorsal tooth is located approximately above the ventral projection in the basal half of the appendage in *P. coomansi*. The holotype of *P. gracilis* has the tooth and ventral projection also wide apart, but the scytheshaped ventral side is slender as in *P. coomansi*. Finally, both specimens of *P. reslae* have the ventral side of the pale stripe over the synthorax with a distinct emargination, while this stripe is straight in both other species. The female differs structurally from other common Sulawesi *Protosticta* species, especially *P. geijskesi*, by its shorter valve and terebra, and the absence of an erect hind margin of the prothorax; in coloration it is characterized by the large pale spot in abdominal segment 9.

Remarks

Etymology. – *Coomansi*, after Mr. Louis Coomans de Ruiter (1898-1972). Coomans de Ruiter lived in Sulawesi (Manado, Ujung Pandang) from 1938 to 1942, was extremely interested in collecting Odonata, and has discovered many interesting and new species in Sulawesi.

Habitat. – Mostly confined to brooklets and foothill streams from c. 100 m up to 1000 m above sea level. It is not confined to densely shaded small streams, but has also been found along the Salo Tandung, a rivulet of c. 10 meter wide, only locally shaded by rather open secondary forest. The larvae were possibly living in the small seepage areas present, but the adults were collected from shrubs hanging from the river banks. Most specimens, however, do come from densely forested areas, where the specimens hang in the shade all day, but are most active when spots of sunlight reach the stream.

Distribution. – Widespread in Central Sulawesi, not observed in the southeastern peninsula, and uncommon in the northern peninsula north of Palu, and in the southwestern peninsula (Fig. 111).

Protosticta geijskesi sp. n.

(Figs 17-20, 58-59, 80, 92, 100, 112)

Type material. – Holotype male: SW Sulawesi: c. 15 km NNE Malili, tributary of Sg. Malili, fast flowing clear water, half shaded, 150 m, 2°32’S 121°12’E, 2 May 1991 (J. van Tol) in RMNH [JvT 1923]. – Paratypes: ‘S. Baebunta / donker boschbeekje / 25/8/’40’ and ‘L.A.A.M. leg.’ [indicating the Baebunta river, shaded forest stream, 25 August 1940, collected by L.A.A. Maurenbrecher], 2 males, in RMNH [JvT 1917-1918]; SW Sulawesi: c. 15 km NNE Malili, tributary of Sg. Malili, fast flowing clear water, half shaded, 150 m, 2°32’S 121°12’E, 2 May 1991, 3 males (J. van Tol) 2 in RMNH, 1 in MBBJ [JvT 1921-1922, 1924]; 30 km N of Wotu, Sg Anoa, waterfall, ponded sites and small tributaries, 2°20’30”S 120°47’45”E, 23 Oct 1993, 1 male (J. van Tol) [JvT 1499]. Other material (excluded from type series, arranged approximately from north to south). – **Sulawesi**: Sabang, Dampelas, 30 Jan 1941, 1 males (J.J. van der Starre) [JvT 1891]; Same site, 28 Nov 1940, 1 male (J.J. van der Starre) [JvT 1894]; 58 km N of Majene, Onan, Sg Parabaya, 19 Nov 1993, 5 males (J.P. & M.J. Duffels) [JvT 6010, 6015, 6032-6034]; Madjene, 8 Nov 1939, 30 Nov 1939, 13 Nov 1940, 23 Apr 1940, 3 males 1 female (J.J. van der Starre) [JvT 1910-1913]; Kolonedale, 8 Aug 1941, 3 males (J.J. van der Starre) [JvT 1914-1916]; 28 km NE of Luwuk: S Bantayan nr crossing road Kajutanju-Siuna, c. 60 m [100 m on label], 0°47’S 123°00’E, 89JvT006, 30 Jan 1989, 2 males (J. van Tol) [JvT 1895, 1896]; Same site, 89JvT14, 7 Oct 1989, 11 males (J. van Tol) [JvT 1898-1908]; 15 km NNE of Luwuk, Sg Biak at road Biak-Poh, 0°49’S 122°50’E, 89JvT013, 6 Oct 1989, 1 male (J. van Tol) [JvT 1897]; NNW of Batui, Batui river at Sinsing camp, 90 m, 89JvT023, 1°09’S 122°21’E, 15-17 Oct 1989, 1 female (J. van Tol) [JvT 1909]; same site, 14-17 Oct 1989, 1 male (much damaged) 1 female (J.P. Duffels) in ZMAN [JvT 16878-16879]. – SE Sulawesi: S of Sanggona: Mokowu river near Mokowu camp, 150 m asl, 3°48’S 121°39’E, 20 Oct 1989, 1 male (J. Huisman) [JvT 1975]; Same site, 89JvT031, 29-31 Oct 1989 and 5-6 November 1989, 70 males, 2 females (J. van Tol) [females JvT 5144, 11886]; S of Sanggona, Gunung Watuwila, Sg Lalonduwasi nr Centipede camp, c. 1050 m, 89JvT035, c. 3°49’S 121°40’E, 3 males (J. van Tol) [JvT 5194-5196]; Moramo, Sg. Moramo, 200 m, S8939, 16-17 Nov 1989, 3 males (R. de Jong) [JvT 1976-1978]. – SW Sulawesi. – c. 40 km over road N of Wotu, brooklet on steep slope, 500 m, 2°15’S 120°46’E, 91JvT020, 29 Apr 1991, 1 male 1 female (J. van Tol) [JvT 1919, 2031]; 45 km ENE Malili, Salura, brooklets E side Danau Matana, 2°31’45”S 121°29’00”E, 450 m, 19 Oct 1993, 19 males (J. van Tol) [JvT 1420-1423, 1425-1428, 1430-1439, 1441]; W of Matano village, near Danau Matana, 15-16 Sep 1993, 6 males (M.T. Wasscher) [JvT

16710, 16713, 16716, 16717, 16725, 16789]; 5 km S of Soroako, forest stream, 25 Sep 1993, 3 males (M.T. Wasscher) [JvT 16747-16748, 16758]; Palopo, km 17, 400 m, 11 May 1941, 3 males 1 female (H. & E. Vonk); 10 km NW Palopo, Salo Tandung, c. 400 m, 2°58'S 120°07'E, 91JvT015, 27 Apr 1991, 9 males 1 female (J. van Tol) [JvT 5145-5154]; 10 km WNW Palopo near Tojambu, 800- 1000 m, July/August 1991, 13 males 3 females (Yohan R.) [JvT 11800-11802, 11873-11885]; W of Sabbang, tributary of Sg Ronkong, 150-200 m; 2°36'00"S 120°12'45"E, 3 males (J. van Tol) [JvT 1702-1704]; Masamba, inland, 2°30'S 120°25'E, 1-2 Nov 1993, 9 males (Yohan R.) [JvT 2035-2043, 16790-16791]; NW Palopo, tributary of Sg Lamasi, 2°51'15"S 120°06'15"E, 2 Nov 1993 (J. van Tol) [JvT 1715]; Tojambu area, 7 males 2 females (Gala) [JvT 16361-16369]; 20 km NW Palopo, Sg Lowi, 2°51'00"S 120°04'45"E, 4 males 3 females (J. van Tol) [JvT 1718- 1724]; Bonthain, Malino, 1000 m, 29 Jun 1936, 5 males, 3 females (L.J. Toxopeus) [JvT 1847, 1848, 1851-1856]; S. Celebes, Lompa-Battau, 3000', März 1896, 1 male (H. Fruhstorfer) [JvT 1850]; Celebes [no further details, ex Museum Paris], 1 male [JvT 1849]. – **Buton**: N. Pulau Buton, a few kms inland from Labuhan Tobelo, Sg Labuhan Tobelo, 150 m, 4°26'30"S 122°59'E, 89JvT040, 13 Nov 1989, 4 males (J. van Tol) [JvT 1925-1928], all in RMNH, except given otherwise; part of the series from Masamba, Tojambu and Sanggona will be deposited in MBBJ.

Description

Variable species or a complex of microspecies. The species in the present sense encompasses virtually all specimens with inferior appendages in ventral view as a 'boxing glove' (Fig. 20), i.e. with a strongly swollen tip and a slender, inwards pointing inner-tooth close to the top. Several populations of the *geijskesi* species- group from the southwestern-most part of the island are considered distinct, and are here described as *Protosticta pariwonoi*.

Male [holotype, JvT 1923]. – Head. Labium yellowish brown, anterior part of median lobe and palps brown; labrum bluish white, anterior one-fifth to one-fourth black; mandibles black to brownish black, dirty white against labrum, otherwise completely black; anteclypeus bluish white; postclypeus and remaining part of head shining black; antenna with scapus brownish black, pedicellus and flagellum brown (flagellum broken off in holotype).

Thorax. Pronotum (Figs 58-59) with anterior and median lobe predominantly creamish white, posterior lobe black; anterior margin of anterior lobe with transverse ridge; posterior lobe with hind margin somewhat raised into a short subtriangular 'horn'. Synthorax (Fig. 80) with mesepisternum without antehumeral stripe, generally glossy brownish black without metallic shine; pale stripe over mesepimeron and metepisternum and over lower side of metepimeron; pale coloured fascia anterior to metapleural suture anteriorly passing to brownish black well before metakatepisternum. Legs dirty yellowish, somewhat darker against joints. Wing length 24 mm; reaching to one-third of abdominal segment 6; Arculus distal to Ax2; origin of R4+5 at subnodus; five cells between origin of IR3 and R3; six to seven cells between Cux (Ac) and place where CuP meets hind margin of wing.

Abdomen. Length including appendages 38 mm. Slim and slender with segments 1-2 somewhat inflated, segments 8-10 distinctly swollen; segment 1 creamish white with narrow posterior brown ring; dorsum of segment 2 dark brown, lateral sides passing to yellowish white; dorsum of segments 3-7 brown, segments 4-6 anteriorly with dorsal brown marking laterally tapering, thus forming an antero-lateral pale spot; dorsum of tergites 8-9 blue (Fig. 17), segment 8 with medio-anterior triangular marking, and also with postero-lateral black markings, margins of segment 9 black; segment 10 black. Anal appendages (Figs 17-19) with superiors curved moderately inwards, with indistinct dorsal process from c. 1/4 from base onwards, extending just beyond half-length from base, top simple without scythe-like wide part; inferiors converging in basal half, distal part more slender and diverging, tip sharply curved inwards and approximately perpendicular to body axis; tip swollen as a 'boxing glove' (Fig. 20), innertooth ('thumb') rather short and pointing somewhat antero-dorsadly.

Female [JvT 1718, 20 km NW Palopo]. – As the male, but abdomen much shorter. Head as male, but mandibles pale coloured (bluish or creamish); pronotum as male, but 'horns' at posterior lobe more distinct, approximately as long as height of posterior lobe; segment 1 of abdomen creamish white, lateral sides of tergites creamish; segments 2-7 dorsally brownish black, anterior one-fourth to one-fifth paler; segment 9 dark brown with large oval, creamish coloured latero-posterior spot on tergite, not quite reaching ventral and posterior margin (Fig. 92); segments 8-10 in dorsal view (Fig. 100) nearly completely dark, the pale spots only just visible laterally; segment 10 short; valves (Fig. 92) long, reaching distinctly beyond appendages, stylus long and slender.

Variation. – Much variation in measurements, shape of prothorax, and shape of anal appendages. Hind margin of prothorax with erect parts of hind margin long or short. The inferior appendages with tips round to oval of various sizes, and with the 'thumb' from a relatively stout (Fig. 20) to a nearly filamentous tooth. Specimens from the Lompobatang mountain (Malino, Bonthain) are large, do not possess 'horns' on the hind margin of the prothorax, but the anal appendages of the male are clearly different from *P. pariwonoi* males, and come closest to *P. geijskesi.* The precise relationships and status of the populations here lumped under the names of *P. geijskesi* and *P. pariwonoi* should be studied when more material has become available, especially from the southwestern peninsula.

Measurements. – Much variation between populations. Males: Buton (n=4) abdomen (including appendages in all measurements given) 40 (39-41) mm, hind wing 26 (25-27) mm; Mokowu (n=5) abdomen 41 (39-41) mm, hind wing 25 (25-26) mm; Luwuk (n=5) abdomen 39 (38-41) mm, hind wing 25 (24- 27) mm; Kolonedale (n=3) abdomen 37 (34-40) mm, hind wing 23 (22-25) mm; NNE Malili (n=4) abdomen 39 (38-40) mm, hind wing 24 (23-25) mm; Baebunta (n=1) abdomen 33 mm, hind wing 21 mm [sic!]; Madjene (n=2) abdomen 41 mm, hind wing 27 (27-27) mm; NW Palopo (n=5) 40 (39-41) mm, hind wing 26 (26-27) mm; Lompobatang (n=7) abdomen 44 (42-46) mm, hind wing 29 (28-30) mm.

Remarks

Etymology. – *Geijskesi*, after my teacher, colleague and friend Dirk Cornelis Geijskes (1907-1985), former curator at the National Museum of Natural History, Leiden.

Habitat. – Not uncommon in lowlands, where it is the dominant species; much less common above 500 m, but also found on Gunung Watuwila (c. 1000 m), and Gunung Lompobatang (unknown altitude). Records are from various kinds of streams, mostly small streams in half-shade, to forest rivulets of several meters wide. *P. geijskesi* is less common on spring brooks in dense shade. It has also been found in semicultivated areas, and severely disturbed forest. Females are very uncommon in collections. I found only two females among 70 males at the foothill stream of Gunung Watuwila.

Distribution (Fig. 112). – Widespread in central and southeastern Sulawesi; not recorded from most of the northern peninsula (Gorontalo, Minahasa), and also absent from the mountainous areas between Palu and Rantepao (e.g. Lore Lindu National Park). In the southwestern peninsula it is uncommon. A larger form, here assigned to *Protosticta geijskesi*, has repeatedly been collected on the slopes on Gunung Lompobatang. A closely related species, *P. pariwonoi*, is inhabiting the lowlands of this presently severely disturbed area.

Protosticta gracilis Kirby

(Figs 22-25, 60-61, 81, 107, 111)

Protosticta gracilis Kirby, 1889: 302. – Holotype male 'Menado Wallace' [white rectangular label], 'Tond.' [white round label], '68.3' [white rectangular label] '*Protosticta gracilis* type' [blue rectangular label, Kirby's hand] in BMNH [examined]. – Kirby 1890: 133 (catalogued); Kimmins 1970: 174 (list of types in BMNH); Davies & Tobin 1984: 107 (catalogued); Tsuda 1991: 8 (catalogued); Bridges 1994: VII.100 (catalogued).

Description

A stout and robust species of *Protosticta*.

Male [holotype]. – Head. Labium creamish yellow at base, labial palps and remaining part of labium brown; mandibles creamish yellow with anterior border with narrow brown stripe; labrum creamish white, anterior one-third brownish black; anteclypeus creamish white; postclypeus brownish black; remaining part of head

semi-glossy brownish black with two paler spots next to lateral ocelli.
Thorax. Pronotum (Figs 60-61) matt; median lobe ochraceous; anterior lobe, especially in centre, somewhat darker, central part protruding with hind margin of middle part reverse V-shaped, lateral parts erect; posterior lobe black without conspicuous latero-posterior lobes ('horns'). Synthorax (Fig. 81) brownish black, mesepisternum without antehumeral stripe; creamish yellow fascia over metepisternum; ventroposterior side of metepimeron creamish white. Legs pale brown, joints somewhat darker. Wings with dark veins; R4+5 arising significantly proximal to subnodus (Fig. 107); IR3 arising only 1/6th to 1/4th of length of a cell distal to subnodus; CuP reaching hind margin of wing at level of R3, ten cells between Cux and place where CuP meets hind margin of wing; fore wing with 21 or 22 Px, hind wing with 18 Px.
Abdomen. Dorsum of segment 1 anteriorly with pale brown crescent-shaped marking, remaining part of segment 1 and segments 2-7 brown to brownish black, somewhat darkening posteriorly; anterior onesixth of segment 8 brownish black, remaining part of segment 8 and segment 9-10 blue (Fig. 21). Anal appendages (Figs 21-25) black; superiors in dorsal view with a subconical basal part with underside hollow, ending in a short, glossy tooth; distal part of superiors curved inwards, ending in a flattened disc (Fig. 23); inferiors with ventral side semi-glossy, distal part straight with top curved 90° inwards, at c. one-third from the base a strong, very long and somewhat dorsadly curved tooth with a transverse brownish yellow band over terminal part of main stem.

Female. – Unknown.
Measurements – Male (n=1) abdomen (including appendages) 43 mm, hind wing 30 mm.
Comparative notes. – Similar to *P. coomansi*, from which it mainly differs by the structure of the anal appendages of the male. See further under *P. coomansi*.

Remarks

Habitat and distribution (Fig. 111). – The only specimen known was collected by A.R. Wallace, almost certainly at Tondano, northern Celebes. Wallace collected in the vicinity of Tondano (Rurukan) in late June and early July 1859 (see Wallace 1890 [1962]: 193). He actually stayed at Tondano a few days after 29 June, so early July, only. He visited the waterfalls at the outlet of the lake, where probably the present specimen was taken. The area is now completely cultivated (own observations). Although the Minahasa, especially the easternmost part around Menado, was well explored in the 1930's and 1940's, the species has not turned up on any of these sites.

Protosticta linduensis sp. n.

(Figs 26-29, 62-63, 82, 112)

Type material. – Holotype male: 'Celebes, Polewali, 23 Oct 1940, J.J. van der Starre' [identified as *Protosticta* spec. H by M.A. Lieftinck] [JvT 1857] in RMNH. – Paratypes: Same data, 1 male [JvT 1858]; 10 km WNW Palopo, river above km 23 from Palopo. 800 m. 2°56'S 120°07'E. July/Aug 1991, 2 males (purchased from native collector Yohan R.) [JvT 1859, 1860]; 50 km SE Palu: Lore Lindu NP nr Dongi Dongi shelter, 950 m, 9 Dec 1985 sample A, 1 male (J. van Tol) [JvT 1861]; W. of Palopo: Tojambu, 2 Nov 1993, 1 male (Gala) [JvT 16360]; Lore Lindu NP, Kamarora, 01°11'53"S 120°08'16"E, 1 male (J. van Tol) [JvT 16644] all in RMNH, but one male from Palopo in MBBJ.

Description

Moderately large species with remarkable, broad anterior lobe of prothorax and very slender anal appendages.
Male [holotype, JvT 1857]. – Head. Labium dark yellow; labrum blue with brownish anterior border; anteclypeus yellow, pale but not concolorous with labium; postclypeus and remaining part of head black; antennae black.
Thorax. Pronotum (Figs 62-63) with anterior lobe laterally with scale-like expansions, central part brown and lateral parts ochraceous; median lobe pale yellowish white without distinct characters; posterior lobe brownish black with lateral corners acute, hind margin nearly straight with shallow (specimens from Polewali), or more distinct (specimens from Dongi Dongi) emarginations. Synthorax (Fig. 82) chestnut brown, somewhat darker between

mesopleural (humeral) sutures; bluish yellow fascia over mesepimeron and metepisternum running anterior to metakatepisternum over metastigma, leaving the metapleural suture, ending against hind margin midway between humeral and metapleural suture; subequal dark stripe over metapleural suture parallel to pale fascia; remaining ventro-posterior part of metepimeron brownish yellow. Legs greyish with joints of femur to tibia somewhat darker. Wings (26 mm) reaching halfway abdominal segment 6; Arculus well distal to Ax2; origin of R4+5 at or proximal to subnodus; 5-6 cells between origin of IR3 and R3; 6-8 cells between Cux (Ac) and place where CuP meets hind margin of wing.
Abdomen. Length including appendages 40 mm. Segments 1-2 considerably inflated, segments 8-10 strongly inflated; segment 1 creamish white, segment 2 pale brown with latero-anterior two-thirds brownish yellow; segment 3-7 anteriorly with pale ring, followed by a brown ring passing to brownish yellow in posterior parts, each segment posteriorly with dark ring; segment 8 with anterior one-fourth brown, remaining part blue surrounded by brownish black ring; segment 9 blue on dorsum; segment 10 brownish black (Fig. 26). Anal appendages (Figs 26-29) slender; superiors smoothly curved ventro-proximad, dorsal tubercle triangular, not sharp as in most other Sulawesi species; inferiors shorter, strongly curved inwards, the inner subterminal tubercle ('thumb') long and curved inwards (cf. Fig. 29).
Female. – Unknown.
Measurements. – Male (n=5) abdomen including appendages 40-41 mm; hind wing 26-27 mm.

Variation. – The anterior lobe of the pronotum is dark brown or pale; the structure of the anterior lobe of the pronotum shows variation; especially the specimen from Kamarora (JvT 16644) has a conspicuously wider and more erect hind margin than other specimens.

Comparative notes. – Although *P. linduensis* is superficially similar to *P. geijskesi*, the peculiar shape of the anterior lobe of the prothorax is diagnostic. Moreover, the dorsum of abdominal segment 8 is only blue in the distal 50-70%, while it is completely blue in *P. geijskesi*. It is most closely related to *P. marenae* sp. n., in which, however, the anterior lobe of the prothorax is much less widened laterally. Also, the top of the inferior appendage is much more slender in *P. linduensis* than in *P. marenae* (compare Figs 28 and 32, which are drawn to scale).

Remarks

Etymology. – *Linduensis*, after one of the localities, the Lore Lindu National Park, Central Sulawesi.
Habitat. – All specimens collected by myself were found in dense forest. The specimen from Dongi Dongi was found hanging along a foothill brook with only a few centimetres of water flowing through a steep and narrow ravine in (at that time) hardly disturbed tropical rain forest. Only one specimen was discovered between numerous examples of *Protosticta coomansi* sp.n.
Distribution. – Geographically western Central Sulawesi (politically partly Southwestern Sulawesi) (Fig. 112).

Protosticta marenae sp. n.

(Figs 30-33, 64-65, 83, 93, 101, 112)

Type material. – Holotype male: S of Palu, Gimpu, 450 m, 1°40'46"S 120°03'30"E, 2 Apr 1997, 1 male (J. van Tol) [JvT 16579]. – Paratypes 9 males 1 female: Central Sulawesi, 65 km SSE Palu: Lore Lindu NP nr Marena shelter, 600 m, 14 Dec 1985 sample B, 2 males (J. van Tol) [JvT 1862-1863]; same locality, 15 Dec 1985 sample B, 2 males (J. van Tol) [JvT 1864- 1865]; same locality, 16 Dec 1985 sample C, 2 males (J. van Tol) [JvT 1866-1867]; close to previously mentioned locality: foothill brooklet nr Anaksungai Mbewe, alt 700 m, 17 Dec 1985 sample B, 1 male (J. van Tol) [JvT 1868]; S of Palu, Gimpu, 450 m, 1°40'46"S 120°03'30"E, 2 Apr 1997, 2 males 1 female (J. van Tol) [JvT 16580, 16581, 16583]. All specimens in RMNH, but 2 males to be deposited in MBBJ.

Description

Medium-sized species, characterized by shape of anterior border of prothorax, horn-like structures at posterior margin of prothorax, shape of inferior appendage of male (Fig. 33), and black dorsum of abdominal segment 10.

Male [holotype, JvT 16579]. – Head. Labium brown; labrum bright creamish white with medio-anterior two-fifths black, laterally tapering in width; mandibles black with only inner base pale coloured; anteclypeus bright creamish white; postclypeus and remaining part of head black. Antennae brownish black.

Thorax. Pronotum (Figs 64-65) with anterior lobe dark brown, except for a longitudinal yellowish stripe close to lateral corners, shaped as long dish with raised borders, characteristically 'V'-shaped in cross-section, laterally somewhat wider than centre; median lobe yellowish, with two low tubercles; posterior lobe black with bluish metallic shine, lateral corners tapering into slender, laterally pointing processes perpendicular to body axis. Synthorax (Fig. 83) base colour black, in most specimens with metallic shine; metepisternum with parallel-sided greenish-white coloured fascia parallel to metapleural suture, with lower side over metastigma, posteriorly tapering towards interpleural suture; dark fascia over metapleural suture dark brown to black, somewhat wider than pale fascia anterior to it; remaining part of metepimeron creamish white. Legs greyish, joints somewhat darker. Wing length 24 mm; wings reaching just beyond abdominal segment 5, origin of Arculus distal to Ax2; origin of R4+5 at or even distal to subnodus; five cells between origin of IR3 and R3; seven cells between Cux and place where CuP meets hind margin of wing.

Abdomen. Length including appendages 38 mm. Brownish, relatively pale, with first segment creamish, segments 2-6 brown on dorsum except for posterior dark brown one-sixth part, latero-anteriorly with creamish white spots, segment 7 dark brown except for latero-anterior creamish spots; segment 8 with dorsoanterior one-fifth and lateral sides brownish black, remaining part blue; segment 9 with dorsum blue, lateral sides brownish black; segment 10 black. Appendages (Figs 30-33) brownish black; superiors smoothly curved ventro-proximad, distal half flattened but not conspicuously wider than base, c. half-way with triangular tubercle; inferiors in ventral view smoothly curved outwards from base, with top curved inwards, tip strongly tapered and curved dorsadly, subterminal inner-tooth short and rather bluntly shaped.

Variation. – No apparent variation in structural details in the type series.

Female [JvT 16580, Gimpu]. – General coloration similar to male, but head with mandibles bluish white; pronotum with anterior lobe markedly different, and not conspicuously widened, only simply thickened, remaining part similar to male; abdomen with pale markings of segments 2-7 more pronounced than in male, segment 8 short, dark brown, with large creamish spot latero-anteriorly against margin of tergite; segment 9 brownish black with large paired lateral spot not touching in dorsal view and not touching margin of tergite; segment 10 brownish black, valve straight and long, reaching far beyond segment 10.

Remark: Some doubts remain whether this specimen indeed represents the female of *P. marenae* sp. n. Especially the anterior lobe of the pronotum differs more from the male than noted in other species.

Measurements. – Males (n=7) abdomen including appendages 37 (36-37) mm; hind wing 24 (23-24) mm.

Comparative notes. – Based on the shape of the inferior appendages, the largely black mandibles, and a black dorsum of abdominal segment 10 similar to *Protosticta geijskesi* sp. n. Presumably sistertaxon of *Protosticta linduensis* sp. n., a relationship that is especially apparent by the shape of the anterior lobe of the prothorax. It is, however, much smaller than *P. linduensis*, and especially the tip of the inferior appendage is much smaller. Also, *P. linduensis* has the lateral sides of the anterior lobe of the pronotum more conspicuously enlarged, and the distal half of the superior appendages widened.

Remarks

Etymology. – *Marenae*, after the shelter 'Marena' near the type locality close to the Lore Lindu National Park.

Habitat. – Found along rather shallow brooklets through relatively open, somewhat disturbed rain forest. Other species on these sites included *Protosticta coomansi* sp. n. and *Disparocypha biedermanni* Ris.

Distribution. – Central Sulawesi (Fig. 112). Only known from two sites close together, and certainly not common or widespread in the area.

Protosticta maurenbrecheri sp. n.

(Figs 34-36, 66-67, 84, 110)

Type material. – Holotype male: 'Sulawesi, c. 10 km NW Palopo (km 15 road Palopo-Rantepao): Salo Tandung, c. 400 m asl. Width 10 m, large boulders, torrents, seepage areas. Rather open secondary forest overhanging from bank, otherwise not shaded. c. 2°58'S 120°07'E. 27 Apr 1991. Sample 91JvT15. Leg. J. van Tol' [JvT 1869] in RMNH. – Paratypes 4 males: C. Celebes (Loewoe), Masamba, S. Baeboenta, 17 Apr 1940, 12 May 1940, 25 May 1941, 4 males (L.L.A. Maurenbrecher) [JvT 1870-1873] (in RMNH). Several of the paratypes are in poor condition due to damage by psocids. Specimens collected by Maurenbrecher labelled by Lieftinck as '*P. bivittata*'.

Description

Rather robust species; immediately recognizable by the presence of a pale antehumeral stripe of synthorax, in combination with a bilobed hind margin of the anterior lobe of the prothorax.

Male [holotype, JvT 1869]. – Head. Labium at base ochraceous, median lobe and palps chestnut-brown; mandibles bluish yellow to ochraceous, not concolorous to labrum; labrum bluish white with anterior onefourth to one-third with parallel-sided black stripe; anteclypeus concolorous with labrum; postclypeus and remaining part of head brownish black to black; scapus and flagellum brown; pedicellus dirty yellow.

Thorax. Pronotum (Figs 66-67) with anterior and median lobe bright creamish white, posterior lobe brownish black; anterior lobe with anterior transversal ridge much narrower in the centre than at lateral sides, widest part brownish covered with very short spiny setae, hind margin bilobate, shortly erect; median lobe without distinct characters; posterior lobe flat, hind margin nearly straight, but with lateral triangular process curved outwards. Synthorax (Fig. 84) chestnutbrown, ventrally somewhat paler, with brightly bluishwhite coloured lateral fasciae; antehumeral stripe close to dorsal carina narrowing posteriorly, ending well before hind margin of synthorax; pale, parallel-sided stripe over mesepimeron and metepisternum relatively wide and running parallel to metapleural suture, anteriorly just reaching mesokatepisternum, not covering metakatepisternum; ventral pale coloration of metepimeron widening posteriorly. Legs greyish yellow, joints brown. Wings nearly reaching posterior margin of abdominal segment 5; Arculus just distal to Ax2, origin of R4+5 approximately at subnodus; five cells between origin of IR3 and R3; seven cells between Ac (Cux) and place where CuP meets hind margin of wing; pterostigma nearly rectangular.

Abdomen. Segment 1 dorsal side ochraceous, lateral side yellowish; segment 2-6 dorsally predominantly ochraceous, anteriorly (especially latero-anteriorly) much paler, nearly creamish white, and posterior onefifth to one-sixth of each segment chestnut-brown to brownish black; segment 7 dark brown with anterior one-fourth dirty yellow; segment 8-10 dorsally blue, latero-posterior sides of tergites 8-9 black, lateral side of segment 10 black. Anal appendages (Figs 34-36) black; superiors rather slender with large dorsal tooth at c. two-fifth from the base, length of tooth approximately equal to diameter of appendix, insignificant ventral process at c. one-third from the top; inferiors with sturdy base, the more slender terminal parts curved outwards, near the top sharply curved inwards; top oblong triangular with inner-tooth very small in comparison to other species.

Female. – Unknown.

Measurements. – Male abdomen including appendages for specimens from Masamba (n=4) 41 mm, specimen from Palopo 47 mm; hind wing for specimens from Masamba 23 mm, the specimen from Palopo 25 mm.

Comparative notes. – Easily distinguishable from other Sulawesi *Protosticta* species by the presence of an antehumeral stripe, its considerable size, and the bilobate hind margin of the anterior lobe of the prothorax. It is similar in general appearance to *P. bivittata* , but it lacks the 'inner-horns' at the hind margin of the posterior lobe of the prothorax, and the strong inner-tooth of the inferior appendix (cf. Fig. 9).

Remarks

Etymology. – *Maurenbrecheri*, after Mr. L.L.A. Maurenbrecher, who collected odonates on Sulawesi in the 1940's for M.A. Lieftinck.
Habitat. – The type was found hanging in shrubs along a rivulet through semi-cultivated area at c. 400 m above sea level. Only one specimen was found among ten specimens of *Protosticta geijskesi* sp. n., a common lowland species in that region. Sungai Baebunta near Masamba is also a lowland locality, now situated in cultivated area. My own efforts in this area have not revealed any specimen of this beautiful species.
Distribution. – Central Sulawesi (politically Southwest Sulawesi), south of the central mountain ranges (Fig. 110).

Protosticta pariwonoi sp. n.

(Figs 37-39, 68-69, 85, 94, 102, 112)

Type material. – Holotype male: 'Indonesia, Sulawesi / E. of Maros: Bantimurung area, Sg. / Pattunuang Asue. Fast flowing stream / through disturbed forest on limestone. Large / boulders, ponded areas, clear water / 5°03'S 119°41'E. Sample 91JvT07 / 17 and 20 Apr 1991 / Leg. J. van Tol' in RMNH [JvT 5241]. – Paratypes: SW Celebes: Maros, Patunuang Asue, 23, 24, 25 Sep 1983, 4 males 1 female (S.S. Pariwono) [JvT 5230-5233, 5256, 5261]; Maros, Bantimurung, Biseang Labboro, 7, 8 and 10 Oct 1983, 6 males 3 females (S.S. Pariwono) [JvT 5234-5240, 5258-5260]; E of Maros, Bantimurung Area, Sg. Pattunuang Asue. 5°03'S 119°41'E. Sample 91JvT07, 17 and 20 Apr 1991, 5 males 1 female (J. van Tol) [JvT 5241-5244, 5252, 5257]; c. 30 km E of Maros, Cakar Alam near Desa Layia. Sg. Labang, and tributary. c. 5°00'S 119°50'E. 91JvT10 and 91JvT11. 20 Apr 1991, 10 males (J. van Tol) [JvT 5245-5251, 5253- 5255] all in RMNH, but 3 males and 1 female to be deposited in MBBJ.

