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Title: Studies on phylogeny and biogeography of damselflies (Odonata) with emphasis on the Argiolestidae

Issue Date: 2013-12-19

Studies on phylogeny and biogeography of damselflies (Odonata) with emphasis on the Argiolestidae

PROEFSCHRIFT

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van Rector Magnificus prof. mr. C.J.J.M. Stolker,
volgens besluit van het College voor Promoties
te verdedigen op donderdag 19 december
klokke 16.15 uur

door

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Geboren te Hilversum in 1974

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Het onderzoek voor dit proefschrift werd verricht bij Naturalis Biodiversity Center, Leiden, en is mede mogelijk gemaakt door Stichting European Invertebrate Survey (EIS) – Nederland, Leiden.

Vincent J. Kalkman

**Studies on phylogeny and biogeography
of damselflies (Odonata) with emphasis
on the Argiolestidae**

2013

LEIDEN

Disclaimer

None of the zoological names and combinations in this thesis are published for purpose of zoological nomenclature. This is a disclaimer with reference to Article 8.2 of the International Code for Zoological Nomenclature (ICZN 1999).

Cover plate: Selection of Argiolestidae, illustration by A.G. Orr

Kalkman, V.J. 2013.

Studies on phylogeny and biogeography of damselflies (Odonata) with emphasis on the Argiolestidae. PhD thesis, Leiden University. 224 p.

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INTRODUCTION

Damselflies and dragonflies (Odonata) are, compared to most groups of insects, well studied and a relatively high percentage of the world's dragonfly fauna has been formally described. They are popular with amateur odonatologists and play an important role in conservation policy. The wealth of information on damselflies and dragonflies found in books or on internet seems to indicate that nearly everything on them is known. Nonetheless no proper overview of patterns of diversity or conservation status was available at the start of this project. Furthermore, while the classification of dragonflies was rather stable at the end of the last century, scientific justification for the system in use at that time was poor.

The stability of the classification system for the families did not signify the end result of a well resolved phylogeny, but merely reflected the lack of true progress during the 20th century.

Much of the work conducted for this thesis was focused on what was at the time known as the family Megapodagrionidae. It was suspected that this family included several, not necessarily closely related, lineages. Based on molecular data this group was divided into eight families. The distribution of the largest of these new families, the family Argiolestidae, includes Africa, Australia, mainland Southeast Asia and the Malesian region. The diversity patterns found in the latter region are still only partially understood and well-based phylogenetic reconstructions of groups occurring in this area are rare, especially so for aquatic invertebrates.

The above mentioned gaps in knowledge on dragonflies and damselflies led to the following four objectives for this thesis:

1. To describe the patterns of global diversity of damselflies and dragonflies and summarize the main processes thought to have led to these patterns. (Chapter 1)
2. To describe how damselflies and dragonflies under threat of extinction are distributed across the globe and to summarize the main processes that might have created these patterns. (Chapter 2)
3. To develop a hypothesis on the phylogeny of damselflies in general and the Megapodagrionidae *sensu lato* in particular, based on molecular data. (Chapters 3, 4, 5)
4. To contribute to the understanding of the diversity patterns of dragonflies and damselflies in Australia and the Malesian region and to reconstruct the history of Argiolestidae in this area. (Chapters 6, 7)

Part I

Diversity and conservation

I. GLOBAL DIVERSITY OF DRAGONFLIES (ODONATA) IN FRESHWATER

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Citation: Kalkman, V.J., V. Clausnitzer, K.-D.B. Dijkstra, A.G. Orr, D.R. Paulson & J. van Tol 2008. Global diversity of dragonflies (Odonata) in freshwater. – *Hydrobiologia* 595: 351-363.

Larvae of almost all of the 5,680 species of the insect order Odonata (dragonflies and damselflies) are dependent on freshwater habitats. Both larvae and adults are predators. The order is relatively well studied, and the actual number of species may be close to 7,000. Many species have small distributional ranges, and are habitat specialists, including inhabitants of alpine mountain bogs, seepage areas in tropical rain forests, and waterfalls. They are often successfully used as indicators for environmental health and conservation management. The highest diversity is found in flowing waters in rain forests of the tropics, the Oriental and Neotropical regions being the most speciose. This paper discusses diversity, summarises the biogeography of dragonflies in the different biogeographical regions and gives the total number of species and genera per family per biogeographical region. Examples are given of areas of particular diversity, in terms of areas of endemism, presence of ancient lineages or remarkable recent radiations but no well-based review of areas with high endemism of dragonflies is available so far. The conservation status of dragonflies is briefly discussed. Species confined to small remnants of forest in the tropics are most under threat of extinction by human activities.

INTRODUCTION

With 5,680 extant species, dragonflies are a relatively small order of insects. Their size and colour and their diurnal and often conspicuous behaviour make them a popular group for both professional and amateur entomologists. Dragonflies are among the most ancient of winged insects, dating back well into the Permian (Grimaldi & Engel 2005). They include the largest insect that ever lived, the griffenfly *Meganeuropsis permiana* Carpenter, with a wingspan of c. 70 cm. Dragonflies are recognised by their long, slender abdomen; large globular eyes, often making up a large portion of the head; short antennae; and long wings, which have a conspicuous nodus and usually a pterostigma. They possess a unique mechanism of indirect sperm transfer: sperm are produced in the testes situated at the abdomen

tip, but the secondary copulatory organs that transfer them to the female lie on the ventral side of the abdomen base. Sperm must be transferred externally to this organ before copulation. This copulatory organ is used not only to inseminate, but also to remove the sperm of the female's previous mates. Sperm competition in Odonata was first reported by Waage (1979) and stimulated numerous studies, making dragonflies one of the most studied animal groups in terms of reproductive behaviour. Another unique feature of odonates is the strongly modified labium of the larva, which can be extended at great speed to seize prey.

The extant dragonflies are divided into two suborders, the Zygoptera or damselflies and the Anisoptera or true dragonflies (fig. 1). Until recently a third suborder, Anisozygoptera, was recognised, with two extant species from Japan



Figure 1. (a) The damselfly *Neurobasis ianthinipennis* female, Indonesia, West Papua, Yapen, Ambaidiru, July 2006.

Photo: Vincent Kalkman.

(b) The dragonfly *Protorthemis coronata*, Indonesia, West Papua, Borne, July 2006. Photo: Vincent Kalkman.



and the eastern Himalayas. The Anisozygoptera, which have some features recalling Zygoptera, are now often included in Anisoptera (as done here), or combined with them under the new name Epiprocta. Zygopterans have a broad head with widely separated eyes and similar fore and hind wings. Most species rest with wings closed. The larvae are slender and rely mainly on two or three caudal gills for respiration. Anisoptera are on average larger and more robust than Zygoptera. Their hind wings are distinctly broader at their base than the fore wings and in most families the

eyes touch on top of the head. At rest most species spread their wings. The larvae are typically much sturdier than those of Zygoptera and lack caudal gills: oxygen is absorbed through gills in the rectum. A general outline of odonate diversity is given by Silsby (2001). A checklist of all dragonflies including synonyms and references is found on <http://www.odonata.info> (van Tol 2005).

Dragonfly larvae live in freshwater environments and only a few species tolerate brackish conditions, two of which even live in salt marshes and

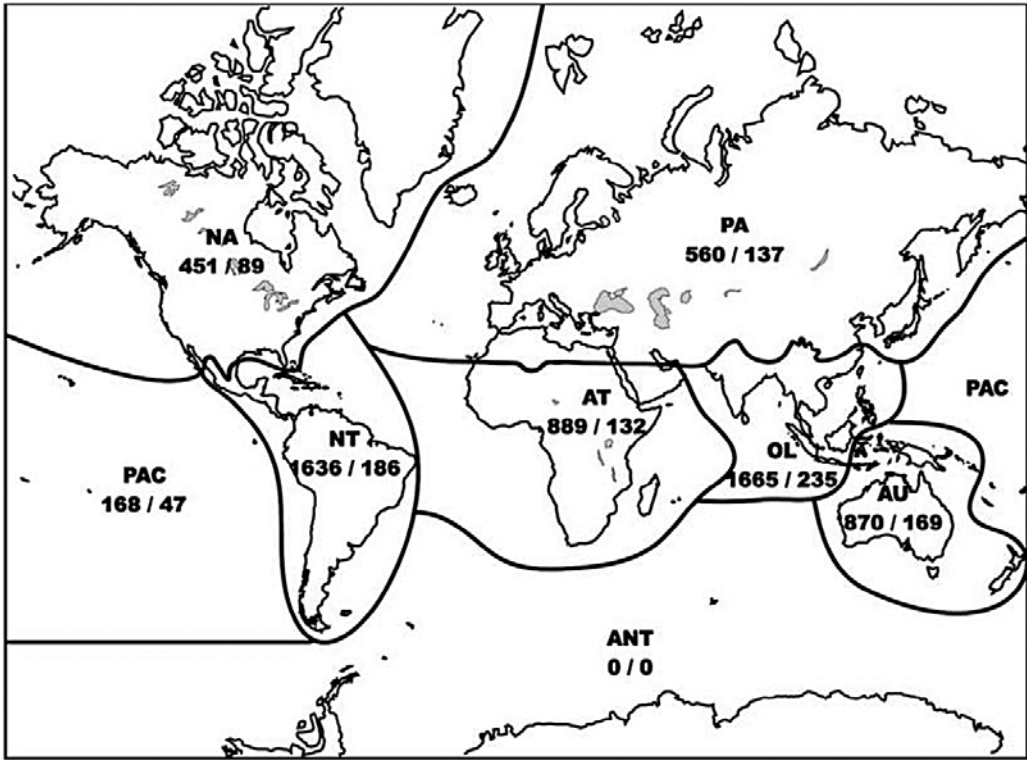


Figure 2. Diversity of dragonflies per biogeographical region (species number/genus number). PA – Palearctic, NA – Nearctic, NT – Neotropical, AT – Afrotropical, OL – Oriental, AU – Australasian, PAC – Pacific Oceanic Islands, ANT – Antarctic.

