Phylogeny and biogeography of the Platystictidae (Odonata)

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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.

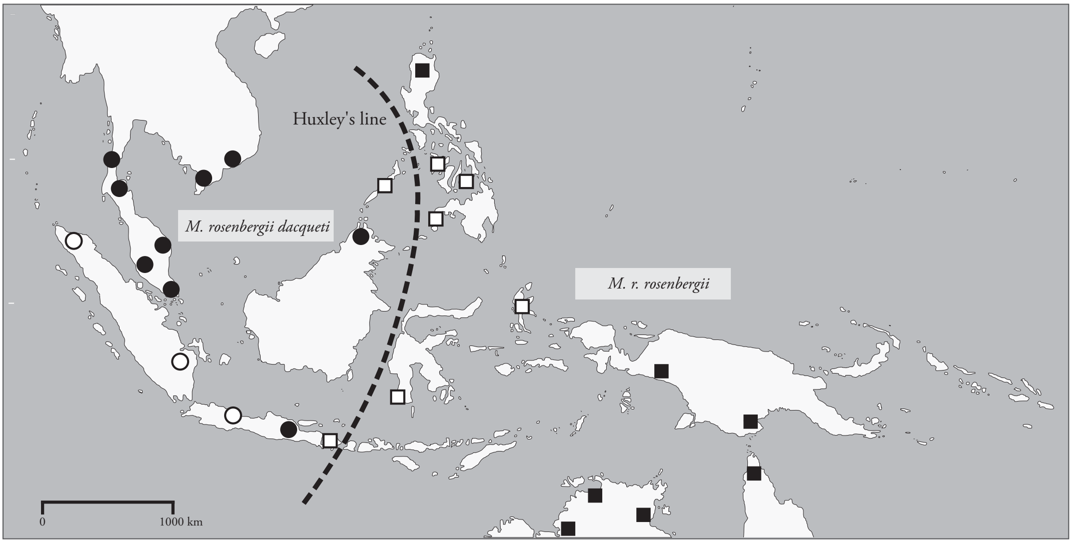
The example of *Macrobrachium* also raises another issue, namely the mechanism or mechanisms by which present patterns have evolved. Based on current knowledge of the palaeogeography of the region, island-hopping along terranes or island arcs during the Cenozoicum has been hypothesized to explain the 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