Description

Relatively robust and large species, with similar general appearance as *Protosticta geijskesi*, but with much larger and also otherwise differing inferior appendages (see Fig. 39); anterior margin of prothorax wider than in *P. geijskesi*.
Male [holotype, JvT 5241]. – Head. Labium greyish white, tips of palps darker, brown; labrum bluish white, anteriorly with a narrow brownish black band; mandibles shiny black except for a paler spot in the basal corner against the labrum; anteclypeus bluish white; postclypeus and remaining part of head black; antenna concolorous brown (flagellum of right antenna broken).
Thorax. Pronotum (Figs 68-69) with anterior lobe brown, posterior lobe brownish black; anterior margin of anterior lobe curved distad, corners somewhat less than centre; sides conspicuously swollen; median lobe pale yellow; posterior lobe with raised hind margin and two 'horns' curved apicad; much variation in size of horns. Synthorax (Fig. 85) dark brownish black, black between humeral sutures, with parallelsided pale stripe parallel to metapleural suture running over mesepimeron and metepisternum touching metastigma; metepimeron creamish white with brown marking against metapleural suture rectangular at ventral side, pointed dorsally. Legs greyish brown. Wing length 25 mm; wings with origin of Arculus half the length of Ax2 distal to Ax2; origin of R4+5 at subnodus; nearly six cells between origin of IR3 and R3; six to seven cells between Ac (Cux) and place where CuP meets hind margin of wing.
Abdomen. Length including appendages 38 mm. First segment dark yellow with posterior brown ring; second segment brown with subrectangular latero-anterior marking; segments 3-6 dorsally brown, leaving anteriorly a creamish white ring and posteriorly passing to brownish black; segment 7 brownish black with latero- anteriorly an ovoid yellow marking; segments 8 and 9 blue on dorsum, only with minor brownish black markings in latero-distal corners; segment 10 black. Appendages (Figs 37-39) with superiors dark brownish black, slender; dorsal triangular process at approximately three-fifths from base, also an inconspicuous process at innerside at approximately four-fifths from base; inferiors in ventral view distal half with slender base and top as well-developed 'boxing glove', thumb thin and slender, connected by membranaceous (chitinized) structure; outer tip acute and somewhat curved inwards.
Female. – As the male, but mandibles creamish white, not black as in male (similar to *P. geijskesi*); anterior lobe of prothorax with anterior margin not laterally

flattened as in male, although somewhat produced and erect; inner horns of hind lobe of posterior lobe of prothorax slender. Abdomen much shorter than male; segment 2 narrowest segment, abdomen gradually widening posteriorly; segment 1 creamish white except for dark crescent shaped dorso-posterior marking; segment 2 dark on dorsum with pale coloration in ventro-anterior three-quarters towards sternites; segments 3-7 with dorsum brownish black, gradually paler towards sternites, with pale anterior twinspot leaving anteriorly a median dark dorsal stripe; tergite 8 (Fig. 102) dorsally brownish black with creamish white marking in latero-anterior threequarters, sternite 8 pale creamish white, base of valve segment 8 pale creamish white, top black; segment 9 dark brownish black, laterally with pale central oval spot, valve (Fig. 94) of segment 9 dark, top of terebra pale coloured except for black dorsal line, stylus long and slender; segment 10 dark.

Variation. – There is some variation in the length of the ‘horns’ at the hind margin of the prothorax.

Measurements. – Male (n=23) abdomen including appendages 39 (36-42) mm, hind wing 26 (24-28) mm; female (n=5) abdomen including appendages 33 (31-35) mm, hind wing 24 (23-25) mm.

Comparative notes. – Very similar to *P. geijskesi* (see key for characters), confined to the southernmost part of the southwestern peninsula of Sulawesi. The much more robust top of the inferior appendage and the swollen sides of the anterior lobe of the prothorax are diagnostic characters; in most specimens also the shape of the hind margin of the prothorax with ‘horns’ distinctly different from specimens here assigned to *P. geijskesi*. Specimens from Gunung Lompobatang (SW Sulawesi) above c. 1000 m, although much larger than specimens from populations in Central and Southeastern Sulawesi, are assigned to *P. geijskesi*.

Remarks

Etymology. – Named after Scipio S. Pariwono (born 1919 in Gorang Gareng, Eastern Java, mainly lived in Bogor, Indonesia) (formerly named Liem Swie Liong), a former assistant to A.M.R. Wegner at Nongkodjadjar and A. Diakonoff in MBBJ. Through numerous field trips, mr. Pariwono has contributed significantly to our knowledge of the Odonata of Indonesia, especially of Java, Borneo and Sulawesi. Mr. Pariwono made collecting and reconnaissance trips to Sulawesi with M.A. Lieftinck in 1982, and with J. van Tol in 1989.

Habitat. – Own records pertain to specimens collected around Bantimurung, where this species is not uncommon along rivulets through rather open, somewhat disturbed riverine forest on limestone. *Protosticta bivittata* is another species reported from this area, but that species is less common, and presumably also more seasonal. *P. pariwonoi* was also observed along a tributary of one of the streams, which was flowing through dense forest, where the most common species was *P. coomansi*.

Distribution. – Only known from the extreme southwest of Sulawesi (surroundings of Maros, Bantimurung) (Fig. 112).

Protosticta reslae sp. n.

(Figs 40-42, 70-71, 86, 111)

Type material. – Holotype male: ‘Celebes. Polewali 6/8/40 [= 6 Aug 1940]. J.J. van der Starre’ and ‘*Protosticta* spec. nov. E’ [Lieftinck’s hand] [JvT 1876] in RMNH. – Paratype 1 male: Same envelope as holotype, 1 male [labelled as paratype] [JvT 1877] in RMNH.

Description

Robust species, with inferior appendage stoutly built, and superior appendage relatively broad.

Male [holotype, JvT 1876]. – Head. Labium with palps and anterior side of median lobe dark brown, remaining part pale brown; mandibles bluish white with anterior one-fourth brownish black; labrum bluish white, with anterior one-fourth with a parallelsided black stripe; anteclypeus bluish white as labrum, postclypeus and remaining part of head black; area below antennae and median ocellus glossy, dorsal surface velvet black.

Thorax. Pronotum (Figs 70-71) with anterior lobe brown, relatively narrow, anterior and posterior margin parallel-sided with an irregular, transverse ridge partly running along anterior margin; median

lobe dirty greyish white (? due to preservation); hind lobe brownish black, simply built with lateral corners only somewhat curved upwards. Synthorax (Fig. 86) brownish black with metallic shine; no antehumeral stripe; creamish fascia over metepisternum straight on anterior side, but with irregular ventro-posterior margin, fascia wide over stigma, constricted just above stigma; dark stripe over metapleural suture extending to halfway metepimeron, posteriorly tapering towards suture; remaining part of metepimeron creamish white. Wing length 32 mm; Arculus just distal to Ax2, origin of R4+5 well proximal to subnodus; seven cells between origin of IR3 and R3; eleven cells between Ac (Cux) and place where CuP meets hind margin of wing. Abdomen. Length including appendages 45 mm. Slender, brown and paler than most other species of Sulawesi. Segments 1-2 relatively little swollen, segments 8-10 strongly inflated, segment 7 setose on dorsal side; segment 1-7 with inconspicuous coloration, segment 1 brown with somewhat paler centre, segments 2-7 concolorous brown, although somewhat darker against hind margin of each segment; distal 7/8th of dorsum of segment 8, and segment 9-10 with blue marking (obscured by post mortem changes in the types) . Appendages (Figs 40-42) with superiors brownish black, in dorsal view a blunt dorsal toothlike tubercle at 3/4th from base, scythe-shaped terminal part extending for three-quarters of the distal part of superior, stronger developed than in *P. coomansi*. Inferiors also dark brown, structure of top comparable to *P. coomansi*, but inner tooth stronger developed.
Female. – Unknown.
Measurements. – Paratype wing length 32 mm, abdomen including appendages 48 mm..

Comparative notes. – Similar to *P. coomansi*, based on shape of inferior appendage and blue marking of abdominal segment 10. It can be distinguished from *P. coomansi* and *P. gracilis* by the shape of the superior and inferior appendages of the male. The superior appendage is robust and scythe-shaped, with a blunt dorsal tooth in the distal half (Fig. 40). Inferior appendage in ventral view rather similar, but more robust than in *P. coomansi* (Fig. 42).

Remarks

Etymology. – *Reslae*: a combination of characters, in which the abbreviation of the Royal Entomological Society of London (RESL) can be detected. The RESL was the organizer of Project Wallace (Dumoga Bone National Park, northern Sulawesi) in 1985, which formed the immediate reason for me to start a study on the Odonata of Sulawesi.
Distribution. – Only known from the type locality Polewali in the topographically southwestern part of central Sulawesi (Fig. 111).

Protosticta rozendalorum sp. n.

(Figs 43-46, 72-73, 87, 95, 103)

Type material. – Holotype male: 'Indonesia, Sangihe Islands: NW slope of Gunung Sahendaruman (SSW of Liwung): 2°32'N 125°32'E. Primary forest and forest edge, water trickle and small streams. 600- 650 m. 12-19 May 1985' (type actually collected 19 May 1985) (F.G. Rozendaal) [JvT 1879] in RMNH. – Paratypes: Same site (one without proper label), 14 and 19 May 1985, 2 males 1 female (F.G. Rozendaal) [JvT 1880-1882]; Manganitu, riverine gardens, coconut, plantations, secondary growth, 3°35'N 125°32'E, 10 May 1985, 1 male (F.G. Rozendaal) [JvT 1878] all in RMNH.

Description

Medium-sized species, which is not closely related to any of the species occurring in Sulawesi. Immediately distinguishable from other *Protosticta* treated in this paper by the shape of the inferior appendages of the male.
Male [holotype, JvT 1879]. – Head. Labium dark creamish white, labial palps brown; mandibles with anterior side variable in colour, brown or pale; labium bluish white with a black stripe along the anterior margin, c. one-third the height of labium, with basiomedial V-shaped emargination; anteclypeus creamish white; postclypeus and frontal part of head glossy black; dorsal surface of head velvet black. First segments of antenna brown, flagellum brownish black. Thorax. Pronotum (Figs 72-73) with anterior lobe black, shape rather simple with anterior margin with rim, median lobe brownish black, lateral tubercles only little elevated, posteriorly brown; hind lobe black, flat without erect parts. Synthorax (Fig. 87) brownish black

with pale parts creamish; antehumeral stripe absent; fascia over mesepisternum nearly par- allel-sided, only tapering dorso-posteriorly; dark stripe over metapleural suture with sharp outline on metepimeron, where somewhat irregular. Legs greyish. Wing length 26 mm; pterostigma pale bordered against veins, most narrow anteriorly against Costa; Arculus just distal to Ax2, origin of R4+5 at or just anterior to subnodus; five cells between origin of IR3 and R3; nine cells between Ac (Cux) and place where CuP meets hind margin of wing.

Abdomen. Length including appendages c. 40 mm. Rather slender, only segments 9-10 somewhat inflated; segment 1 creamish yellow with dorsum pale brown and a posterior dark brown ring; segment 2 brown with latero-anterior two-thirds of tergite creamish yellow; segment 3 brown, much darker posteriorly and a latero-anterior creamish yellow marking; segments 4-7 brown, somewhat darker posteriorly and a latero-anterior creamish yellow marking on each segment; segment 8 with posterior 5/6th of dorsum pale blue, anteriorly and laterally bordered with dark brown, ventral part of tergite creamish; segment 9 with dorsum pale blue, ventral part brownish black; segment 10 brownish black. Appendages (Figs 43-46) brownish black; superiors smoothly curved inwards, innerside halfway with triangular tooth directed ventrad, at approximately three-quarters from base a low tubercle at base of an elongate emargination to the top; inferiors in ventral view with basal half straight, then pointed 90° outwards, and then again directed posteriad; top smooth and shining, in ventral view a subquadrangular structure with short basal innertooth, in dorsal view consisting of a terminal hook with a subterminal innertooth, which are connected by a delicately chitinized veil.

Variation. – No notable structural variation in paratypes.

Female. – As the male, but mandibles pale coloured, abdominal segment 8 short, dorsum dark brown, gradually paler towards sternites; segment 9 anteriorly and posteriorly dark brown, also centre of dorsum dark brown, lateral sides with much paler brownish coloured markings; segment 10 dull castaneous; valves long, projecting considerably beyond appendages (Figs 95, 103).

Measurements. – Males (n=4) abdomen including appendages 41 (38-42) mm, hind wing 26 (24-26) mm; female (n=1) abdomen including appendages 33 mm, hind wing 25 mm.

Comparative notes. – The structure of the superior appendage of the male is unlike that of any of the Sulawesi species. The structure of the inferior appendage of the male is more or less similar to that in *P. geijskesi* and related species.

Remarks

Etymology. – *Rozendalorum,* after Mr. and Mrs. Frank and Carla Rozendaal, ornithologists with a keen interest in Odonata, and collectors of the present species.

Habitat. – Collected together with *Protosticta simplicinervis* Selys and *Rhinocypha frontalis* Selys in a small shaded stream.

Distribution. – Sangihe Islands; only known from the type locality.

Protosticta simplicinervis Selys

(Figs 47-49, 74-75, 88, 96, 104,108, 113)

Protosticta simplicinervis Selys, 1885: cxlv. Lectotype male (here designated) 'Mirabassa / Celebes', and '*Protosticta simplicinervis* Selys' in Selys hand, and several labels from M.A. Lieftinck, in IRSN [examined]. – Kirby 1890: 133 (catalogued); Davies & Tobin 1984: 107 (catalogued); Van Tol 1987: 154 [record Dumoga Bone]; Tsuda 1991: 8 (catalogued).

Protosticta annulata Fraser, 1926: 492. Holotype male: Celebes, Menado (Mohari) in RMNH [examined]. – Lieftinck 1930: 138 [synonymized with *P. simplicinervis*]; Lieftinck 1971: 73 [type examined; synonymized with *P. simplicinervis*]; Davies & Tobin 1984 (catalogued as synonym of *P. simplicinervis*); Tsuda 1991: 209 (catalogued as synonym of *P. simplicinervis*); Bridges 1994 (catalogued as synonym of *Protosticta simplicinervis*).

Protosticta sp. – Askew et al. 1989: 118 [examined].

Description

Large and robust species with relatively long abdomen, immediately recognizable by the paired protuberance on the middle lobe of the prothorax, and the characteristic shape of the inferior appendages.

Male. – Head. Labium with labial palps brown, median lobe anteriorly brown, rest of mentum creamish white; labrum bluish white with anterior margin black, dark margin in the middle c. half the height of labrum, strongly tapering towards lateral corners; mandibles with anterior margin bluish white with black markings; anteclypeus bluish white, postclypeus shiny black; remaining part of head black with glossy shine anteriorly and velvet black on dorsal surface; two tufts of long setae behind lateral ocelli directed distad.

Thorax. Pronotum (Figs 74-75) with anterior and median lobes predominantly pale coloured, hind lobe dark brown; anterior lobe medially more or less flat; lateral sides depressed in the middle resulting in anterior and posterior ridge; median lobe medio-anteriorly with paired conical structure; posterior lobe simple with only extreme lateral corners somewhat raised, no horn-like structures. Synthorax (Fig. 88) very dark brownish black with purple shine, light coloured parts creamish or bluish white; antehumeral stripe absent, pale stripe over mesepimeron and metepisternum parallel-sided, approximately four-fifths the width of metepisternum; dark stripe over metapleural suture, fading to brown on metepimeron; rest of metepimeron creamish white. Legs pale. Wings (Fig. 108) reaching to halfway abdominal segment 6; Arculus distal to Ax2; origin of R4+5 just proximal to subnodus; four cells between origin of IR3 and R3; seven cells between Cux and place where CuP meets hind margin of wing.

Abdomen. Segments 1-2 somewhat inflated; segments 8-10 strongly inflated, nearly flat on dorsum; dorsum of segments 1-2 ochraceous, lateral sides creamish white; segments 3-7 brown with paler anterior part gradually increasing from 1/10th on segment 3 to 1/5th on segment 7; dorsum of segments 8-10 with distinct pale blue spot, consisting of an oblong semi-circular marking on posterior 4/5th of segment 8, a complete blue segment 9, and segment 10 blue except for a narrow brownish black ring on segment 10. Appendages (Figs 47-49) pale ochraceous, superiors in dorsal view directed medio-ventrad, top somewhat club-shaped, but not distinctly wider than base, dorsal side with conspicuous spine halfway; inferiors in ventral view with top glossy pale brown, bent 90° inwards, with its very tip sharply bent dorsad; subterminal tooth directed medio-dorsad.

Female. – As male, including the paired conical protuberance on the median lobe of prothorax; coloration of abdominal segments 1-7 also as in male, segment 8 brown with latero-anterior pale markings, segment 9 (Figs 96, 104) with dorsal line dark, posterior 2/5th of segment dark, but pale towards sternites; latero-anterior part pale; segment 10 brown, darker on dorsum; appendages short, brown; valves brownish black, top of terebra pale coloured, stylus long and slender.

Measurements. – Male (n=10) abdomen including appendages 43 (39-47) mm, hind wing 28 (25-30) mm; female (n=6) abdomen 39 (37-41) mm, hind wing 30 (29-32) mm.

Variation. – No notable geographical variation. The specimen from Sangihe is not markedly different from the Sulawesi specimens.

Comparative notes. – Males and females can easily be distinguished from other Sulawesi species of *Protosticta* by the conical structures (protuberances) on the dorsum of the median lobe of the prothorax. A species group in its own.

Material examined

In total 37 males and 19 females, including lectotype male and paralectotype male ‘Mirabassa / Celebes’ (in IRSN), and the holotype of *Protosticta annulata* Fraser, and further as follows: Sangihe Islands: NW slope Gn Sahendaruman (SSW Liwung), 3°32’N 125°32’E. 600-650 m, 12-15 May 1985, 1 male 1 female (F.G. Rozendaal) in RMNH [JvT 1973-1974]. – N Sulawesi (Celebes), localities arranged from west to east: Sabang Dampelas; Toli Toli; Leok; Ile Ile 500-800 m; Gorontalo heuvelland Kwandang alt 200 m; Dumoga Bone National Park, several stations 200-600 m; Tondano: pool between Airmadidi and Tondano 600 m; surroundings Ranotongkor; Mapanget; Pineleng, 250 m (various collectors) in RMNH, IRSN, collection D.A.L. Davies. – Central Sulawesi. c. 10 km WNW Palopo near Tojambu (Puncak), 800-1000 m, c 2°56’N 120°07’E, Jul/Aug 1991 (native collector Yohan), 1 male 5 females; Masamba inland, river and tributaries, c. 2°30'S 120°25'E, 1-2 Nov 1993, 2 males (Yohan R.).

Remarks

Habitat. – Found along densely shaded small streams, as well as along more open larger streams. I am uncertain about the breeding habitat of this species. Most likely the larvae are living in small shaded streams rather than in the large streams. As far as I am aware, all records from larger streams are close to brooklets or creeks.

Distribution. – Central Sulawesi (uncommon), and the dominating *Protosticta* of the northern peninsula (north of Dampelas), also Sangihe Islands (Fig. 113). The species has repeatedly been found by professional collectors around Palopo (Tojambu, Masamba), but I have been unable to find this species here myself. Thus, the precise habitat of this species in that area remains uncertain.

Note. – While males of most *Protosticta* species are dominating in collections, females of *P. simplicinervis* are remarkably common in the material examined.

Protosticta vanderstarrei sp. n.

(Figs 50-53, 76-77, 89, 97, 105, 109, 113)

Type material. – Holotype male: 'Celebes, Polewali, 23 Oct 1940 (J.J. van der Starre)' [JvT 1883] in RMNH. – Paratypes 13 males and 2 female: Same site and same collector as holotype, 23 Oct 1940, 2 males [JvT 1884, 1888], 6 Aug 1940, 1 female [JvT 1887]; Lindoe-vlakte, loc. XVIII [near Lake Lindu], alt. 850 m, 8 Aug 1940, 2 males (one incomplete) [JvT 1885- 1886]; 30 km N of Wotu: Sg Anoa, waterfall near bridge Wotu-Tentena, 650 m, 23 Oct 1993, 1 male (J. van Tol) in RMNH [JvT 1500]; N of Madjene, Onan, Sg. Parabaya, 5 males 1 female (J.P. Duffels) [JvT 6019, 6020, 6028-6031] in ZMAN, 1 male in RMNH; S of Palu, Lore Lindu NP: Kamarora, small brooklets, 700 m, 7-8 Apr 1997, 2 males (J. van Tol) in RMNH, MBBJ [JvT 16636, 16638]; same, first large river crossing trail to Nokilalaki, 9 Apr 1997, 1 male (J. van Tol) [JvT 16655] in RMNH.

Additional material, excluded from type series. – Celebes, Ile Ile, 5-800 m, Dec 1930, 1 male 1 female (S. Heinrich) [identified as *Protosticta* sp. – by Lieftinck] in RMNH [JvT 1889, 1890]; 65 km SSE of Palu: Lore Lindu NP near Marena shelter, 600 m, 17 Dec 1985, 2 males (J. van Tol) in RMNH, MBBJ [JvT 1874-1875]. I have also seen a male from Northern Sulawesi, Dumoga Bone National Park, 1985, in coll. D.A.L. Davies, Cambridge.

Description

Small species with very dark synthorax, especially so since it lacks pale coloration on metepimeron; general appearance as *Drepanosticta* rather than *Protosticta*.

Male [holotype, JvT 1883]. – Head. Labium concolorous ochraceous; labrum bluish white with narrow brown-black anterior border, wider in middle than lateral corners; mandibles shining bluish white; anteclypeus bluish white, postclypeus and remaining part of head black; antennae with scapus brown, pedicellus pale ochraceous, flagellum pale brown.

Thorax. Pronotum (Figs 76-77) with anterior and posterior lobe brownish black; anterior lobe erect, but not turned posteriad; median lobe pale yellow without significant characters (specimens from the Lindu valley have a brown median lobe); posterior lobe flat, hind margin hardly indented. Synthorax (Fig. 89) very dark chestnut brown, dorsally nearly black, with only one lateral pale yellowish stripe above metastigma parallel to second lateral suture, stripe pointed anteriorly, wider dorsal part stops aslant before posterior margin of synthorax; metepimeron and metakatepisternum dark without pale marking. Legs greyish yellow, joints of femora and tibiae greyish brown, also a grey ring at one-third from joint of femur. Wing length 21 mm; pterostigma subquadrate with oblique inner corner; Arculus just distal to Ax2 (Fig. 109); origin of R4+5 in fore and hind wing approximately at subnodus; six cells between origin of IR3 and R3; nine cells between Ac (Cux) and place where CuP meets hind margin.

Abdomen. Length including anal appendages 32 mm. Segments 1 and 2 somewhat inflated, segments 8-10 relatively little wider than preceding segments; segment 1 ochraceous with lateral crescent-shaped brown marking connected with hind margin; segment 2 castaneous with a small latero-anterior spot; segment 3-6 brown, anteriorly c. one-fifth to oneeighth ochraceous, but dorsally with narrow brown stripe, segments 7-8 brownish black, segment 7 somewhat paler anteriorly; segment 8 without any trace of pale coloration; segments 9-10 blue, ventro-laterally bordered with black, hind margin of segment 10 black; ventral side of abdominal segments 8-9 blue; anal appendages (Figs 50-53) relatively short, superiors laterally inflated, top rectangular, dorsal tubercle stout; inferiors club-shaped, tapering towards the top, ending in short S-curve, subterminal innertooth very slim and slender, nearly filamentous.

Female. – As the male, in coloration; abdomen shorter and less slender than that of male, segments 3- 7 brown, but anterior one-sixth to one-fifth creamish yellow, segment 8 brown with latero-anterior twinspot, segment 9 (Figs 97, 105) pale blue with a brown dorsal stripe, somewhat widening posteriorly, ventral side of tergite also brown, segment 10 and appendages brownish black; valves castaneous, projecting just beyond appendages, stylus long and slender.

Measurements. – Male abdomen including appendages 32-34 mm; hind wing 21-22 mm; female abdomen 23 mm, hind wing 21 mm.

Variation. – Not much variation in structural details, apart from the pterostigma, which is subquadrate to rhomboidal, with distal side straight to rather convex. Middle lobe of pronotum sometimes without dark markings, but in some specimens with rather extensive dark brown spot, fading towards edges (‘burnt’). Significant variation in coloration of last abdominal segments. Specimens with extensive blue markings (as in JvT 16636 from Kamarora) have a lateral blue line along lateral margin of tergites 8, dorsum of segment 9 fully blue, and dorsum of segment 10 blue except from narrow black line along hind margin; sternites of segment 8 and 9 blue; innerside of superior appendages pale coloured. Another specimen from Kamarora (JvT 16655) with only small pale dorsal markings on abdomen: segment 9 with subtriangular paired white spot in anterior half, a small twinspot dorsally near hind margin, segment 10 with only a small rounded twinspot near anterior margin; sternites blue as in JvT 16636. A specimen from Wotu (JvT 1500) with very extensive markings, viz. with a small blue twinspot in anterior half of segment 8. Specimens collected near Gimpu (Lore Lindu NP) (JvT 1874, 1875) completely lack pale dorsal abdominal markings, but have blue coloured sternites as described above. Most older material too much discoloured to examine pale coloration.

Comparative notes. – Not similar to any of the other Sulawesi platystictids here assigned to *Protosticta*. As indicated elsewhere, the correct generic assignment of this species has to await a generic revision of the Platystictidae. The general appearance is more similar to *Drepanosticta*, but its structural details studied so far are too generalized to postulate another generic position than *Protosticta*.

Remarks

Etymology. – *Vanderstarrei*, after Mr. J.J. van der Starre, who travelled extensively along the coasts of Sulawesi in the early 1940’s, collecting many interesting Odonata in areas previously unexplored and even poorly investigated today. Mr. Van der Starre also collected the holotype of this species.

Habitat. – One of the labels gives ‘overhangende takken boschbeek’ (overhanging branches forest stream); presumably not in lowland areas. My own observations indicate that *P. vanderstarrei* occurs only in low densities at strongly shaded sites in dense forest. Larvae possibly live in seepage areas or trickles, a habitat encountered on all sites where this species was collected. Most sites between 500 and 850 m.

Distribution. – Widespread in Central Sulawesi, apparently very local in the northern peninsula.

Unplaced specimens

I have been unable to attribute three specimens to any of the species described in this paper. They are incomplete or damaged, but almost certainly they represent three different, undescribed species.

Mamasa, along brooklet, 1550 m, 11 Apr 1991, 1 male (J. van Tol) in RMNH [JvT 19353]. Teneral specimen, with anal appendages rather damaged. The structure of the anal appendages reminds of *Protosticta maurenbrecheri*, but the synthorax lacks the antehumeral stripe.

Ile Ile, 500-800m, Anf. 12.30 [= early December 1930], 1 male (G. Heinrich) in RMNH. Specimen misses last abdominal segments. The anterior lobe of the prothorax has some resemblance to *P. marenae*, but it is sufficiently different to suppose that it represents an undescribed species.
Sulawesi Utara, Dumoga Bone Nat. Park, river Tumpah (200 m), X-1985. Station 045 (R. Bosmans & J. Van Stalle, 1 female (in IRSN) [JvT 16880]. This specimen is different from any other female of *Protosticta* I have seen, based on the coloration of the last abdominal segments and the structure of the prothorax. Unfortunately, it is also too much damaged to be described as a new species.

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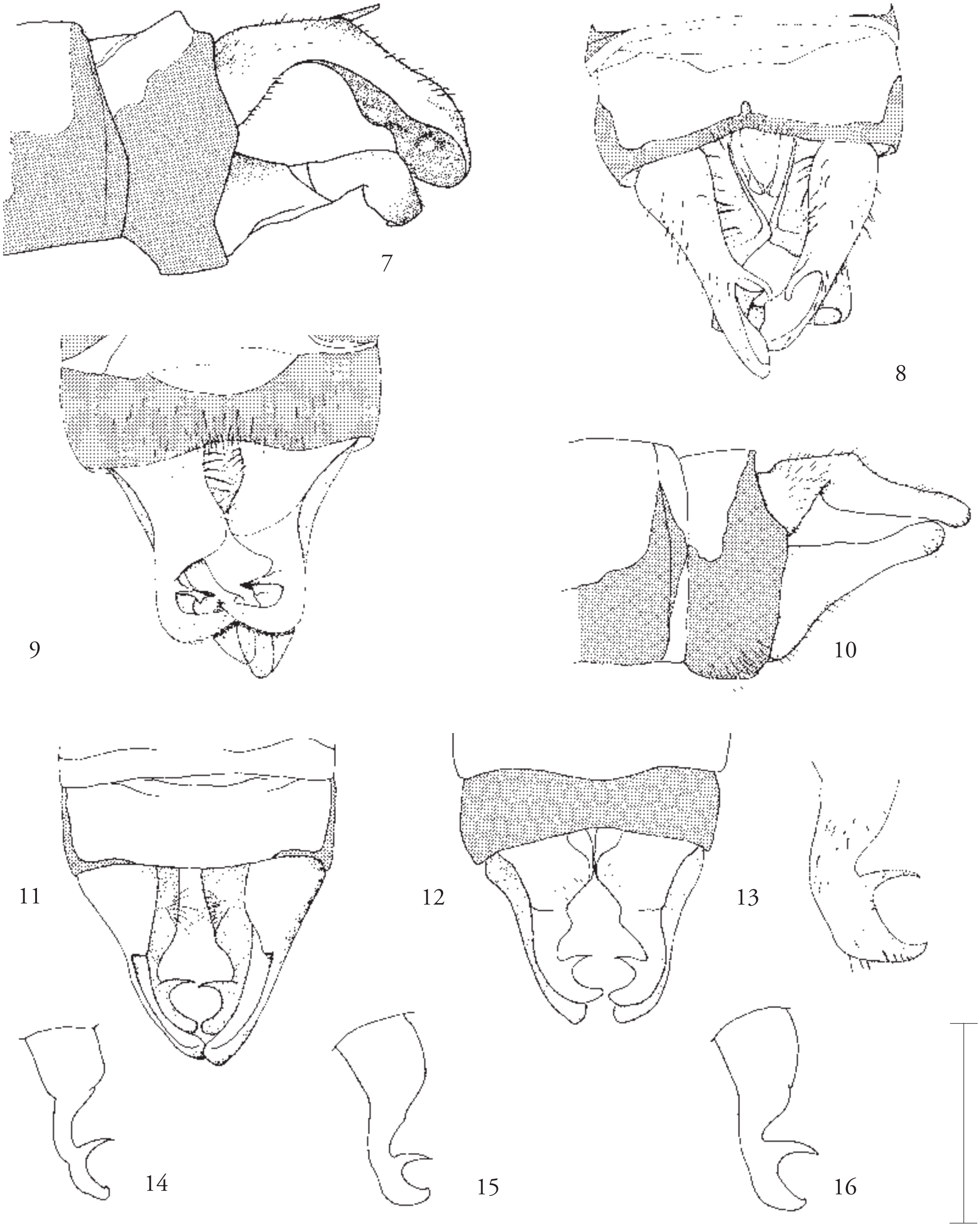
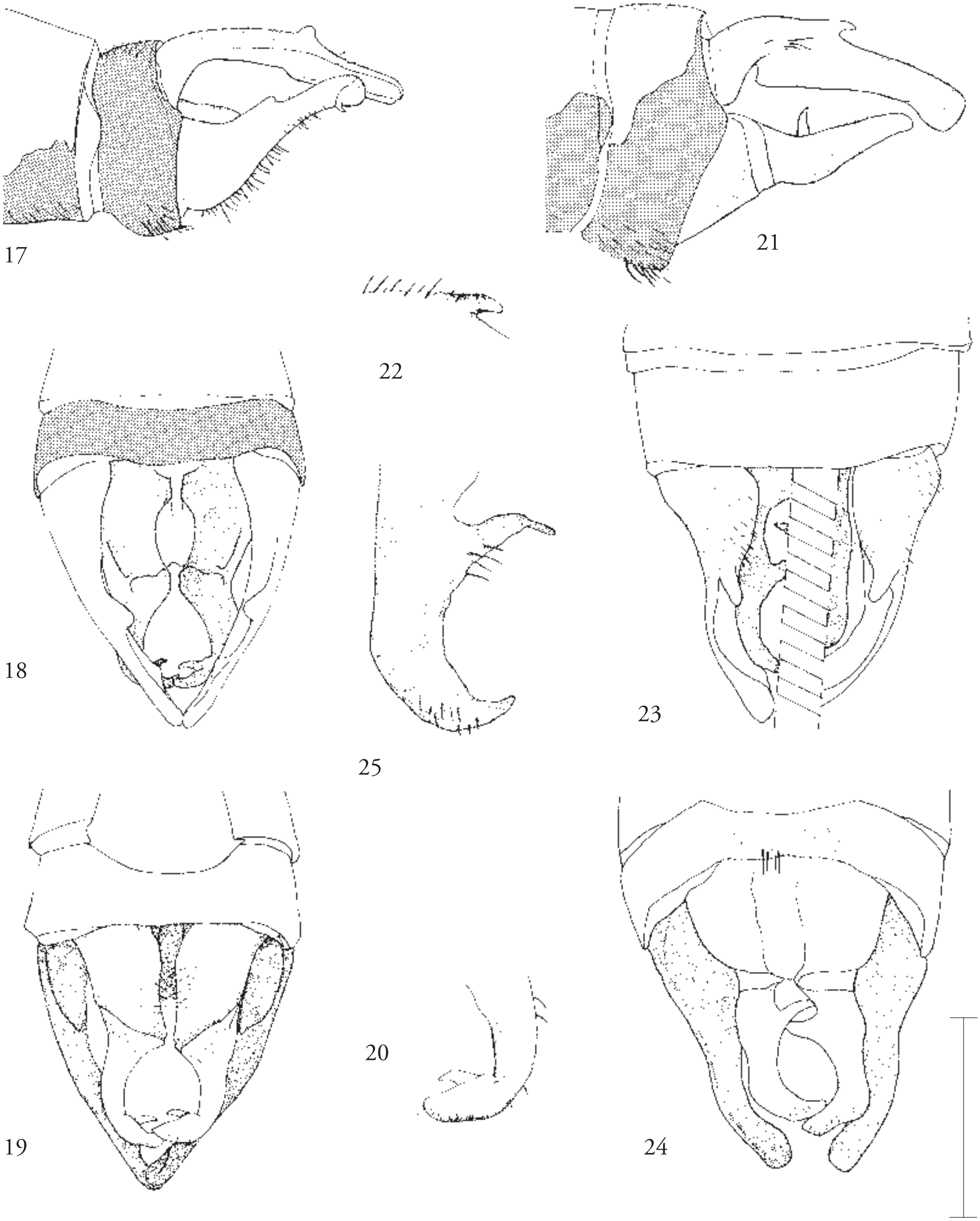
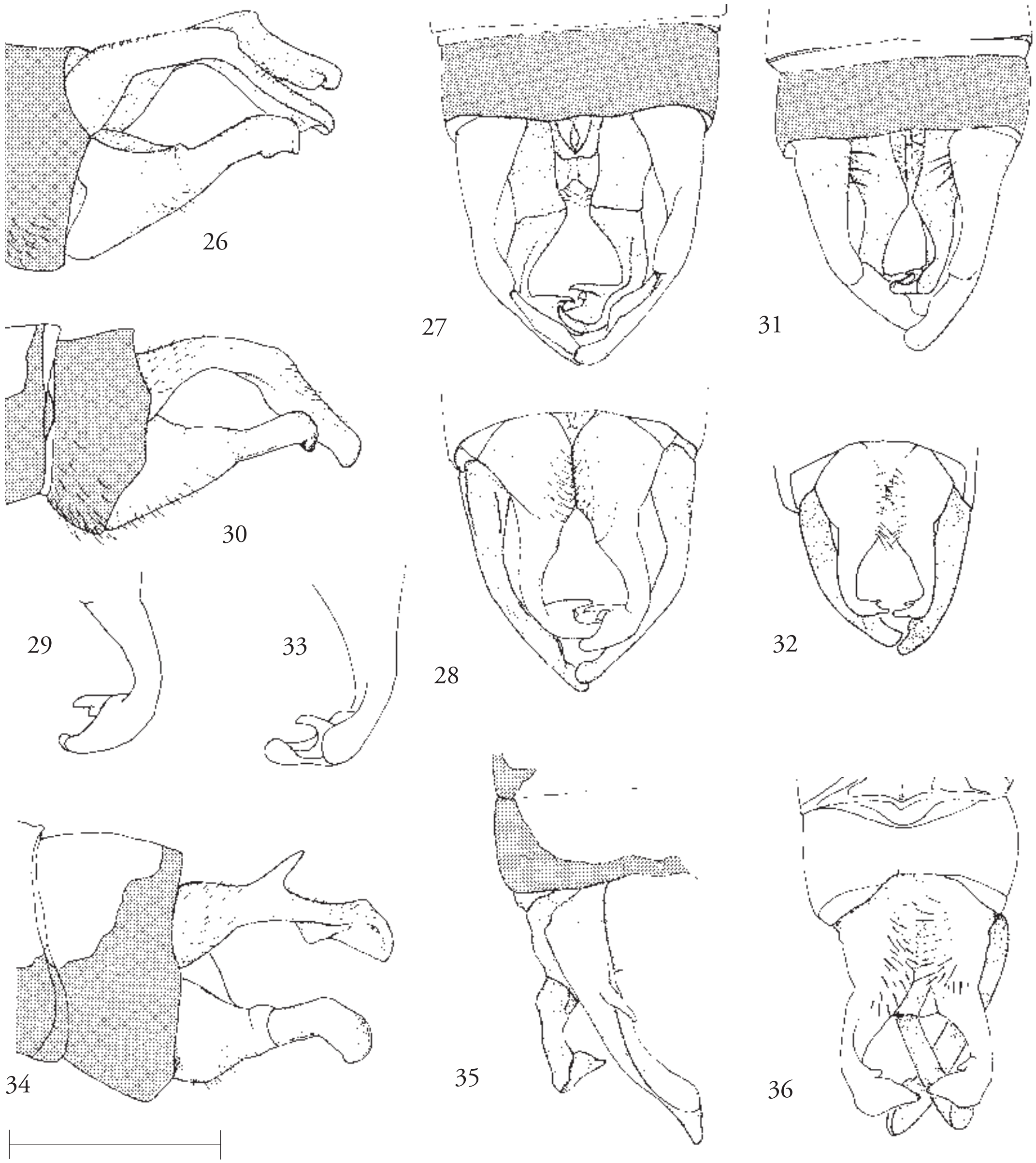


Figures 7-16. Last abdominal segments and anal appendages of male. – 7-9, *Protosticta bivittata* Lieftinck. 7, left lateral; 8, dorsal; 9, ventral view (JvT 1842, SW Sulawesi, Bantimurung area, 31 May 1982). – 10-16, *Protosticta coomansi* sp. n., 10, left lateral; 11, dorsal; 12, ventral view (JvT 16606, C. Sulawesi, N of Gimpu, 4 Apr 1997), 13, same, inferior appendage, high magnification (JvT 16661, SW Sulawesi, Loewoe, Todjamboe, 18 Jul 1936), 14, same, inferior appendage ventral view (JvT 2033, SW Sulawesi, Maros area); 15, same (JvT 16582, C Sulawesi, Gimpu); 16, same (JvT 2009, C. Sulawesi, Leok). Scale bar 1 mm (for all figures, except for fig. 13 = 0.5 mm).