mangroves. Both running and standing waters are used, while a few species are semi-terrestrial or inhabit water held in tree holes, leaf axils and other phytotelmata. Many species have small distributional ranges, and are habitat specialists, including inhabitants of alpine mountain bogs, seepage areas in tropical rain forests, and waterfalls. Larvae prey on all kinds of small animals up to the size of tadpoles and small fish. Larvae take from a few weeks to 7 years to develop. Emergence takes place above water on plants or on the shore, after which most species leave the water edge to mature. Males return to the water to search for females or to establish territories. Females often only return to mate and to oviposit. Information on the life history and behaviour of odonates is thoroughly summarised in Corbet's (1999) review of odonate behaviour and ecology.

SPECIES DIVERSITY

Information on the number of species of odonates is derived from the Global Species Database Odonata prepared for the Catalogue of Life (van Tol 2005). Taxa were assigned to one or more of the biogeographical regions based on the authors information and several key references (e.g., Lieftinck 1949, Watson et al. 1991, Westfall & May 1996, Okudaira et al. 1999, Needham et al. 2000, Tsuda 2000, Wang 2000). Subspecies were not considered. Table 1 enumerates the number of genera and species per family for each biogeographical region. Family-level classification of odonates is poorly resolved, although most families are broadly accepted. The most recent contribution to the higher classification of dragonflies was published by Rehn (2003). With the

Table 1. (a) Number of species per family per biogeographical region. (b) Number of genera per family per biogeographical region.

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
(a)									
Aeshnidae	57	42	127	44	138	76	13	–	441
Amphipterygidae	–	–	3	2	5	–	–	–	10
Austropetaliidae	–	–	7	–	–	4	–	–	11
Calopterygidae	37	8	61	20	60	4	–	–	171
Chlorocyphidae	3	–	–	41	80	15	–	–	135
Coenagrionidae	95	101	370	197	185	170	88	–	1084
Cordulegastridae	18	9	1	–	27	–	–	–	49
Chlorogomphidae	5	–	–	–	40	–	–	–	41
Corduliidae	20	50	37	17	57	54	12	–	239
Dicteriadidae	–	–	2	–	–	–	–	–	2
Epiophlebiidae	1	–	–	–	1	–	–	–	2
Euphaeidae	11	–	–	–	65	1	–	–	69
Gomphidae	127	100	273	149	358	42	–	–	966
Hemiphlebiidae	–	–	–	–	–	1	–	–	1
Isostictidae	–	–	–	–	–	41	5	–	46
Lestidae	17	19	38	17	39	29	3	–	148
Lestoideidae	2	–	–	–	4	9	–	–	13
Libellulidae	121	107	352	245	190	184	32	–	1012
Macromiidae	6	9	2	37	50	16	–	–	122
Megapodagrionidae	2	–	130	38	28	57	5	–	260
Neopetaliidae	–	–	1	–	–	–	0	–	1
Perilestidae	–	–	18	1	–	–	–	–	20
Petaluridae	1	2	1	–	–	6	–	–	10
Platycnemididae	23	–	–	33	130	37	–	–	210
Platystictidae	–	1	42	–	119	29	1	–	191
Polythoridae	–	–	58	–	–	–	–	–	58
Protoneuridae	1	3	94	37	57	52	–	–	245
Pseudolestidae	7	–	–	–	15	–	–	–	22
Pseudostigmatidae	–	–	18	1	–	–	–	–	19
Synlestidae	6	–	1	10	17	8	–	–	37
Synthemistidae	–	–	–	–	–	35	9	–	43
Total	560	451	1636	889	1665	870	168	0	5680
Undescribed	75-100	5-10	400-500	100-125	300-400	175-250	30-40	0	1085-1425
(b)									
Aeshnidae	14	13	15	6	18	19	7	–	48
Amphipterygidae	–	–	2	1	1	–	–	–	4
Austropetaliidae	–	–	2	–	–	2	–	–	8

Table 1. cont.

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Calopterygidae	8	3	3	3	10	1	—	—	16
Chlorocyphidae	3	—	—	3	14	4	—	—	18
Coenagrionidae	15	15	38	15	23	24	12	—	90
Cordulegastridae	3	1	1	—	5	—	—	—	5
Chlorogomphidae	1	—	—	—	1	—	—	—	1
Corduliidae	6	8	2	6	7	16	3	—	41
Dicteriadidae	—	—	2	—	—	—	—	—	2
Epiophlebiidae	1	—	—	—	1	—	—	—	1
Euphaeidae	5	—	—	—	12	1	—	—	12
Gomphidae	33	14	26	20	43	9	—	—	92
Hemiphlebiidae	—	—	—	—	—	1	—	—	1
Isostictidae	—	—	—	—	—	11	1	—	12
Lestidae	3	2	2	1	5	3	3	—	8
Lestoideidae	1	—	—	—	1	2	—	—	3
Libellulidae	31	27	44	53	56	45	16	0	143
Macromiidae	2	1	2	1	2	2	—	—	4
Megapodagrionidae	2	—	14	6	10	6	3	—	39
Neopetaliidae	—	—	1	—	—	—	—	—	1
Perilestidae	—	—	2	1	—	—	—	—	3
Petaluridae	1	2	1	—	—	2	—	—	5
Platycnemididae	4	—	—	9	8	11	—	—	25
Platystictidae	—	1	1	—	5	2	1	—	6
Polythoridae	—	—	8	—	—	—	—	—	8
Protoneuridae	1	2	14	4	8	1	—	—	25
Pseudolestidae	1	—	—	—	3	—	—	—	3
Pseudostigmatidae	—	—	5	1	—	—	—	—	6
Synlestidae	2	—	1	2	2	3	—	—	8
Synthemistidae	—	—	—	—	—	4	1	—	4
Total	137	89	186	132	235	169	47	0	642

advent of molecular techniques, revision of family-level classification may be expected.

In total 5,680 species of Odonata are known, 2,739 belonging to the suborder Zygoptera (19 families) and 2,941 to the suborder Anisoptera (12 families). Table 1 and fig. 2 show that the tropics support by far the most species of dragon-

flies. Besides higher diversity at the species level, the number of families is also much greater in the tropics (fig. 3). Twelve of the 31 families are restricted mostly to running waters within tropical forest habitats. The two largest families (Coenagrionidae and Libellulidae) are believed to be relatively recent (Rehn 2003). Almost all ubiquitous species belong to these two families and they

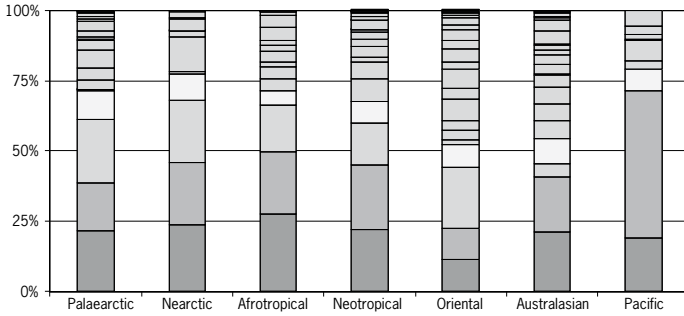


Figure 3. Percentages of species belonging to a family for the seven different biogeographical regions. The four largest families are at the bottom with from bottom to top: Coenagrionidae, Libellulidae, Gomphidae and Aeshnidae.

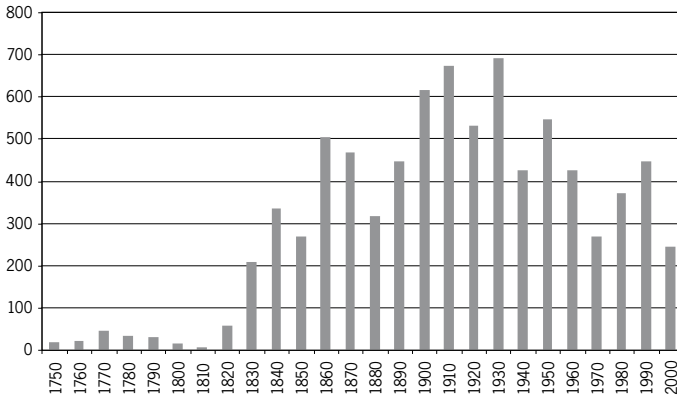


Figure 4. Rate of description of new taxa in Odonata.

dominate in unshaded habitats with stagnant water (both artificial and natural, e.g., savannas). Both families include species with the greatest migratory capacity, including those with distributions spanning more than one continent and almost all species found on isolated islands.