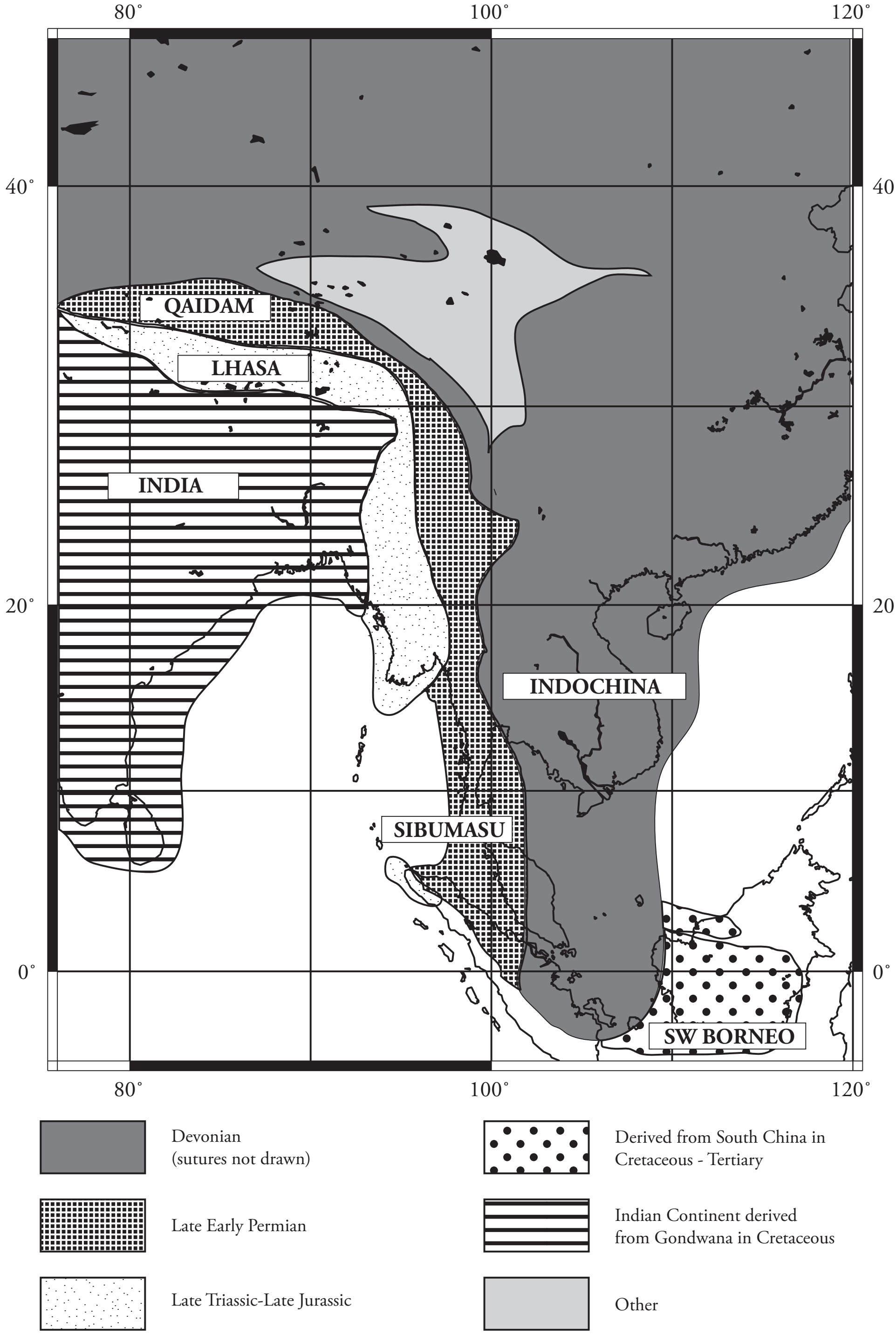


Figure 2. Distribution of principal terranes of east and southeast Asia. Sutures, especially of Devonian age, not indicated (simplified after Metcalfe 2001)

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**

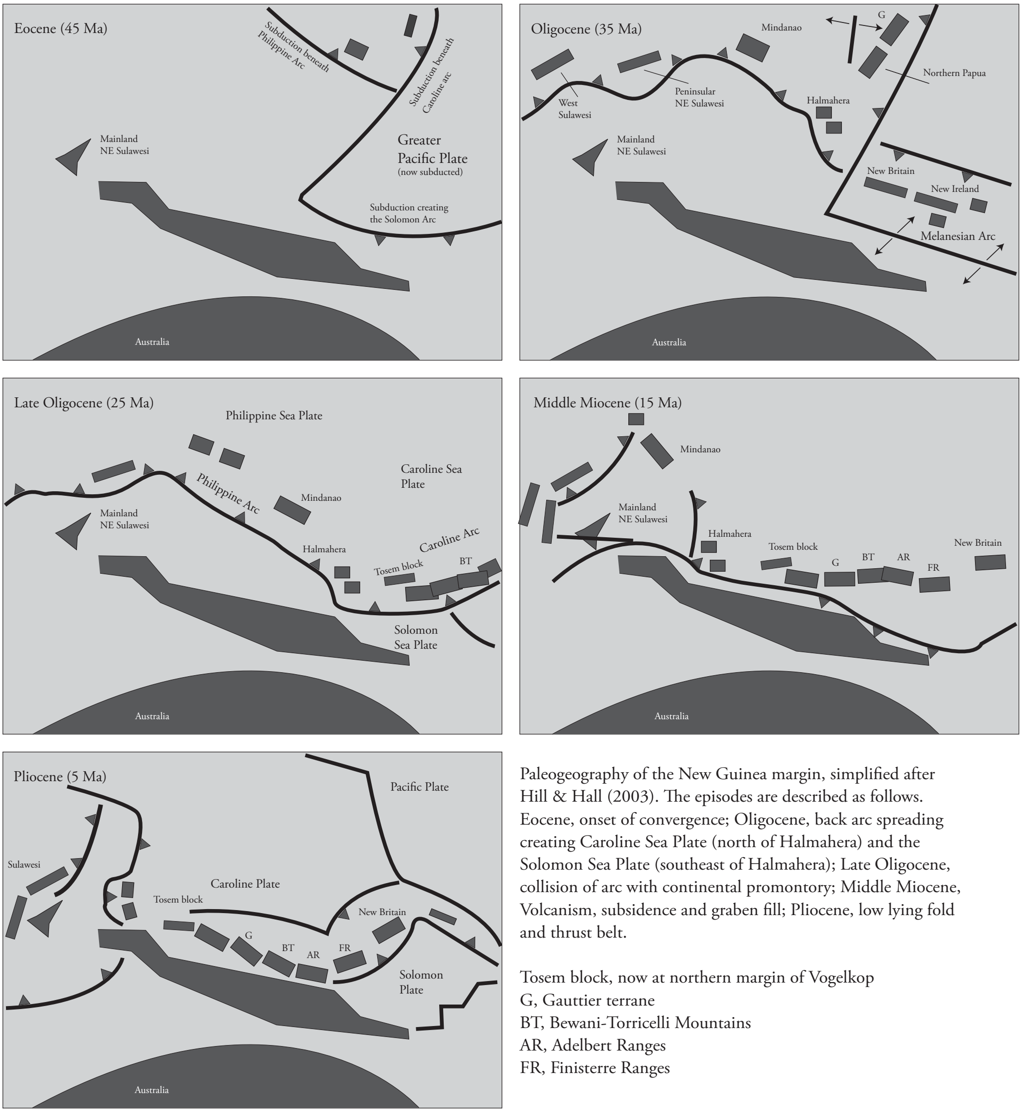
The geological evolution of southeast Asia during the Cenozoicum has been extensively studied and discussed by Hall and collaborators (e.g., Hall 2001, 2002) and with special attention to the northern margin of the Australian continent by Hill and Hall (2003). Hall's reconstructions, and particularly 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.