Figures 17-25. Last abdominal segments and anal appendages of male *Protosticta*. – 17-20, *P. geijskesi* sp. n. 17, left lateral; 18, dorsal; 19, ventral view; 20, appendix inferior in ventral view at higher magnification (JvT 1891, NW Sulawesi, Sabang, Dampelas, 30 Jan 1941. – 21-25. *Protosticta gracilis* Kirby. 21, left lateral; 22, dorsal tooth of superior appendage in lateral view; 23, dorsal view (piercing straw indicated); 24, ventral view; 25, appendix inferior in ventral view (all holotype, NE Sulawesi, Manado, Tondano). Scale bar 1 mm (for figures 17-19, 21, 23-24), 0.5 mm (for figures 20, 22, 25).



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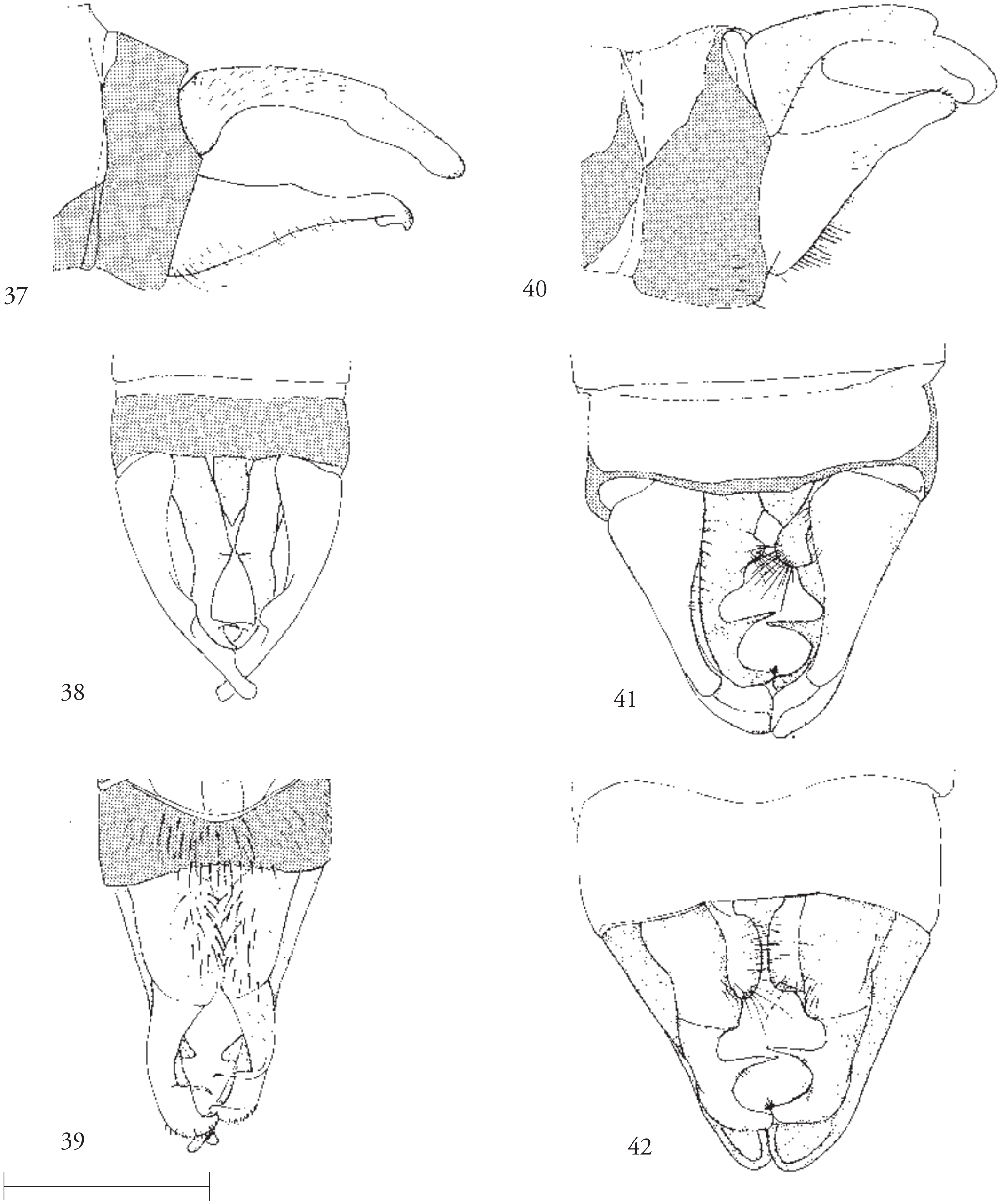

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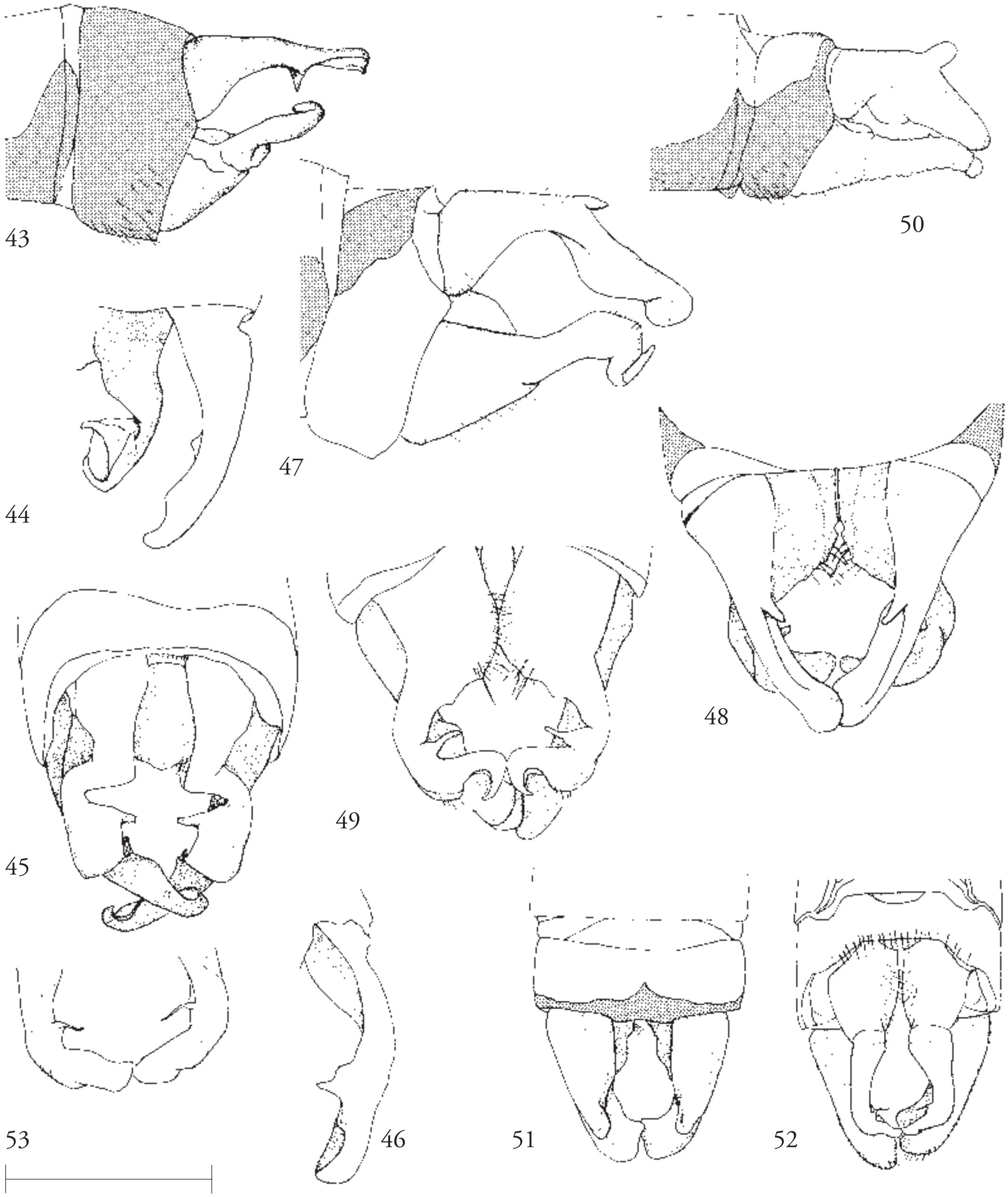

Figures 43-53. Last abdominal segments and anal appendages of male *Protosticta*. – 43-46, *P. rozendalorum* sp. n., left lateral, dorsal and ventral view, and (46) innerside of right superior appendages (JvT 1878, N. of Sulawesi, Sangihe Is., Manganitu, 1985). – 47-49, *P. simplicinervis* Selys, left lateral, dorsal and ventral view (JvT 1947, NE Sulawesi, Mapanget, 28 Jul 1940). – 50-53, *P. vanderstarrei* sp. n., left lateral, dorsal and ventral view (JvT 1888, SW Sulawesi, Polewali, 23 Oct 1940).
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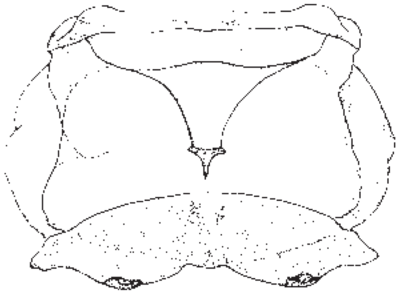

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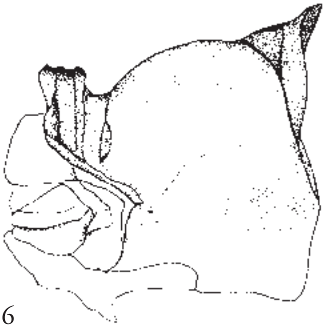

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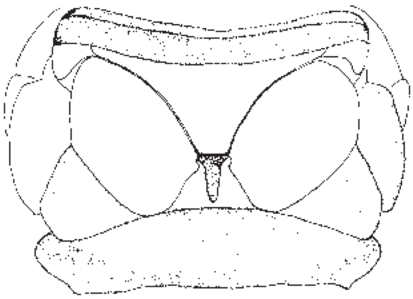

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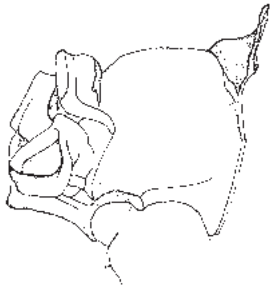

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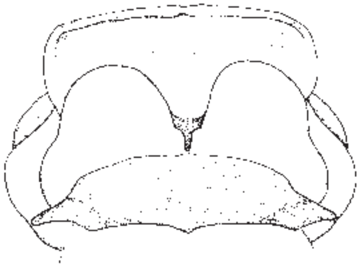

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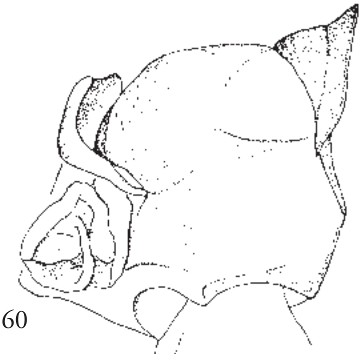

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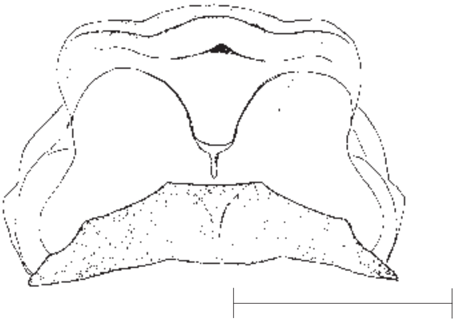

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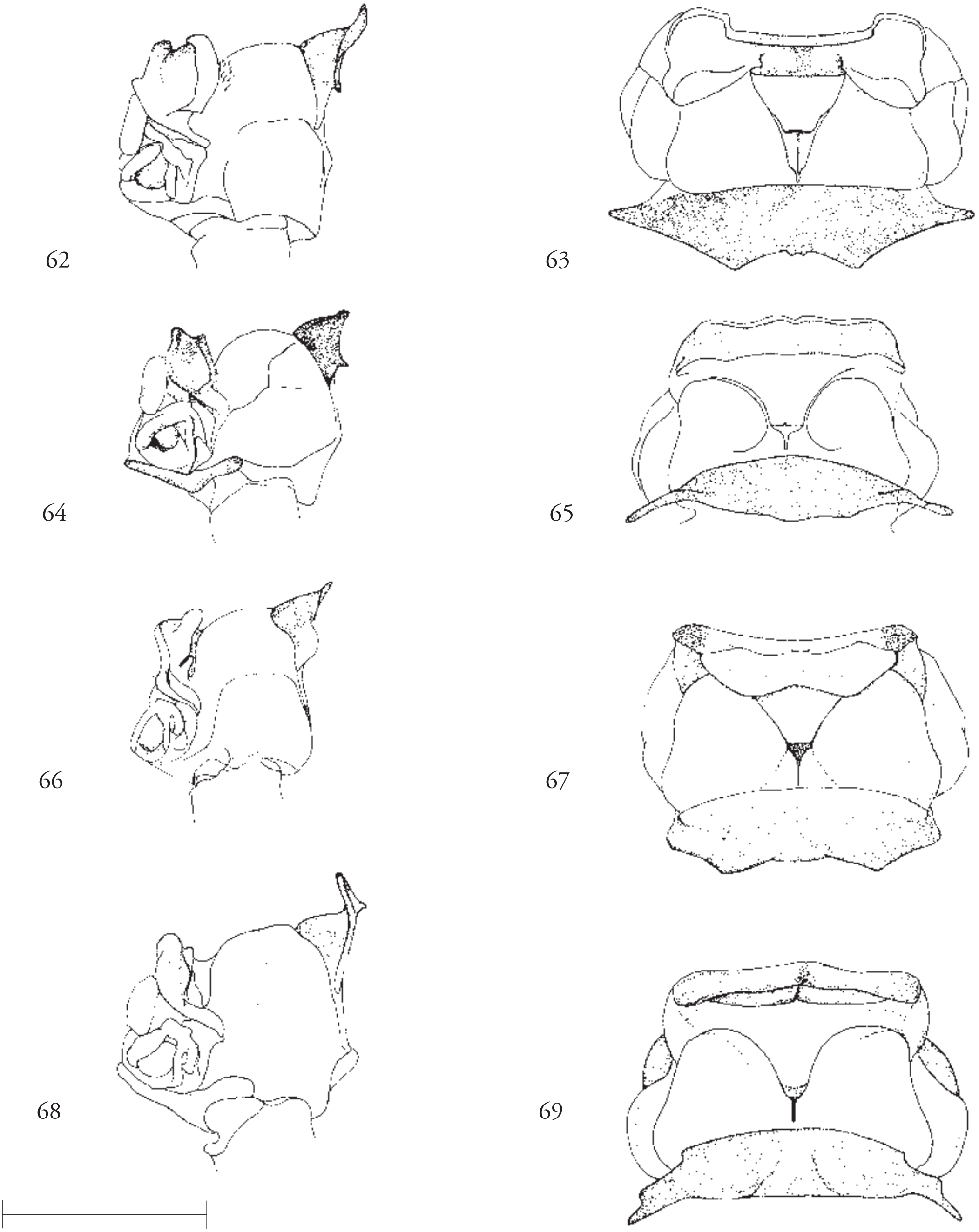
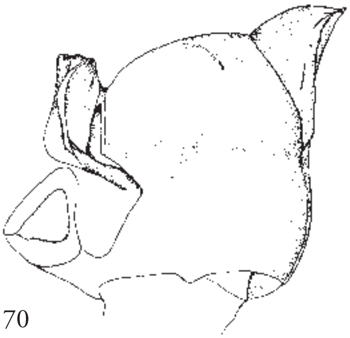
Figures 54-61. Pronotum of *Protosticta* species in left lateral and dorsal view. – 54-55, *P. bivittata* Lieftinck (JvT 1842, SW Sulawesi, Bantimurung area, 31 May 1982). – 56-57, *P. coomansi* sp. n. (JvT 16853, C. Sulawesi, N. of Gimpu, 16 Dec 1985). – 58-59, *P. geijskesi* sp. n. (JvT 1891, C. Sulawesi, Sabang, Dampelas, 30 Jan 1941). – 60-61, *P. gracilis* Kirby (holotype). Scale bar 1 mm.



Figures 62-69. Pronotum of *Protosticta* in left lateral and dorsal view. – 62-63, *P. linduensis* sp. n. (JvT 1861, C Sulawesi, Lore Lindu NP, 9 Dec 1985). – 64-65, *P. marenae* (JvT 1866, C Sulawesi, Lore Lindu NP, 16 Dec 1985). – 66-67, *P. maurenbrecheri* sp. n. (JvT 1873, C Sulawesi, S. Baebunta, 17 Apr 1940). – 68-69, *P. pariwonoi* sp. n. (JvT 5230, SW Sulawesi, Bantimurung area, 24 Sep 1983). Scale bar 1 mm.



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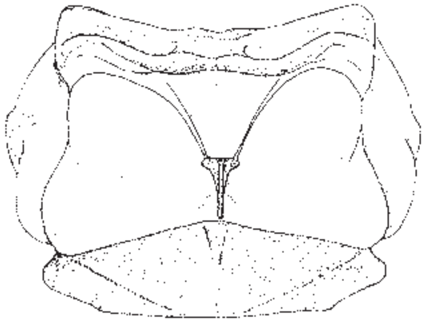

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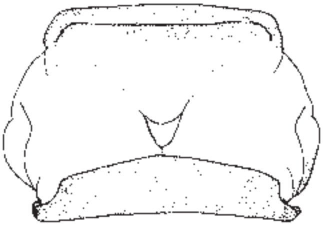

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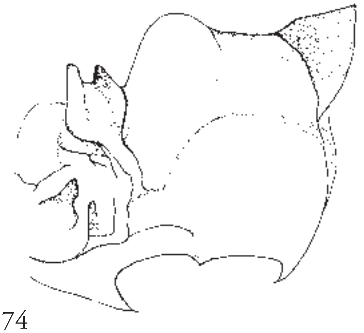

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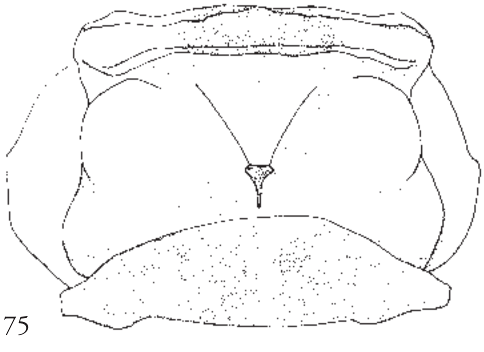

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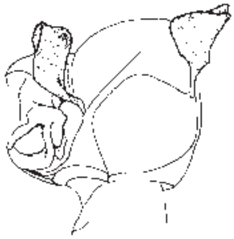

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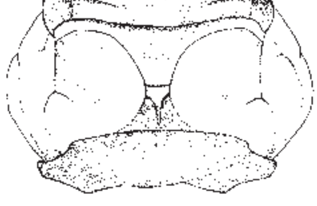

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Figures 70-77. Pronotum of *Protosticta* in left lateral and dorsal view. – 70-71, *P. reslae* sp. n. (JvT 1876, SW Sulawesi, Polewali, 6 Aug 1940). – 72-73, *P. rozendalorum* sp. n. (JvT 1878, Sangihe Is). – 74-75, *P. simplicinervis* Selys (JvT 1947, NE Sulawesi, Mapanget, 28 Jul 1940). – 76-77, *P. vanderstarrei* sp. n. (JvT 1885, C Sulawesi, Paloe, Lindu valley, 8 Aug 1940). Scale bar 1 mm.


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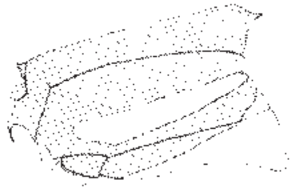
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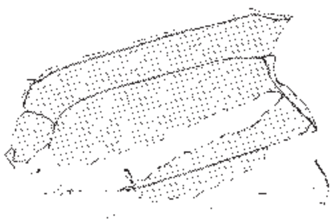
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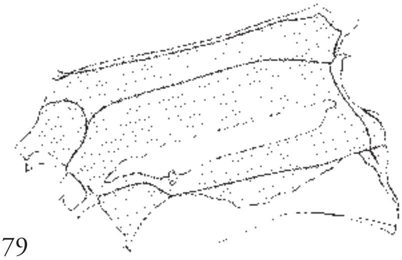
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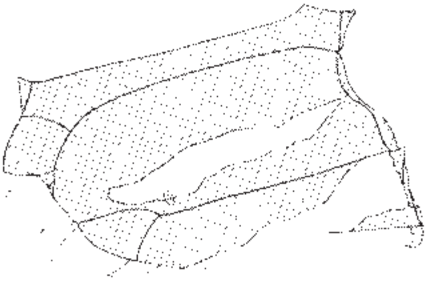
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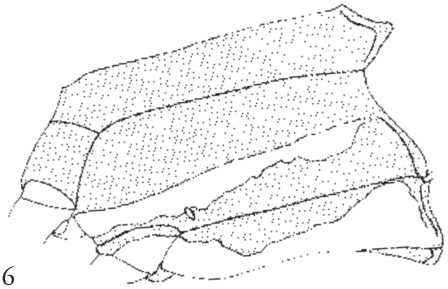
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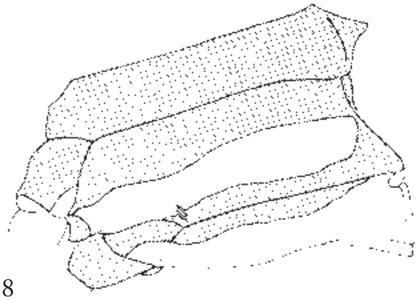
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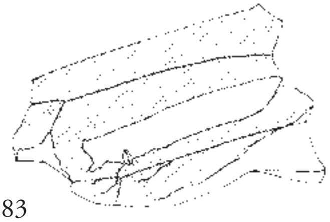
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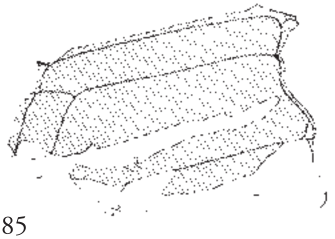
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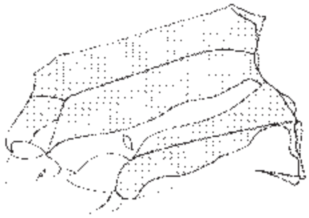
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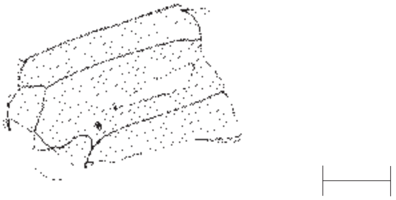
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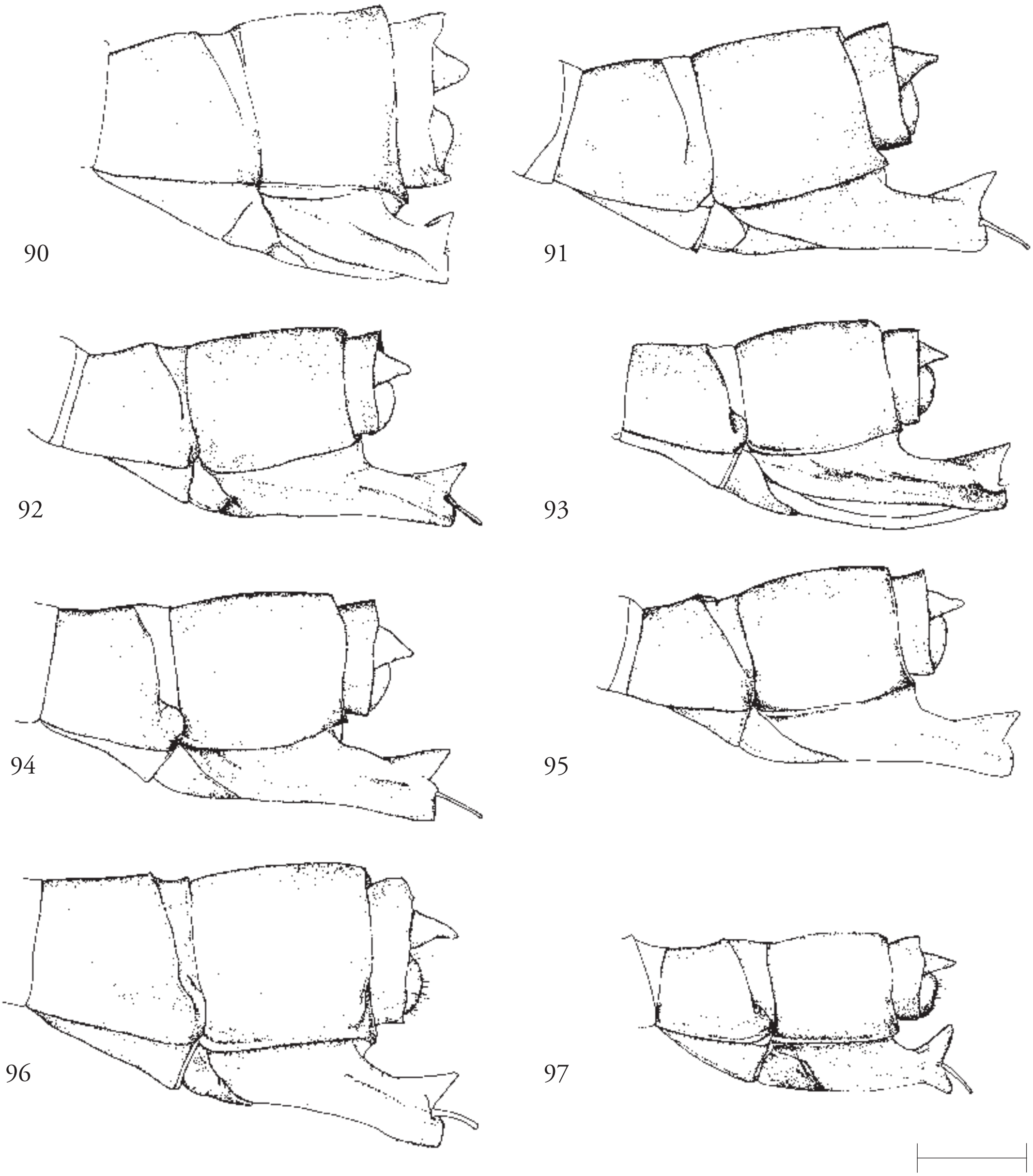
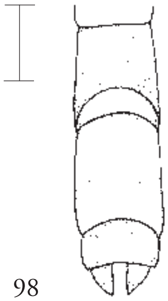
Figures 78-83. Synthorax of *Protosticta* in lateral view. – 78, *P. bivittata* Lieftinck (JvT 1842, SW Sulawesi, Bantimurung area, 31 May 1982). – 79, *P. coomansi* sp. n. (JvT 16661, SW Sulawesi, Loewoe, Todjamboe, 18 Jul 1936). – 80, *P. geijskesi* sp. n. (JvT1917, C Sulawesi, S. Baebunta, 25 Aug 1940). – 81, *P. gracilis* Kirby (holotype); 82, *P. linduensis* sp. n. (JvT 1861, C Sulawesi, Lore Lindu NP, 9 Dec 1985). – 83, *P. marenae* sp. n. (JvT 1862, C Sulawesi, Gimpu area, 14 Dec 1985). – 84, *P. maurenbrecheri* sp. n. (JvT 1873, C Sulawesi, S Baebunta, 17 Apr 1940). – 85, *P. pariwonoi* sp. n. (JvT 5230, SW Sulawesi, Bantimurung area, 24 Sep 1983). – 86, *P. reslae* sp. n. (JvT 1876, SW Sulawesi, Polewali, 6 Aug 1940). – 87, *P. rozendalorum* sp. n. (JvT 1878, Sangihe Is, Manganitu, May 1985). – 88, *P. simplicinervis* Selys (JvT 1943, N Sulawesi, Dumoga Bone NP, 20 May 1985). – 89, *P. vanderstarrei* sp. n. (JvT 1888, SW Sulawesi, Polewali, 23 Oct 1940). Scale bar 1 mm.