It is estimated that between 1,000 and 1,500 species of dragonflies await description (table 1). If this is true, the actual number of extant species may be close to 7,000. The Oriental, Australasian and especially the Neotropical regions hold the highest number of undescribed species. In the latter, new species are still discovered more rapidly than descriptions are published (Paulson 2004). The fauna of Africa is relatively well known and relatively depauperate. Overall the families Platystictidae, Protoneuridae, Gomphidae and Corduliidae are believed to hold relatively many undescribed species. They are typically inconspicuous odonates with small ranges, often confined to seepages or small runnels in tropical forest.

Gomphidae, Corduliidae and also Chlorogomphidae in Southeast Asia are difficult to collect as they spend little time at the waterside. The two largest families, Coenagrionidae and Libellulidae, are relatively well known, because most species are conspicuous and many favour open habitats, although in absolute numbers they still represent a large proportion of species to be described. This is especially so for the Coenagrionidae in South America. Since 1970 an average of 38 species have been described annually (fig. 4). With an undiminished rate of description an estimated 95% of all species will be described in 2030.

PROCESSES INFLUENCING DIVERSITY OF DRAGONFLIES

Factors influencing the distribution of dragonfly diversity can be divided into historical (geological) and ecological factors. Both determine current species diversity, while composition at family and

genus level is predominantly determined by the first. Dragonflies are an ancient group, and present-day distribution reflects the distribution of the families before the break-up of Pangaea and subsequent supercontinental schisms. However, more well-founded phylogenetic reconstructions are needed before a satisfactory synthesis of this subject can be written.

Today's patterns of dragonfly diversity correspond largely with the present climatological zones. Temperature accounts for a sharp increase of diversity from the poles to the equator, while precipitation obscures this pattern by reducing diversity in areas of low precipitation, resulting in 'gaps' in diversity. Diversity of tropical odonates is at least partly explained by the high diversity of aquatic habitats in tropical forests (Orr 2006), especially in montane areas (Oppel 2005). Mountains not only provide a greater contemporary diversity of habitats, but also a greater potential for survival in regional refugia. The relative long-term stability of forest habitats (also in the short term, the limited seasonality), which provides opportunities for animals with a specialist lifestyle, might also explain the high diversity of tropical odonates.

Speciation events in dragonflies can be directly linked to isolation events in the geological past such as Andean orogeny (De Marmels 2001) and isolation in refugia in southern Europe during the ice ages (Sternberg 1998). Polhemus (1997) showed how a single coenagrionid founder evolved into 22 species of *Megalagrion* on the Hawaiian Islands. Speciation was not only promoted by isolation after the colonisation of newly formed volcanic islands, but also by habitat specialisation (stagnant water, seepage, phytotelmata and swift streams) within an island. Speciation has also been promoted by the isolation of patches of tropical forest due to climatological factors (Dijkstra & Clausnitzer 2006). Large river systems such as the Amazon and Congo basins, forming an ever-changing mosaic of land and water, probably also facilitated

speciation, but distribution patterns in these regions are known insufficiently to verify this hypothesis.

A BRIEF OUTLINE OF ODONATE BIODIVERSITY WITHIN THE BIOGEOGRAPHICAL REGIONS

Palaeartic

Large parts of the Palaeartic are relatively species poor when compared with areas at the same latitude in North America. Europe for instance has only slightly more than half the number of species of Texas. Exceptions are Japan, Korea and the part of China included in the Palaeartic. The faunal diversity in these areas is at least as high as in North America and is far richer than in Europe. In China the Palaeartic fauna merges gradually into the Oriental fauna. This transition zone is very rich compared to the other parts of the Palaeartic and harbours many species not occurring elsewhere in the Palaeartic. The large differences in diversity between different parts of the Palaeartic are largely due to the advance of glaciers during the Pleistocene ice ages, which impoverished the fauna in the western two-thirds of the Palaeartic. Here the main mountain ranges and seas run east-west (e.g., the Mediterranean Sea, the Pyrenees, Alps and Himalayas) thus forming a barrier for northern species retreating southwards. Similar factors also apply today as Oriental species can easily penetrate into the Palaeartic, but northward expansion of African and Oriental species into the western Palaeartic is hampered by the same barriers as those limiting southward retreat in the past. The ice ages also promoted speciation by isolating species in various refugia, especially evident in Europe. Most Palaeartic species with a more northern distribution are widespread, several ranging from Europe to eastern Russia or even into the Nearctic. Whether after the ice ages these wide-ranging species colonised the eastern Palaeartic from the western Palaeartic or vice versa is still a point of debate (Kosterin 2005).

Nearctic

The dragonfly fauna of the Nearctic is richer than that of most of the Palaearctic. As in the Palaearctic, the eastern part of the Nearctic is richer than the western part, and most eastern states in the USA have larger species lists than all of Europe. This is presumably because the humid East has had a continuous connection with the wet tropics to the south, and numerous tropical species have moved into southeastern USA, while the West has gone through arid periods when odonate dispersal was interrupted and aquatic faunas were presumably extirpated by glaciation. The species of the wet forests on the west coast of Mexico are restricted from advancing northward by thorn forest and then desert, but species of the moister uplands of the Mexican Plateau have also moved north into the southwestern states. Thus the latter region is a centre of diversity and endemism in North America, as are the north-eastern and south-eastern coastal plains, Allegheny-Appalachian uplands, Ozarks, Great Plains, and Pacific coast. Stream-dwelling gomphids are especially likely to show restricted distributions and diversification, and they comprise the largest odonate family in the eastern Nearctic. However, many odonate species, both northern and southern, are wide-ranging over the entire moist eastern half or all across the continent. Others are restricted to the West, often both arid and humid parts of it, as ultimately it is the presence of water bodies that determines their distributions. Some of even the largest odonate families appear to show different origins in the Nearctic, for example coenagrionids and libellulids mostly from the tropics and gomphids and corduliids mostly from northern latitudes. There is a substantial boreal fauna; Canada holds 208 species, but many of them are restricted to the southeastern border region, including tropical genera such as *Hetaerina*, *Argia*, and *Pantala* (Catling et al. 2005). Special features of the Nearctic include the presence of two petalurids, a Pacific Northwest montane species (*Tanypteryx hageni*) with nearest relative in Japan and a southeastern lowland species (*Tachopteryx thoreyi*); certain

genera (*Tanypteryx*, *Lanthus*, *Stylogomphus* and *Hagenius*) that show a distinct relationship between eastern Asia and eastern Nearctic; and a very recent radiation of *Enallagma* (Brown et al. 2000).

Afrotropical

It is notable that, among tropical faunas, the Afrotropical fauna is relatively poor and its composition is nearest that of the Holarctic, with few families and a large proportion of Coenagrionidae and Libellulidae (Dijkstra & Clausnitzer 2006). This may be explained by the relatively unstable climatological history of the continent, which favoured species capable of colonising recent or temporary habitats. The extent of tropical forest in Africa is believed to have contracted substantially during periods with a cooler and drier climate. As a consequence the 'old' African fauna seems to be largely gone, although relicts remain in isolated areas that were apparently more stable. Examples are the genera *Pentaplebia* (Amphipterygidae) and *Nubiolestes* (Perilestidae) in the Cameroon highlands and *Coryphagrion* (Pseudostigmatidae) in the East Coast forests, which all have their only relatives in tropical America. The families Synlestidae and Megapodagrionidae, which have a global but rather fragmented distribution, are largely restricted to South Africa and Madagascar, respectively. On the other hand, the present-day extent of forest and other tropical habitats, such as the continent's famous savannahs, has allowed remarkable speciation in a few genera (e.g., *Chlorocypha*, *Pseudagrion*, *Paragomphus*, *Phyllomacromia*, *Orthetrum* and *Trithemis*). These groups often have strong Asian affinities, suggesting palaeotropical faunal exchange followed by rapid radiation in periods with a more favourable climate. A small but interesting element in the fauna of the eastern coast and Indian Ocean islands are genera of probably Papuan- Australian origin (*Hemicordulia*, *Teinobasis*), that probably reached Africa by wind-aided trans-oceanic dispersal. The highest odonate diversity, as well as the greatest number of range-restricted species, is found in the Guineo-Congolian forest, which stretches from Senegal to west-

ern Kenya. The richest area is the Cameroon highlands and the surrounding Lower Guinea lowland forest. The Upper Guinean forest, Congo Basin and Albertine Rift are other core areas within this forest belt. Outside it, coastal East Africa (including the Eastern Arc Mountains), the Ethiopian highlands and South Africa are notable for their endemism. Although the approximately 175 odonate species of Madagascar include distinctly Afrotropical elements, 60% of Anisoptera and almost 95% of Zygoptera species are endemic. Endemism and diversity is greatest on the island's wet eastern coast.