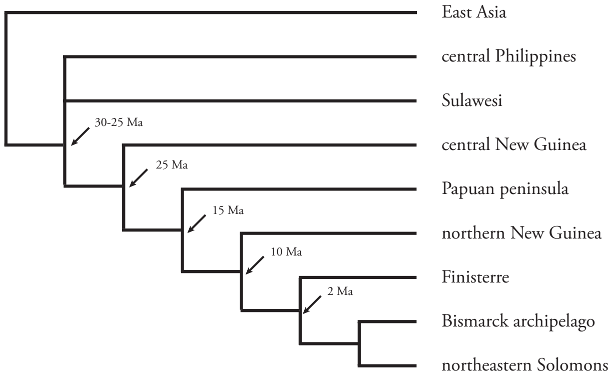


Figure 5. Geological area cladogram of southeastern Asia (from Beuk, 2002).

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

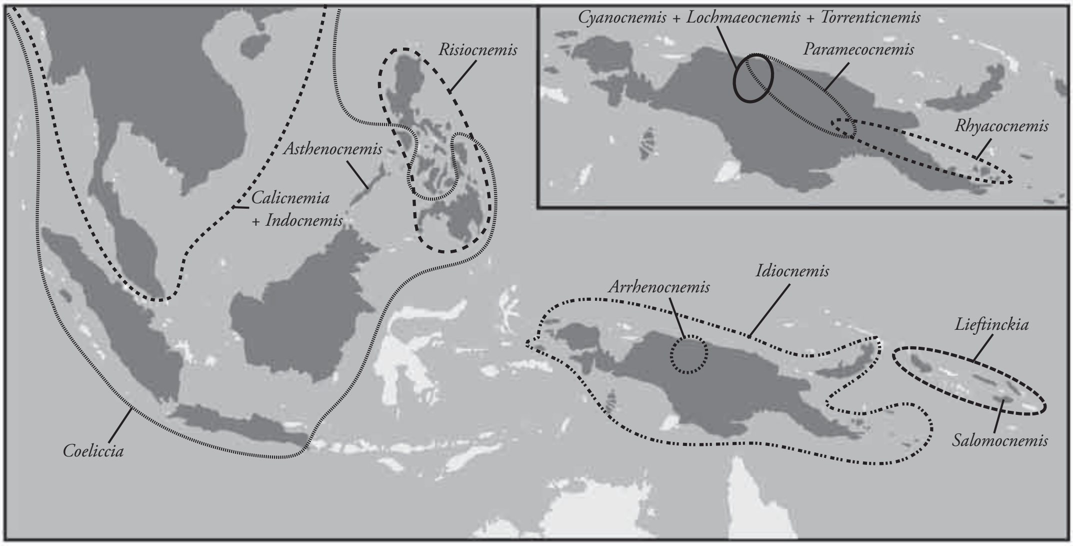


Figure 6. Distribution of the Calicnemiinae (Odonata, Platycnemididae).