Figures 90-97. Last abdominal segments of female, left lateral view. – 90, *P. bivittata* Lieftinck (JvT 1841, SW Sulawesi, Bantimurung area, 31 May 1982). – 91, *P. coomansi* sp. n. (JvT 16617, C Sulawesi, Gimpu, 4 Apr 1997); 92, *P. geijskesi* sp. n. (JvT11886, SE Sulawesi, Mokowu, 29 Oct 1989). – 93, *P. marenae* sp. n. (JvT 16580, C Sulawesi, Gimpu area, 2 Apr 1997). — 94, *P. pariwonoi* sp. n. (JvT 5257, SW Sulawesi, Bantimurung area, 17 Apr 1991). – 95, *P. rozendalorum* sp. n. (JvT 1882, Sangihe Is., Gn Sahendaruman, 12-19 May 1985). – 96, *P. simplicinervis* Selys (JvT 1942, N Sulawesi, Dumoga Bone NP, 30 Apr 1985). – 97, *P. vanderstarrei* sp. n. (JvT 1887, SW Sulawesi, Polewali, 6 Aug 1940). Scale bar 1 mm.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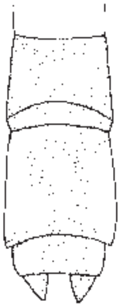
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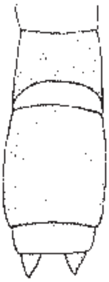
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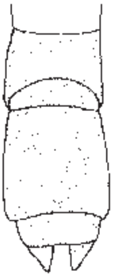
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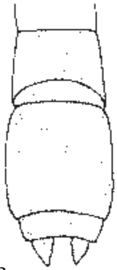
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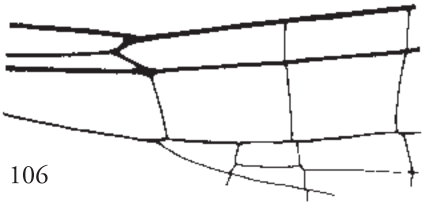
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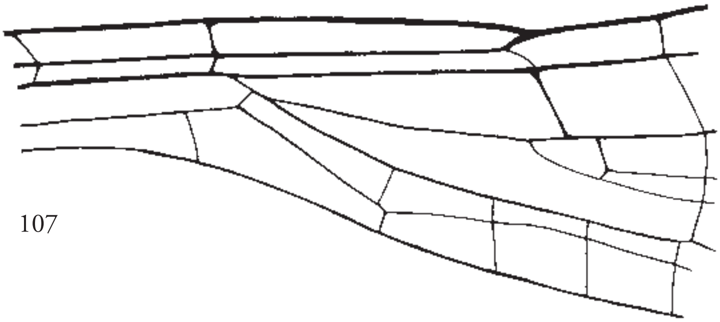
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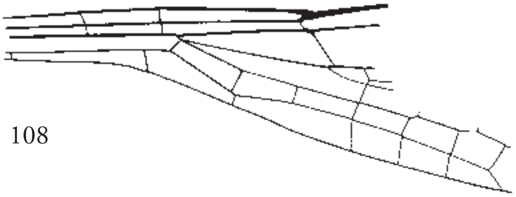
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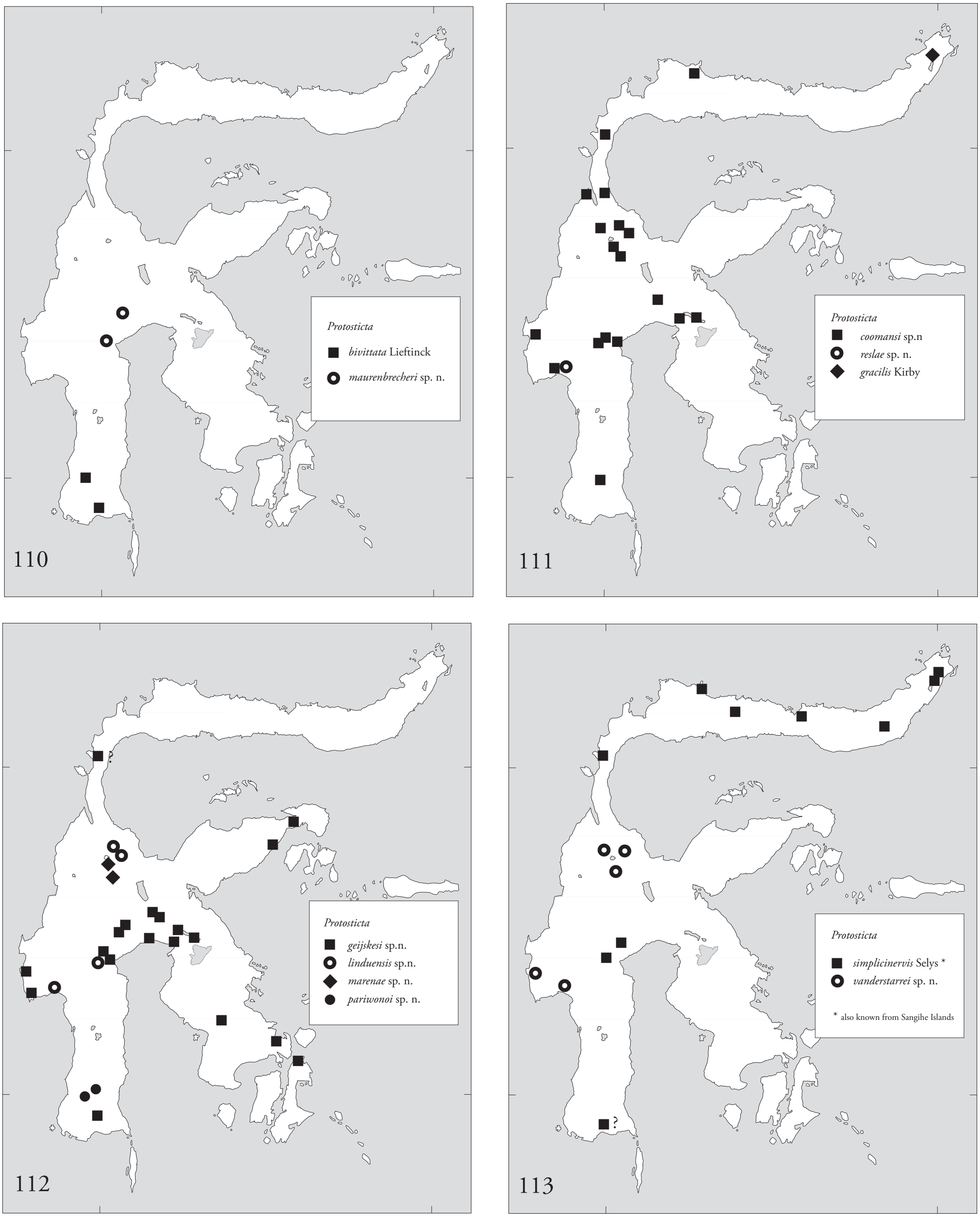
Figures 98-105. Last abdominal segments of female, dorsal view. All data as in figs. 90-97. – 98, *P. bivittata* Lieftinck. — 99, *P. coomansi* sp. n. – 100, *P. geijskesi* sp. n. – 101, *P. marenae* sp. n. – 102, *P. parinonoi* sp.n. – 103, *P. rozendalorum* sp. n. –104, *P. simplicinervis* Selys. – 105, *P. vanderstarrei* sp. n. Scale bar 1 mm.

Figures 106-109. Wing characters of *Protosticta* species. – 106, *P. bivittata* Lieftinck. – 107, *P. gracilis* Kirby. – 108, *P. simplicinervis* Selys. – 109, *P. vanderstarrei* sp. n. (JvT 1888, SW Sulawesi, Polewali, 23 Oct 1940). Various magnifications.



Figures 110-113. Distribution of *Protosticta* species in Sulawesi.

7. The Odonata of Sulawesi and adjacent islands. Part 6. Revision of the genus *Drepanosticta* Laidlaw (Zygoptera: Platystictidae)

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Abstract

The genus *Drepanosticta* Laidlaw is revised for Sulawesi and adjacent islands. *D. ephippiata* Lieftinck is redescribed, and *D. bicolor* sp. n. (Buton Island), *D. hamulifera* sp. n. (Kabaena Island), *D. penicillata* sp. n. (central Sulawesi) and *D. watuwilensis* sp. n. (SE Sulawesi) are described as new to science. A key to the males is provided. Based on the structure of the posterior margin of the pronotum, *D. ephippiata* presumably represents a monophyletic clade with the *Drepanosticta lymetta* and *D. megametta* species-groups, including spp. from the mainland of New Guinea. This group is distributed from Mindanao (Philippines) eastward to the northern Moluccas, northern New Guinea and the Solomon Islands. The newly described species are morphologically quite diverse; they are presumably most closely related to species occurring SE of Sulawesi.

Introduction

The platystictid genus *Protosticta* Selys shows remarkable radiation in the Indonesian island of Sulawesi (Celebes) (van Tol, 2000), while only one species of *Drepanosticta* Laidlaw is known from that area until now. The present paper revises the material of the genus *Drepanosticta* from Sulawesi, and the adjacent islands of Buton and Kabaena. No specimens are available from the islands of Saleyer, Sangihe, Talaud or the Sula islands. These islands are relatively poorly investigated, although one species of *Protosticta* is known from Sangihe (van Tol, 2000).

Drepanosticta ephippiata was described by Lieftinck (1937) from Tondano, not far from Manado in the northern arm of Sulawesi. Although it is confined to the northern arm and the central part of the island, and Pulau Peleng (Banggai archipelago), it still appears to be the most common and widespread species of *Drepanosticta* of Sulawesi. Four other species, newly described in the present paper, have more restricted ranges and are only known from the southern centre, the southeastern arm of Sulawesi, or the adjacent islands of Buton and Kabaena. These areas were mainly explored during the last twenty years during field work that started with Project Wallace (1985) in the northern peninsula, and continued in a series of expeditions organised by the National Museum of Natural History at Leiden, in co-operation with the

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Indonesian universities of Makassar, Manado and Kendari, and the Indonesian Institute of Sciences (Jakarta and Bogor).

This paper is one of a series revising the Platystictidae of Southeast Asia (van Tol, 2000, 2005, in press), preparing a reconstruction of the phylogeny of this family. It is also a contribution to the revision of the Sulawesi odonate fauna.

Methods

Specimens were studied using stereomicroscopes (Leica MZ16A, Olympus). Illustrations were prepared using a camera lucida on the MZ16A. A Nikon D70S digital camera equipped with a 60 mm Micronikkor lens with bellows was used for the illustrations of the synthorax. Measurements are in millimetres, and were taken using a standard ruler (abdomen, wings), or an ocular ruler in a microscope (pterostigma, anal appendages). JvT numbers are preserved with the specimens studied, using a small label with the specimen, or written on the 5x3 inch label card in the envelope with the specimen. All specimens are preserved in the collection of papered specimens of the National Museum of Natural History (Leiden, The Netherlands), except if indicated otherwise.

Notes on phylogeny and biogeography

Affinities of Platystictidae of Sulawesi. – These paragraphs provide a preliminary analysis of the affinities of the Sulawesi Platystictidae, and hypothesize a scenario of their historical biogeography. Detailed studies of the phylogeny are in progress. The phylogenetic relationships and distribution patterns of the Sulawesi *Drepanosticta* species may contribute to understanding the historical relationships of the various parts of the island. This group of species does not show the radiation into a series of closely related taxa, as has been found in Sulawesi for the genus *Protosticta* (van Tol, 2000), or in the Philippines and the Moluccas for the genus *Drepanosticta* (van Tol, 2005, in press). The Sulawesi species here assigned to *Drepanosticta* are quite diverse in morphological characters. They presumably have their closest affinities to species distributed east of Sulawesi. This is in contrast with the *Protosticta* species of Sulawesi, which have distinct western phylogenetic relationships.

D. ephippiata belongs to a clade with a distinct autapomorphy, a pair of processes on the hind margin of the pronotum, which otherwise occurs in the Philippines (Mindanao) (van Tol, 2005), the Moluccas (van Tol, in press), New Guinea (Lieftinck, 1932) and the Solomon Islands (van Tol, unpublished). Two presumably monophyletic groups within this clade were characterized by van Tol (2005), viz. the *D. lymetta* and the *D. megametta* group. Within this clade, the *D. megametta* group is well characterized by the flat processes. The other species can be divided into three groups, viz. the *D. lymetta* group s.s., an unnamed group confined to northern New Guinea, and the *D. ephippiata* group (*D. ephippiata* only), of which the relationships are presently not well understood. The Sulawesi *D. ephippiata* differs from the other species by the tapering, rather than widening, posterior processes of the posterior lobe of the pronotum.

The other species dealt with in the present paper are characterized by a simple hind margin of the posterior lobe of the pronotum, a distinct pale stripe over the metepisternum (Figs 31-35), and large dorso-ventrally compressed superior anal appendages. Species with such characters are also known from Flores, viz. *D. floresiana* Lieftinck, and Lombok, viz. *D. berlandi* Lieftinck (Lieftinck, 1939). The remarkably shaped superior anal appendage is a synapomorphy for the species of this group. The variation within the group of species of Sulawesi, however, is large and the phylogenetic relationships are subject to further analysis.

Notes on the historical biogeography. – Platystictidae are poorly dispersing, stenotopic odonates, and active 'island hopping' is not a plausible scenario. If the distribution of the present species or their ancestors is the result of dispersal with the islands rafting along the continental plates, the relationships of the Sulawesi platystictids would reflect the tectonic history of the region.

Figure 1. Distribution of *Drepanosticta* species in Sulawesi. [*Revised version*].

The biogeography of Southeast Asia and the Pacific is still poorly understood, especially due to the complex geological history of the region, but also since well-founded phylogenetic reconstructions with estimates of the timing of splitting of lineages are virtually absent (Turner et al., 2001). The palaeohistory of Sulawesi is particularly complicated. The island consists of at least four palaeo-islands, which merged only between five and ten million years ago. Some of these palaeo-islands may have had a sub-aerial history for more than twenty million years, but others may have been submerged until they collided with other islands or continental fragments.

The genus *Protosticta* is widespread in the mainland of Southeast Asia and Borneo, and reaches its eastern limit in Sulawesi (van Tol, 2000). Species recently described from the Philippines and assigned to *Protosticta* (van Tol, 2005) only share the loss of the Ab vein, a doubtful synapomorphy with the type species *Protosticta simplicinervis* (Selys) from Sulawesi. Anyhow, no platystictids with characters of *Protosticta* are known east of Wallacea. So, while *Protosticta* seems to represent a western element in the dragonfly fauna of Sulawesi, the *Drepanosticta* species of Sulawesi clearly belong to lineages with northern, eastern or southern ranges.

While the genus *Protosticta* is well represented in the southwestern arm of Sulawesi (van Tol, 2000), there are no records of *Drepanosticta* form that area. This is a clear indication of the poor dispersal power of the species in *Drepanosticta*. The southwestern part of the island already has approximately the same position to Borneo for about 45 million years (e.g., Wilson & Moss, 1999). Although it is still uncertain whether this palaeo-island has ever been connected to Borneo, both areas have certainly been closer together during periods of lower levels of the oceans, e.g. during the last ice ages. Still, exchange between Borneo and Sulawesi of poorly dispersing biotas, such as Platystictidae, must have been difficult for the last 45 million years. Although the monophyly of all Sulawesi *Protosticta* has not been ascertained, the Bornean and Sulawesi species are certainly more closely related than those of Sulawesi and the mainland, or Sulawesi and the Philippines. If Borneo and Sulawesi have never been connected, this would include (at least) one *Protosticta* dispersal event between both islands. The absence of sister-group relationships between the *Drepanosticta* species of Borneo and Sulawesi, and the complete absence of *Drepanosticta* from the southwestern arm, suggests poor faunal exchange between both regions.

Drepanosticta ephippiata, here assigned to a clade characterized by a pair of processes on the posterior margin of the pronotum, is widespread in the northern peninsula, and is also known from the Banggai archipelago and (doubtfully) from the region between Rantepao and Palopo. The distribution of the clade shows distinct congruence with island arcs that were formed during the Eocene, when the Australian plate moved northward and subducted under the Philippine plate, forming the Philippine Arc. At least during the Eocene (35 Ma) this island arc included from west to east peninsular north-eastern Sulawesi, Mindanao and parts of the Moluccas, including Halmahera (Hill & Hall, 2003). Along the eastern margin of the Philippine plate the north-south oriented (South) Caroline Arc was formed at the collision zone with the Greater Pacific Plate. These two island arcs came more or less in line in west-east orientation, due to back-arc spreading, during the Late Oligocene (25 Ma). The Caroline Arc collided from west to east to the Australian plate from the Late Miocene (10 Ma), a process continuing up to today. Due to clockwise turning of the Caroline plate, the position of certain islands changed rapidly. Halmahera, for instance, had a position east of and close to the Vogelkop peninsula during the Middle Miocene (15 Ma).

Biogeographical reconstructions indicate that the eastern Philippines are inhabited by several monophyletic groups, which seem to have moved, or have been moved, from the Papuan region in western direction. Several aquatic groups, including the Calicnemiinae (Platycnemididae) (Gassmann, 2005; van Tol & Gassmann, in press), show distributions including New Guinea and the Philippines, but excluding the Moluccas and Sulawesi. Polhemus (1995) and Polhemus & Polhemus (1998) hypothesized a pre-Eocene 'Inner Melanesian arc system' for such patterns. It is unusual that such distributions include the northern Moluccas and Sulawesi. However, the odonate genus *Diplacina* Brauer (Libellulidae) represents another monophyletic group with such a distribution pattern. *Diplacina* species are generally more dispersive. The sister-group of the Sulawesi species *Diplacina militaris* Ris occurs on Mindanao (*D. bolivari*), while *D. militaris* is represented in Sulawesi with two parapatric subspecies (van Tol, 1987). One subspecies, *D. militaris dumogae* Van Tol is confined to the northern arm, while the nominal subspecies is distributed over the rest of Sulawesi. The genus *Diplacina* is also found with many species in New Guinea, eastward into the d'Entrecasteaux and Bismarck Islands, and with several species in the Moluccas (Halmahera, Ambon).

Some, perhaps all, of the remaining species of Sulawesi *Drepanosticta* share unique characters with a group of species with southern and eastern distributions, including *D. berlandi* Lieftinck (Lombok) and *D. floresiana* Lieftinck (Flores), and even the Papuan species *D. auriculata* (Selys) (see Lieftinck, 1938: p. 81-82, Fig. 18). In Sulawesi, this group is at least represented by *D. penicillata* sp. n., but may also include some or all of the other new species described in the present paper. Sister-group relationships between Sulawesi and the Lesser Sunda Islands have previously been found for prasiine cicadas (Duffels, 1990) and butterflies (Holloway, 1990), but these relationships were mainly found for species confined to the drier zones of both areas. Species of such habitats usually have significantly higher dispersal power. Further range extension northward on Sulawesi may have been prevented by climatic conditions. However, such a scenario cannot easily be understood for the stenotopic and poorly dispersing *Drepanosticta* species of Sulawesi. Dispersal events from the Lesser Sunda Islands to Sulawesi (or visa versa) are thus less likely. The alternative hypothesis would include the arrival of the Sulawesi lineage on one or more of the island fragments forming Sulawesi. Unfortunately, there is little geological support for a sub-aerial history of the fragments now forming Central and Southeastern Sulawesi. Neither the position of Central Sulawesi close to NW Australia during the Eocene, nor the history of the southeastern peninsula, provide a palaeogeographical key to such relationships (see Hill & Hall, 2003).

In conclusion, the Sulawesi *Drepanosticta* fauna shows complex relationships to faunal elements of both northern and southern origin, but apparently not with Bornean elements. The results of ongoing phylogenetic studies, based on analysis of both morphological and molecular characters, will provide the basis to test the hypothesis of the historical biogeography of this family in Sulawesi.

List of *Drepanosticta* species of Sulawesi

Drepanosticta Laidlaw, 1917

D. ephippiata Lieftinck, 1937
Distribution. – North and Central Sulawesi; Banggai archipelago.
D. bicolor sp. n.
Distribution. – Buton Island.
D. hamulifera sp. n.
Distribution. – Kabaena Island.
D. penicillata sp. n.
Distribution. – Central Sulawesi.
D. watuwilensis sp. n.
Distribution. – Southeastern Sulawesi.

Key to males of *Drepanosticta* species of Sulawesi and adjacent islands

1. Hind margin of pronotum with a pair of curved processes, approximately as long as median line of median lobe of pronotum (Figs 2-3) . . . . *D. ephippiata* Lieftinck
– Hind margin of pronotum straight, or lateral corners with a sharp edge, but without a pair of curved processes (e.g. Figs 8-9) 2
2. Synthorax black, except for a dirty yellow marking over posterior part of mesopleural suture, and a dirty yellow marking starting at hind margin of synthorax near interpleural suture, running anteriad over metepisternum and metepimeron, continuing over ventrum . . . . *D. bicolor* sp. n.
– Synthorax brownish black with conspicuous pale yellow stripe over metepisternum; ventrum pale yellow 3
3. Inferior appendage in ventral view stout, width of terminal part about one-sixth total length of appendage (Fig. 29); setae of tip of inferior appendage not in a tuft . . . *D. watuwilensis* sp. n.
– Inferior appendage in ventral view slender, width of terminal part (perpendicular to body axis) about one-tenth total length of appendage (Figs 16, 23); tip of inferior with a tuft of brown setae. 4
4. Tip of inferior appendage with a sharp tooth directed dorso-axiad (Fig. 16); transverse occipital carina with angulate lateral extremities. Distribution: Kabaena . . . . . . *D. hamulifera* sp. n.
– Tip of inferior appendage smoothly curved (Fig. 23); transverse occipital carina poorly developed; lateral extremities hardly visible. Distribution: Central Sulawesi. . . . .*D. penicillata* sp. n.

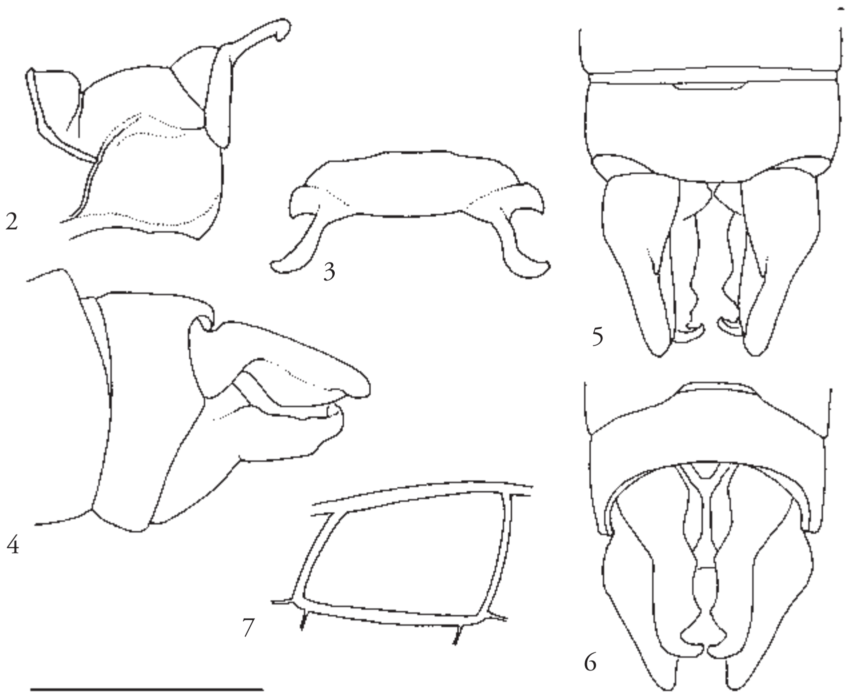
Systematic part

Drepanosticta ephippiata Lieftinck
Figs 1-7, 31

Drepanosticta ephippiata Lieftinck, 1937: 72 [original description, relationships discussed]. – Lieftinck 1971: 86 [lectotype designated].

Material examined (31 specimens, including lectotype). – Northern Sulawesi: Tondano (type locality), 1935, 2 males; Manado, 19 May 1940, 1 male 1 female; Mapanget, 23 Jun 1940, 2 males; same site, 11 Aug 1940, 3 males 1 female; Pineleng, 14 Jul 1940, 2 males; Toli Toli, 6 Nov 1940, 1 female; same site, 5 Dec 1940, 6 males; Dampelas, 28 Nov 1940, 2 males 1 female; Airmadidi, 1 Dec 1940, 1 male; Kakaskasen [not found], 26 Dec 1940, 1 female; Dumoga-Bone National Park, 4 Jun 1985, 1 male 1 female. – Central Sulawesi: Tojambu (between Rantepao and Palopo), 29 Oct 1993, 1 male 1 female (purchased from insect dealer, locality uncertain). – Banggai Peninsula: Pulau Peleng, 31 Jul 1941, 2 males 1 female.

Description. – Small, brown species; distinguishable from other Sulawesi species by a pair of slender processes on posterior margin of posterior lobe of pronotum.
Male [JvT 11842, Celebes, Toli Toli]. – Head. Labium dirty ochreous, mandibles bluish white with anterior border brown, labrum bluish white, anterior one-fourth with brownish black border, gena dirty white, parts against the eye brownish black; anteclypeus bluish white; remaining part of head mat black with metallic lustre, underside of eyes shining black; occipital area with



Figures 2-7. *Drepanosticta ephippiata* Lieftinck, male. – 2, pronotum, left lateral view; 3, posterior lobe of pronotum, dorsal view; 4, anal appendages, left lateral view; 5, idem, dorsal view, 6, idem, ventral view; 7, pterostigma, right fore wing. Scale bar 1 mm.

transverse occipital carina distinct, lateral corners acute. Antenna with scapus and base of pedicellus creamish white, rest of pedicellus and flagellum pale brown.

Thorax. – Pronotum (Figs 2-3) with anterior and central part of middle lobe brown, lateral sides of middle lobe and posterior lobe brownish black; anterior lobe simple, posterior lobe with two caudal processes, approximately 1.0-1.5 times the length of median line of posterior lobe, directed 60°, but with tip directed abaxially, distinctly swollen in some specimens, or somewhat wider than base in others. Synthorax (Fig. 31) dark brown, dorsal part mat, densely punctate, lower half of synthorax more shining; dirty yellow stripe over mesepimeron / metepisternum from just above stigma to hind margin, approximately five times as long as widest part just before distal end. Legs unicolorous yellow, but all femora with dirty-coloured rings against tibiae, distal one-fourth of hind tarsus dark; long setae (spines) on legs dark yellow, short setae of tibiae white.

Wings hyaline, reaching to halfway abdominal segment 6, venation brown; Px in fore wing 17, in hind wing 15; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Arculus, especially in hind wing, distinctly distal to Ax2; Ab vein meeting Ac at hind margin of wing; number of cells between Arculus and place where CuP ends in hind margin of fore wing 8; of hind wing 10; CuP reaches hind margin of fore wing at level of Px4, in hind wing at level of Px6; pterostigma (Fig. 7) brown, quadrangular, costal side shorter than subcostal side; veins distal to pterostigma undivided.

Abdomen. – Slender; segment 1 brown, segment 2 brown with a pair of latero-anterior pale spots, segments 3-6 brownish black with basal pale rings against annulae, approximately one-fifth of each segment; segment 7 dark brown, basal one-third paler, segments 8-10 brownish black, without pale markings. Anal appendages (Figs 4-6) rather compact, yellow, superior appendage in dorsal view basally wide,

tapering caudally, with a dorsal tooth approximately one-third from tip, in lateral view from outside hollow; inferior appendage basally very wide, caudal part straight outside, innerside halfway with triangular tooth, leaving a concavity caudally, the tip turned sharply dorso-axially, no tuft of setae.
Female. – As the male, but posterior margin of posterior lobe of pronotum with rather short, triangular, erect projections; abdomen with segment 8 with small pale spot in latero-anterior corner, segment 9 brown, segment 10 and anal appendages pale; valve brown, somewhat extending beyond anal appendage.

Measurements (mm). – Male, abomen including appendages 29, hind wing 20; female, abdomen 28, hind wing 21.
Variation. – Inferior appendages of specimens from Pulau Peleng (off Banggai peninsula) are more slender than in typical specimens from the northern arm of Sulawesi. They are assigned to *D. ephippiata* since no other diagnostic characters were found.
Distribution. – North and central Sulawesi (Fig. 1).

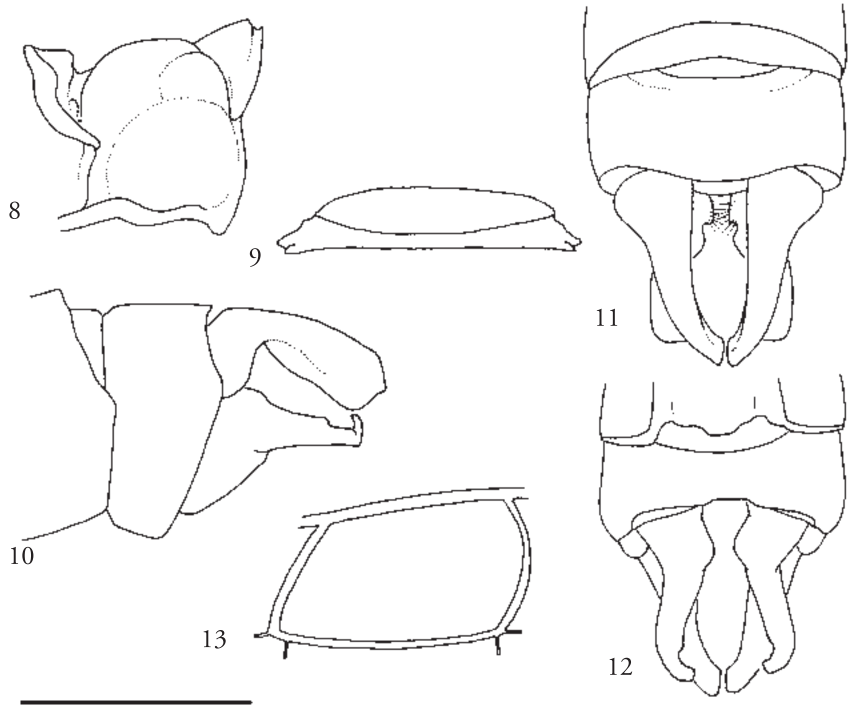
Drepanosticta bicolor spec. nov.

Figs 1, 8-13, 32

Material. – **Holotype** male [JvT 11867]. '1989 RMNH Expedition to Sulawesi / Indonesia. Northern Pulau Buton: / a few kms inland from Labuhan Tobelo: / Jismil camp along Sg Labuhan Tobelo. / Rivulet through hardly disturbed primary evergreen rain forest. Boulders covered / with calcareous deposit. 150 m asl. / 4°26'30"S 122°59'00"E. 18 Nov 1989; / sample 89JvT040. Leg. J. van Tol'.

Etymology. – *Bicolor*, for the two-coloured ventrum of the synthorax. An adjective.

Description. – A dark large *Drepanosticta*, with conspicuous black and ivory white ventrum; posterior margin of posterior lobe with sharp corners, but without a paired process.
Male [holotype, JvT 11867]. – Head. Labrum, mandibles and anteclypeus bluish white, anterior border of labrum brownish black, c. one-third the height of labrum medially, tapering towards corners; rest of head black, shining on clypeus and against eyes, rest coriaceous; inconspicuous striae against eyes, transverse occipital carina poorly developed, hardly recognizable lateral extremities. Antenna with scapus brownish black, pedicellus dirty yellow, flagellum brown.
Thorax. Pronotum (Figs 8-9) dirty yellow, except for brown or brownish black anterior border of anterior lobe, central parts of paired convex structures of median lobe, and posterior lobe; anterior lobe with anterior margin erect, but not expanded; posterior lobe simple, hind margin straight, laterally turned c. 90° ventrad. Synthorax (Fig. 32) mat brownish black, except for dirty yellow posterior margin consisting of triangular marking in lower posterior corner of mesepisternum, a broadly triangular marking along posterior margin of metepisternum, and a larger pale marking on metepimeron, covering c. one-third of metepimeron, dorsally starting as continuation of marking on metepisternum, and obliquely towards ventral side, which continues ventrally over poststernum.
Legs with remarkable dirty yellow coxae, femora dirty yellow, with weak dark rings c. halfway, also dark rings against joints with tibiae; tibiae pale brown.
Wings hyaline, venation brown; Px in fore wing 17, in hind wing 17; R4+5 arising at or just proximal to nodus; IR3 arising c. halfway first cell distal to subnodus; Ab vein meeting Ac at or just before hind margin of wing (Y sessile or sub-sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 8, of hind wing 10; CuP reaching margin of hind wing at level of Px4 in fore wing, Px6 in hind wing; pterostigma (Fig. 13) brownish black, the central part brown; proximal side oblique, distal side convex; several veins posterior to pterostigma divided.
Abdomen. – Variegated; segments 3-7 brownish black, segments 8-10 and anal appendages mat black; pale marking dirty yellow as follows: segment 1 completely pale, segment 2 pale towards sternites; segment 3 with large triangular markings in ventro-anterior corners, and a pale ring of c. one-fifth the length of segment at c. one-fifth from hind margin, dorsally broken by dark line; segments 4-5 with pale rings at anterior margin



Figures 8-13. *Drepanosticta bicolor* sp. n., male. – 8, pronotum, left lateral view; 9, posterior lobe of pronotum, dorsal view; 10, anal appendages, left lateral view; 11, idem, dorsal view, 12, idem, ventral view; 13, pterostigma, right fore wing. Scale bar 1 mm.

and c. one-fifth from posterior border of segment, both c. one-fifth segment-length and dorsally broken by brown line; segment 6 only with anterior pale ring of one-fifth segment-length; segments 7-8 with large pale markings in ventro-anterior corners of tergite, c. one-third segment-length (marking op segment 8 much shorter since segment is much shorter); segments 9-10 concolorous black. Anal appendages (Fig. 10-12) with superiors in dorsal view slender, tapering towards top, distal two-thirds dorso-ventrally compressed, the distal part c. two times longer than high, to tip acute; inferiors with base stout, distal half narrow, straight, hardly tapering, the inferiors somewhat diverging, the tip turned axio-dorsad.
Female. – Unknown.

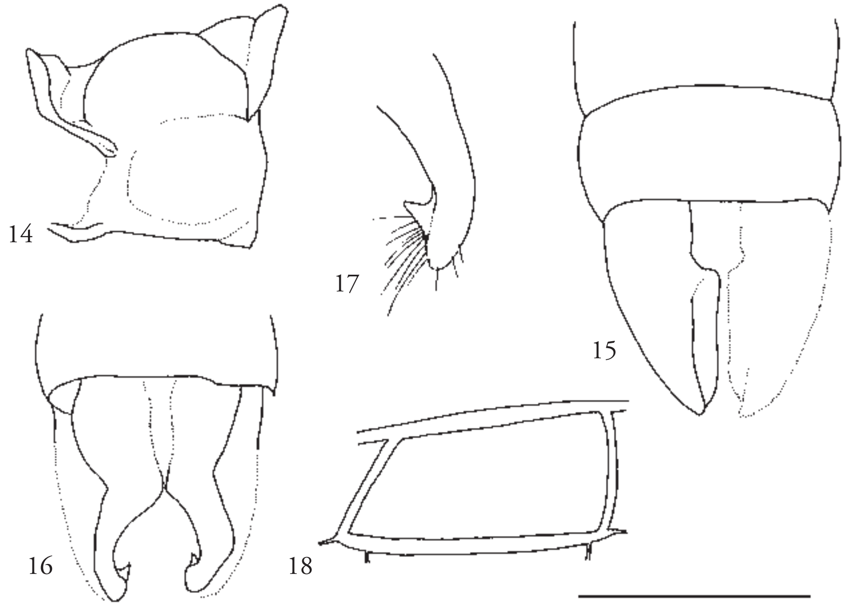
Measurements (mm). – Male, abdomen including appendages 37, hind wing 24.

Remarks. – A rare species. Only one specimen was discovered during five days of field work; the only other platystictid on this site was *Protosticta geijskesi* Van Tol, a common and widespread lowland species in Sulawesi.
Distribution. – Buton Island (off southeastern Sulawesi) (Fig. 1).

Drepanosticta hamulifera sp. nov.

Figs 1, 14-18, 33

Material. – Holotype male [JvT 11872]: '1989 RMNH Expedition to Sulawesi / Pulau Kabaena (S of Sulawesi) 4 km S of Tengkeno. 5-8 Nov 1989 / Leg. R. de Jong / S8928R. – Cave camp. 300 m. Open / riverine forest along Sg. Lakambula' [hand-written label 6 Nov 1989]. – Paratypes: Same site, 2 males 2 females [JvT 11868-11871]. The paratypes in poor condition.



Figures 14-18. *Drepanosticta hamulifera* sp. n., male. – 14, pronotum, left lateral view (mirrored from a right lateral view illustration); 15, anal appendages, dorsal view; 16, idem, ventral view; 17, idem, detail of inferior appendage; 18, pterostigma, right fore wing. Scale bar 0.5 mm for fig. 17; 1 mm for all other figs.