Oriental

The Oriental region is, together with the Neotropical region, by far the most species-rich of the eight regions recognised here. In China the Oriental and Palearctic faunas merge gradually along a climatic gradient. The Chlorogomphidae and Euphaeidae are largely confined to the Oriental region although both have outlying species occurring in the Palearctic, and several families such as the Chlorocyphidae, Platynemididae, Platystictidae and Pseudolestidae are exceptionally well represented. Within the region, several loosely defined subregions, each with a characteristic dragonfly fauna, may be recognised: i.e., the Indian subcontinent, Sundaland, the Philippines, and the main landmass of southeast and east Asia (including tropical and subtropical China, but excluding the Malaya peninsula). The latter subregion exhibits the highest diversity in both species and genera of the entire Oriental region, presumably owing to its large area, numerous mountain ranges intersected by major rivers, and mosaic of forest types. Particularly speciose is the area including the north of Thailand, Laos and Vietnam together with tropical China, recognised by some as distinct faunistic sub-region (van Tol & Rozendaal 1995, Wilson & Reels 2003). Within the Indian sub-region the greatest number of species and endemics occurs in tropical forest refugia. Richest are the tropical and subtropical forests to the south of the Himalayas, including Sikkim, North Bengal and the Khasi Hills, with

other centres of diversity in the Western Ghats and Nilgiris and the wet south-western and central part of Sri Lanka (Lahiri 1989, Bedjanič 2004). Extensive semi-arid parts of the subcontinent host a depauperate and unexceptional fauna. Present-day Sundaland is divided into several large land masses which were contiguous as recently as 8,000 years ago when sea levels were lower. Highest levels of endemism and species richness occur in north Borneo among forest stream dwellers in montane and mixed dipterocarp forest, but Java, Sumatra and the Malay peninsula all host distinctive faunas. The fauna of the Philippines has a high number of endemics (more than 60% of the named species) sharing elements with both the Oriental and the Australasian fauna. Its numerous islands have facilitated speciation, resulting in a high number of endemic species in genera such as *Drepanosticta*, *Amphicnemis*, *Teinobasis*, *Risicnemis* and *Oligoaeschna* (Hämäläinen & Müller 1997).

Australasian region

The Australasian dragonfly fauna is very distinct with a strong representation of small families either largely confined to the region or showing a relict distribution. For several families a large percentage of the world fauna is restricted to the Australasian region: Austropetaliidae (36%), Isostictidae (89%), Lestoideidae (69%), Petaluridae (60%) and Synthemistidae (81%). Hemiphlebiidae and Cordulephyinae (Corduliidae) are both endemic for continental Australia. The Austropetaliidae are only shared with the southern Andes and are therefore believed to be of Gondwanian origin. The Petaluridae and the Synlestidae are good examples of families showing a relict distribution. The majority of dragonflies of the Australian continent occur in the eastern Great Dividing Range and in the adjacent narrow coastal strip to the east of this, and in the wetter parts of the southwest. Greatest diversity is to be found in the north-eastern wet tropics of Queensland. The dry interior of the continent has a depauperate fauna of widespread eurytopic species. The New Zealand fauna is poor with only 17 species (Rowe 1992) including two species of Petaluridae. New Guinea is very

species-rich with a high percentage of endemics, owing to the perhumid tropical conditions and a highly dissected, mountainous topography that creates numerous isolated stream systems, each including a wide altitudinal range. New Guinea was formed during the mid-late Caenozoic when the northward moving Australian plate collided with island arcs to the north, resulting in massive uplifting and orogenesis. The island arcs were part of a complex archipelago that probably played a part in faunal exchange between the Oriental region and the Australasian region, resulting in unexpected affinities between the Philippines and New Guinea (van Tol & Gassmann 2005). New Guinea and Australia were connected as recently as 8,000 years ago and generally have strong biogeographical affinities. They share a high diversity of Megapodagrionidae, Isostictidae and Synthemistidae. However considering their shared history the differences in the dragonfly fauna is remarkable. Especially striking is the absence of Platystictidae and Platycnemididae in Australia and conversely the virtual lack of Gomphidae and Brachytroninae (Aeshnidae) in New Guinea (Liefstinck 1949). The Moluccas and Lesser Sundas (Nusa Tenggara) have probably never been connected to either the Oriental region or the Australasian region. The islands of Lesser Sundas have a drier climate than the rest of the Indonesian archipelago but their faunas are generally commensurate with island area. Most of the species on these islands, including the many endemics, are of Oriental origin (Liefstinck 1953). The Moluccan fauna is largely derived from New Guinea, is rather depauperate, and is perhaps most notable for its lack of the genus *Neurobasis* (Calopterygidae), present in New Guinea, Sulawesi and the Philippines. The island of Sulawesi was formed by the collision of several elements of Laurasian origin and Gondwanian origin. The dragonfly fauna is therefore a blend of species of Australasian and Oriental origin, although the latter dominate (van Tol & Gassmann 2005). No current review of Sulawesi dragonflies is available, but it is known that the fauna is less species-rich than might be expected (van Tol 1987). The family Chlorocyphidae shows exceptional higher-level diversity, as does

Borneo, which perhaps dates back to the most recent connection of the two land masses 42 mya.

Pacific

As might be expected, the Pacific is species poor. Species present can be divided into two groups: those with a very small area of distribution, being often confined to a single island or island group, and highly vagile eurytopic species which occur on most Pacific islands, and which generally also occur throughout much of the Oriental or Australasian regions (or both). Even in Hawaii this phenomenon occurs, although the widespread species originate from the Americas. Both the widespread species and the endemics belong mainly to the Coenagrionidae and the Libellulidae. In the Coenagrionidae the colonisation of an island or group of islands was often followed by speciation events leading to a group of closely related species. This has occurred on Hawaii (*Megalagrion*), Pohnpei (*Teinobasis*), Fiji (*Nesobasis* and *Melanesobasis*) and Samoa (*Pacificagrion* and *Amorphostigma*). An exception to this pattern is New Caledonia, which drifted away from continental Australia at the end of the Cretaceous, and is moderately species rich. It has an interesting fauna showing distinct affinities with Australia and New Guinea and has numerous endemic species and several endemic genera (Davies 2002).

Neotropical

Although North and South America have numerous genera and species in common, this is primarily because the boundary between them is political rather than biogeographical. Nevertheless, the two faunas are quite distinct, with a strong faunal break at middle elevations around the Mexican Plateau, many Nearctic species in temperate habitats on that plateau, and tropical species surrounding it in the lowlands (Paulson 1982). Dispersal was apparently much greater from south to north when Panama emerged in the Pliocene to provide a pathway between the continents, and that dispersal continues today. The Polythoridae, Dicteriadidae and Neopetaliidae are endemic to the region, the latter confined to the southern Andes while the former

Table 2. Examples of areas with a high number of endemic dragonflies.

Biogeographical region	Name of area	Number of species	Number of endemic species	Estimate of endemism (%)
Afrotropical	Ethiopia	96	12	13
	South Africa	160	30	19
	Madagascar	175	135	77
Oriental	Taiwan	142	21	15
	Borneo	272	124	46
	Hainan	127	20	16
	Sri Lanka	116	53	46
Palaeartic	Northwest Africa (Morocco, Algeria and Tunisia)	70	4	6
	Japan	215	74	34
Neotropical	Cuba	80	5	6
	Costa Rica	265	32	12
	Venezuela	489	90	18
Australasian	Sulawesi	124	55	44
	New Zealand	17	10	59
	Pacific Hawaii	36	26	72
	New Caledonia	55	22	40

two are distributed in the tropics. Largely confined to this region are the Austropetaliidae, Perilestidae and Pseudostigmatidae. The latter includes 18 species of very elongate spider-eating, phytotelmata-breeding damselflies which are among the most remarkable odonates. Significant regions of odonate diversification include the Mexican Plateau, Chiapas to Honduras highlands, Costa Rica-Panama highlands, northern Andes, eastern Andean foothills, tepuis of the Guyana Shield, Guyana lowlands, Atlantic forests of Brazil, Rio Parana' basin, and southern Andes. In the last, Gondwanian groups, including the Austropetaliidae, Neopetaliidae, Petaluridae, and Gomphomacromia, are prominent. This leaves the huge Amazon basin, poorly known but presumably with its own regions of endemism. The Neotropical fauna equals that of the Oriental region in both modern (species) and ancient (family) diversity. The complexity of the mountain ranges extending from Mexico to Chile and the varied climates along their length have produced a great variety of odonate habitats,

as well as providing repeated opportunities for speciation, and *Argia*, with 108 named species, is the star of this show. Other characteristic neotropical genera that have diversified widely in the region include *Heteragrion*, *Palaemnema*, *Acanthagrion*, *Telebasis*, *Phyllogomphoides*, *Progomphus*, *Erythrodiplax* and *Micrathyria*. High biodiversity is the rule for all of the countries in this region, but nevertheless, the Neotropical fauna is the least known in the world. The highest known local diversity of odonates is in South America, with 186 species at a single site in southern Peru. Much of the fauna of the West Indies comes from adjacent Mexico and South America, but the large Greater Antillean islands have numerous endemics, including *Hypolestes* of poorly known affinities.

Antarctica

No species are known from this region and it is unlikely that any species of dragonfly will reproduce there although it is not impossible that some species might be found as vagrants.