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

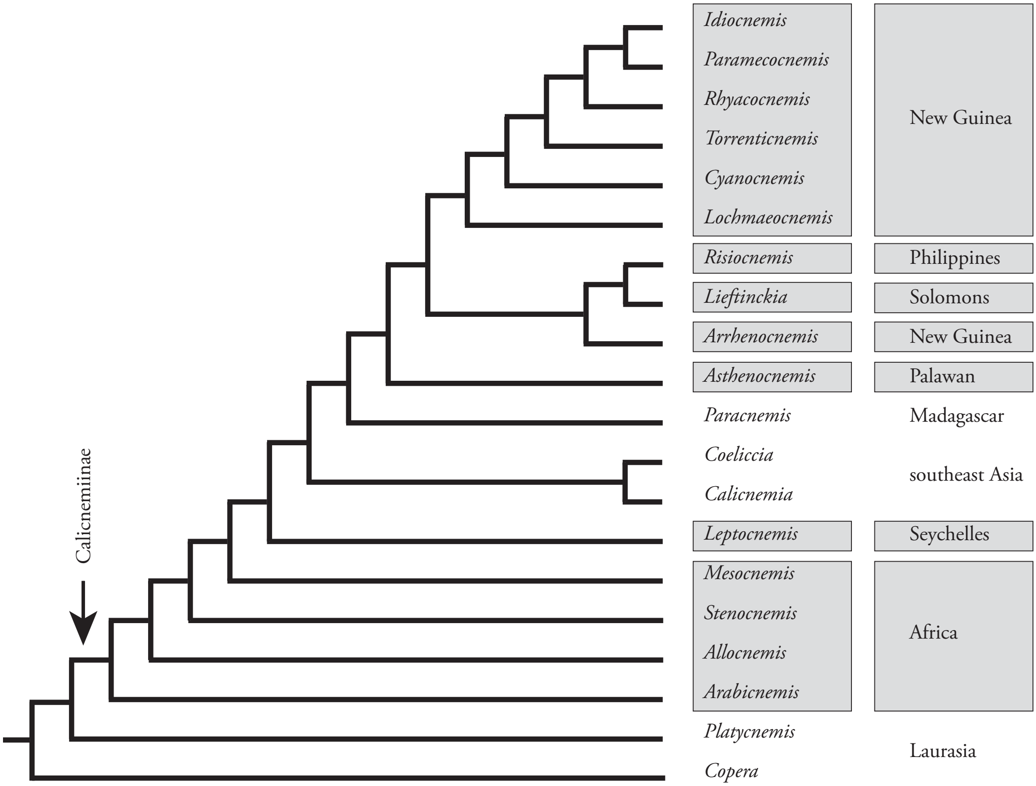


Figure 7. Simplified cladogram of the Calicnemiinae (Odonata: Platycnemididae). The distribution of the clades (area cladogram) is given as shaded areas to the right.

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

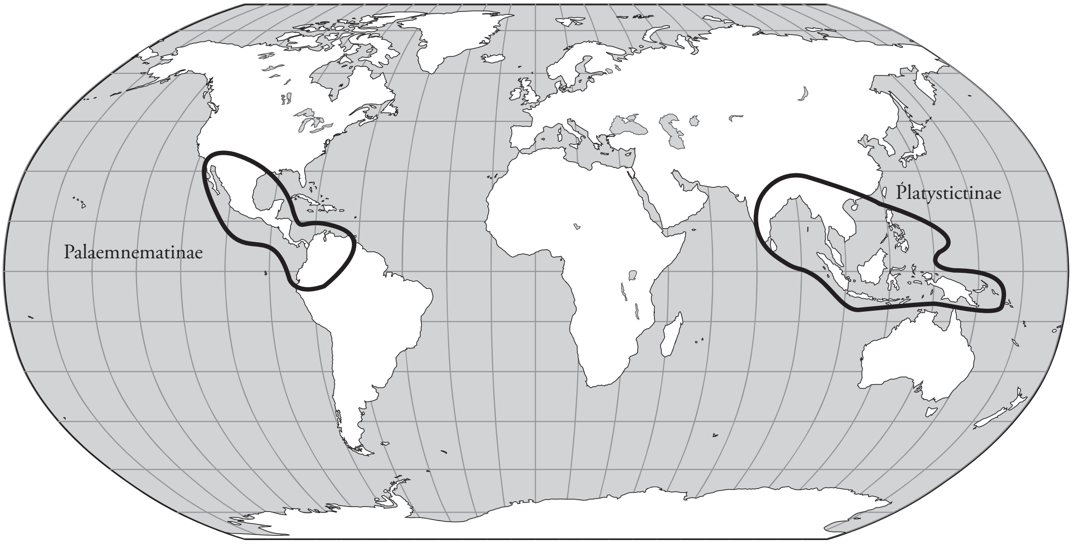
Tol 2005), one in the Sinostictinae, *Sinosticta* Wilson, and one in the Palaemnematinae, *Palaemnema* Selys. The total number of species described per subfamily is presently (van Tol unpublished) 124 in Platystictinae, two in Sinostictinae and 42 in Palaemnematinae.