Etymology. – *Hamulifer* (L.), hammer-carrying, for the shape of the superior appendage. An adjective.

Description. – Large *Drepanosticta*, hind margin of pronotum triangular, without conspicuous processes; synthorax and abdomen variegated due to conspicuous stripe over metepisternum and double pale markings on several abdominal segments; tip of inferior appendage with triangular tooth directed medio-anteriad, provided with tuft of setae; dorsum of distal half of abdominal segment 9, and segment 10, blue.
Male [holotype, JvT 11872]. – Head. [Labrum and anteclypeus damaged, but labrum bluish white with broad anterior brownish black border straight and not tapering towards corners], mandibles bluish white without dark anterior margin; rest of head black, shining against eyes, rest coriaceous, striate part against eyes posterior to antennae inconspicuous, very small pale spot lateral of lateral ocelli; transverse occipital carina well developed with angulate lateral extremities. Antenna with scapus brown, pedicellus dirty yellow, flagellum brown.
Thorax. Pronotum (Fig. 14) dirty yellow, but posterior half of lateral lobes, and median portion of posterior lobe brown; anterior margin of anterior lobe semi-erect; lateral portion of posterior lobe semi-erect, no processes. Synthorax (Fig. 33) brownish black, especially posterior portion shining, rest semi-mat; wide greenish white stripe over metepisternum against interpleural suture, rather narrow anteriorly, running over metastigma, ending rounded well before posterior margin of metepisternum; metakatepisternum dark, but pale against metacoxa, metepimeron with pale marking in lower half, acute in anterior corner, widening posteriorly and covering full width of hind margin. Legs pale dirty yellow; femora with dark rings against joints with tibiae.
Wings hyaline, venation brown; Px in fore wing 16, in hind wing 14; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting

Ac just before hind margin of wing (Y sub-sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 9, of hind wing 10; CuP reaching hind margin of fore wing at level Px5, of hind wing at Px6; pterostigma (Fig. 18) pale brown; proximal side oblique, distal side convex; length subcostal side c. 2.2 times the height; few veins distal to pterostigma divided.

Abdomen pale brown, only posterior parts of segments 3-7 and segments 8-9 darker brown; pale dirty yellow markings as follows: segment 1 nearly fully dark yellow except for median part, segment 2 in antero-lateral two-thirds; segments 3-6 anterior one-sixth and crescent-shaped paired marking of one-fifth the segment length at one-sixth from posterior margin, but these markings diminishing in height from segment 3 to segment 6; segment 7 with pale ring in anterior one-fifth of segment, marking extending further posteriad against sternite; segment 8 with triangular marking in ventro-anterior corner; segment 9 with blue marking, covering approximately posterior half of segment, rounded anteriorly; segment 10 with bluish white dorsal marking. Anal appendages (Figs 15-17) pale, except for dark bases; superiors in dorsal view broad at base, gradually tapering towards top, distal three-quarters dorso-ventrally flattened, club-shaped, c. as long as high; inferiors in ventral view narrow, distal half clasper-like, distally rounded with a very short spine directed ventro-apicad, the rounded tip with dense brush of c. twenty long stout setae.

Female. – As the male, but smaller, and coloration probably more distinct (only teneral specimens available); last abdominal segments very short.

Measurements (mm). – Male: abdomen, including anal appendages, 46, hind wing 24; female: abdomen 37, hind wing 23.

Distribution. – Kabaena island (Fig. 1).

Drepanosticta penicillata sp. nov.

Figs 1, 19-24, 34

Material. – Holotype male. ‘Indonesia. C Sulawesi / 40 km N of Wotu: just N of / Batas. Small stream nr bridge / road Wotu-Tentena at km 4 / Disturbed primary forest; w= 2-4 m, / d=0.1–0.3 m, shade. Boulders. / 1200 m; 2°13’30”S 120°46’30”E / 24 Oct 1993; J. van Tol’. [JvT 1533]. – Paratypes: Same data, 1 male [JvT 1534]; C. Sulawesi, 30 km N of Wotu: Sg. Anoa, waterfall near bridge Wotu–Tentena, 650 m, 2°20’30”S 120°47’45”E, 23 Oct 1993, J. van Tol, 1 teneral female [JvT 1501].

Etymology. – *Penicillatus*, provided with a tuft of hairs, for the brush of hairs of the inferior appendages of the male. An adjective.

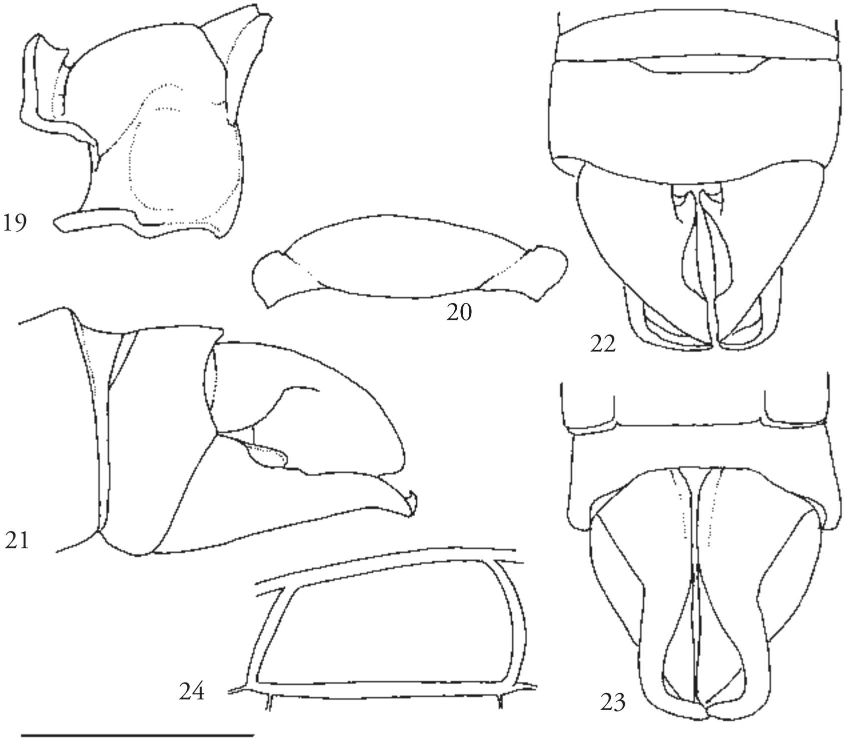
Description. – Large species; male with simple structure of prothorax and enormously developed superior appendage; synthorax with extensive pale markings; distal part of segment 9 and segment 10 pale, most probably blue or yellow.

Male [holotype male, JvT 1533]. – Head. Labium and maxillae pale yellow, mandibles bluish white without dark anterior border, labium white with anterior one-fourth brownish black, anteclypeus white, rest of head brownish black, especially vertex with purple shine; transverse occipital carina poorly developed, lateral extremities hardly visible.

Thorax. Pronotum (Figs 19-20) rather pale, with anterior lobe simple and completely yellow; middle lobe dirty white with small dark markings central on paired tubercle; lateral lobe pale white with a larger median dark marking; posterior lobe brownish black, but lateral corners somewhat paler, simple, median part flat, lateral corners somewhat erect, just expanding outside flat plane. Synthorax (Fig. 34) general coloration dark dorsally and lower parts yellow as follows: mesepisternum brownish black, mesokatepisternum brownish black except for centroposterior corner, mesepimeron yellow but area against mesopleural suture dark brown; metepi–sternum, metakatepisternum and metepimeron all yellow, but metapleural sutue distinctly marked with brown stripe.

Legs with coxae all yellow, femora yellow with dark ring of one-fifth or one-sixth the femur length, approximately at same distance from tibia as width of ring; femora against tibiae also dark, tibiae brown, and tarsi pale brown.

Wings hyaline, venation brownish black; Px in fore



Figures 19-24. *Drepanosticta penicillata* sp. n., male. – 19, pronotum, left lateral view; 20, posterior lobe of pronotum, dorsal view; 21, anal appendages, left lateral view; 22, idem, dorsal view, 23, idem, ventral view; 24, pterostigma, right fore wing. Scale bar 1 mm.

wing 16, in hind wing 15; R4+5 arising at nodus, IR3 arising halfway first cell distal to subnodus; Arculus just distal to Ax2; Ab vein meeting Ac at hind margin of wing (Y-vein sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 8, of hind wing 9; CuP meeting hind margin of fore wing at level of Px4, of hind wing at level of Px5; pterostigma (Fig. 24) pale brown, the proximal corner acute, the distal side convex, c. 2.2 times wider than high; veins distal to pterostigma undivided.

Abdomen. Segment 1 shining, dorsally with dark semicircle on otherwise yellow segment, segment 2 dorsally brown, anteriorly leaving approximately one-third of segment free, widening posteriorly to cover full segment width caudally, rest yellow; segments 3-7 brown, with yellow lateral spots anteriorly; segments 3-5 also with yellow lateral spots at c. three-quarters of segment-length; segment 8 dark brown, lateral sides anteriorly with yellow marking extending posteriorly to meet side margin just before segment border; segment 9 dark brown, posterior one-fifth with blue ring, not reaching the lateral corners; segment 10 dorsally yellow, and ventrally brown. Anal appendages (Figs 21-23) with superiors mat brownish black, enormously developed, inner margin curved sharply ventro-axiad, inner margin subterminally with small inward directed tubercle, lower portion very large with anterior border curved, and anteriorly nearly touching base in lateral view; inferiors pale yellow with inward directed tip brown, in ventral view slender, softly curved 90° outward; curved part slender, hardly tapering, the tip with dense tuft of short setae.

Female. – Characters hardly discernable; only female in poor condition (considered as conspecific based on extensive pale coloration of abdomen, and site at close distance from type locality).

Measurements (mm). – Male. Abdomen, including appendages, 42, hind wing 25.

Distribution. – Central Sulawesi (Fig. 1).

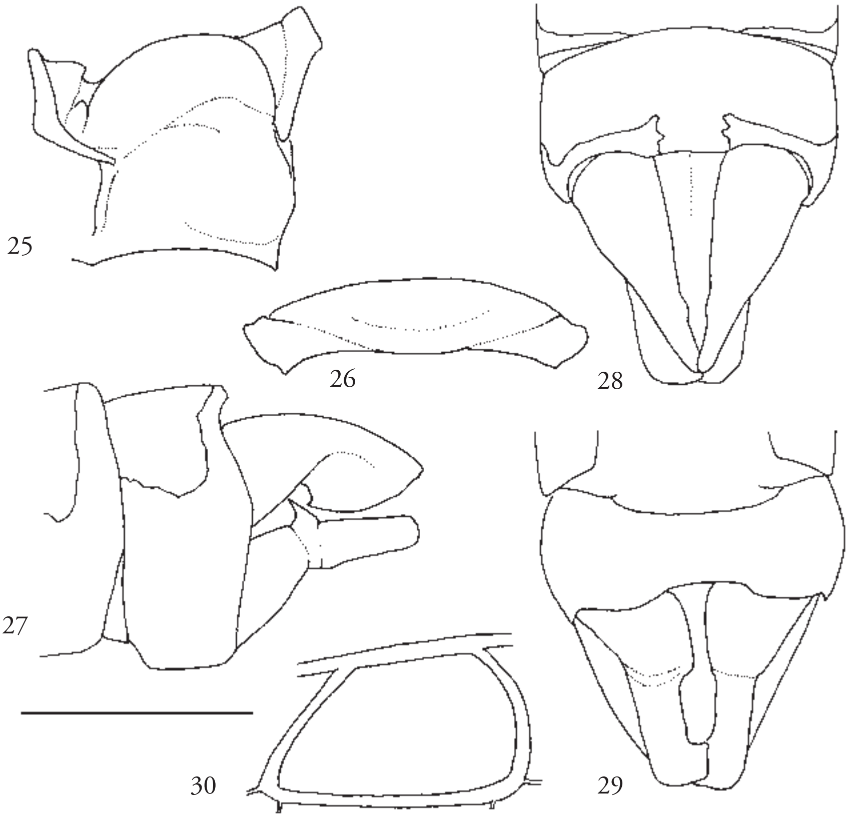
Drepanosticta watuwilensis sp. nov.

Figs 1, 25-30, 35

Material. – Holotype male [JvT 11863]: '1989 RMNH Expedition to Sulawesi / Indonesia Sulawesi Tenggara: S of / Sanggona: Gunung Watuwila. Sungai / Lalonduwasi near Centipede camp. Small / shaded stream in very steep valley. / Clear running water of boulders. Small / pools. c. 3°49'S 121°40'E. c. 1050 m / asl. Sample 89JvT035. 2-4 Nov 1989 / Leg. J. van Tol' [with hand-written date 2 Nov 1989]. – Paratypes: same data, 2 males (JvT 11864-11865); Sulawesi Tenggara, S of Sanggona: Mokowu river near Mokowu camp, foot of Watuwila Mts, 150 m asl, 3°48'S 121°39'E. Rivulet with ponded areas, clear water, bottom with boulders, some sand. Largely shaded. 29-31 Oct 1989. J. van Tol [with hand-written date 29 Oct 1989], 1 male [JvT 11866].

Etymology. – *Watuwilensis*, for the type locality Gunung (= Mountain) Watuwila. An adjective.

Description. – Relatively large species of *Drepanosticta*, with conspicuous pale stripes over metepisternum and metepimeron; pronotum simple; superior appendages distally dorso-ventrally compressed, enormously developed. Differs from similar *D. penicillata* sp. n. by the shape of pterostigma, more pronounced lateral extremities of postoccipital carina, and stouter inferior appendage, which lack a terminal tuft of setae.
Male [holotype, JvT 11863].– Head. Labrum, mandibles and anteclypeus bluish white, anterior one-fourth of labrum with brownish black stripe, tapering towards anterior corners; anterior border of mandibles not darker; rest of head black, clypeus, frons and parts of head against eyes shining, rest coriaceous with metallic lustre, fine longitudinal striae posterior to antennae; transverse occipital carina well developed, lateral extremities angulate. Antenna with scapus black, pedicellus pale brown, flagellum brownish black, but paler against pedicellus.
Thorax. Pronotum (Figs 25-26) generally brownish black, but lateral corners of anterior lobe, and latero-anterior corner of median lobe dirty yellow; anterior lobe semi-erect, the anterior margin folded, more distinct in lateral corners; posterior lobe simple, without posterior processes, hind margin straight, laterally bent 135° ventrad. Synthorax (Fig. 35) brownish black with dirty yellow stripes over metepisternum, from anterior corner over metastigma gradually fading to brown toward posterior margin; metapleural suture with straight brown stripe, anteriorly continuing over dorsal half of metakatepisternum, the posterior part running more dorsad over suture; rest of metepimeron dirty yellow. Legs relatively dark, femora with superficial dark markings except for a pale ring near joints with tibiae, which are also dark.
Wings hyaline, venation brownish black; Px in fore wing 18, in hind wing 18; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting Ac near hind margin of wing (Y subsessile); number of cells between Arculus and place where CuP meets hind margin of hind wing 11; CuP reaching hind margin of wing at level of Px6 in fore wing, at level of Px7 in hind wing; number of cells between Arculus and place where CuP meets hind margin of fore wing 10, of hind wing 11; pterostigma (Fig. 30) brownish black, subcostal side c. 1.8 times wider than high, the proximal corner sharp, posterior margin irregularly convex, costal side ca half as long as subcostal side; many vein distal to pterostigma divided.
Abdomen. Variegated due to double pale markings on many segments; base dark brown, with pale markings as follows: segment 1 with lateral yellow spots, sharply defined, dorsally half rounded; segment 2 somewhat paler in latero-anterior corners; segments 3-6 with two pairs of oval spots, one in latero-anterior corner, one at c. three-fifths the segment length, marking somewhat smaller on segment 6; segment 7 with pale marking in latero-anterior third; segment 8 as segment 7, but marking continues posteriorly along lateral



Figures 25-30. *Drepanosticta watuwilensis* sp. n., male. – 25, pronotum, left lateral view; 26, posterior lobe of pronotum, dorsal view; 27, anal appendages, left lateral view; 28, idem, dorsal view, 29, idem, ventral view; 30, pterostigma, right fore wing. Scale bar 1 mm.

margin of tergite; segment 9 with blue marking medio-posteriorly, lateral parts of tergite brownish black; segment 10 with blue dorsal marking. Anal appendages (Figs 27-29) somewhat shorter than segment 9, the inferiors somewhat longer than superiors; superior black, except for tip, in dorsal view base broad, strongly tapering, in lateral view club-shaped with broad and straight ventral margin; inferiors brownish black, the tips brown; base broad, distal half stout and parallel-sided at base, the tip turned 90˚inward, blunt.
Female. – Unknown.

Measurements (mm). – Male, abdomen including appendages 44, hind wing 28.

Distribution. – Southeastern Sulawesi.
Remarks. – A relatively common platystictid on Gunung Watuwila above 1000 m, while only one specimen was found among 60 specimens of *Protosticta geijskesi* Van Tol along the foothill river at 150 m asl.

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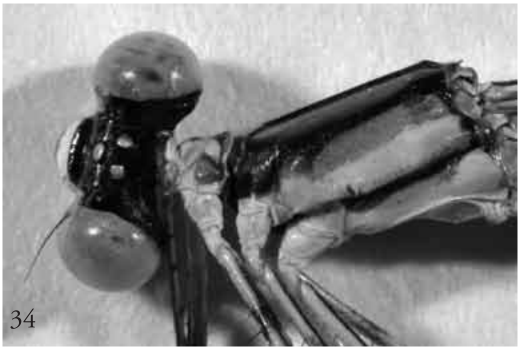
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Figures 31-35. *Drepanosticta* Laidlaw of Sulawesi, head and thorax. – 31, *D. ephippiata* Lieftinck [JvT 11852]; 32, *D. bicolor* sp. n. [JvT 11687]; 33, *D. hamulifera* sp. n. [JvT 11782]; 34, *D. penicillata* sp. n. [JvT 1534]; 35, *D. watuwilensis* sp. n. [JvT 11864].

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8. The Platystictidae of the Moluccas and Misool (Odonata)

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With 62 figures

Key words: Platystictidae, *Drepanosticta*, new species, Moluccas, systematics, biogeography.

Abstract

The Platystictidae of the Moluccas and Misool (Indonesia) are revised. All species are assigned to *Drepanosticta* Laidlaw. Representatives of this genus are known from the larger islands in the region, viz. Halmahera, Bacan, Obi, Ambon, Buru, Seram, and from the Kai island group. Aru is poorly studied for odonates, and no platystictids are known. Nine new species are described, viz. *Drepanosticta halmahera* sp. n., *D. rudicula* sp. n., *D. sembilanensis* sp. n. and *D. siu* sp. n., all from Halmahera; *D. bifida* sp. n. and *D. psygma* sp. n. from Bacan; *D. misoolensis* sp. n. from Misool; *D. amboinensis* sp. n. from Ambon and *D. obiensis* sp. n. from Obi. Two previously described species, *D. robusta* Fraser (Kai) and *D. moluccana* Lieftinck (Buru), are redescribed and illustrated. A key to all species is provided, as well as preliminary notes on phylogenetic relationships and biogeography. Halmahera platystictids show sister-group relationships with species from Bacan or, remarkably, Misool. The Moluccan *Drepanosticta* species are assigned to the *D. lymetta* and *D. megametta* species groups, which are also known from the Philippines and the Papuan region, and the *D. moluccana* group, presumably confined to the southern Moluccas. The role of the middle Eocene South Caroline Arc in the distributional history of the *Drepanosticta* species is discussed.

Introduction

Drepanosticta Laidlaw is one of the most speciose genera of zygopteran odonates worldwide, and the largest genus of Southeast Asia by far. Presently it includes 106 valid species in the Oriental and Papuan regions (van Tol 2006). New species were recently described from the mainland of Southeast Asia (Asahina 1984; Hämäläinen 1999; Wilson & Reels 2003), Hainan (Wilson & Reels 2001), the Philippines (van Tol 2005) and New Guinea (Theischinger & Richards 2005). Several authors have anticipated that the generic division of the Platystictidae of Southeast Asia needs major changes to define monophyletic groups. Recently, two new genera were erected to receive species that could not be assigned to *Platysticta* Selys, 1860, *Protosticta* Selys, 1885 or *Drepanosticta*. *Sinosticta* Wilson was described for a small group of species from southern China (Wilson 1997), and *Sulcosticta* Van Tol for another small group from the Philippines (van Tol 2005). Wilson (1997) also erected the new subfamily Sinostictinae for the aberrant genus *Sinosticta*, sharing several characters with the strictly New World subfamily Palaemnematinae. The

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phylogenetic relationships of the Platystictidae are still poorly understood, and are subject of a study (van Tol in prep.).

The present paper provides a revision of the Platystictidae species of the Moluccas and Misool (Indonesia), including descriptions of nine new species all assigned to the genus *Drepanosticta*. The genus *Protosticta* Selys, which is represented with many species in Sulawesi, is unknown east of Wallacea. The island of Misool does not belong to the Indonesian province of the Moluccas (Maluku); biogeographically it is considered part of the Papuan region. However, one species of *Drepanosticta* from Misool appeared to be very closely related to a species confined to Halmahera and is included in this paper. The Indonesian province of the Moluccas encompasses a land area of about 78,000 km^2, of which the islands of Wetar, Yamdena, Aru, Seram, Buru, Taliabu, Obi, Halmahera and Morotai/Rau are larger than 2000 km^2. The area of sea of the province stretches over 776,500 km^2 (Monk et al. 1997).

The region between Sulawesi and New Guinea is relatively poorly studied for Odonata. Field work focusing on, or with significant results of, odonates is restricted to (collections including Platystictidae with an [a] sign; all material preserved in RMNH, except if mentioned otherwise). Ternate: 1861 (H. A. Bernstein), 1995 (J. van Tol). Halmahera: 19th century (P.J.M. Lorquin, in IRSNB), 1861 (H. A. Bernstein) [a], 1931 and 1933 (M. J. van Diejen), 1951 (Amsari & Manis, names of collectors not on labels) [a], 1981 (A.C. Messer & P.M. Taylor, in USNM), 1995 (J. van Tol) [a]. Morotai: 1861-1862 (A. H. Bernstein). Bacan: 1953 (A. M. R. Wegner) [a], 1985 (F.G. Rozendaal) [a]. Buru: 1921-1922 (L.J. Toxopeus) [a], 1941 (J.J. van der Starre) [a]. Obi: 1862 (H. A. Bernstein), 1953 (A.M.R. Wegner) [a]. Seram: 1912 (H. Elgner) [a]. Ambon: 1921 (L.J. Toxopeus), 1941 (J.J. van der Starre), 1948, 1949 (M.A. Lieftinck) [a], 1961 (A.M.R. Wegner) [a]. Saparua I., 1949 (M.A. Lieftinck). Aru: 1908 (H. Merton) (Ris 1913), 1910-1912 (H. Elgner), 1938 (P. Buwalda), 1939 (R.G. Wind). Kai: 1908 (H. Merton), 1922 (H.C. Siebers) [a]. Tanimbar: 1938 (P. Buwalda). Several of the islands west of or around the Vogelkop of New Guinea have been studied for odonates as well; only the results of Lieftinck's field work in Misool (1948) are included in the present paper.

The first record of Platystictidae from the Moluccas is *Platysticta bicornuta* Selys (= *D. bicornuta* (Selys)) for Ceram (Seram) (Ris 1915). The identification of this specimen has been changed several times, and its status is still uncertain. Fraser (1926) described *Drepanosticta robusta* from Kei Island, and Ris (1929) recorded *D. auriculata* (Selys) from Buru, noting that also the female *D. bicornuta* from Seram in Ris (1915) may pertain to this species. Lieftinck (1949) renamed the Buru material as *D. moluccana* Lieftinck, and provisionally included the Seram female under this name as well. Redescriptions of previously described species are included in the present paper.

Material and methods

This paper is exclusively based on material in the Leiden museum (RMNH). Most specimens remained largely unstudied for more than fifty years, although M. A. Lieftinck had provisionally sorted them by species. Recent material was collected by Mr. F. G. Rozendaal in Bacan in 1985, and by myself during field work in Halmahera in 1995. In total 295 specimens were studied, including the types of the previously described *Drepanosticta robusta* Fraser and *D. moluccana* Lieftinck (both in RMNH). Per island the numbers of specimens are: Halmahera 28, Bacan 226, Obi 10, Ambon 16, Buru 7, Kai 2 and Misool 6. Specimens were studied using binocular microscopes (Leica MZ16A, Olympus). Illustrations were prepared with a camera lucida on a Leica MZ16A. Measurements are in millimeters, and were taken using a standard ruler (abdomen, wings), or indirectly measured from illustrations (pterostigma, anal appendages). JvT numbers are preserved with the specimens studied, written on a label with the specimen(s), or on the 5 × 3 inch label card in the envelope with the specimen.

Morphological terminology follows Watson & O'Farrell (1991). Special terminology of the head of Platystictidae follows Calvert (1931) and Cowley (1936). Note that the term 'transverse occipital carina' was used in the text by these authors for a structure named 'postoccipital carina' in the illustrations. Only the term 'transverse occipital carina' is in use since that time.

Acronyms used for collections: IRSNB, Royal Belgian Institute of Natural Sciences, Brussels; USNM, US National Museum of Natural History (Smithsonian Institution), Washington DC; RMNH, National Museum of Natural History Naturalis, Leiden.

Phylogeny and biogeography

Phylogeny. The phylogeny and historical biogeography of the Platystictidae of Southeast Asia are the subject of ongoing studies by the author (van Tol in prep.). The following notes represent preliminary remarks on the relationships of the Moluccan species. Based on morphological characters, the *Drepanosticta* species of the region can be divided in three presumably monophyletic groups characterized by one or more unique characters.

Drepanosticta megametta group. Within the genus *Drepanosticta* this group is characterized by a pair of processes on the posterior lobe of the pronotum, which are flat and of which the tips are only slightly wider than the base (e.g., Figs 3-4).

Other, non-unique (symplesiomorphic), characters of the species of this group include the unicolorous brown vertex anterior to the ocelli; the unmodified anterior lobe of the pronotum; the simple anal appendages with superiors provided with a more or less distinct spine approximately halfway on the inner surface; the inferior appendages are long and slender, distally compressed, in ventral view emarginate; the synthorax is brown with inconspicuous paler markings. These characters also occur in other, presumably monophyletic groups of *Drepanosticta*.

Distribution. Two species are known from the Philippines, viz., *D. megametta* Cowley (Mindanao) and *D. centrosaurus* van Tol (Mindanao) (van Tol 2005), and at least one undescribed species from the Bismarck Islands belongs here. Three species described in this paper from Misool and Halmahera are assigned to this group.

Drepanosticta lymetta group. This group is characterized in the genus *Drepanosticta* by a pair of processes on the posterior lobe of the pronotum, of which the tip (of the processes) is club-shaped or forked (e.g., Figs 21-22). Other, non-unique, characters of the species of this group include unicolorously brown vertex anterior to the ocelli; the unmodified anterior lobe of pronotum; the relatively simple anal appendages, with superiors straight, long and slender (e.g. Figs 23-25), lacking the distinct spine on the inner surface, and inferiors slender with tip turned medio- dorsad; synthorax castaneous without conspicuous pale stripes.

Distribution. Five species are known from the Philippines (*D. clados* van Tol from Mindanao, *D. furcata* van Tol from Siquijor, *D. hermes* van Tol from Mindanao, *D. lymetta* Cowley from Mindanao and *D. taurus* Needham & Gyger from Mindanao) (van Tol 2005). An undescribed species from Biak is very similar to the Philippine species of this group, while several species from the mainland of New Guinea also share the group characters as given above. Four species from Halmahera and Bacan described in this paper are assigned to this group.

Drepanosticta moluccana group. This group is characterized in the genus *Drepanosticta* by a transverse pale stripe of the vertex. Other, non-unique, characters of the species of this group include the more or less squarish corners of the posterior margin of the pronotum, not provided with a pair of posterior processes; the anal appendages with superiors relatively short and simple, their outer surface smoothly curved and with a small dorsal denticle; inferiors with distal half straight, the tip bent axiad; synthorax with a distinct pale band over metepisternum and (partly) metepimeron.

Distribution. Southern Moluccas (Kei, Obi, Buru, Ambon, and presumably also Seram). *D. moluccana* was described by Lieftinck (1938). *D. robusta* Fraser is known from Kei; the male is poorly described and only known from one incomplete specimen. Two new species are described in this paper from Ambon and Obi. All four species are morphologically very similar.

Biogeography. Nearly all species of *Drepanosticta* have small to extremely small ranges (e.g. van Tol 2005), defining areas of endemism of freshwater habitats (Van Tol & Gassmann 2007). Many are island endemics. The Moluccan species generally follow this pattern (Fig. 1).

Island endemicity in the Moluccas varies distinctly between various groups of insects. Island endemism is rather low in butterflies (e.g. five out of 200 species in Halmahera, and one out of 214 on Ambon). Comparing the various regions of the Moluccas, only c. 11% of the butterfly species are endemic to the Northern Moluccas (incl. Obi), and 15% to the Central Moluccas (Vane-Wright & Peggie 1994: Table 2). De Jong (1998) also stressed the distinct similarities between butterfly faunas of Halmahera (Northern Moluccas) and Seram (Central Moluccas). Since these islands have very different geological histories, he claimed an overwhelming and permanent role for dispersal rather than island rafting of these island biota. Such patterns are also common in several groups of well-dispersing odonates, e.g., Libellulidae, but island endemicity is the rule in many families of Zygoptera in this region (e.g. Protoneuridae, Isostictidae).

The strongest pattern links of the butterflies of the Northern and Central Moluccas are to New Guinea (Vane-Wright & Peggie 1994). Such a pattern was not found for the butterfly faunas of Halmahera and Misool, as described below for the sister species *Drepanosticta halmahera* sp. n. and *D. misoolensis* sp.n. Vane-Wright & Peggie did, however, find a link

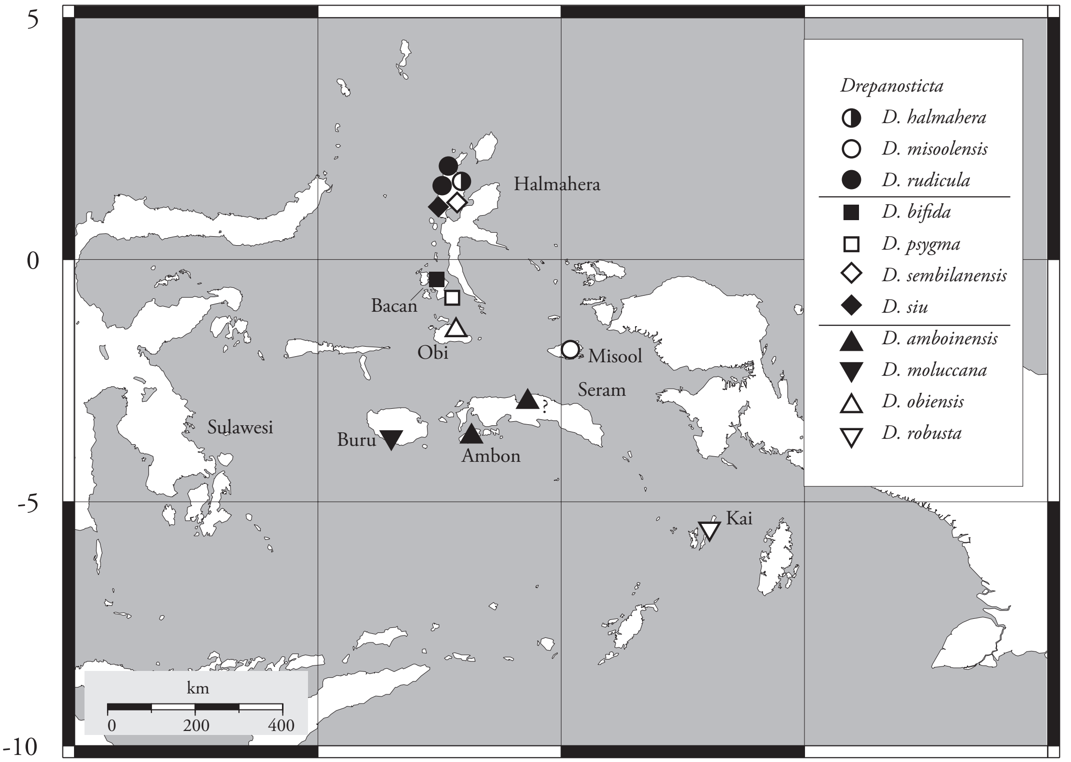


Figure 1. Distribution of *Drepanosticta* species in the Moluccas. Round symbols are used for the species of the *D. megametta* group, quadrangular symbols for those of the *D. lymetta* group, and triangular symbols for those of the *D. moluccana* group.

between the Northern Moluccas and Biak, which seems to be reflected in the *D. lymetta* group as well. The *D. lymetta* and *D. megametta* species groups as distinguished above and based on presumed synapomorphies of their members, reveal a distinct biogeographic pattern along the southern margin of the Philippine Sea Plate (Fig. 2). Several groups of aquatic insects, such as aquatic and semi-aquatic Hemiptera (e.g. Polhemus 1995), and the odonate family Platycnemididae (Gassmann 1999, 2000, 2005, Gassmann & Hämäläinen 2002) show similar patterns. This general pattern seems to have originated largely as a consequence of the geological history of the Philippine and Caroline Arcs (Hall 2002; Hill & Hall 2003).