AREAS OF ENDEMICITY

No well-based review of areas with high endemism of dragonflies is available. However, this is intended in the near future as part of a Global Dragonfly Assessment. Regional projects to identify areas of endemism carried out so far include an analysis of endemism in freshwater biotas partly based on Zygoptera for New Guinea and on Zygoptera and Anisoptera in eastern Africa (Polhemus et al. 2004, Darwall et al. 2005) and are presently being prepared for southern and western Africa by the IUCN Freshwater Biodiversity Assessment Programme. Some examples of levels of endemism in different regions are summarised in table 2, showing large inter-area differences between areas in absolute and relative numbers of endemic species. Species in the temperate region have wide distributions and the percentage of localised species is low, whereas faunas with both high absolute and relative endemism are mainly found in moist tropical forests. Although at present there is no sound basis for identifying the most important areas of endemism, it goes without question that the faunas of the islands of New Guinea, Sulawesi, Sri Lanka and Madagascar are exceptionally rich in endemics (see table 2). It is noteworthy that the percentage of endemic Zygoptera is almost always much higher than the percentage of endemic Anisoptera. Examples of this are Madagascar (60% in Anisoptera, 95% in Zygoptera), the Philippines (31%, 86%) and Sri Lanka (30%, 68%).

HUMAN-RELATED ISSUES

Dragonflies have little economic value, although they are used as food and as magical or medicinal resources at a local scale, and to an unknown extent may influence populations of disease vectors. The group features prominently in nature management in the temperate regions of the world (Westfall & May 1996, Kosterin et al. 2004, Sahlén et al. 2004) and they are often used as indicators for environmental health and conservation

management (Corbet 1999). Their sensitivity to structural habitat quality (e.g., forest cover, water chemistry) and amphibious habits make dragonflies well suited for use in evaluating environmental change in the long term (biogeography, climatology) and in the short term (conservation biology), both above and below the water surface (e.g., Clark & Samways 1996, Sahlén & Ekestubbe 2001, Clausnitzer 2003, Foote & Hornung 2005, Osborn 2005). Dragonflies are often used in both fundamental and applied research because of the relative ease with which they can be observed and their broad array of behaviours. In many regions reliable identification literature is available, so species can be determined fairly easily by the layman. This enables mapping schemes conducted by volunteers, facilitating the use of distributional data on dragonflies in management. From a global perspective, odonates are among the best known insect groups with respect to taxonomy and distribution, and, apart from butterflies, probably no other group of insects receives so much attention from the general public and has so many organisations devoted to its study. An overview of the conservation and research status of the world's Odonata can be found in Clausnitzer & Jödicke (2004).

Many species in the temperate region have shown a dramatic decline in distribution and abundance since the second half of the 20th century (Westfall & May 1996, Sahlén et al. 2004, Inoue 2004). This has been caused by habitat destruction, eutrophication, acidification and pollution of aquatic habitats in general, and the canalisation of streams and rivers. Most of these species are not under immediate threat of extinction as they have wide ranges. A marked exception comes from the Ogasawara Islands, Japan, where five endemic species are on the verge of extinction due to the introduction in the 1980s of an *Anolis* lizard (Karube 2005). At least in parts of Europe, some of the species considered threatened recovered since the 1990s as result of improved water management. Recently it has become evident that many dragonflies of temperate regions are re-

sponding, both in distribution and phenology, to global climate change (Ott 2001). The ranges of common and widespread southern species are expanding in Europe but there is as yet no strong evidence that northern species are decreasing as a result of the rising temperatures, as might be expected.

Most of the world's dragonflies are restricted to the tropics, especially to forest, where the diversity of the group is greatest. Tropical species of open landscapes are generally better able to colonise new habitats than species confined to forest, and therefore have wider ranges on average and seem to be less influenced by habitat alteration. A clear exception is a number of South African endemics which declined due to shading of their habitat by invasive alien trees (Kinzig & Samways 2000), and recovered after removal of the trees (Samways 2004). Destruction of tropical forest is probably the most important threat to global odonate diversity, potentially resulting in the extinction of numerous species. Unfortunately these species are often poorly known, making it difficult to say whether a species is genuinely rare or merely overlooked. Evaluating the conservation status of most naturally rare species is hardly possible. Examples of data deficiency are known from Africa (e.g., Dijkstra & Clausnitzer 2006), South America (Paulson 2006), the Oriental region (Orr 2004) and New Guinea. More fieldwork is thus essential to establish the true ranges of these species and to determine areas of endemism within larger tropical forest areas. There is, however, no doubt that species confined to small remnants of forest in areas under high human pressure are endangered. Examples of such sites include many of the Philippine islands, Hawaii, the small pockets of forest in the Eastern Arc Mountains of East Africa and the Caribbean islands of Cuba, Hispaniola and Jamaica, but a well-founded overview of threatened areas of high importance for dragonflies is wanting. Especially susceptible are species depending on forest on small islands such as those of the Seychelles (Samways 2003). Here the disappearance of forest-

cover not only results in alteration of the habitat but also may change precipitation patterns.

Dragonflies have shown to be useful for nature management and conservation, and recently an increased effort is being made to make information on dragonflies available for both scientists and policymakers. Important initiatives taken are the update of the IUCN red list, the 'Pan-Africa Freshwater Biodiversity Assessment' started by the IUCN (Darwall et al. 2005), which includes dragonflies among other taxa, and the 'Global Dragonfly Assessment' initiated in 2005. The latter should hopefully result in a more detailed overview of the areas of endemism and conservation priority in the coming years.

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2. ODONATA ENTER THE BIODIVERSITY CRISIS DEBATE:

THE FIRST GLOBAL ASSESSMENT OF AN INSECT GROUP

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Citation: Clausnitzer, V., V.J. Kalkman, M. Ram, B. Collen, J.E.M. Baillie, M. Bedjanič, W.R.T. Darwall, K.-D.B. Dijkstra, R. Dow, J. Hawking, H. Karube, E. Malikova, D. Paulson, K. Schütte, F. Suhling, R. Villanueva, N. von Ellenrieder & K. Wilson 2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. – *Biological Conservation* 142: 1864-1869.

The status and trends of global biodiversity are often measured with a bias towards datasets limited to terrestrial vertebrates. The first global assessment of an insect order (Odonata) provides new context to the ongoing discussion of current biodiversity loss. A randomly selected sample of 1500 (26.4%) of the 5680 described dragonflies and damselflies was assessed using IUCN's Red List criteria. Distribution maps for each species were created and species were assigned to habitat types. These data were analysed in respect to threat level for regions and habitat types. We have found that one in 10 species of dragonflies and damselflies is threatened with extinction. This threat level is among the lowest of groups that have been assessed to date, suggesting that previous estimates of extinction risk for insects might be misleading. However, Odonata only comprise a small invertebrate order, with above-average dispersal ability and relatively wide distribution ranges. For conservation science and policy to be truly representative of global biodiversity a representative cross-section of invertebrates needs to be included.

INTRODUCTION

The loss of biodiversity that the world faces today dominates recent scientific and popular publications (Myers & Knoll 2001, Pimm & Brooks 2000). Long-term projections leave little hope for as many as half the species on earth (Jenkins 2003, Pimm et al. 1995, Pimm & Brooks 2000). But forecasts of biodiversity change are often based on unrepresentative data sets of limited taxonomic scope. Until recently, the most widely used and comprehensive conservation assessments have been for three vertebrate groups only (i.e. mammals, birds and amphibians) (Ceballos & Ehrlich 2006, Stattersfield & Capper 2000, Stuart et al.

2004), while the highest extinction risk and therefore greatest loss of biodiversity is expected to be suffered by invertebrates (Thomas et al. 2004, Hadfield 1993), specifically insects (Dunn 2005). However, knowledge of the threat status of invertebrates is limited, and therefore rarely considered in measures of global biodiversity change, although evidence suggests they might respond in different ways to anthropogenic threat (Thomas et al. 2004). Since invertebrates are more speciose than vertebrates and in most cases less well known, the task of comprehensively assessing their conservation status is both challenging and time-consuming. In the short-term a more feasible sampled

approach has been developed which increases the taxonomic coverage of the Red List through inclusion of representative subsets of invertebrates and plants, so providing a more representative indicator for the status of biodiversity (Baillie et al. 2008).

The IUCN Red List of Threatened Species™, www.iucnredlist.org (herein Red List) (IUCN 2008) has been documenting the threat status of flora and fauna for more than 40 years and is widely considered to be the most comprehensive dataset on the conservation status of species worldwide (Rodrigues et al. 2006). Here we show the status of the first insect order to be assessed on a representative global scale for the IUCN Red List of Threatened Species: A randomly selected subsample (26.4%) of all dragonflies and damselflies (Odonata) (Baillie et al. 2008). Until now only a selection of vertebrate taxa, the reef-building corals (Carpenter et al. 2008), the freshwater crabs (Cumberlidge et al. 2009) and a few plant groups (e.g. cycads and conifers) are adequately represented in the Red List (Baillie et al. 2004). Forty-two percentage of the described vertebrates have been assessed for the Red List, whereas only 0.3% of invertebrates have been assessed to date (IUCN 2007). This discrepancy needs to be rectified if any acceptable level of understanding of the status of the world's species is to be sought. The current focus on vertebrates may provide a limited and highly biased view of species extinction risk. Previous mass extinctions have shown that an extrapolation from vertebrates to invertebrates (Labandeira & Sepkoski 1993) may not be applicable.