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).



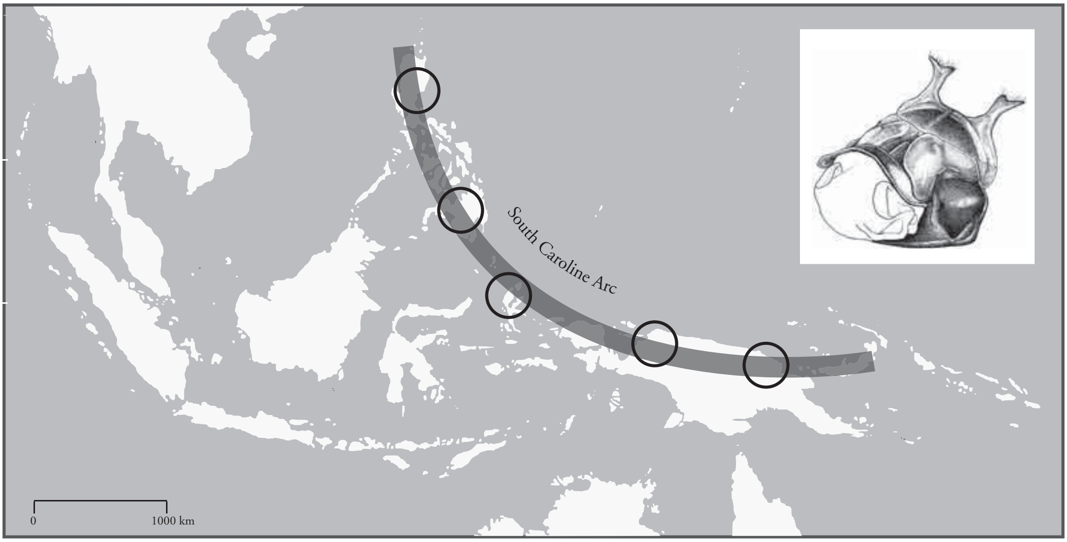


Figure 9. Distribution of the *Drepanosticta lymetta* group.

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*.

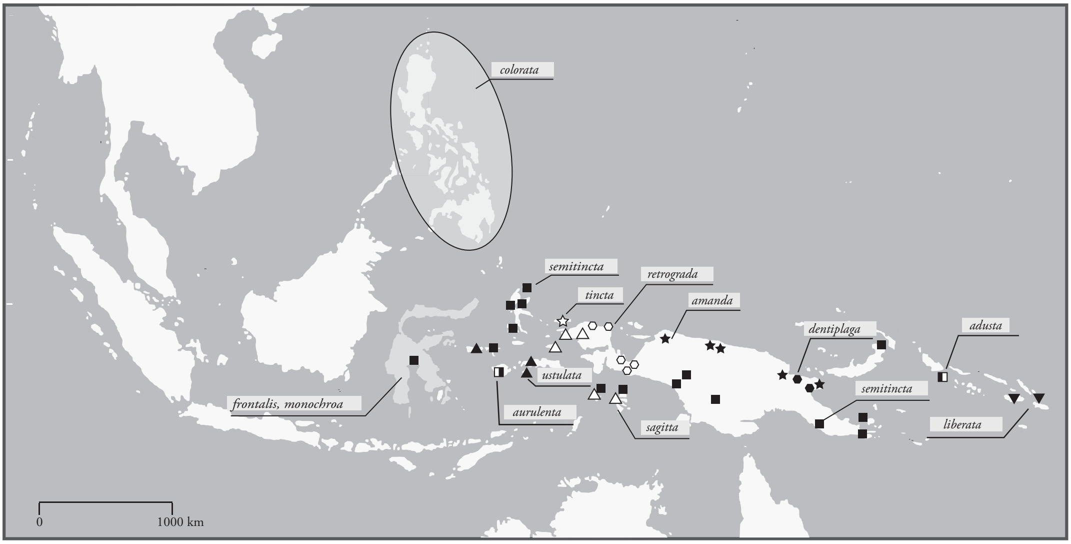


Figure 10. Distribution of the *Rhinocypha tincta* group.