The Philippine Arc was formed by subduction of the Indo-Australian plate under the Philippine Sea plate, a process that started about 45 Ma. Parts of this Philippine Arc are now forming the islands of the eastern part of the Philippines, while during the early phase (Middle Eocene, about 40 Ma) parts of Sulawesi and Halmahera may have been parts of this arc as well, the so-called Sulawesi – East Philippines – Halmahera Arc. The Caroline Arc was formed, also at about 40 Ma, at the eastern margin of the Philippine plate due to subduction of the Greater Pacific plate (now subducted) under the Philippine plate. It consisted of an island arc which now predominantly forms the northern half of New Guinea. This arc had an original position far more to the north, while its orientation was nearly north-south. It moved south and rotated clockwise since the Oligocene, forming one island arc with the Philippine arc. From the Late Miocene (10 Ma) it accreted from west to east with 'proto-New Guinea', a process continuing up to today. The orientation of the Philippine arc, including Halmahera, changed from east to west into more south to north, due to a complicated set of tectonic processes. The area north of Halmahera became larger due to back-arc spreading, forming the Caroline Sea Plate. The Caroline plate pushed the clockwise-rotating Philippine plate (since 25 Ma) in western direction towards Eurasia. Docking of parts of the arc against the north-western Philippines that started in the Late Miocene (10 Ma), resulted in the origin of western Luzon and some small islands due to the subduction

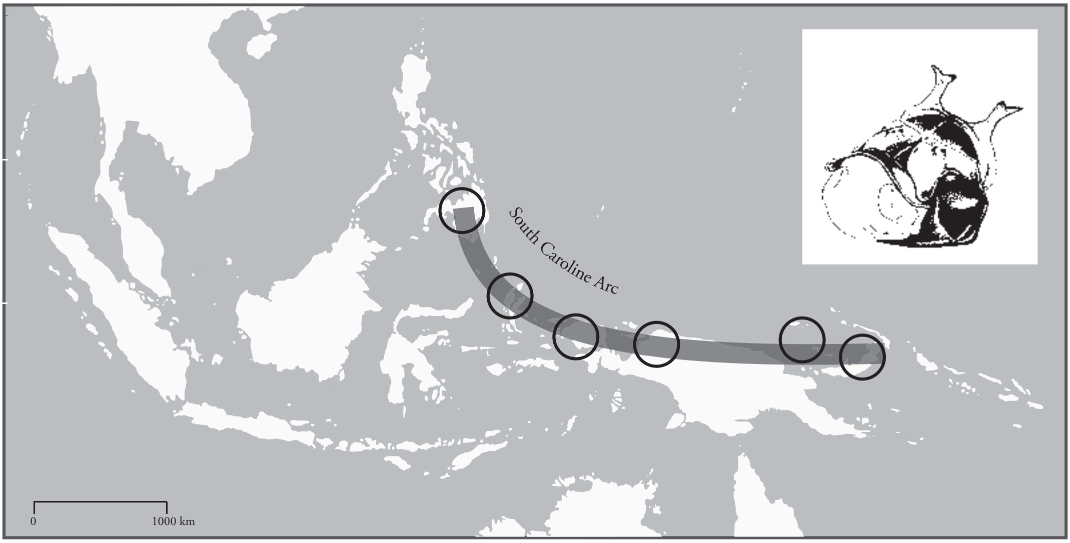


Figure 2. The South Caroline Arc and the distribution of species of the *Drepanosticta lymetta* (including the more distantly related species from New Guinea) and *Drepanosticta megametta* groups in Southeast Asia. The pronotum is that of *D. lymetta* Cowley male (modified after van Tol & Gassmann, 2007).

of the South China Sea Plate under the Philippine Plate. Later on, parts of the arc formed, for instance, the island of Mindanao by amalgation of extant islands along the eastern margin of Eurasia (Pubellier et al. 1996).

The various ancient island arcs seem to have played an important role in the origin of present distribution patterns of invertebrates of this region. This was demonstrated by Gassmann (2005), who reconstructed the phylogeny of the odonate subfamily Calicnemiinae (Platycnemididae). Representatives of this family frequently occur in the same habitats as the Platystictidae. The calicnemiine genus *Risiocnemis* Cowley, confined to the Philippines, appeared to be the sister-group of the genera *Lieftinckia* Kimmins plus *Salomocnemis* Lieftinck, both from the Solomon islands. This clade forms a monophyletic group with all genera from New Guinea (and possibly with the genus *Asthenocnemis* Lieftinck from the Philippines). The calicnemiine platycnemidids are not known from Australia, Halmahera and Sulawesi. These data suggest that the present pattern is due to rafting of odonates on islands of the Philippine arc in western direction.

A similar distributional history is hypothesized for the Moluccan and Philippine Platystictidae, although the timing of dispersal in western direction may have been different, as indicated by the presence of this family on Halmahera and Sulawesi. The *D. lymetta* group is at least represented on Biak. Closely related clades occur in New Guinea (van Tol in prep.) and Sulawesi (van Tol, in press). Further analysis has to reveal the phylogenetic position of the Moluccan species, and their role in the distributional history of the family. Platystictidae confirm that the phylogenetic relationships of various groups of insects of the region between New Guinea and the Philippines seem to indicate a historical biogeography of the region hardly foreseen some years ago.

List of species of Platystictidae of the Moluccas

***Drepanosticta megametta* group**

1. *Drepanosticta halmahera* sp. n.
   Distribution: Halmahera
2. *Drepanosticta misoolensis* sp. n.
   Distribution: Misool
3. *Drepanosticta rudicula* sp. n.
   Distribution: Halmahera

***Drepanosticta lymetta* group**

4. *Drepanosticta bifida* sp. n.
   Distribution: Bacan
5. *Drepanosticta psygma* sp. n.
   Distribution: Bacan
6. *Drepanosticta sembilanensis* sp. n.
   Distribution: Halmahera
7. *Drepanosticta siu* sp. n.
   Distribution: Halmahera

***Drepanosticta moluccana* group**

8. *Drepanosticta amboinensis* sp. n.
   Distribution: Ambon
9. *Drepanosticta moluccana* Lieftinck, 1938
   Distribution: Buru
10. *Drepanosticta obiensis* sp. n.
    Distribution: Obi
11. *Drepanosticta robusta* Fraser, 1926
    Distribution: Kai

Species excluded from the list of Moluccan Platystictidae

Drepanosticta bicornuta (Selys). Misidentification. – A record from Seram (Ris 1915), as *Platysticta bicornuta*, was rectified to *D. auriculata* (Selys) by Ris (1929). Confirmed records of this species are confined to New Guinea.

Drepanosticta auriculata (Selys). Misidentification. – The previous record from Seram (Ris 1929), changed to *D. moluccana* Lieftinck (with question mark) by Lieftinck (1949). Although the specimen was not examined by me, it seems unlikely that it is identical to *D. moluccana*, which is confined to Buru.

Key to the males of *Drepanosticta* from the Moluccas and Misool

1. Posterior margin of posterior lobe of pronotum with a pair of conspicuous processes, which are

distally wider than basally, apex club-shaped, fan-shaped or bifid (e.g. Figs 16, 28); occiput with distinct transverse occipital carina, usually with angulate lateral extremities; vertex brown or black, concolorous with rest of head 2

— Posterior margin of posterior lobe of pronotum sharp or with elongate triangular corners; apex sharp, not wider than base (Fig. 46); occiput with inconspicuous transverse occipital carina, lateral extremities absent or indistinct; vertex with transverse pale stripe (*D. moluccana* group) 8

2. Superior anal appendage with denticle or tooth in basal half; denticle sometimes rather inconspicuous (e.g. Fig. 18) (*D. megametta* group) 3

— Superior anal appendage basally round, without sharp denticle or tooth (e.g. Fig. 25) (*D. lymetta* group) 5

3. Denticle on superior appendage particularly well visible in dorsal view, less so in lateral view (Figs 17–18); superior appendages in lateral view with upper and lower side subparallel. Distribution: Halmahera . . . .*Drepanosticta rudicula* sp. n.

— Denticle on superior appendage particularly well visible in lateral view, less so in dorsal view (Figs 5-6); superior appendages in lateral view club-shaped 4

4. Inferior anal appendage in ventral view slender (Fig. 13); hind wing length c. 19 mm. Distribution: Misool . . . . *Drepanosticta misoolensis* sp. n.

— Inferior anal appendage in ventral view stout (Fig. 7); hind wing length c. 22 mm. Distribution: Halmahera . . . . . . *Drepanosticta halmahera* sp. n.

5. Ventrum of synthorax black or brownish black; apical T-shaped part of posterior processes of pronotum approximately as slender as the stalk (Fig. 22) 6

— Ventrum of synthorax dirty yellow; apical T-shaped part of posterior processes of pronotum distinctly heavier than the stalk (Fig. 34) 7

6. Superior anal appendages with distinct ventral subterminal triangular process (Fig. 41). Distribution: Halmahera . . . . *D. siu* sp. n.

— Superior anal appendages with ventral side subterminally smoothly rounded (Fig. 23). Distribution: Bacan . . . . *D. bifida* sp. n.

7. Inferior anal appendages distinctly longer than superiors (Fig. 35); posterior processes of pronotum T-shaped. Distribution: Halmahera . . . . *D. sembilanensis* sp. n.

— Inferior and superior appendages of equal length (Fig. 29); posterior processes of pronotum more or less fan-shaped. Distribution: Bacan . . . . *D. psygma* sp. n.

8. Distribution: Kei Island (the male of this species is only known from one teneral, incomplete specimen) . . . . *D. robusta* Fraser

— Distribution: Ambon, Buru, Obi 9

9. Inferior anal appendages ventrally with distinct subapical constriction, just before inward bent tip (Fig. 55); pale stripe over metepisternum conspicuous 10

— Inferior anal appendages ventrally without, or with hardly discernable, subapical constriction (Fig. 49); pale stripe over metepisternum inconspicuous. Distribution: Ambon . . . . *Drepanosticta amboinensis* sp. n.

10. Terminal part of inferior anal appendages c. two times as long as wide at the top (Fig. 55). Distribution: Buru . . . . *Drepanosticta moluccana* Lieftinck

— Terminal part of inferior anal appendages more than three times as long as wide at the top (Fig. 61). Distribution: Obi . . . . *Drepanosticta obiensis* sp. n.

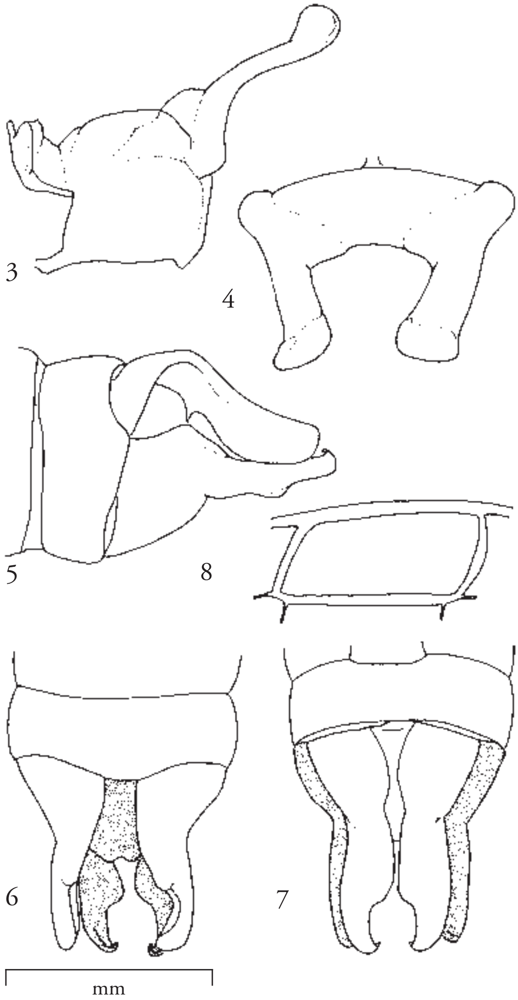
Drepanosticta megametta group

Drepanosticta halmahera van Tol, sp. n.

Figs 1, 3-8

Type material. Holotype male [JvT 10997]: ‘Indonesia (Maluku Utara)/NW Halmahera. 24 km SW of Tobelo/ Rivulet S of Tunuo camp (PT Widuri Utama/Timberindo), tributary of Sg Tunuo/c. 1°32’N 127°54’ E. Alt 150-200 m/22 Sep 1995. Leg. J. van Tol/Slowly flowing rivulet 6-8 m, in somewhat/disturbed primary rain forest. Mostly shaded/ Clear water. 10-30 (50) cm’.
Paratype: 1 male [JvT 10996], same data as holotype.

Medium-sized *Drepanosticta*, with anal appendages

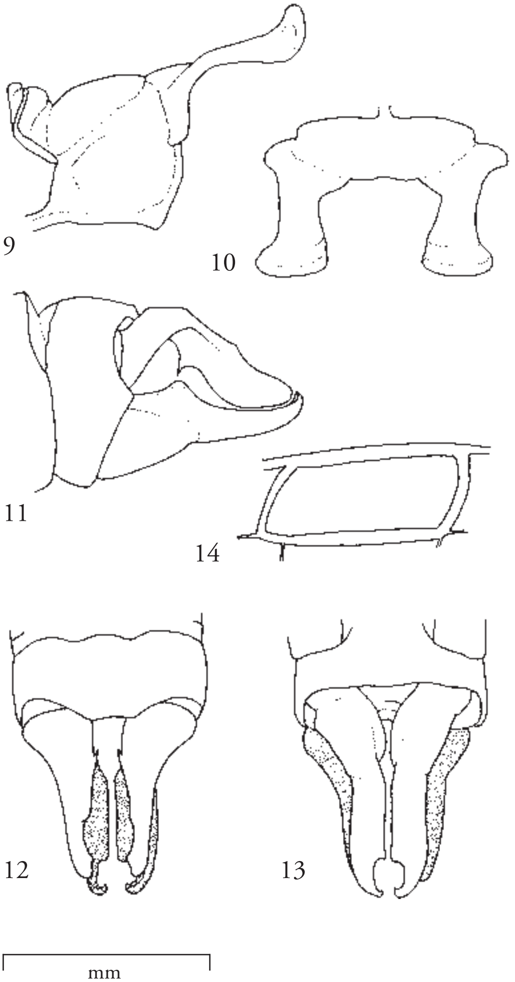


Figures 3-8. *Drepanosticta halmahera* sp. n., male. – 3, pronotum, left lateral view. – 4, posterior lobe of pronotum, dorsal view. – 5, anal appendages, left lateral view. – 6, idem, dorsal view. – 7, idem, ventral view. – 8, pterostigma, right fore wing.

distinctly different from other species known from Halmahera: superiors in lateral view down-curved, inferiors in ventral view constricted in distal half; ventrum black.

Male [holotype, JvT 10997]: Head. Labrum, anteclypeus and mandibles bluish white, anterior onesixth of labrum brown, mandibles with lower anterior corner against eye brownish black; rest of head brownish black; transverse occipital carina welldeveloped, lateral extremities angulate. Antennae with scapus brownish black, pedicellus dirty yellow, flagellum brown.

Thorax. Pronotum (Figs 3-4) pale brown, anterior lobe erect, widened anteriorly in lateral corners; median part posterior lobe somewhat darker than rest of pronotum, with posterior processes stout, flat over synthorax, curved inwards, the top widened and thickened, squarish at distal margin, length approximately as median line of median lobe. Synthorax with coloration as follows: mesepisternum pale brown, middorsal carina black, mesinfraepisternum brownish black, mesepimeron anteriorly brownish black, posterior from stigma (on metepisternum) pale brown, and dark brown on suture; metepisternum posterior from stigma mostly pale brown, and anterior from stigma brownish black except for triangular marking against stigma; metinfraepisternum brownish black, metepimeron brownish black, except for a broad triangular marking against posterior margin. Legs dirty yellow, hardly darker on joints. Wings hyaline, venation brown; Px in fore wing 17, in hind wing 15; R4 + 5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting Ac just before hind margin of wing (Y short-stalked); pterostigma (Fig. 8) brown, rather elongate, 2.2 times as wide as high, the proximal corner oblique, but not angulate, anterior and posterior side nearly parallel- sided; cells distal to pterostigma undivided. Abdomen brown, segments 8-10 brownish black, segments with pale markings (annules) as follows: anterior one-eighth of segment 3 dirty yellow, anterior one-sixth of segments 4-5 yellow, anterior one-fourth of segments 6-7 pale and with sagittiform markings, which are somewhat bluish white. Anal appendages (Figs 5-7) brown, inferiors surpassing superiors; superiors in dorsal view constricted near base, distal two-fifths dorso-ventrally flattened, dorsally at three-fifths from base a small blunt process (denticle), at c. two-fifths from base a sharp tooth, directed ventro-axiad; superiors in lateral view with base raised dorsad and distal threefifths turned ventrad; inferiors in ventral view with base strongly tapering, distal half basally straight, parallel-sided, distal two-fifths of distal half constricted,



Figures 9-14. *Drepanosticta misoolensis* sp. n., male. – 9, pronotum, left lateral view. – 10, posterior lobe of pronotum, dorsal view. – 11, anal appendages, left lateral view. – 12, idem, dorsal view. – 13, idem, ventral view. – 14, pterostigma, right fore wing.

dorso-ventrally compressed, the tip turned dorso-axiad.

Female. Unknown.

Measurements. Male, abdomen including anal appendages 34 mm, hind wing 22 mm.
Etymology. *Halmahera* (Gr.), after the type locality. A noun in apposition.
Distribution (Fig. 1). Halmahera (Moluccas, Indonesia).

Drepanosticta misoolensis van Tol, **sp. n.**

Figs 1, 9-14

Type material. Holotype male [JvT 23603]: [Printed label]: 'Misool Id (W.)/0-75 m/8.ix.-20.x.1948/M.A. Lieftinck', [on envelope in MAL's hand]: 'Fakal/19.9.48' and 'nec *bicornuta*, cpd with type Genova X.'59'. Paratypes (four male, one female), same data as holotype, but dates 20 Sep (female, JvT 23605), 23 Sep (male, JvT 23602), 4 Oct (two males, JvT 23600 and 23601), and 7 Oct (male, JvT 23604).

Posterior lobe of pronotum with pair of conspicuous flat processes; rather similar to *D. rudicula* sp. n., but basal interior denticle of superior appendage best visible in lateral view, and inferior appendages with distinct subterminal constriction.

Male [JvT 23603]. Head. Labrum, anteclypeus and mandibles bluish white, anterior one-sixth of labrum brown, mandibles with brownish black marking in latero-anterior corner against eye; postclypeus brown; rest of head mat-black; transverse occipital carina well developed, lateral extremities angulate. Antennae with scapus brownish black, pedicellus dirty yellow, flagellum broken.
Thorax. Pronotum (Figs 9-10) pale brown, median portion of posterior lobe dark brown, lateral lobes dirty yellow; anterior lobe medially expanded; posterior lobe with a pair of posterior processes, stout, wide at base, distally gradually widening, the broad top turned somewhat dorsad; length of process approximately the length of median line of median lobe. Synthorax variegate brownish black with paler medium-brown stripes as follows: dorsal carina black, black coloration of mesepisternum against dorsal carina from anteriormost corner widening posteriorly towards hind margin; mesinfraepisternum brownish black; mesepimeron with black marking anteriorly covering full width of mesepimeron, tapering posteriorly towards lower posterior corner; markings of metepisternum similar to mesepimeron, but metastigma distinctly pale; metepimeron brownish black except for a subsquarish pale marking against posterior margin. Legs dirty yellow, hardly darker on joints. Wings hyaline, venation brown, Px in fore

wing 16, in hind wing 14; R4+5 arising just distal to nodus, IR3 arising halfway first cell distal to subnodus; Arculus just distal to Ax2; Ab vein meeting Ac just before hind margin of wing (Y-vein short-stalked); CuP meeting hind margin in fore wing at level of Px5, in hind wing at level of Px 10; number of cells between Arculus and place where CuP meets hind margin of fore wing 9, of hind wing 14; pterostigma elongate, c. 2.3 times as wide as high, proximal corner oblique, posterior side only somewhat convex; some cells distal to pterostigma divided.
Abdomen brown, segments 9-10 brownish black; pale markings on segment 2-7 distinct, ivory white, as follows: segment 2 with elongate triangular marking anteriorly, and a paired crescentshaped marking latero-anteriorly; segments 3-6 with pale annule in anterior one-sixth, segment 7 with pale sub-squarish marking medio-anteriorly, c. one-sixth length of segment. Anal appendages brown, inferiors surpassing superiors in length; superiors in dorsal view wide at base, strongly tapering in basal third, distal two-thirds dorso-ventrally compressed, with ventrally directed sharp triangular tooth at base of distal portion, best visible in lateral view; superiors in lateral view with raised basal third, the distal two-thirds bent obliquely ventrad; inferiors in ventral view tapering in basal twofifths, distal three-fifths parallel-sided at base, then constricted on innerside, the tip slender, curved medio-axiad.

Female [JvT 23605]. Available female rather teneral; largely pale brown, generally as the male; posterior projections of pronotum distinct, as in the male, but shorter; shape of last abdominal segments damaged and distorted.

Measurements. Male, abdomen including appendages 30 mm, hind wing 24 mm; female, abdomen c. 26 mm, hind wing 19 mm.

Etymology. *Misoolensis* (L.), after the type locality. An adjective.
Distribution (Fig. 1). Misool (off western New Guinea, Indonesia).

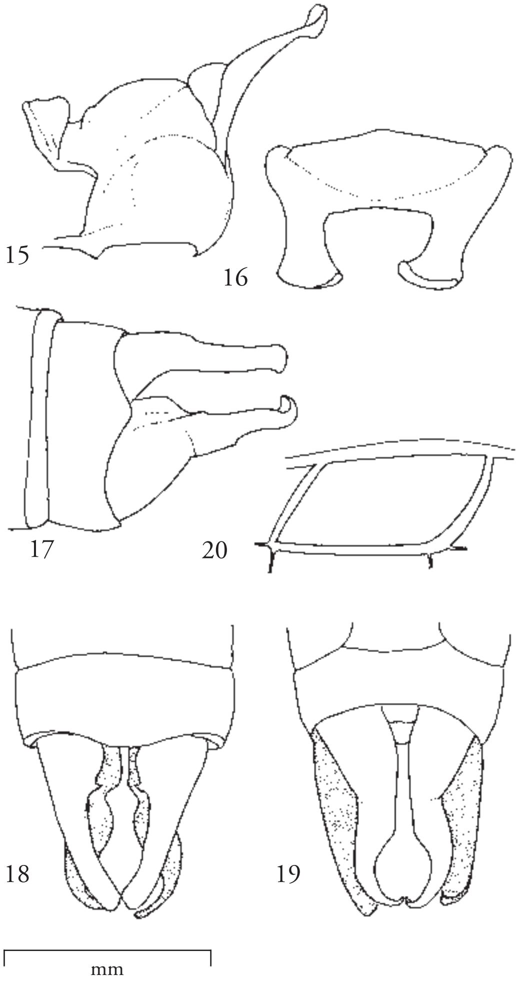
Drepanosticta rudicula van Tol, **sp. n.**

Figs 1, 15-20

Type material. – Holotype male [JvT 10940] 'Indonesia (Maluku Utara)/NW Halmahera. 23 km SW of Tobelo/ Basecamp PT Widuri Utama Timberindo/1°32'40" N 127°54'30" E. Alt 150-200 m. 20 Sep 1995. Leg. J. van Tol/Slowly flowing rivulet, and forest pools, in/somewhat disturbed primary rain forest/ Shaded. Clear water. 20-80 cm'. Paratypes (11 males, 4 females) (all Halmahera): Tolewang, 12-25 Oct 1951, 1 male; 20 km SSW of Tobelo, Sg. Gotoro W of Telaga Paca, c. 1°34' N 127°56' E, 150-200 m, 13-15 Sep 1995, J. van Tol, 7 males, 3 females; same data as holotype, 3 males, 1 female.
Other material (excluded from type series). Noord-Halmaheira (Bernstein), 1 male [JvT 19947] [incomplete].

Medium-sized *Drepanosticta*, general coloration brownish black, ventrum of synthorax black, with flattened processes on posterior margin of pronotum, anal appendages slender, of equal length, superiors with basal interior spine, which is well visible in dorsal view (in *D. misoolensis* sp. n. best visible in lateral view); inferiors in ventral view tapering towards tip (in *D. misoolensis* distinctly constricted subterminally).

Male [based on JvT 10668]. Head. Labrum and anteclypeus bluish white, anterior one-fifth of labrum black, mandibles brownish black with large, subsquarish white marking in basal corner against anteclypeus; rest of head black, postclypeus and frons shining, rest coriaceous, transverse occipital carina well-developed, lateral extremities angulate. Antennae with scapus brownish black, pedicellus dirty yellow at base, darkening against flagellum, flagellum castaneous.
Thorax. Pronotum (Figs 15-16) dorsally brown, lateral lobes dirty yellow, anterior lobe castaneous, erect, with distinctly wider and flattened parts on both sides of median line, median lobe brown, although portions against lateral lobes paler; posterior lobe with median lobe brownish black, lateral parts and processes pale brown; paired process short and stout, approximately length of median line of posterior lobe, both processes wide apart, the distal one-third expanded, distal margin squarish and thickened. Synthorax nearly black, but faint paler markings as follows: mesepisternum except



Figures 15-20. *Drepanosticta rudicula* sp. n., male. – 15, pronotum, left lateral view. – 16, posterior lobe of pronotum, dorsal view. – 17, anal appendages, left lateral view. – 18, idem, dorsal view. – 19, idem, ventral view. – 20, pterostigma, right fore wing.

for dorsal carina, posterior half of mesepimeron, metepisternum posterior to metastigma, and a small triangular marking in posteriormost portion of metepimeron (synthorax unicolorously castaneous in other specimens). Legs dirty yellow, femora with dark rings against joints with tibiae. Wings hyaline, reaching to halfway segment 6 of abdomen; venation brown; Px in fore wing 17, in hind wing 16; R4 + 5 arising at or just distal to nodus; IR3 halfway first cell distal to subnodus; Ab vein meeting Ac just before hind margin of wing (Y short-stalked); CuP meeting hind margin of fore wing at level of Px 5, in hind wing at level of Px 10; number of cells between Arculus and place where CuP meets hind margin of hind wing 14; pterostigma (Fig. 20) brown, 1.7 times as wide as high, proximal and distal side more or less parallelsided, proximal corner sharp, but not angulate; cells distal to pterostigma undivided.

Abdomen. Segments 1-2 brown, segments 8-10 black, other segments brown with paler markings as follows: anterior one-tenth of segment 3, anterior one-sixth of segments 4-6, anterior one-fifth of segment 7. Anal appendages (Figs 17-19) dark brown, superiors in dorsal view stout in basal onethird, more slender in flattened distal two-thirds, with short triangular process at one-third from base, directed ventro-axiad; inferiors with basal two-fifths relatively slender, parallel-sided, distal three-fifths bent outward and then inward again, especially on inner surface, the tips bent dorsad and touching.

Female [JvT 10810]: Similar to the male, but posterior processes of pronotum shorter and terminally hardly expanded; pale markings somewhat larger and more conspicuous than in holotype, abdominal segments 8-10 brownish black, valves black, terebra brown, both just surpassing the pale brown anal appendages; stylus brownish black.

Variation. Females vary in structure of the hind margin of pronotum. Some specimens have conspicuous processes similar to those of the male [JvT 10810], while an otherwise indistinguishable female (based on shape of anterior margin of pronotum) has a rounded posterior margin of the pronotum without any indication of a process [e.g. JvT 10671].

Measurements. Male, abdomen including anal appendages 32 mm, hind wing 22 mm (specimen JvT 10939 much smaller, with hind wing 20 mm, abdomen incl. appendages 28 mm); female, abdomen 32 mm, hind wing 23 mm.

Etymology. *Rudicula* (L.), spoon, for the shape of the prothoracic process. A noun in apposition.
Distribution (Fig. 1). Halmahera (Moluccas, Indonesia).

Drepanosticta lymetta group

Drepanosticta bifida van Tol, **sp. n.**

Figs 1, 21-26

Type material. — Holotype male [JvT 23730]: 'Salawaku river/ Batjan Isl. 150-100 m, 13 Jun 1953' [two stamped labels] [collected by A.M.R. Wegner], in RMNH.
Paratypes: same data as holotype, 12-14 Jun 1953: 139 males, 10 females; Sibela Mtn, 1 Jul 1985, 12 males, 1 female; Sibela Mtn, 3 Jul 1985, 4 males, 1 female; Ake Songu river, 9 Jul 1985, 1 male; Timber camp, 15 Jul 1985, 2 males (all in RMNH).

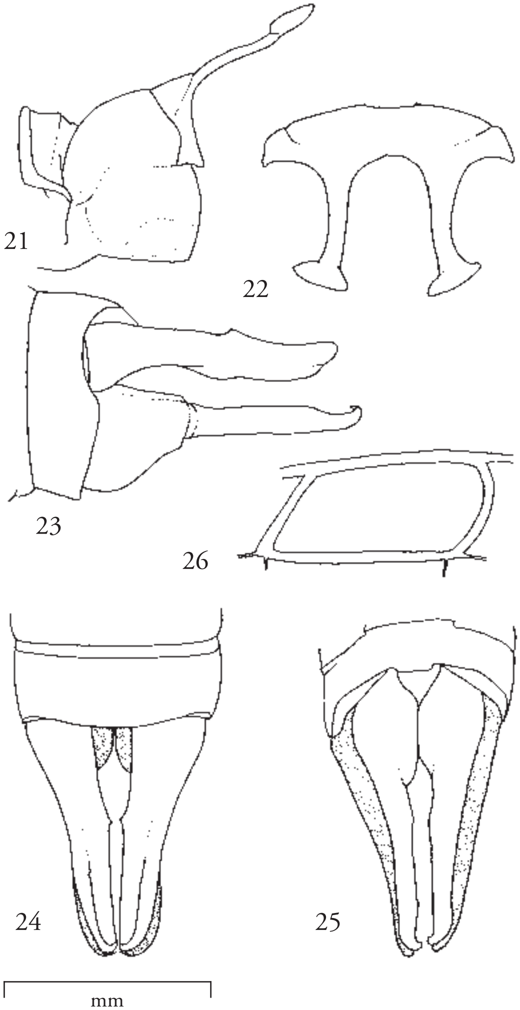
Rather small, castaneous species with pair of bifurcate processes on posterior margin of pronotum. Ventrum of synthorax dark. Differs from other species from Bacan, *D. psygma* sp. n., by dark ventrum of synthorax and very short median line of posterior lobe of pronotum (less than half the length of process).

Male [holotype, JvT 23730]. Head. Labrum, mandibles and anteclypeus bluish white; anterior margin of labrum with narrow brown border, not reaching lateral margin, mandibles with darker margin, especially in corner against eye; rest of head brownish black, but brownish transverse stripe in front of median ocellus; frons and clypeus, and narrow stripe along eyes shining, rest coriaceous; a series of longitudinal striae posterior to antennae; transverse postoccipital carina distinct, with angulate lateral extremities.
Thorax. Pronotum (Figs 21-22) castaneous, lateral lobes darker brown; anterior lobe semi-erect; posterior lobe with paired process, approximately as long as median line of median lobe, rather close together, subparallel, nearly flat over synthorax, straight, the top bifurcate, both fingers subequal, although inner finger somewhat more sturdy (variable between specimens); synthorax castaneous, ventro-posterior portion somewhat shining, rest mat. Legs dirty yellow, femora with narrow dark rings against tibiae. Wings hyaline, venation brown; Px in fore wing 16, in hind wing 15; R4+5 arising at subnodus, IR3 in anterior half of first cell distal to subnodus; Arculus distal to Ax2; Ab vein meeting Ac at hind margin of wing (Y sessile); number of cells between Arculus and place where CuP meets hind margin of hind wing 14; CuP meeting hind margin of fore wing at level of Px6, in hind wing at Px10; pterostigma (Fig. 26) pale brown, c. 1.9 times as wide as high, proximal side oblique, distal side convex, c. perpendicular to subcosta; few cells distal to pterostigma divided.
Abdomen. Segments 1-7 castaneous, segments 8-10 brownish black; pale markings on abdomen inconspicuous, as follows: latero-anterior corner of segment 3 pale marking approximately onesixth length of segment; pale rings on segments 4-6 of one-fifth, one-fourth and one-third of segment length; segment 7 with pale markings of c. two-fifths length of segment in latero-anterior corner. Anal appendages (Figs 23-25) castaneous, inferiors surpassing superiors, both longer than segment 8 of abdomen; superiors in dorsal view slender, subparallel, c. halfway a small sharp tubercle on innerside; terminal half of superiors dorso-ventrally flattened, with blunt dorsal tooth just posterior to inner tubercle; inferiors also very slender, especially terminal three-fifths, straight except for tip, which is sharply bent medio-dorsad.

Female. Similar to the male, but paired posterior process of pronotum more slender, the top ending in short triangular knob, wings somewhat wider than in male, pterostigma distinctly higher; segments 8-10 of abdomen and valve brownish black; valves and terebra reaching to same level as anal appendages, stylus dark and slender, distinctly surpassing level of anal appendages.

Measurements. Male, abdomen including appendages 30 mm, hind wing 21 mm; female, abdomen 32 mm, hind wing 24 mm.

Etymology. *Bifidus* (Latin), two-fingered, for the shape of the posterior process of the pronotum. An adjective.
Distribution (Fig. 1). Bacan (Moluccas, Indonesia).



Figures 21-26. *Drepanosticta bifida* sp. n., male. – 21, pronotum, left lateral view. – 22, posterior lobe of pronotum, dorsal view. – 23, anal appendages, left lateral view. – 24, idem, dorsal view. – 25, idem, ventral view. – 26, pterostigma, right fore wing.

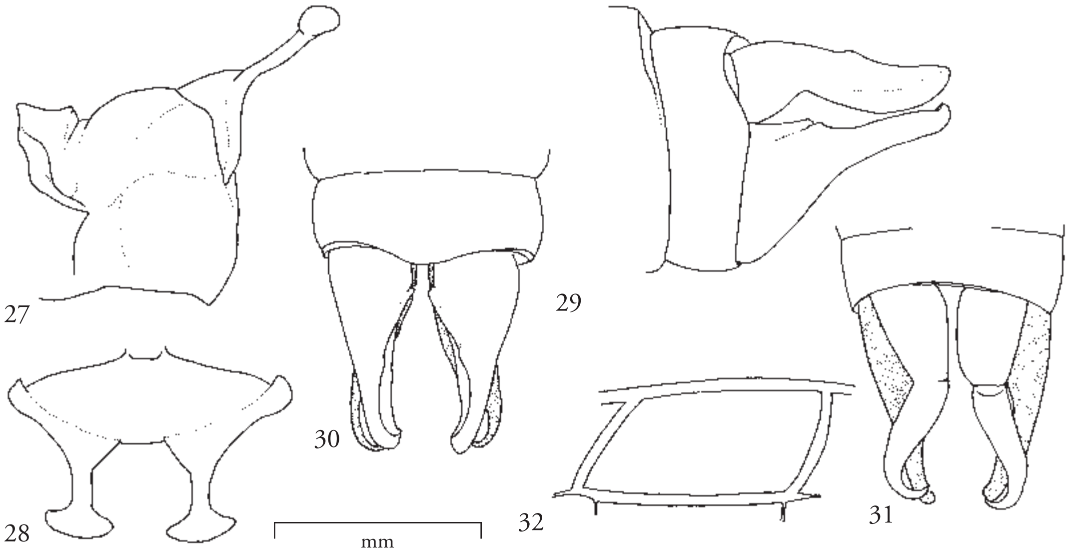
Drepanosticta psygma van Tol, **sp. n.**

Figs 1, 27-32

Type material. Holotype male [JvT 23542]: 'Salawaku river/ Batjan Isl. 150-100 m' and '13 Jun 1953' [leg. A.M.R.Wegner]. Paratypes (45 males, 8 females): same data as holotype, 12-14 June 1953, 41 males, 5 females; Gn. Sibela, trib. Ake Wayauna, 0°43' S 127°35' E, 850-1000 m, primary forest, natural clearing, 1 July 1985, F. G. Rozendaal, 2 males, 2 females; same, but 750 m, 2 males, 1 female.