With the exception of Antarctica, Odonata are widespread and abundant on all continents, although centres of species richness typically occur in tropical forests (Kalkman et al. 2008). Odonata spend their larval life in aquatic habitats and use a wide range of terrestrial habitats as adults. The larvae are critical in regard to water quality and aquatic habitat morphology such as bottom substrate and aquatic vegetation structure. Adult

habitat selection is strongly dependent on vegetation structure, including degrees of shading. As a consequence dragonflies show strong responses to habitat change such as thinning of forest and increased erosion. Ubiquitous species prevail in disturbed or temporary waters, while pristine streams, seepage and swamp forests harbour a wealth of more vulnerable, often localised species. Different ecological requirements are linked to different dispersal capacities. Species with narrow niches often disperse poorly, while pioneers of temporal habitats (often created by disturbance) are excellent colonisers, making Odonata a particularly good group for evaluating habitat connectivity. In summary, Odonata are an easy-to-study group and are useful for monitor the overall biodiversity of aquatic habitats and have been identified as good indicators of environmental health (Corbet 1999, Kalkman et al. 2008).

METHODS

Red List assessments

From a comprehensive list of the 5680 described extant Odonata (Kalkman et al. 2008), 2000 species were sampled at random, of which 1500 (26.5%) were used for conservation assessment. The selected species were checked for their taxonomic status by specialists and if necessary replaced by another species from the same realm and family from the additionally 500 randomly selected species. The sample size of 1500 is a manageable subset to be assessed, which is taxonomically and geographically representative of the whole group (Baillie et al. 2008). We used the Red List Categories and Criteria of the International Union for Conservation of Nature to determine the global threat status of Odonata species (IUCN 2001). The combined expertise of a large international network of Odonata specialists was employed to assess the species, and then each assessment was peer-reviewed by two independent experts. The Red List Categories and Criteria (IUCN 2001) have been widely used and constitute a well-established system, which in an objective framework determines the threat status of

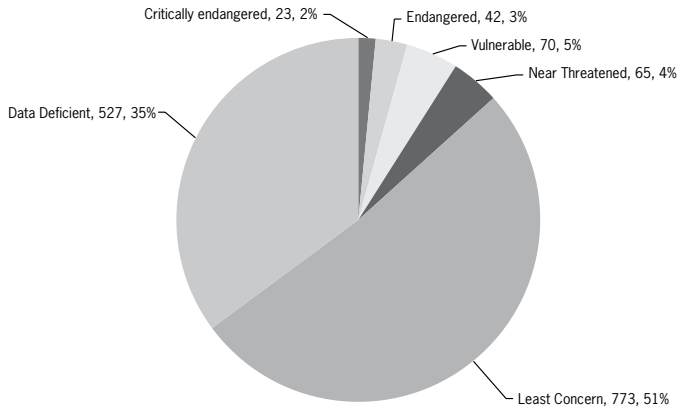


Figure 1. Global extinction risk of Odonata. Total numbers and percentage of Odonata assigned to a Red List Category (n total species = 1500).

a broad range of species (see Mace et al. 2008 for an updated and critical overview). The Red List Categories and Criteria use quantitative measures to classify species into categories of extinction risk according to measures of distribution, population abundance trends, rate of decline, geographic range information, and fragmentation (see Rodrigues et al. 2006). Categories range from “Least Concern” with very little probability of extinction to high risk “Critically Endangered”. The “threatened” categories (Vulnerable, Endangered, Critically Endangered) often serve as a key piece of information used in setting priority measures for biodiversity conservation.

Analysis of geographical patterns and habitat associations

Distribution maps for each species were created, based on point locality data, from which broad polygons that join the known locations were drawn (see Schipper et al. 2008 for detailed methods). Range maps were mapped onto a hexagonal grid of the world (each cell approximately 22,300 km²). This means that data were analysed using a geodesic discrete global grid system, defined on an icosahedron and projected to the sphere using the inverse Icosahedral Snyder Equal Area (ISEA) Projection. This corresponds to a hexagonal grid composed of individual units (cells) that retain their shape and area (approximately 22,300 km²) throughout the globe. These are more suitable for a range of ecological applications than the most commonly used

rectangular grids. Threatened species richness was then calculated for each cell, relative to the richest cell (nine threatened species). Distribution maps were used to assign each species to biogeographic realms. Further data on broad habitat type (lentic and lotic for the aquatic larval habitats; forest, shrubland and grassland for the habitats adjacent to the larval habitats) were collated for each species in the assessment process and number of species per habitat type was analysed.

RESULTS

More than half of the Odonata species were listed as Least Concern (fig. 1). One in 10 species was found to be threatened (assigned an IUCN Red List category of critically endangered, endangered, or vulnerable), while 35% had to be listed as Data Deficient (fig. 1). Odonate species richness is clustered in the Neotropical and Indo-Malayan realms, which contain almost 60% of the world’s Odonata diversity (fig. 2). Threatened species are as well clustered in tropical areas, especially in the Indo-Malayan realm (fig. 3). The lowest threat level is found in the Nearctic realm, with about 80% of the species listed in the Least Concern Category. The Oceanic realm harbours the lowest species number, but at the same time the highest number listed as Data Deficient (fig. 2). The majority of the Odonata species depends on lotic (flowing) waters and on forest (fig. 4).

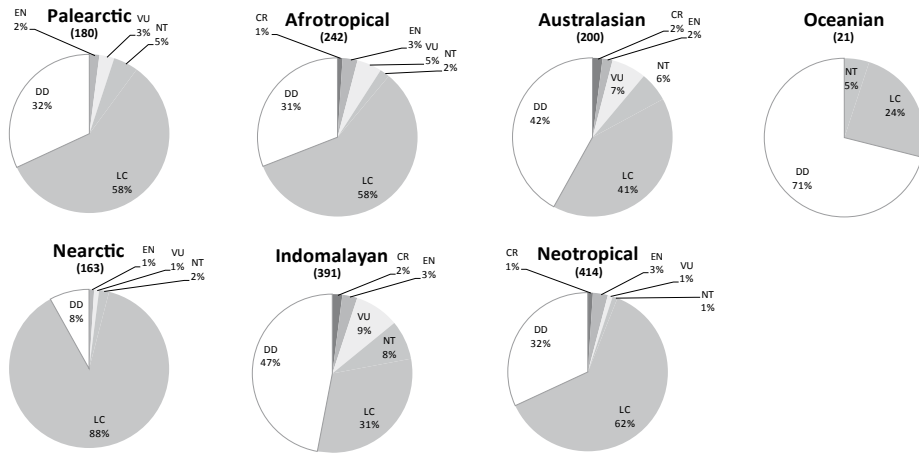


Figure 2. Regional extinction risk of Odonata. Threat levels of Odonata as percentages with respect to the number of species within each biogeographic realm assigned to a Red List Category. Total numbers given in brackets, percentages listed in the table; note: a species can be found in more than one realm.

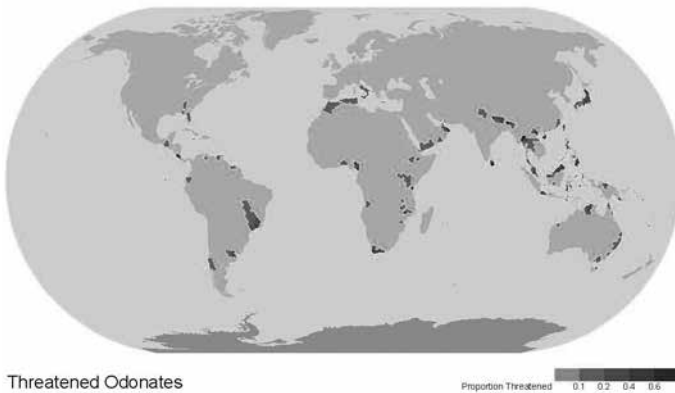


Figure 3. Global map of threatened Odonata. Global species richness map of threatened Odonata, given as a proportion of those species assigned vulnerable, endangered, and critically endangered conservation status, based on the Red List assessment. The apparent absence of threatened species in severely impacted regions as Madagascar and India's Western Ghats is explained by the extreme data deficiency for Odonata in these regions.

In both habitat types the percentage of Data Deficient species is higher than in the other habitat types. Species in lotic waters were found to be at greater risk than those in lentic (standing) waters (fig. 4), while the threat level between the terrestrial habitat types is more or less identical.