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.

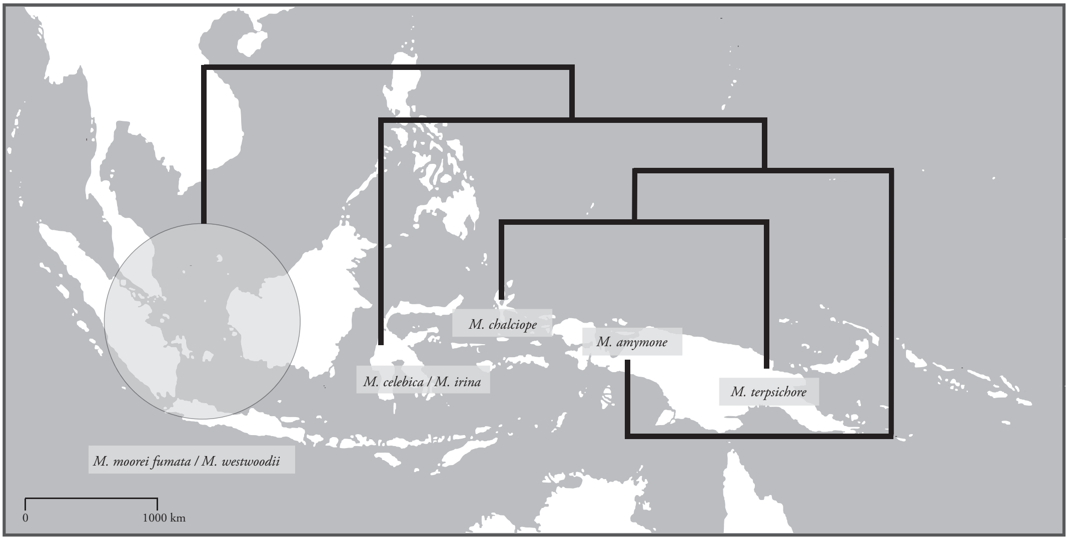
When the distributions of the species are used to define areas of endemism and are plotted on a map, the area cladogram (Fig. 11) is congruent with the geological area cladogram of Beuk (2002b).

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

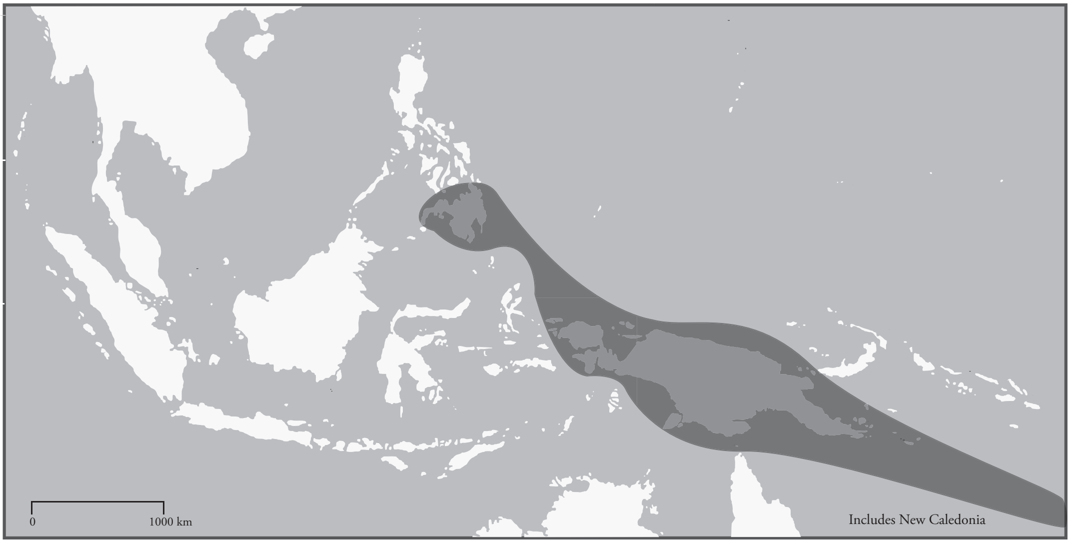


Figure 12. Distribution of the *Rhagovelia novacaledonica* group (from Polhemus, 1995).