Larger than *D. bifida* sp. n., also from Bacan; processes of posterior lobe of pronotum club-shaped; pale stripes over synthorax. Ventrum of synthorax yellow, and median line of posterior lobe of pronotum longer, more than half the length of posterior process.

Male [holotype JvT 23542]. Head. Labrum, mandibles and anteclypeus ivory white, anterior border of labrum brown, medially c. one-sixth the height of mandible and tapering towards latero-anterior corners; rest of head brownish black, but small transverse marking in front of median ocellus, black parts in front of median ocellus shining, rest coriaceous, postocular carina well developed, lateral extremities angulate. Antennae with scapus brown, pedicellus dirty yellow, flagellum brown. Thorax. Pronotum (Figs 27-28) castaneous, but lateral lobes and median portion of posterior lobe darker; posterior margin of posterior lobe with paired process with broad base, strongly constricted, the top knob-like or club-shaped, lying flat over synthorax. Synthorax castaneous, but metepisternum nearly fully dirty yellow, except for posterior margin; metepimeron dirty yellow with large rectangular brown marking anteriorly, c. threequarters length of metepimeron. Legs dirty yellow, but narrow black rings near joints with tibiae. Wings hyaline, venation brown; Px in fore wing 17, in hind wing 16; R4+5 arising at nodus, IR3 halfway first cell distal to subnodus; Ab vein meeting Ac at hind margin of wing (Y sessile); number of cells between Arculus and place where CuP meets hind margin of hind wing 20; CuP meeting hind margin of fore wing at level of Px6, of hind wing at level of Px13; pterostigma (Fig. 32) pale brown, proximal side oblique, distal side convex, c. 1.9 times as wide as high; cells distal to pterostigma undivided.
Abdomen. Segments 1-7 shining castaneous, segments 8-10 brownish black with pale, usually dirty yellow, markings as follows: anterior one-eighth of segment 3 with triangular median spot and a more elongate marking in ventro-anterior corner; segments 4-6 anterior one-sixth pale, most distinct medio-anteriorly; segment 7 somewhat paler anteriorly, but without distinct marking. Anal appendages (Figs 29-31) castaneous or brownish black, inferiors surpassing



Figures 27–32. *Drepanosticta psygma* sp. n., male. – 27, pronotum, left lateral view. – 28, posterior lobe of pronotum, dorsal view. – 29, anal appendages, left lateral view. – 30, idem, dorsal view. – 31, idem, ventral view. – 32, pterostigma, right fore wing.

superiors; superiors in dorsal view stout at base, distal fourfifths dorso-ventrally compressed, the flattened part at least four times as long as high, the top obliquely cut; inferiors in vental view stout at base, distal three-fifths slender, straight, nearly parallel-sided, the tip tapering bent axiad, but hardly dorsad.

Female. Similar to the male, but posterior projections of pronotum very slender, thread-like, and perpendicular to posterior lobe; segments 9-10 of abdomen short, valve and terebra long, surpassing level of anal appendages; stylus long.

Measurements. Male, abdomen including appendages 36 mm, hind wing 24 mm; female, abdomen 35 mm, hind wing 26 mm.

Etymology. *Psygma* (Gr.), fan, for the shape of the prothoracic processes. A noun in apposition.
Distribution (Fig. 1). Bacan (Moluccas, Indonesia).

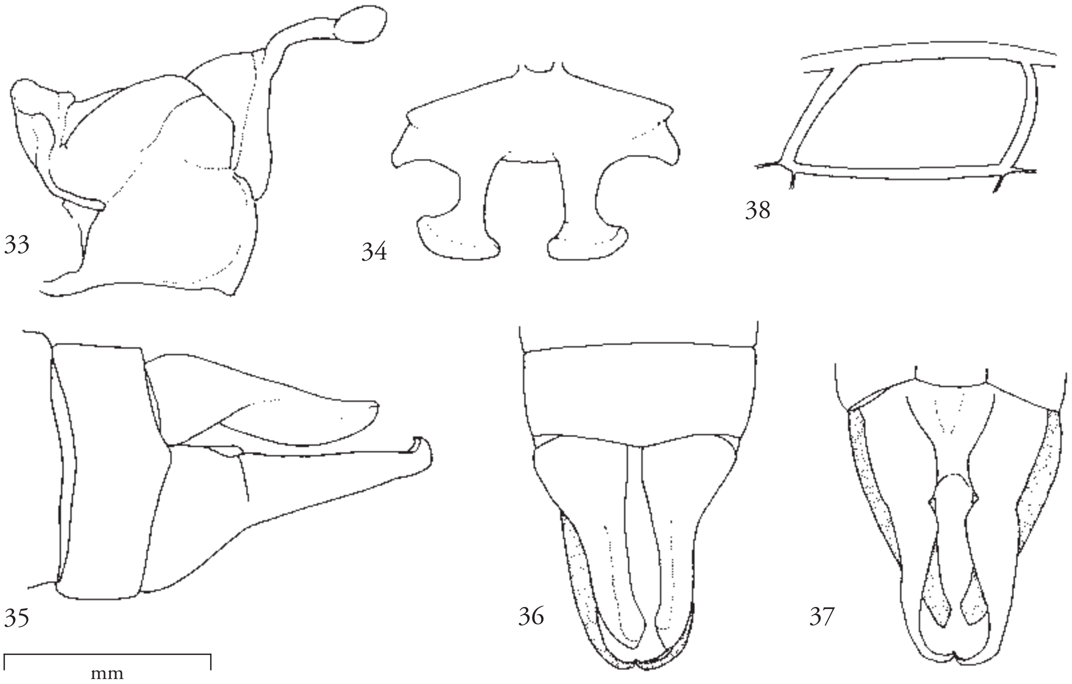
Drepanosticta sembilanensis van Tol, **sp. n.**

Figs 1, 33-38

Type material. Holotype male [JvT 23495]: 'Isl. Halmaheira/ Mt Sembilan 600 m/27/9-6/10 1951' [printed], '8 Oct 1951' [printed] and 'Gn. Sembilan' [handwritten].
Paratypes (2 males) (all Halmahera): Same data as holotype, but 4 Oct 1951, 1male [JvT 23494]; 20 km SSW of Tobelo. Along Sg Gotoro W of Telaga Paca, c. 1°34'N 127°56'E, 150-200 m, 13-15 Sep 1995, J. van Tol, 1 male [JvT 10812].

A large and robust species of the *D. lymetta* complex; ventrum of synthorax pale; general appearance castaneous, superior anal appendages of male distinctly shorter than inferiors, superiors elongate club-shaped without tooth or denticle.

Male [holotype, JvT 23495]. Head. Labrum, mandibles and anteclypeus yellow (bluish yellow), labrum and mandibles with narrow anterior brownish black border, approximately one-tenth the height of labrum, but somewhat more extensive in middle; rest of head black, coriaceous, transverse occipital carina well-developed, with lateral extremities angulate.



Figures 33-38. *Drepanosticta sembilanensis* sp. n., male. – 33, pronotum, left lateral view. – 34, posterior lobe of pronotum, dorsal view. – 35, anal appendages, left lateral view. – 36, idem, dorsal view. – 37, idem, ventral view. – 38, pterostigma, right fore wing.

Antennae with scapus brown, pedicellus dirty yellow, flagellum brown.

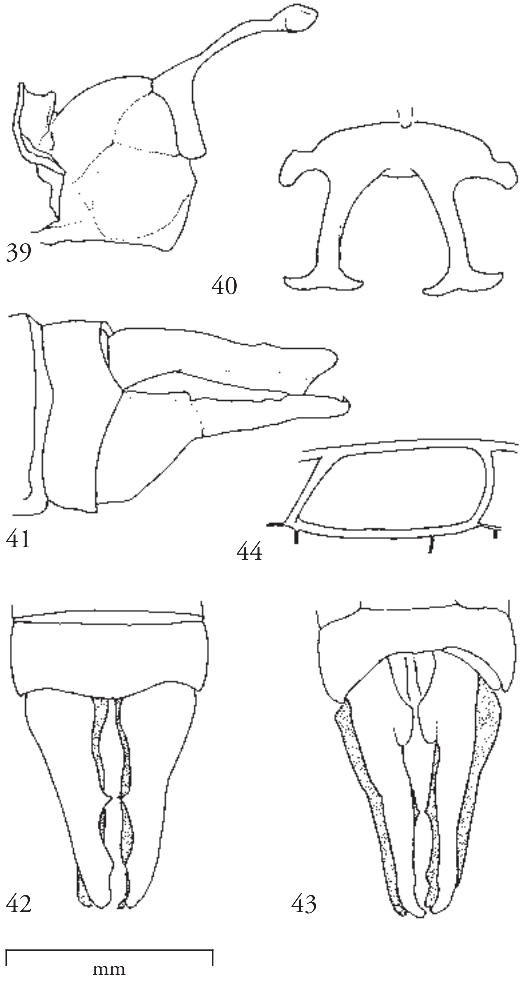
Thorax. Pronotum (Figs 33-34) with anterior lobe brown, median part flat, the sides distinctly erect, median lobe castaneous, lateral lobes darker, posterior lobe dark brown, especially medially, with a pair of posterior processes, T-shaped, stout and flat, the transverse terminal part approximately as long as the stem, total length of process approximately middorsal length of median lobe. Synthorax dark brown, but lower half castaneous, no antehumeral stripe. Legs dirty yellow, femora near joints with dark rings. Wings hyaline, venation brown; Px in fore wing 18, in hind wing 17; R4+5 arising at or just distal to nodus; IR3 arising halfway first cell distal to subnodus; Arculus distinctly distal to Ax2; Ab vein joining Ac at or just before hind margin of wing (Y unstalked or very short-stalked); CuP reaching hind margin of fore wing at Px5, of hind wing at Px10; number of cells between Arculus and place where CuP meets hind margin of fore wing ten, of hind wing 15; pterostigma (Fig. 38) castaneous, c. 1.9 times as wide as high, proximal corner angulate, cells distal to pterostigma undivided.

Abdomen. Segments 1-7 castaneous, and segments 8-10 brownish black, paler medio-anterior markings on dorsum of segments as follows: onetenth of segment 3, one-sixth of segment 4, onefifth of segment 5, and one-sixth of segment 6. Anal appendages (Figs 35-37) brown, the inferiors darker; inferiors distinctly surpassing superiors; superiors elongately club-shaped, without denticles or spines; inferiors slender, nearly straight, the top sharply bent inwards, the tips dorsad and touching.

Female. Unknown.

Measurements. Male, abdomen including anal appendages 39 mm, hind wing 27.5 mm.

Etymology. *Sembilanensis*, for the type locality Gunung Sembilan. An adjective.



Figures 39-44. *Drepanosticta siu* sp. n., male. – 39, pronotum, left lateral view. – 40, posterior lobe of pronotum, dorsal view. – 41, anal appendages, left lateral view. – 42, idem, dorsal view. – 43, idem, ventral view. – 44, pterostigma, right fore wing.

Distribution (Fig. 1). Halmahera (Moluccas, Indonesia); apparently widespread in northern half of the island, but uncommon.

Drepanosticta siu van Tol, **sp. n.**

Figs 1, 39-44

Type material. Holotype male: 'Isl. Halmahera/Mt. Siu 600-700 m/27/9-6/10 1951' [stamped on envelope], 'G. Siu' [handwritten] and '28 Sep 1951' [stamped] [JvT 23492].

Paratypes: Halmahera, Mt. Sembilan, 600 m, 27 Sep-6 Oct 1951, 3 males 2 females [JvT 23487-23491]; Halmahera, Tuguaer-Tasao, 100-150 m, 20-24 Sep 1951, 1 female [JvT 23486].

Very similar to *D. bifida* sp. n. from Bacan, with dark ventrum of synthorax, but males differ in the structure of the paired process of the posterior lobe of the pronotum, and a subterminal ventral triangular projection of the superior appendage.

Male [JvT 23492, holotype]. Head. Labrum, mandibles and anteclypeus creamish white, anterior one-fifth of labrum brownish black, mandibles brownish black along eye, continuing in concave line towards anterior corner near labrum; rest of head black, coriaceous, transverse occipital carina well developed, with lateral extremities angulate. Antennae with scapus brownish black, pedicellus dirty yellow, darkening against flagellum, flagellum brown.

Thorax. Pronotum (Figs 39-40) castaneous, median lobe and central part of posterior lobe somewhat darker; anterior lobe anteriorly erect, without conspicuous emarginations or extensions, posterior lobe with a pair of processes, placed distinctly from lateral corner, the top of each process T-shaped, perpendicular part as wide as stem, process c. as long as median line of median lobe; synthorax concolorous brownish black, only somewhat paler along sutures. Legs dirty yellow, with black markings on all femora near joints of tibiae. Wings clear, venation brown; Px in fore wing 18, in hind wing 17; R4+5 arising just anterior to nodus; IR3 arising in anterior half of first cell distal to subnodus; Arculus distal to Ax2; Ab vein joining Ac just before posterior margin of wing (Y-vein short-stalked); CuP reaching hind margin of hind wing at level of Px11; eleven cells between Arculus and place where CuP meets posterior margin in fore wing, and 15 cells in hind wing; pterostigma (Fig. 44) castaneous, approximately 2.1 times as wide as high, proximal corner angulate; some cells distal to pterostigma divided.

Abdomen. Segments 1 and 9-10 dark brown, other segments castaneous, with paler markings anteriorly on segments as follows: one-tenth of segment 2, one-eighth of segment 3, one-sixth of segment 4 and one-eighth of segment 5. Anal appendages (Figs 41-43) with superiors brown, inferiors brownish black, superiors long and slender, the top hollowed with subterminal blunt and short tooth, and very short denticle c. halfway on inner side; inferiors just surpassing superiors, straight except for tapering tip, which is bent 90° inward.

Female. Similar to the male, but posterior processes of pronotum more delicate. Abdominal segments 9-10 short, valves and terebra approximately as long as anal appendage; stylus dark and slender, well surpassing level of anal appendage.

Variation. Two females [JvT 23486, 23489] lack the posterior processes of the pronotum, and are doubtfully conspecific; the other female [JvT 23488] is in one envelope with a male [JvT 23487].

Measurements. Male, abdomen including anal appendages 33 mm, hind wing 22 mm; female, abdomen 32 mm, hind wing 22 mm.

Etymology. *Siu*, for the type locality Gunung Siu. A noun in apposition.
Distribution (Fig. 1). Halmahera (Moluccas, Indonesia).

***Drepanosticta moluccana* group**

***Drepanosticta amboinensis* van Tol, sp. n.**

Figs 1, 45-50

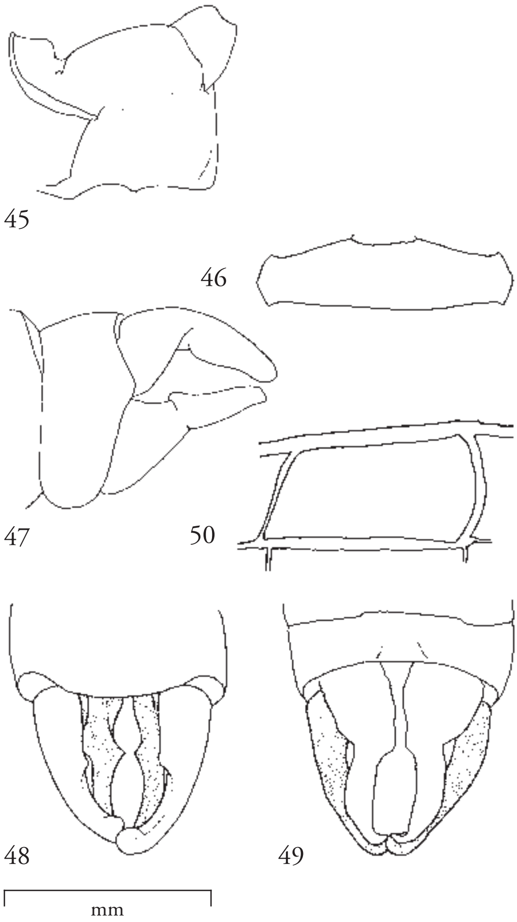
Platysticta bicornuta. - Ris, 1915: 89 (1 female, Ceram) [misidentification, fide Lieftinck, 1949]
Drepanosticta auriculata. - Ris, 1929: 141–142 (Ceram only).
Drepanosticta moluccana Lieftinck (female Ceram only). – Lieftinck, 1949: 82.

Type material. Holotype male [JvT 23556]: 'S. Moluccas / Ambon x.1949 / M.A. Lieftinck' [printed label with black border], and 'Ambon 12.10.49' [hand written, in purple], and '*Drepanosticta* sp. n.' [in Lieftinck's hand].
Paratypes (all Ambon): Ambon, 5 Nov 1948, 5 males 2 females [235548-23554]; same data as holotype, 4 males [JvT 23555, 23557-9]; as holotype, but date 9 Oct 1949, 1 male 1 female [JvT 23560-1]; Ambon island, mountain brook, 150 m, 20 Apr 1961, A.M.R. Wegner, 1 male [JvT 23562]; Mt Salahuhi, 600 m, 26 Oct 1961, 1 female [JvT 23563].
Other material (excluded from type series). Ceram, 1 female (see Ris, 1915) [not studied, doubtfully conspecific].

Structurally similar to *D. moluccana* Lieftinck, but synthorax without distinct pale metepisternum and metepimeron, presumably not due to preservation conditions; the inferior appendages lack the subterminal constriction, as present in *D. moluccana* and *D. obiensis* sp. n.

Male [holotype, JvT 23556]. Head. As *D. moluccana* (see below), but pale markings of mandibles and labrum bluish white; anterior one-third of labrum dark; pale stripe over frons similar as in *D. moluccana*. Thorax. Pronotum (Figs 45-46) as in *D. moluccana*, but somewhat darker. Synthorax much darker, paler stripes over metepisternum and metepimeron hardly recognizable; legs somewhat paler. Wings hyaline, venation brown; Px in fore wing 16, in hind wing 15; R4+5 arising just anterior to nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting Ac at hind margin of wing (Y sessile); CuP reaching hind margin of fore wing at level of Px 4, in hind wing at level of Px 6; ten cells between Arculus and place where CuP meets hind margin of hind wing; pterostigma (Fig. 50) rather dark, otherwise as in *D. moluccana*.
Abdomen. Generally darker than *D. moluccana*, but last segment paler; anal appendages (Figs 47-49) dirty yellow, the top of inferiors somewhat different from *D. moluccana*, in ventral view without distinct subterminal constriction, although tip turned inward and somewhat dorsad.

Female. Similar to the male; pale markings of abdomen more extensive; last abdominal segments short; valves and terebra short, not surpassing level of anal appendages.



Figures 45-50. *Drepanosticta amboinensis* sp. n., male. – 45, pronotum, left lateral view. – 46, posterior lobe of pronotum, dorsal view. – 47, anal appendages, left lateral view. – 48, idem, dorsal view. – 49, idem, ventral view. – 50, pterostigma, right fore wing.

Measurements. Male, abdomen including anal appendages 35 mm, hind wing 23 mm; female, abdomen 31 mm, hind wing 24 mm.

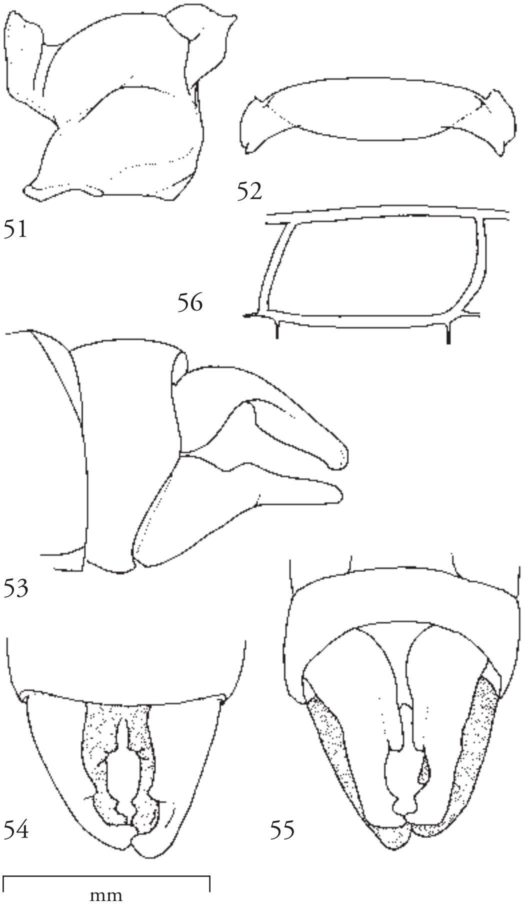
Etymology. *Amboinensis* (L.), for the type locality, the island of Amboina (Ambon). An adjective.
Remark. It is uncertain whether the female from Seram, mentioned since Ris (1915) under various names, is indeed conspecific with the specimens from Ambon.
Distribution (Fig. 1). Ambon (southern Moluccas, Indonesia), and possibly Seram.

Drepanosticta moluccana Lieftinck
Figs 1, 51-56

Drepanosticta auriculata (partim). – Ris, 1929: 141–142 (Buru only).
Drepanosticta moluccana Lieftinck, 1938: 82-83 (original description [as ‘nom. nov’] for specimens of *D. auriculata* from Buru).

Medium-sized *Drepanosticta*, brown with paler markings on synthorax and abdomen; pronotum without posterior processes, appendages short and simple; inferior appendages in ventral view rather stout, the terminal part c. two times as long as wide, subterminally with distinct constriction; the closely related *D. obiensis* sp. n. with more slender inferior appendages.

Male [based on JvT 21410]. Head. Labrum, mandibles and anteclypeus bluish white, labrum with anterior two-fifths brown, mandibles with anterior one-sixth brown; gena pale, rest of head variegated with brown; a narrow transverse paler brown stripe over frons between antennae just in front of anterior ocellus; postocular lobe and occiput pale brown; fine longitudinal striae between eye and ocelli, rest of head coriaceous; transverse occipital carina poorly developed, without extremities. Antennae with scapus pale brown, pedicellus brown, anteriorly black, flagellum brown.
Thorax. Pronotum (Figs 51-52) predominantly pale brown, but lateral lobe darker; lateral parts of anterior lobe and median lobe paler, anterior lobe simple, erect, but anterior border not widening, posterior lobe simple as well, the lateral parts with sharp edge in line with median portion, laterally rounded ventrad. Synthorax dorsally medium brown, dorsal carina paler, dark stripe over dorsal half of mesepisternum against dorsal carina; metepisternum ivory white and metepimeron dirty yellow, a stripe over metapleural suture distinctly darker. Legs dirty yellow, dark rings on femora of all legs as follows: an inconspicuous ring close to coxa, a more distinct ring at one-third the femur-length from tibia, and a narrow ring at joints with tibiae. Wings hyaline, venation middlebrown, Costa darker; Px in fore wing 17, in hind wing 16; R4+5 arising



Figures 51-56. *Drepanosticta moluccana* Lieftinck, male. – 51, pronotum, left lateral view. – 52, posterior lobe of pronotum, dorsal view. – 53, anal appendages, left lateral view. – 54, idem, dorsal view. – 55, idem, ventral view. – 56, pterostigma, right fore wing.

at nodus (hind wing) or well anterior to nodus (fore wing); IR3 arising halfway first cell after subnodus; Ab vein meeting Ac at or just before hind margin of wing (Y sessile or very short-stalked); CuP reaching hind margin of wing at level of Px4 in fore wing, at level of Px5 in hind wing; nine cells between Arculus and place where CuP meets hind margin of hind wing; pterostigma (Fig. 56) castaneous, proximal side oblique, distal side somewhat convex, c. 1.8 times as wide as high; cells distal to pterostigma undivided. Abdomen. Segment 1 somewhat expanded posteriorly, pale brown, but with small triangular dark marking near annule with segment 2; segment 2 brown, antero-lateral corner pale; segments 3-5 anterior three-quarters pale brown (middle part dark than rest, and anteriorly paler), rest of segments dark brown, but somewhat variable; segment 6 anterior one-fifth dirty yellow, rest brown to brownish black against segment 7; segment 7 dark brown, but somewhat paler in latero-anterior onefourth; segments 8-9 dark mat-brown; segment 10 paler, shining. Anal appendages (Figs 53-55) ochreous; superiors in dorsal view curved inward, with small flat dorsal tubercle at half the appendage length, distal half dorso-ventrally compressed, elongate club-shaped; inferiors with distal half parallelsided, the tip constricted, compressed and turned dorsad.

Female. Only known specimen damaged.

Measurements. Male, abdomen including appendages 36 mm, hind wing 24 mm.

Material examined. All specimens from Buru (in RMNH). Nal'besi, 26 Apr 1921, L. J. Toxopeus, 1 male [holotype, JvT 3049]; Leksoela, Aug 1921, 1 male [JvT 14740]; Buru Station 2, L.J. Toxopeus, 1 female, [JvT 19948]; Leksoela, 8 Nov 1941, J. J. van der Starre, 4 males [JvT 19892-4, 21410].

Remark. Toxopeus (1924) includes ecological data of the locality. Buru station 2 is described as follows: '. . . a fairly big waterfall called the Wa'ha (in Malay: Air Berbunyi, i.e. Thundering Water). This stream springing from the rocks at about 1300 ft is powerfully fed by subterranean channels and at a height of some 650 ft the falls begin in successive cascades . . .'.

Distribution (Fig. 1). Buru (Moluccas, Indonesia).

Drepanosticta obiensis van Tol, **sp. n.**

Figs 1, 57-62

Type material. – Holotype male [JvT 23567] 'Obi, Kali Telaga, 6 Aug 1953' [leg. A. M. R. Wegner].
Paratypes [all in RMNH]. Obi, Kali Telaga, 6 Aug 1953, [leg. A.M.R. Wegner], 3 males [JvT 23564-6]; same 31 Oct 1953, 2 males [JvT 23568-9]; same, 2 Nov 1953, 2 males 1 female [JvT 23570-2]; Obi, Laiwui, 21 Oct 1953, 1 male [JvT 23573].

In general, structurally similar to *D. moluccana*, but pale stripes over metepisternum and metepimeron less conspicuous, the dark stripe over metapleural suture narrower; abdomen generally paler; inferior appendages in ventral view subterminally distinctly constricted, the terminal part slender, more than two times as long as wide.

Male [holotype, JvT 23567]. Head. Mandibles and labrum bluish white, anterior two-fifths of labrum dark.
Thorax. Pronotum (Figs 57-58) not conspicuously different from *D. moluccana.* Synthorax with metepisternum and metepimeron dark yellow, a narrow dark stripe over metapleural suture. Legs dirty yellow, the dark rings very conspicuous. Wings hyaline, venation brown, Costa brownish black; number of Px in fore wing 17, in hind wing 16; R4+5 arising at nodus, IR3 arising halfway first cell distal to subnodus; Ab vein meeting Ac before hind margin of wing (Y-vein short-stalked); CuP reaching hind margin of fore wing at level of Px4, of hind wing at level of Px6; ten cells between Arculus and place where CuP meets hind margin of hind wing; pterostigma (Fig. 62) castaneous; many cells distal to pterostigma divided.
Abdomen rather pale, segment 1 brown, segment 2 brown, except for a pale triangular spot in lateroanterior corner, segment 3 with anterior one-eighth dirty yellow, broken by dark line in middle, then posteriorly three-eights brown (anterior and posterior parts paler), posterior-most one-quarter dark brown, a pale brown region between both dark rings; segments 4-5 with similar markings, but pale area between dark rings much darker, nearly brown on segment 5; segments 6-7 with anterior one-fourth pale, especially on segment 7 broken by dark median line; segments 8-10 dark. Anal appendages (Figs 59-61) ochreous, similar to *D. moluccana*, but medio-dorsal tooth on superiors more distinct and sharper, inferiors as in *D. moluccana*, but more slender.

Female: As male, but rather pale; valves and terebra approximately as long as anal appendages.

Measurements. Male, abdomen including appendages 33 mm, hind wing 20.5 mm; female abdomen 32 mm, hind wing 23 mm.

Etymology. *Obiensis* (L.), for the type locality. An adjective.

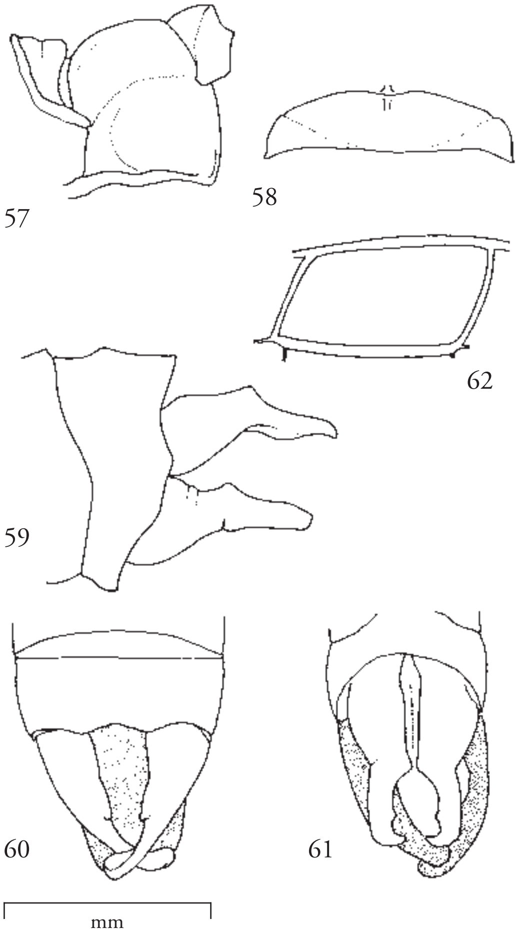
Distribution (Fig. 1). Obi (Moluccas, Indonesia).

Drepanosticta robusta Fraser

Fig. 1

Drepanosticta robusta Fraser, 1926: 491-492 (original description, Kei Island, Gn Daab). – Lieftinck, 1971: 110 (lectotype female in RMNH).

As already indicated in the original description, the male is teneral, incomplete (missing abdominal segments 7-10) and in poor condition. Although the pronotum is much distorted, it seems that the structure of the hind margin of the posterior lobe of the pronotum resembles the species of the *D. moluccana*-group; also the smoothly rounded transverse occipital carina, and the transverse pale stripe over the vertex indicate a close relationship to *D. moluccana*. The female lectotype is in good condition, and is presumably conspecific; generally pale brown, distinct transverse paler stripe between antennae, transverse occipital carina indistinct, lateral extremities absent; pronotum with hind margin posterior lobe rounded without posterior processes; metepimeron and metepisternum very pale.
Male [based on paralectotype, JvT 15407]. Head. Labrum, mandibles and anteclypeus dirty white, without dark anterior border [possibly due to teneral state]; remaining part of head brown, with broad pale stripe between antennae, also covering anterior half of median ocellus; an oval marking abaxially of lateral ocelli, somewhat larger than the ocelli; occiput also paler than rest of head; transverse occipital carina hardly visible, no lateral extremities.
Thorax. Pronotum simple, brown; anterior lobe simple, with anterior margin erect, without distinct extensions; posterior lobe short, with very short triangular projections on hind margin, c. one-fourth the



Figures 57-62. *Drepanosticta obiensis* sp.n., male. – 57, pronotum, left lateral view. – 58, posterior lobe of pronotum, dorsal view. – 59, anal appendages, left lateral view. – 60, idem, dorsal view. – 61, idem, ventral view. – 62, pterostigma, right fore wing.

length of the posterior lobe itself. Synthorax (damaged) brown, with presumably distinct pale stripe over metepisternum, and another stripe over metepimeron, divided by a narrow brown stripe over metapleural suture. Legs (only right middle leg available) yellow. Wings hyaline, venation pale brown, Px in fore wing 16, in hind wing 15; R4+5 arising at nodus, IR3 arising halfway first cell distal to subnodus; Arculus distal to Ax2; Ab vein meeting Ac well before hind margin of wing (Y-vein stalked); number of cells between Arculus and place where CuP meets hind margin of hind wing 10; CuP meets hind margin of fore wing at level of Px5; of hind wing at level of Px6; pterostigma pale brown, trapezoidal, only distal side somewhat convex; some cells distal to pterostigma divided.
Abdomen (broken at base of segment 4). Pale brown with extensive dirty yellow markings.

Female [lectotype]. Head. Labrum, anteclypeus and mandibles dirty yellow; anterior one-third of labrum indistinctly castaneous, mandibles with very narrow brownish black anterior border; rest of head dark brown, but indistinct brown transverse stripe between antennae before median ocellus; transverse occipital carina indistinct, lateral extremities absent. Antenna with scapus brownish black, pedicellus brown, flagellum brown.
Thorax. Pronotum pale brown to dirty yellow, lateral lobes somewhat darker; anterior lobe simple, without broader parts; posterior lobe very short, without posterior projections. Synthorax predominantly pale ochreous brown; mesepimeron pale brown, dorsal carina not darker, but mesopleural suture with narrow, distinct mat-black stripe ending just before posterior margin of synthorax; mesepisternum brownish black, upper and lower sides over sutures darker, posteriorly with indistinct elongate triangular paler marking; metepimeron and metepisternum pale ochreous brown, but metapleural suture with narrow, but distinct, black stripe. Legs dirty yellow, but dark rings on tibiae against joints with femora. Wings hyaline, venation brown; Px in fore wing 15, in hind wing 14; R4+5 arising at nodus; IR3 circa halfway first cell distal to subnodus; Arculus just distal to Ax2; Ab vein meets Ac well before hind margin of wing (Y-vein short-stalked); CuP meeting hind margin of fore wing at level of Px4, of hind wing at level of Px6; number of cells between Arculus and place where CuP meets hind margin of fore wing 9, of hind wing 10; pterostigma somewhat wider than high; veins distal to pterostigma undivided.
Abdomen pale brown, with dirty yellow markings as follows: segment 1 lateral third on both sides, segment 2 latero-anterior one-fourth indistinctly paler; segment 3 anterior one-third; segment 4 anterior one-fifth; segments 5-6 anterior onefourth, all dorso-medially

interrupted by longitudinal dark stripe; segments 7-10 castaneous, valves somewhat darker; valves and terebra long, extending well beyond anal appendages.