DISCUSSION

The global threat status of Odonata

Only 10% of the assessed Odonata were found to

be threatened, a relatively low figure compared with 31% of amphibians and 20% of mammals (IUCN 2007), but similar to the level of threat for birds at 12% (IUCN 2007). However, a relatively high proportion (35%) of the species is Data Deficient (DD), akin to that for amphibians (Stuart et al. 2004). Many species in tropical forest habitats in particular are poorly studied and often known only from the type specimen. Expert judgement, e.g. IUCN (2007) on the status of those habitats where most DD species are found (e.g. large forest blocks such as the Amazon and

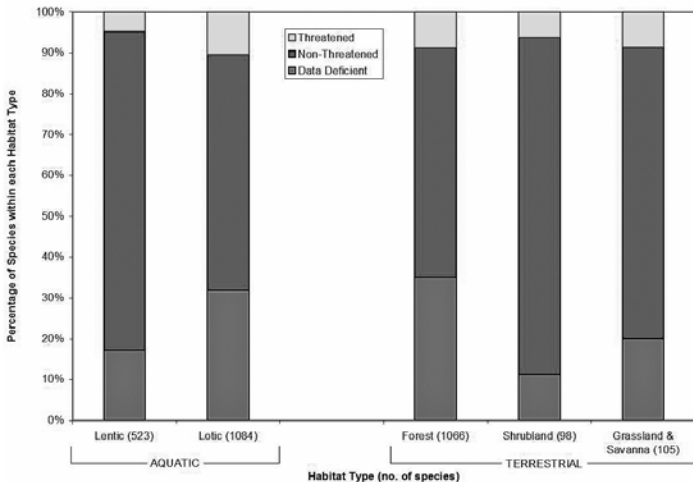


Figure 4. Extinction risk of Odonata in habitat types. Odonata threat levels in aquatic habitats as percentages with respect to all species within each habitat type. Threatened species are categorised as critically endangered, endangered, or vulnerable; and non-threatened species are categorised as near threatened or least concern. Total numbers given in brackets; note: a species can be found in more than one habitat type (n total species = 1492; for eight species no habitat information was available).

Congo) suggests that 10-20% of these species are likely to be threatened, thus bringing the overall percentage of threatened species close to 15%.

Areas and habitats with a high threat level

Threatened species appear to be clustered in the Indo-Malayan and Australian realms (fig. 2). This is largely due to the high percentage of endemics in the Indonesian archipelagos combined with the anthropogenic threat to the species of large scale logging of lowland forest on many islands, while in Australia, climate change is having an especially strong impact on freshwater systems (for a global review on threats affecting Odonata see articles in Clausnitzer & Jödicke, 2004). As in many other taxa, island endemic species of Odonata are the most threatened. This is true not only for species restricted to islands such as the Philippines, but also for those species restricted to terrestrial habitat islands such as remnant forest patches in Sri Lanka (see fig. 3). In fact, the only two documented extinctions of Odonata have occurred on islands: *Megalagrion jugorum* (Perkins 1899) from Maui in the Hawaiian Islands, and *Sympetrum dilatatum* (Calvert 1892) from Saint Helena.

That species inhabiting lotic waters are at greater risk than those in lentic waters (fig. 4) may be partly due to lotic habitats being less predictable

in space and time. Species in lentic systems tend to be more generalised and have a higher dispersal capacity (Corbet 1999), resulting in larger ranges and wider ecological preferences, and therefore lower extinction risk (see articles in Clausnitzer & Jödicke 2004, Hof et al. 2005). Higher environmental pressure on lotic waters may also be responsible for the increased risk to species in these habitats, but this remains uncertain.

Comparison with other taxa

The relatively low level of threat to Odonata when compared to other groups assessed by IUCN is unexpected, as freshwater habitats are often considered as “particularly at risk” (Dudgeon et al. 2006, Dunn 2005, Naiman et al. 2006). There are several possible factors to explain this. Many Odonata species are able to live in partially degraded habitats, are capable of rapidly colonising new or restored habitats, and when compared with birds, mammals, and amphibians, can maintain viable populations in relatively small remnants of habitat. Odonata are also largely unaffected by hunting or trade, unlike birds, mammals or other invertebrates, notably butterflies. It will be interesting to see whether other freshwater invertebrates will show similar results, once assessed in a representative way. In addition, the highest diversity of Odonata is found in tropical forests,

which are not considered to be the most endangered habitat types (Hoekstra et al. 2005, Wright & Muller-Landau 2006) and which are also thought to be under less immediate impact of climatic change (Wright & Muller-Landau 2006). Although threat level is higher for forest species (fig. 4), this is most often due to increased human pressures on those species restricted to forest fragments, mountaintops, and island localities, while those species inhabiting large forest blocks are assessed as being at lower risk. Species inhabiting peatland bogs are also considered to be at a low risk as many of these habitats, such as those in Scandinavia, remain still widely unaffected (Sahlén et al. 2004). However, as climate change is predicted to have a significant impact in these habitats and associated species in the future (Hoekstra et al. 2005), the level of threat is likely to rise, which eventually will be shown by the RLI.

Research needed

Odonata are currently the only insect group for which a representative global assessment of conservation status has been completed and analysed. This assessment succeeds in providing an indication of the level of global threat across a freshwater invertebrate group but it also identifies a high level of Data Deficiency, meaning there is insufficient information to assess their status. Given the current lack of representation for invertebrates in global biodiversity assessments the importance in obtaining a comprehensive assessment for odonates has to be a priority, requiring extensive new field surveys. This holds especially true for most forests in tropical areas. The data gap in tropical countries is a taxa-wide problem and does not only apply to Odonata (see Collen et al. 2008). Invertebrates have been insufficiently represented not only when gauging the status of biodiversity but also when estimating rates of change in species status. The approach of the Red List Index (Baillie et al. 2008, Butchart et al. 2004, 2007) will allow for the first time the opportunity to monitor the global status according to the Red List criteria. It will be used to calculate the movement of species between threat categories over

time and generate trends in extinction risk. The RLI can currently be calculated for birds, as all described species in this taxonomic group have been assessed for the Red List on at least two separate occasions. The RLI has been adopted by the Convention on Biological Diversity to measure progress toward its 2010 target of significantly reducing the current rate of biodiversity loss by the year 2010 (decision VI/26) (Balmford et al. 2005) and more recently as a measure for the UN Millennium Development Goals [7.7 Proportion of species threatened with extinction (www United Nations Development Goals)]. However, it will only succeed as an informative measure of the status of global biodiversity if non-vertebrate species are also included in a representative way. Thus the Odonata need to be re-assessed in future in regular intervals. Ongoing assessments of Odonata, for instance as part of the IUCN African freshwater assessment, will increase the amount of odonate species for which RLI can be applied in due course.

Conservation actions

Conservation actions need to be implemented especially for tropical island species. Habitat degradation and pollution put especially great pressure on species confined to a small area. If we are to better understand the status of biodiversity in freshwater ecosystems then odonates provide an excellent easy-to-use indicator group (Clausnitzer 2004, Sahlén & Ekestubbe 2001, Samways & Steytler 1996, Suhling et al. 2006) with which to start. Specific conservation action plans for every threatened dragonfly can neither be achieved nor realized. Still a canon of general conservation measures do cover many of the threatened species in most areas, especially the most threatened forest species of lotic tropical habitats:

- (1) Prevention of any further deforestation. Forests should be regarded as a natural resource with high conservation priority.
- (2) Afforestation with indigenous trees. This is not only of conservation value for odonates, biodiversity and/or centres of endemism, but also resource management and prevention of flooding, landslides, etc. Afforestation programmes

should focus on the local community level as well as on a large scale governmental level.

- (3) Fire control. Frequent and uncontrolled fires, especially in tropical and subtropical countries, prevent any kind of regeneration. A fire control programme would be quite effective, allowing natural succession.
- (4) Leaving a strip of natural riparian vegetation of at least 20 m on either side of streams and rivers in cultivated and mined landscapes. This would increase landscape heterogeneity, decrease the destructive impact of flooding and increase biodiversity. Such measures would not only benefit heliophobic odonate species of the streams but also forest species which are highly isolated at the moment, as they could use such corridors for dispersal between forest patches.
- (5) Water pollution control measures, e.g. sewage works mining run-off and factory effluent treatment. Restricting and controlling the amount of insecticides and pesticides.
- (6) Protection of watersheds, floodplains, water retention sites, swamps, etc., against adverse impacts of damming and other alterations, such areas are important to prevent flooding and function as water-catchment areas.

ACKNOWLEDGEMENTS

We would like to thank the Esmée Fairbairn Foundation for funding the sampled approach to the Red List Index. Parts of the study were funded by grants from the BMBF (German Ministry for Science and Education) BIOLOG programme (01LC0025, 01LC0404, V. Clausnitzer; 01LC0024, F. Suhling), the Aquashift core-programme of DFG (F. Suhling), SYNTHESIS (K.-D.B. Dijkstra, K. Schütte) and the Rufford Maurice Laing Foundation (B. Collen). Jean Legrand helped during collection work in MNHN (K. Schütte) and The National Museum of Natural History Naturalis, Leiden provided working facilities for K.-D.B. Dijkstra. This document has been produced in part with the financial assistance of the European Union under project EuropeAid/ENV/2004-81917.

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Part 2

Taxonomy and phylogeny

3. REMARKS ON THE TAXONOMY OF MEGAPODAGRIONIDAE

WITH EMPHASIS ON THE LARVAL GILLS (ODONATA)

Vincent J. Kalkman, Chee Yen Choong, Albert G. Orr & Kai Schütte

Citation: Kalkman, V.J., C.Y. Choong, A.G. Orr & K. Schütte 2010. Remarks on the taxonomy of Megapodagrionidae with emphasis on the larval gills (Odonata). – International Journal of Odonatology 13: 119-135.