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

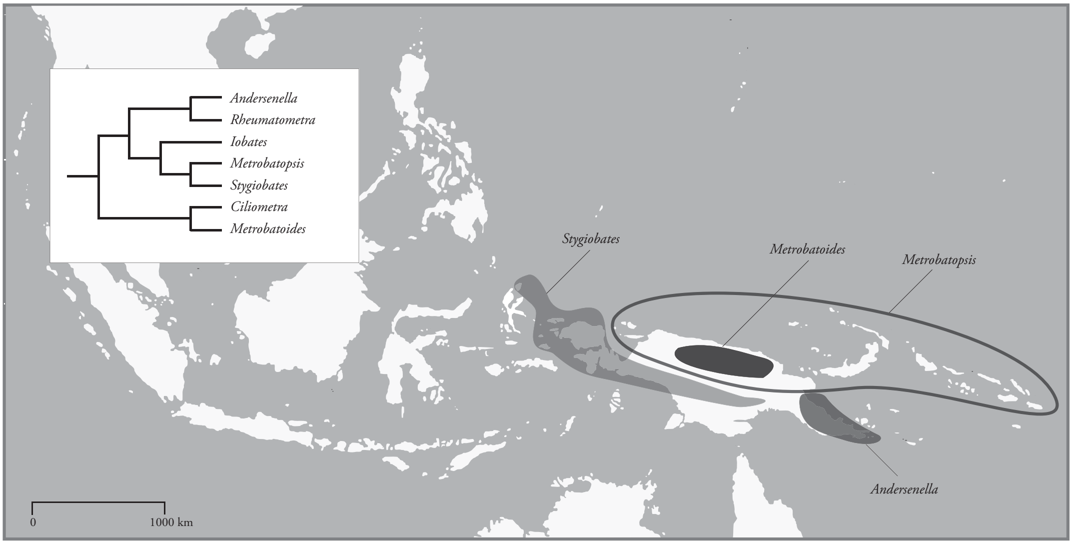


Figure 13. Distribution of genera of Metrobatini (after Polhemus and Polhemus, 2002).

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.

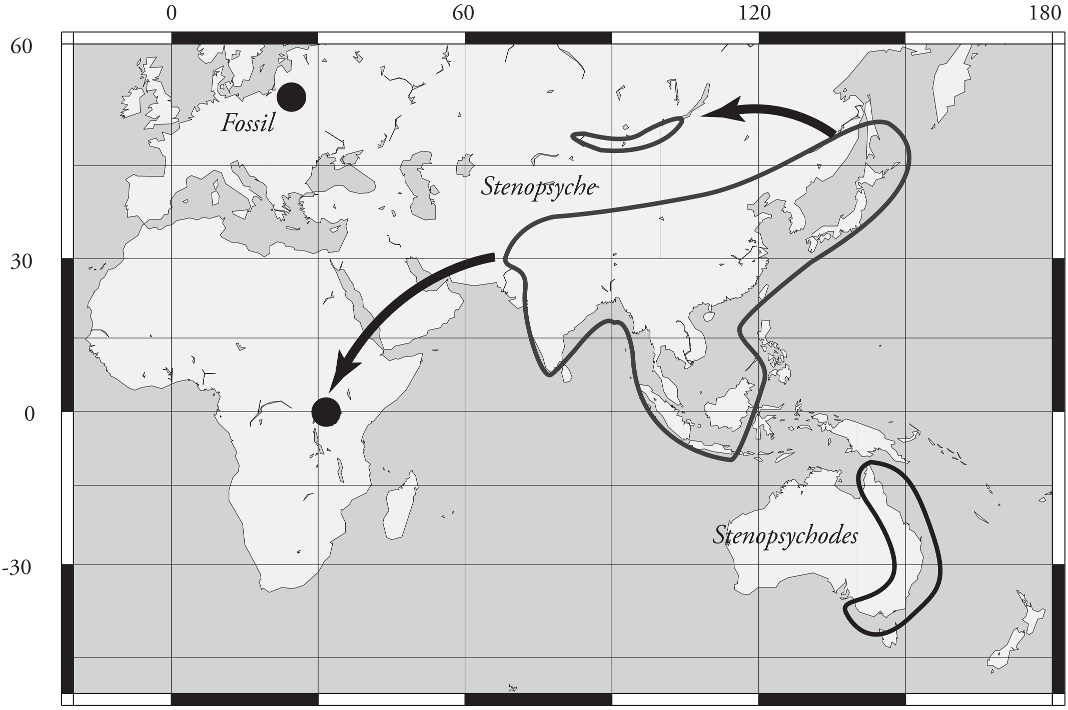
The Gondwanan influence on the Oriental fauna after the docking of India has not been studied yet, but the distribution of the genus *Apsilochorema* Ulmer has been attributed to the accretion of terranes in southeast Asia before India reached the southern margin of Laurasia (Mey 1998, 1999). *Apsilochorema* 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.