Measurements. Male. Abdomen including anal appendages (not measurable), hind wing 23 mm; female abdomen 33 mm, hind wing 24 mm.

Material examined. Lectotype female: 'H.C. Siebers/Kei Eil. 1922/Gn. Daab 149' [printed label, but '149' handwritten]. Paralectotype: Kei Islands, Gn Daab, 1922 (H. C. Siebers), 1 male (teneral and incomplete, with label *Drepanosticta robusta* male sp. nov. [Fraser's hand]).

Distribution (Fig. 1). Kei Island (Moluccas, Indonesia).

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Part 3

Nederlandse samenvatting en curriculum vitae

9. Nederlandse samenvatting

De waterjuffers van de familie Platystictidae voldoen in weinig opzichten aan het algemene beeld van tropische insecten, een rijkdom van kleurrijke soorten met grote vleugelspanwijdte, zich soepel voortbewegend boven de boomkruinen of tussen de lianen. De meeste Platystictidae, die in het Nederlands 'bosjuffers' kunnen worden genoemd, zijn als larven gebonden aan bronbeken of andere kleine stromen in het regenbos, waar zij een onopvallend bestaan lijden tussen organisch materiaal. De volwassen bosjuffers zijn vooral bruin of bruinzwart, soms met blauwachtige tekening op het borststuk. De mannetjes van vele soorten hebben een blauwe vlek op de bovenzijde van de laatste segmenten van het achterlijf; bij de vrouwtjes is een lichte tekening gewoonlijk minder opvallend. Volwassen bosjuffers bijna zonder uitzondering te vinden nabij de biotopen waar de larven kunnen worden aangetroffen. Sommige soorten verplaatsen zich blijkbaar in de nacht iets hoger naar de boomlaag of iets dieper het bos in, maar de meeste kunnen altijd hangend aan twijgen of aan een bladpunt vlak langs de waterkant worden gevonden. Het ontdekken van bosjuffers in het veld vraagt daarom bijzondere aandacht. In het dampende en donkere bos, tussen een wirwar van vegetatie, zijn alleen de blauwe punten van het achterlijf een indicatie van hun aanwezigheid, maar die gelijken onder die omstandigheden verrassend op een waterdruppel aan het eind van een takje. Door langzaam door een beek te lopen worden deze libellen enigszins verstoord, en verraden hun aanwezigheid dan door naar een volgend takje te vliegen.
Over de biologie van deze groep is weinig bekend. Enkele soorten zetten de eieren in planten boven het wateroppervlak af. De volwassen stadia leven vermoedelijk enkele maanden. Over de levensduur van de larven zijn geen gegevens bekend.
Het geringe verbreidingsvermogen van de bosjuffers is zonder twijfel een van de oorzaken van het kleine areaal van de meeste soorten van Zuidoost-Azië. Toch is de familie als zodanig wijd verspreid. Naast een verspreiding in Zuidoost-Azië van Sri Lanka tot op Nieuw Guinea en de Salomon eilanden, met zelfs nog een soort op Palau, komt de familie ook voor in Midden-Amerika. Een dergelijke verspreiding kan alleen tot stand zijn gekomen in een, ook geologisch gesproken, ver verleden.

Dit proefschrift valt in twee delen uiteen. Deel 1 (hoofdstuk 1 en 2) behandelt de evolutie en de zoögeografie. In hoofdstuk 1 wordt de evolutie van de groep geanalyseerd aan de hand van morfologische en moleculaire kenmerken van een selectie van de soorten, en wordt een reconstructie gepresenteerd van de ontstaansgeschiedenis van de huidige verspreidingspatronen van de soorten. Hoofdstuk 2 bevat een overzicht van de huidige kennis van de zoögeografie van aquatische ongewervelden van Zuidoost-Azië. In deel 2 (hoofdstuk 3-8) wordt een bijdrage geleverd aan de kennis van de diversiteit van de bosjuffers van Zuidoost-Azië. Reeds beschreven soorten worden opnieuw beschreven en met elkaar vergeleken. In totaal worden in deze hoofdstukken, die alle reeds eerder werden gepubliceerd, 46 soorten nieuw voor de wetenschap beschreven.

In dit proefschrift wordt getracht een antwoord te geven op de volgende vragen:
(a) welke soorten Platystictidae leven op aarde, met name in Zuidoost-Azië, en hoe zijn deze soorten verspreid?
(b) welke morfologische en moleculaire kenmerken kunnen worden gebruikt om de verwantschappen tussen de soorten te kunnen reconstrueren?
(c) vormt de familie Platystictidae een monofyletische

eenheid, en welke verwantschap bestaat er met ander families van waterjuffers (Zygoptera)?

(d) welke evolutionaire verwantschappen bestaan er tussen de soorten van de bosjuffers, gebaseerd op morfologische en moleculaire kenmerken?

(e) welke 'gebieden van endemisme' kunnen worden herkend op basis van verspreidingspatronen van bosjuffersoorten?

(f) welke relaties kunnen worden gereconstrueerd tussen de herkende gebieden van endemisme, gebaseerd op fylogenetische verwantschappen van de soorten van de Platystictidae, en hoe verhouden deze zich tot relaties tussen gebieden van endemisme gebaseerd op andere groepen organismen?

(g) hoe ontstonden de huidige verspreidingspatronen van bosjuffersoorten, bijvoorbeeld in relatie tot de paleogeografie en paleoclimatologie?

Hoofdstuk 1 bevat een introductie tot de Platystictidae, en een overzicht van wat tot heden bekend is van deze groep waterjuffers. Door het grote aantal soorten en de kleine arealen vormen de soorten van deze groep een ideale keuze voor de biogeograaf. De fylogenetische verwantschappen van de waterjuffers zijn nog steeds onvoldoende bekend. Mogelijk door de ouderdom van de groep zijn morfologische kenmerken vaak moeilijk te interpreteren. Door de Leidse groep libellen-onderzoekers is inmiddels een aanzienlijk aantal soorten van vele verschillende genera uit Zuidoost-Azië bijeengebracht voor moleculair onderzoek. De analyse van deze moleculaire gegevens (16S rRNA en 28S rRNA) bevindt zich nog in een vroeg stadium, maar er is eenduidig naar voren gekomen dat de Platystictidae een monofyletische eenheid binnen de Zygoptera vormen.

Gebaseerd op de morfologie van 53 soorten is vervolgens getracht een reconstructie te maken van de fylogenie van de Platystictidae. De soort *Lestes temporalis* werd als outgroup gebruikt. In totaal werden 38 morfologische kenmerken. In de resulterende 'strict consensus' boom is de soort *Sinosticta ogatai* van Hong Kong het meest basale taxon. De ondersteuning van de takken van deze boom is niet significant. De analyse gebaseerd op moleculaire kenmerken heeft geen grote verschillen aangetoond met de resultaten gebaseerd op de morfologische kenmerken, maar het kleine aantal soorten dat moleculair kon worden onderzocht is hierbij een belemmering geweest.

In de fylogenetische reconstructie gebaseerd op morfologische kenmerken zijn de subfamilies Palaemnematinae en Platystictinae als zustergroepen herkend[1]. Vervolgens splitsen aan de basis van deze boom een aantal soorten van Sri Lanka af. Deze tak van de fylogenetische boom heeft zich naar het noorden niet verder ontwikkeld. Vanuit de grens van Laurazië en het Indiaas schiereiland heeft de verbreiding naar het oosten plaatsgevonden. In de eerste plaats kan hierin een 'West-Malesische tak' worden onderscheiden, met onder meer de soorten van het geslacht *Protosticta*, dat vooral op Sulawesi veel voorkomt. Ook veel *Drepanosticta* soorten die beperkt zijn tot het vasteland en Borneo behoren tot deze 'West-Malesische' tak (zie figuren 56-60 in hoofdstuk 1).

De 'Oost-Malesische tak' heeft meer expansief via een zuidelijke route de Indonesische archipel bezet. De reconstructie toont aan dat deze uitbreiding via Java en Sulawesi heeft plaatsgevonden. Veel soorten van de Filipijnen behoren tot deze tak. Vanuit de Filipijnen werden de noordelijke Molukken en zelfs Nieuw Guinea bereikt.

Een andere groep van Nieuw Guinea, in de analyse gerepresenteerd door *Drepanosticta dorcadion* en *D. conica,* blijkt echter in de morfologische analyse meer verwant aan soorten van Sri Lanka. Nader onderzoek, ook met moleculaire kenmerken, zal moeten aantonen of deze uitkomst van de analyse reëel is, want een paleogeografische verklaring voor deze relatie is niet beschikbaar.

Deze resultaten hebben geleid tot de hypothese dat de Platystictidae mogelijk al ongeveer 100 miljoen jaar geleden zijn ontstaan. Hoewel de familie recent niet in Afrika voorkomt, wordt de hypothese geponeerd dat de groep in dat continent is ontstaan. Als

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[1] Na afsluiting van het manuscript is gebleken dat de subfamilie Sinostictinae ook in de moleculaire analyse de zustergroep is van alle andere Platystictidae.

alternatief zou oostelijk Azië in aanmerking komen. De Afrika-hypothese wordt ondersteund door het feit dat de meest primitieve vormen nu voorkomen in Sri Lanka en de noordrand van de Himalaya. De Palaemnematinae van Zuid-Amerika zijn het nauwst verwant aan het geslacht *Platysticta* van Sri Lanka en zuidelijk India. De Aziatische groep van de Sinostictinae en de Platystictinae zou dan met de verschuiving van India van Afrika naar Azië het gebied hebben bereikt, en zich daarna in oostelijke richting hebben verbreid. Zo'n verspreidingsgeschiedenis is voor enkele andere diergroepen, en voor planten, al aangetoond. De voorgangers van de Palaemnematinae zouden Zuid-Amerika hebben kunnen bereiken door zich van Afrika naar Europa te verplaatsen, en gebruik te maken van een landbrug tussen het noordelijke deel van Europa en Noord-Amerika tijdens het Eoceen, ongeveer 45 miljoen jaar geleden. Er heersten toen tropische omstandigheden in dit gebied. Bij het koeler worden van het klimaat werden de soorten van de Nieuwe Wereld 'naar het zuiden verdrongen'.
De verbreiding van de Aziatische soorten naar het oosten zou vanaf circa 40 miljoen jaar geleden kunnen hebben plaatsgevonden. Er is met name in het vasteland van Azië een grote morfologische diversiteit. Meer naar het oosten neemt deze diversiteit af. Het aantal soorten is op de eilanden van Indonesië wel groot, maar de soorten zijn duidelijk van recentere oorsprong. Zo hebben Borneo en de noordelijke Filipijnen nog een tamelijk grote diversiteit in structuurkenmerken, maar hebben eilanden als Sulawesi en de Molukken vooral 'soortenzwermen'. Zoals hiervoor als opgemerkt wijkt Nieuw Guinea van dit patroon af, en is nader onderzoek noodzakelijk om dit patroon te begrijpen.

Hoofdstuk 2 is een overzichtsartikel van de historische biogeografie van de aquatische ongewervelden van Zuidoost-Azië, met speciale aandacht voor libellen. Van de meeste insectenordes zijn fossielen bekend vanaf het Vroege Perm, of het Midden Carboon (libellen). Hiermee is ook het opbreken van Gondwana (Late Jura) relevant voor ons begrip van de huidige verspreidingspatronen van insectengroepen. Met name de complexe geologische geschiedenis van Zuidoost-Azië wordt samengevat, en geologische 'gebiedscladogrammen' gepresenteerd. De studie van de historische biogeografie wordt ernstig belemmerd door de beperkte informatie over het feit of gebieden, zoals de eilanden van Indonesië, onder dan wel boven water lagen tijdens hun ontstaansgeschiedenis.
In dit hoofdstuk wordt de historische biogeografie van de breedscheenjuffers (Platycnemididae), en dan met name de subfamilie Calicnemiinae, gepresenteerd als een van de eerste voorbeelden van een goed gefundeerde studie van een wijdverbreide groep aquatische insecten. Dit onderzoek werd verricht door co-auteur D. Gassmann. De soorten van Zuidoost-Azië stammen af van Afrikaanse voorouders. De Malesische Calicnemiinae stammen af van voorouders die voorkwamen op het vasteland van Zuidoost-Azië, en zich mogelijk hebben verspreid langs de zogeheten Izu-Bonin eilandboog (40-50 Ma), of langs de 'Inner Melanesian Arc' sensu Polhemus gedurende het Laat Krijt. De groep van de verwante geslachten *Lieftinckia* en *Risiocnemis* (Solomon eilanden en de Filipijnen) vormen een recentere (Oligoceen) uitbreiding naar het westen van de Calicnemiinae, via de Caroline en Filipijnen eilandbogen.
Verscheidene meer beperkte fylogenetische reconstructies en biogeografische analyses van andere groepen zoetwater-ongewervelden worden behandeld, vooral van libellen en water- en oppervlaktewantsen. Gebleken is dat 'gebieden van endemisme' op Nieuw Guinea goeddeels congruent zijn met geologische eenheden, in het bijzonder de '*microterranes*' langs de noordrand van het eiland. Speciale aandacht wordt besteed aan de fauna van Sulawesi. De reconstructie van de historische relaties tussen gebieden van endemisme gebaseerd op fylogenetische reconstructie van o.m. de soorten van het geslacht *Protosticta* Selys, en verschillende libellen van de familie Chlorocyphidae, toont een vergelijkbaar beeld als de geologische geschiedenis van de gebieden (noordarm (zuidwest arm – centraal deel plus zuidoost arm)).
De biogeografische patronen van zoetwaterongewervelden verschillen niet principieel van die van strikt terrestrische taxa. De drijvende kracht bij het ontstaan

van patronen in de soortvorming lijkt de verdeling van land en water tijdens het Cenozoicum te zijn. Het is echter onopgelost welk onderliggende mechanisme de belangrijkste rol bij het ontstaan van deze patronen heeft gespeeld, t.w. vicariantie door het verplaatsen van biotas op de elementen van verschillende eilandbogen, of actieve gesynchroniseerde verbreiding. De extreme milieu-eisen en het gebrekkig verbreidingsvermogen van vele soorten maken een verbreidings-scenario over grote afstanden echter onwaarschijnlijk.

Hoofdstuk 3, het eerste hoofdstuk van het tweede deel, reviDeert de Vietnamese soorten van het genus *Protosticta*. In dit hoofdstuk komt naar voren dat de soorten van het vasteland tamelijk grote arealen hebben. Zo werd de soort *Protosticta grandis* Asahina oorspronkelijk uit noordelijk Thailand beschreven; deze soort bleek in zuidelijk Vietnam plaatselijk vrij talrijk te zijn. Ook twee andere, eerder beschreven soorten, werden oorspronkelijk gemeld uit andere landen in de regio, al moet worden opgemerkt dat de geografische variatie tamelijk groot is en de populaties mogelijk later toch als verschillende soorten zullen moeten worden opgevat. De gecompliceerde situatie blijkt ook uit het feit dat *Protosticta satoi* Asahina in deze publicatie als een goede soort, en niet als ondersoort van *P. khaosoidaoensis* Asahina moet worden gezien, zoals tot op heden werd verondersteld. De nominale soort *P. beaumonti* Wilson, beschreven uit Hong Kong, is waarschijnlijk een synoniem van *P. satoi*, maar het materiaal was ontoereikend om tot een eenduidige conclusie te komen. In de bergen van Tamdao werd een morfologisch identieke, maar zeer donkere vorm van *P. satoi* aangetroffen. Deze wordt beschouwd als conspecifiek met de donkere vorm van *P. beaumonti,* die eerder in de bergen van Guangxi (China) werd gevonden.
Tenslotte worden in dit hoofdstuk twee soorten nieuw voor de wetenschap beschreven van zuidelijk Vietnam. Deze soorten werden vernoemd naar C. Linnaeus, ter gelegenheid van de 250e verjaardag van het verschijnen het de tiende editie van *Systema Naturae*, welk boek wordt gebruikt als uitgangspunt van de zoölogische naamgeving.

Hoofdstuk 4 beschrijft een nieuwe soort *Drepanosticta* van de Filipijnen. Dit artikel is een voorloper van de meer complete bewerking van de bosjuffers van de Filipijnen in hoofdstuk 5. De bewerking is vooral gebaseerd op een collectie bijeengebracht door Roland A. Müller, die professionele verzamelaars naar vele odonatologisch slecht onderzochte gebieden van vrijwel alle eilanden van de Filipijnen heeft uitgestuurd.
Deze uiterst belangrijke collectie, met tientallen onbeschreven soorten libellen, werd in de jaren ’90 van de vorige eeuw door Museum Naturalis verworven.
De bewerking van het materiaal door Dr M. Hämäläinen heeft geleid tot de beschrijving van talloze nieuwe soorten, vooral van het geslacht *Risiocnemis,* behorend tot de familie van de breedscheenjuffers (Platycnemididae). Het voorlopig beeld van Hämäläinen en Müller dat ook een grote, onbekende diversiteit van Platystictidae in het materiaal was vertegenwoordigd, werd door het voorliggend onderzoek bevestigd. In dit hoofdstuk wordt een soort beschreven die sterk afwijkt van wat eerder bekend was van de variatie van *Drepanosticta*. Een voorlopige analyse leidde tot de hypothese dat de zustergroeprelatie tussen de Platystictinae en de Palaemnematinae tenminste terug moet gaan tot het Krijt.

Hoofdstuk 5 vormt een revisie van alle Platystictidae van de Filipijnen, met uitzondering van de wijd verspreide en heterogene *Drepanosticta halterata*-soortengroep, welke nog nadere studie vereist.
De bewerking van de collectie heeft geleid tot de beschrijving van 22 nieuwe soorten; ook de reeds bekende soorten worden beschreven en afgebeeld. Sinds die tijd is overigens gebleken dat ook na de huidige revisie door veldwerk in meer afgelegen gebieden nog vele nieuwe taxa kunnen worden ontdekt.
De bewerking van de soorten van de Filipijnen heeft vele vragen opgeworpen. In de eerste plaats werd vastgesteld dat bijna alle soorten van deze eilandengroep (exclusief Palawan) werden gekenmerkt door variatie in de structuur van het pronotum (halsschild). De soorten van het vasteland van Zuidoost-Azië zijn vooral gekarakteriseerd door grote

structuurverschillen in de anale aanhangselen, maar deze verschillen zijn onder de soorten van de Filipijnen slechts gering. Toch laten de Filipijnse soorten zich op grond van het halsschildkenmerk niet onmiddellijk herkennen als een monofyletische eenheid. Een andere vraag die het Filipijnse materiaal opriep was de status en omgrenzing van de grote genera *Drepanosticta* en *Protosticta*. De meeste tot heden beschreven soorten lieten zich vrij eenvoudig in twee groepen opsplitsen, gebaseerd op aan- (*Drepanosticta*) of afwezigheid (*Protosticta*) van de zogeheten 'Anal bridge' (zie p. 19). Wel moet worden opgemerkt dat M.A. Lieftinck al in 1933 zijn verbazing heeft uitgesproken over het feit dat hij *Protosticta feronia* en *Drepanosticta dupophila* in verschillende genera moest plaatsen gebaseerd op dit kenmerk, terwijl hij op grond van overige kenmerken moest concluderen dat beide soorten 'naaste verwanten' (zustersoorten) waren[2]. Deze constatering heeft echter daarna noch bij Lieftinck, noch bij andere onderzoekers geleid tot verdere groepering van soortengroepen in monofyletische eenheden. Onder het materiaal van Luzon kon, gebaseerd op een veronderstelde synapomorfie van de anale aanhangselen van de mannetjes, een monofyletische groep van drie soorten worden onderscheiden. Deze soorten waren echter variabel in het diagnostisch kenmerk van de genera *Protosticta* en *Drepanosticta*. Aangezien in het kader van dit onderzoek geen fundamentele oplossing kon worden geforceerd, werd als praktische oplossing het genus *Sulcosticta* van Tol opgericht. Hierbij werd uiteraard geen bijdrage geleverd aan de classificatie van de overige Platystictidae, maar werd wel een begin gemaakt met het onderscheiden van monofyletische eenheden.
De soorten van het geslacht *Drepanosticta* konden veelal, op grond van unieke apomorfieën binnen de Platystictidae, in soortengroepen worden onderverdeeld. Gebaseerd op het recente onderzoek dat wordt besproken in hoofdstuk 1 is de positie van de Filipijnse taxa onbevredigend.

Hoofdstuk 6 en 7 presenteren een revisie van de Platystictidae van Sulawesi (Celebes) en enkele omliggende eilanden. De libellen-fauna van dit eiland was tot voor kort een van de minst bekende van het huidige Indonesië.

Hoofdstuk 6 behandelt het genus *Protosticta*. Er worden twaalf soorten herkend, die alle endemisch zijn voor Sulawesi en de omliggende eilanden (Buton en Sangihe eilanden). Dit is een opmerkelijk aantal soorten voor een relatief klein gebied, en er wordt dan ook gesproken van een radiatie van dit genus op Sulawesi, ook al is het nog niet zeker dat alle soorten een monofyletische eenheid binnen het genus vertegenwoordigen.
Drie soorten waren eerder beschreven. Twee soorten werden al in de 19e eeuw herkend, de typesoort van het genus *Protosticta*¸ *P. simplicinervis* Selys, en *P. gracilis* Kirby. Beide soorten werden beschreven gebaseerd op exemplaren uit de Minahassa, het noordoostelijk eind van dit eiland. Lieftinck beschreef *P. bivittata*; deze soort is beperkt tot het zuidwesten van Sulawesi. Er werden tijdens het onderzoek negen nieuwe soorten herkend, en deze worden hier beschreven. Onder meer door eigen veldonderzoek is de verspreiding en de intraspecifieke variatie van de soorten nu redelijk goed bekend. Sommige soorten, zoals *P. geijskesi* van Tol en *P. coomansi* van Tol zijn tamelijk wijd verspreid over het eiland, en beide vertonen een aanzienlijke geografische variatie. Elk riviersysteem lijkt wel een eigen herkenbare populatie te hebben, maar het materiaal was onvoldoende om te kunnen besluiten of hierin nog microsoorten kunnen worden herkend. De status van met name de nominale taxa *P. coomansi* en *P. gracilis* is hierdoor nog niet definitief opgelost. Het is niet onmogelijk dat *P. gracilis* een uiterste van een clinale variatie binnen *P. coomansi* vertegenwoordigt; de correcte naam voor dat taxonomische taxon zou dan overigens *P. gracilis* zijn. *Protosticta geijskesi* van Tol is de soort met de meest wijde verspreiding binnen Sulawesi. In tegenstelling tot de meeste andere soorten komt *P. geijskesi* vooral voor in iets bredere stromen in het laagland. Het centrale deel van Sulawesi is, net als bij vele andere groepen dieren, het meest soortenrijk.

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[2] Lieftinck, M.A., 1933. A synopsis of the Bornean Platystictinae, with descriptions of three new species (Odon.). *Konowia* 11 (4): 281-296.

Hoofdstuk 7 behandelt de soorten van het genus *Drepanosticta* Laidlaw voorkomend op Sulawesi. Soorten van dit genus zijn veel minder talrijk op dit eiland dan de meeste *Protosticta*-soorten. Alleen de eerder beschreven *D. ephippiata* Lieftinck is van een groter aantal waarnemingen bekend. Deze soort komt vooral verspreid voor in het noordelijk schiereiland, en is bekend van enkele plaatsen in Centraal Sulawesi en de Banggai archipel. De andere soorten zijn slechts bekend van één of enkele dicht bijeen liggende vindplaatsen. Er zijn geen waarnemingen van *Drepanosticta* bekend van het zuidwestelijk schiereiland, het best onderzochte gedeelte van Sulawesi. De *Drepanosticta* soorten van Sulawesi zijn veel diverser dan de *Protosticta*-soorten, en vormen geen duidelijke monofyletische eenheid; dit resultaat werd bevestigd door de meer formele analyse zoals beschreven in hoofdstuk 1. *D. ephippiata* moet worden gerekend tot een groep van soorten die verder voorkomt in de zuidelijke Filipijnen. De andere soorten, afkomstig van het centrale en zuidoostelijk deel van Sulawesi, en van de eilanden Kabaena en Buton, hebben de duidelijkste verwantschap tot soorten die verder voorkomen op de Kleine Sunda-eilanden.

Hoofstuk 8 presenteert een bewerking van het materiaal beschikbaar van de Molukken en Misool. In tegenstelling tot het normale patroon, waarin Platystictidae in lage dichtheden voorkomen en daarom in slechts kleine aantallen in collecties zijn gerepresenteerd, waren er van enkele soorten grote series van de Molukken in museum Naturalis. Slechts twee soorten waren eerder beschreven: één soort van Buru, en één van Kei. De revisie voegt negen nieuwe soorten toe aan de kennis van dit gebied. Sommige soorten waren al tientallen jaren geleden door M.A. Lieftinck herkend, maar zij waren nog niet formeel beschreven. De morfologische diversiteit van de soorten in het gebied is vrij gering. Soorten van de noordelijke Molukken kunnen worden gerekend tot twee soortengroepen die voorkomen van de zuidelijke Filipijnen tot in Nieuw Guinea. De andere soorten worden hier gerangschikt in de *D. moluccana* groep, welke is verspreid over Ambon, Buru, Obi en Kai, en mogelijk een zustergroep relatie heeft met een groep van soorten van Nieuw Guinea. De vaststelling van twee zustersoorten op Halmahera en Misool was een van de meer verrassende conclusies van deze revisie.

Curriculum vitae

Jan van Tol werd geboren op 14 januari 1951 in Rotterdam. Enkele jaren later verhuisde hij met zijn ouders naar Den Haag. Na zijn middelbare school opleiding aan het Johan de Witt Lyceum (HBS-B) van 1963 tot 1969, studeerde hij Biologie aan de Rijksuniversiteit (nu: Universiteit) Leiden. Hij behaalde zijn kandidaatsexamen in 1973, en zijn doctoraal examen (cum laude) op 5 oktober 1976. In dat laatste jaar trouwde hij ook met Stans Kofman.

Jan van Tol ontwikkelde zijn belangstelling voor de biologie al op de lagere school. Aanvankelijk was hij vooral geïnteresseerd in vogels. Mede onder invloed van zijn biologieleraar op het lyceum, S. Verploegh, verdiepte en verbreedde zijn belangstelling zich.

Later, als lid van de Nederlandse Jeugdbond voor Natuurstudie in Den Haag, werd zijn belangstelling voor de aquatische fauna gewekt door onder meer Wim J. Kuiper en Erik J. van Nieukerken.

Als doctoraalonderwerpen bestudeerde hij de populatiebiologie van de kuifeend *Aythya fuligula* in de duinplassen van Meijendel (onder leiding van mw. Dr. N. Croin Michielsen), de verspreidingsecologie van water- en oppervlaktewantsen in hetzelfde gebied (onder leiding van Prof. dr. J.T. Wiebes), en tenslotte de relatie tussen de intensiteit van de veeteelt en de samenstelling van de aquatische fauna van sloten in de Duivenvoordse–Veenzijdse Polder (onder leiding van Drs. W.J. ter Keurs).

Kort na het afsluiten van zijn studie werd hij op 1 april 1977 aangesteld bij het voormalige Rijksmuseum van Natuurlijke Historie (Leiden), nu museum Naturalis, als coördinator van het Nederlands bureau van de European Invertebrate Survey. De eerste vier jaar werden de kosten gedekt door een subsidie van het Prins Bernhard Fonds aan Dr. P.J. van Helsdingen.

Samenwerking met Dr. D.C. Geijskes, emeritus conservator van de 'kleine insectenorden', resulteerde in een co-auteurschap van het boek 'De libellen van Nederland' (1983), en een blijvende belangstelling voor die insectenorde. Hij werd in 1986 aangesteld als conservator van de afdeling Hemiptera, Orthoptera & Odonata, nadat hij in 1985 al vier maanden veldwerk had verricht in Sulawesi (Indonesië) en daar voor het eerst met Platystictidae kennismaakte.

Sinds die tijd heeft hij deelgenomen aan veldwerk in Zuidoost-Azië, gedeeltelijk als expeditieleider, naar Sabah (1987), Sulawesi (1989, 1991, 1993, 1997), Halmahera (1995), Kalimantan (2005), Mindanao (2004) en Vietnam (2001 en 2007), en verder reizen ondernomen naar onder meer de Verenigde Staten, Canada, Thailand, Japan en Australië. Hij publiceerde onder meer over de samenstelling van de libellenfauna van Indonesië, en dan met name Sulawesi. Artikelen die betrekking hebben op de familie Platystictidae vormen het taxonomisch deel van dit proefschrift.

Als een jonge conservator met kennis en ervaring van informatietechnologie heeft hij zich in het museum vanaf de jaren '80 van de vorige eeuw met een groot aantal verschillende projecten op dit gebied beziggehouden, zoals de automatisering van de leenadministratie, een tijdschrift-registratiesysteem, en een registratiesysteem voor de collectie van de onderafdeling. Hij was projectleider voor de ontwikkeling van het Natuur Informatie Centrum (NIC) (1996-1998), een infrastructuur met een referentiecollectie van de Nederlandse natuur, een referentiebibliotheek en een geavanceerd informatiesysteem. In 1998 werd hij benoemd tot hoofd van de afdeling entomologie.

Zij belangstelling voor libellen, collectiebeheer, de geschiedenis van de taxonomie, nomenclatuur en informatietechnologie resulteerde in de samenstelling van een electronische catalogus van de Odonata van de wereld. Als *Global Species Database of the Odonata* is deze nu beschikbaar via internet (www.odonata.info) en vormt een onderdeel van de *Catalogue of Life* (www.sp2000.org).

Hij heeft een groot aantal bestuursfuncties vervuld, zoals bij de Stichting Duinbehoud, de Stichting European Invertebrate Survey-Nederland, Stichting Fauna Malesiana, de Nederlandse Entomologische Vereniging (NEV) (voorzitter 1999-2008), en de Uyttenboogaart-Eliasen Stichting. Sinds 2001 is hij *Commissioner* van de *International Commission on Zoological Nomenclature*, en vervult redacteurschappen van enkele wetenschappelijke tijdschriften: *Tijdschrift voor Entomologie* (1988 tot 1997, en sinds 2008), het *Deutsche Entomologische Zeitschrift* (sinds 1996), het *International Journal of Odonatology* (sinds 1998) en *ZooKeys* (sinds 2008).

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Het is een voorrecht te kunnen werken in de wereldberoemde libellencollectie van museum Naturalis, die nu niet alleen de collecties van wijlen Dr. M.A. Lieftinck (vooral afkomstig uit het voormalige Nederlands Oost Indië, en verzameld vóór 1950), en van wijlen Dr. D.C. Geijskes (Suriname) omvat, maar ook de recente aanwinsten in de vorm van de verzamelingen van wijlen Dr. J. Belle (Velp), de heer R.A. Müller (St. Gallen, Zwitserland) (voornamelijk van de Filipijnen) en van Dr. M. Hämäläinen (Espoo, Finland) (voornamelijk van Thailand). De waarde van de Naturalis collectie blijkt uit het feit dat vele soorten nieuw voor de wetenschap in deze dissertatie op grond van deze verzameling konden worden beschreven. Vooral in de laatste fase van het onderzoek, bij het moleculair werk, werden de beperkingen van de collectie toch soms voelbaar, maar Dr. K.-D.B. Dijkstra, Dr. D. Gassmann en ing. V.J. Kalkman (allen te Leiden en gastmedewerkers van de afdeling Entomologie) waren zeer behulpzaam om materiaal van ontbrekende soorten, of verse monsters van reeds beschikbare soorten, voor dit onderzoek beschikbaar te stellen. Dr. Gassmann verzorgde ook de illustraties met behulp van de *Scanning Electron Microscope* van hoofdstuk 1. I am also grateful to my foreign colleagues for making essential specimens available for morphological and molecular study (in alphabetical order) Dr. Jurg Demarmels (Maracay, Venezuela), Dr. Rosser Garrison (Sacramento, CA, USA), Dr. Matti Hämäläinen (Espoo, Finland), Dr. Haruki Karube (Odawara, Japan), Dr. Rodolfo Novelo G. (Veracruz, Mexico), Dr. Graham Reels (Hong Kong, China), Mr. Reagan J. Villanueva (Davao, Philippines), Dr. Keith D.P. Wilson (Brighton, U.K., formerly Hong Kong, China). Ook beheerders van de collecties van het Zoölogisch Museum Amsterdam, the Natural History Museum (London, U.K.), the US National Museum of Natural History (Smithsonian Institution) (Washington, D.C., USA) en het Department of Entomology van Cornell University (Ithaca, NY, USA) waren bereid materiaal onder hun beheer voor onderzoek beschikbaar te stellen.

Ik realiseer me dat het onderzoek aan en het beheer van de collectie alleen goed kunnen worden uitgevoerd als ook de rest van de organisatie soepel draait. Ik dank mijn collega's van het secretariaat, de bibliotheek, de 2D afdeling, de afdeling automatisering, maar ook de minder direct betrokken collega's in Naturalis voor hun prima hulp en collegiale werksfeer. Bij de verwerking van het onderzoek tot publicaties heb ik ook meer direct met enkele collega's mogen samenwerken. De tekenaars Bas Blankevoort, Erik Jan Bosch en mw. Inge van Noortwijk hebben belangrijk illustratiewerk geleverd, met name voor hoofdstuk 4 en 5. De waarde van professioneel tekenwerk kan niet voldoende worden benadrukt, ook niet in de tijd van de *Scanning Electron Microscope* of *AutoImaging* faciliteiten op lichtmicroscopen. Drs. Bastian T. Reijnen (Leiden) en Dr. Henri Thomassen (Leiden, nu Los Angeles, CA, USA) hebben hun expertise op het gebied van moleculair onderzoek willen inzetten om een geheel nieuwe dimensie aan het fylogenetisch onderzoek van de Platystictidae toe te voegen. Recente resultaten van Drs. Frank Stokvis bij het moleculair werk aan libellen konden nog juist als voetnoot worden ingevoegd.

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[1] Numbers in bold refer to illustrations; new names are written in italics.