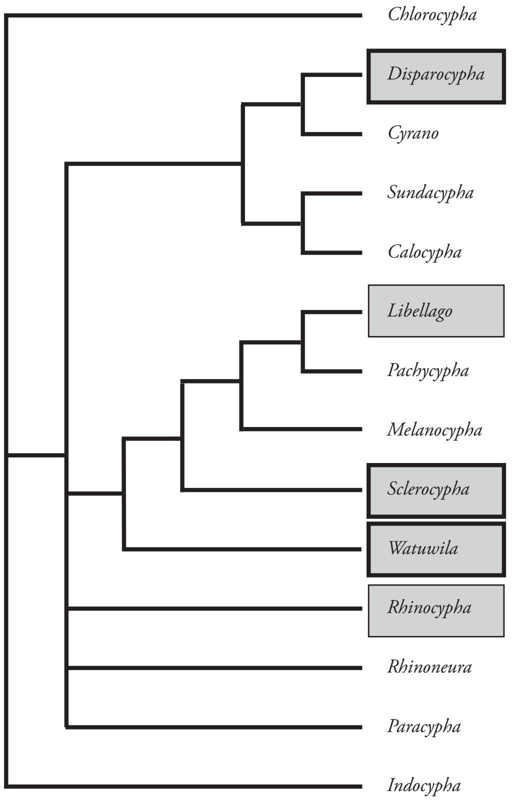


Figure 15. Cladogram of genera of Chlorocyphidae (Odonata) (after van Tol, 1998). Genera occurring in Sulawesi in grey box, genera endemic to Sulawesi in bold border. Chlorocyphidae are very diverse on Sulawesi, even at generic level.

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

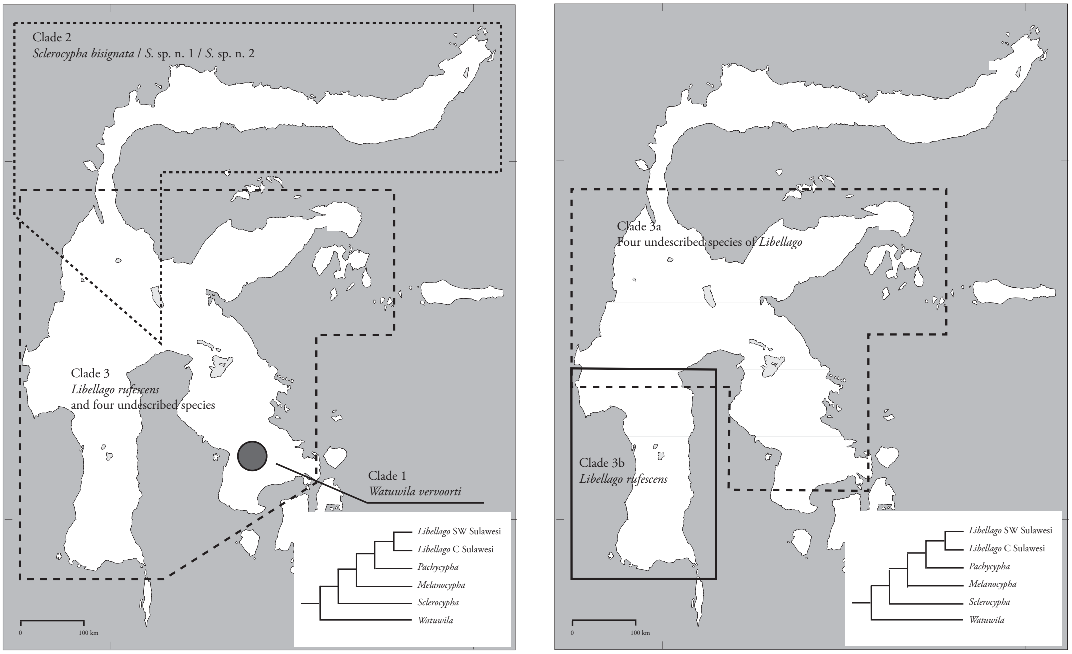


Figure 17. Area relationships in Sulawesi based on phylogenetic relationships of *Libellago*, including *Sclerocypha*, in Sulawesi. – Left: First division in cladogram. – Right. Second division in cladogram.

(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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