A list of genera presently included in Megapodagrionidae and Pseudolestidae is provided, together with information on species for which the larva has been described. Based on the shape of the gills, the genera for which the larva is known can be arranged into four groups: (1) species with inflated sack-like gills with a terminal filament; (2) species with flat vertical gills; (3) species in which the outer gills in life form a tube folded around the median gill; (4) species with flat horizontal gills. The possible monophyly of these groups is discussed. It is noted that horizontal gills are not found in any other family of Zygoptera. Within the Megapodagrionidae the genera with horizontal gills are, with the exception of *Dimeragrion*, the only ones lacking setae on the shaft of the genital ligula. On the basis of these two characters it is suggested that this group is monophyletic.

INTRODUCTION

In the last decade many studies have been devoted to the phylogeny of damselflies (for a review, see Trueman 2007). Studies that included a large selection of species of most families have been most successful in providing an understanding of the limits of families. Notable studies include those of Rehn (2003), who analysed morphological data for over 150 species, and Bybee et al. (2008), who analysed morphological and molecular data for over a 100 species from 30 families. The monophyly for most damselfly families is well established and Calopterygidae, Chlorocyphidae, Euphaeidae, Isostictidae, Lestidae, Platystictidae, 'Disparoneurinae' (= Old World Protoneuridae) and Polythoridae are established as monophyletic groups in Bybee et al. (2008). In addition to this, Coenagrionidae is monophyletic when Pseudostigmatidae and Protoneuridae s.str. are included (Carle et al. 2008; Pessacq 2008). A more recently published phylogeny based on DNA data of 229 species largely agrees with these results (Dumont et al. 2009).

However the Holy Grail of zygopteran phylogeny, a well-resolved tree showing the inter-family relations, remains to be found, although we now at least have some good working hypotheses (Bybee et al. 2008).

One of the most problematic groups in the work of Bybee et al. (2008) and Dumont et al. (2009) is that which includes the families Megapodagrionidae, Pseudolestidae and Amphipterygidae. The only generally recognised member of Pseudolestidae, *Pseudolestes mirabilis* Kirby, 1900, and also the genus *Rhipidolestes*, which is sometimes included in Pseudolestidae, are shown by Bybee et al. (2008) as falling within Megapodagrionidae and are considered here to belong to that family. Amphipterygidae includes the genera *Amphipteryx* Selys, 1853, *Devadatta*, Kirby 1890 (Amphipteryginae), *Pentaplebia* Förster, 1909 and *Rimanella* Needham, 1934 (Rimanellinae), all of which show a convincing synapomorphy in the form of paired, highly plumose, filamentous gill tufts. Neither molecular study cited above recognizes

Amphipterygidae as a monophyletic group. Bybee et al. (2008) did not find *Devadatta* and *Rimanella* to be monophyletic, but the authors suggest that as no molecular data were available for *Rimanella*, a close relationship might yet be found. Similarly Dumont et al. (2009) failed to establish the monophyly of *Devadatta* and *Pentaplebia*. We consider that these results may well represent methodological artefacts and in this paper we consider Amphipterygidae to be monophyletic, falling outside the limits of the Megapodagrionidae. In many publications *Philoganga* Kirby, 1890 is also included in the Amphipterygidae. However, because the larvae lack gill tufts, Novelo-Gutiérrez (1995) removed this genus from the Amphipterygidae, and placed it in Lestoideidae (incorrectly designating it as Diphlebiidae) together with *Diphlebia* Selys, 1869 and *Lestoidea* Tillyard, 1913. The latter two genera are recovered as a monophyletic group in all trees presented by Bybee et al. (2008). These genera are however never grouped with *Philoganga*, which is shown either as a separate lineage or forming a monophyletic group together with *Rimanella*. The position of *Philoganga* thus remains problematic, for which reason we treat it as equivalent to a family under the name '*Philoganga*' leaving Lestoideidae with only *Diphlebia* and *Lestoidea*. Furthermore, in some of the trees presented by Bybee et al. (2008), the Polythoridae also lie within Megapodagrionidae. As with Amphipterygidae, this tropical American group has some well-defined autapomorphies, mainly manifested in the larvae. The abdomen bears dorsal hooks, the caudal gills are swollen, with three to six finger-like projections, and they have latero-ventral abdominal gills on S2-7. The only other family in which abdominal gills occur is the Euphaeidae, where they are found ventro-laterally on S2-8. This apparent similarity suggests a close relation between these families but this is not firmly supported by consideration of adult morphology (Rehn 2003) or by molecular analyses (Bybee 2008). There is no reason, other than certain uncorroborated phylograms of Bybee et al. (2008), to consider the Polythoridae as part of the Megapodagrionidae, and in the following analysis, this family is also disregarded.

vjk is currently studying the taxonomy of the species of Megapodagrionidae occurring east of Huxley's Line: The Philippines, eastern Indonesia, Papua New Guinea, The Solomon Islands, Australia and New Caledonia. This group includes over 80 species and 10 genera and is believed to be monophyletic. The best evidence for their monophyly is to be found in the gills of the larvae, which are placed in a horizontal plane, a character state found in no other group of Zygoptera. With the recent description of the larvae of *Podolestes* (Choong & Orr 2010), *Nesolestes* (Schütte 2010) and the reappraisal of the description of the larva of *Protolestes* (Paulian 1958) it became clear that this character state is not confined to species occurring east of Huxley's Line. The question arises: are horizontal gills found in other genera of Megapodagrionidae? And if so, do the species with horizontal gills form a monophyletic group? In order to answer these questions the present review was made of all described larvae of Megapodagrionidae. During this search it was noted that the shape of the gills was correlated with the presence or absence of setae on the genital ligula or penis shaft. Larval morphology is therefore analysed in association with this easily assessed, unrelated adult male character.

MATERIAL AND METHODS

The review of larval gill morphology was based on published literature. A complete list of references is provided in table 1. The presence or absence of setae on the genital ligula was assessed for all genera from Scanning Electron Microscopy (SEM) images for the Old World genera and from literature and specimens, examined under a stereo light microscope for the New World genera. It must be noted that the setae on the genital ligula are often not drawn and therefore a drawing in which the setae are not shown cannot be used as confirmation of the absence of setae. In order to establish the variation in this character the presence and absence of setae was also studied in a wide selection of genera from all families of Zygoptera.

Table 1. Species of Megapodagrionidae for which the larva is described, their affiliation to morphological groups and their presence or absence of setae on the shaft of the genital ligula. B: balloon megapods; F: fan megapods; L: long-legged megapods; T: tube megapods; ?: group affiliation unknown; +: setae present; -: setae absent.

Genus / species with larva described	Distribution of genus / reference to larval description	Group	Setae
<i>Agriomorpha</i> May, 1933 No larva described	Mainland Asia	?	+
<i>Allolestes</i> Selys, 1869 No larva described	Seychelles	?	-
<i>Allopodagrion</i> Förster, 1910 No larva described	America	?	+
<i>Amanipodagrion</i> Pinhey, 1962 No larva described	Tanzania	?	-
<i>Archaeopodagrion</i> Kennedy, 1939 No larva described	America	?	+
<i>Archiargiolestes</i> Kennedy, 1925 <i>parvulus</i> (Watson, 1977) <i>pusillissimus</i> Kennedy, 1925 <i>pusillus</i> (Tillyard, 1908) <i>Argiolestes</i> Selys, 1862	West Australia Theischinger 1998 Theischinger 1998 Theischinger 1998 New Caledonia, Solomons, Papua New Guinea, Philippines	F	-
<i>fontinalis</i> Lief tinck, 1956 <i>ochraceus</i> (Montrousier, 1864) <i>pectitus</i> Lief tinck, 1949 ¹	Lief tinck 1956, 1976 Lief tinck 1976 Lief tinck 1956, 1976		
<i>Austroargiolestes</i> Kennedy, 1925 <i>alpinus</i> (Tillyard, 1913) ¹ <i>aureus</i> (Tillyard, 1906) ¹ <i>chrysoides</i> (Tillyard, 1913) ¹ <i>icteromelas</i> (Selys, 1862)	East Australia Theischinger 1998 Theischinger 1998 Theischinger 1998 Tillyard 1917; Lief tinck 1976; Theischinger 1998; Hawking & Theischinger 1999 Theischinger, 1998	F	-
<i>isabellae</i> Theischinger & O'Farrell, 1986 <i>Bornargiolestes</i> Kimmins, 1936 No larva described	Borneo	?	+
<i>Burmargiolestes</i> Kennedy, 1925 No larva described	Mainland Asia	?	+
<i>Caledargiolestes</i> Kennedy, 1925 <i>uniseriis</i> (Ris, 1915) ²	New Caledonia Wiley 1955; Lief tinck 1976	F	-
<i>Caledopteryx</i> Kennedy, 1925 <i>maculata</i> Winstanley & Davies, 1982 ³	New Caledonia Lief tinck 1976	F	-
<i>Celebargiolestes</i> Kennedy, 1925 sp. ⁴	Sulawesi Culhane 2005	F	-
<i>Dimeragrion</i> Calvert, 1913 <i>percubitale</i> Calvert, 1913 ¹	America De Marmels 1999	F	+
<i>Griseargiolestes</i> Theischinger, 1998 <i>albescens</i> (Tillyard, 1913) <i>bucki</i> Theischinger, 1998	East Australia Theischinger 1998; Hawking & Theischinger 1999 Theischinger 1998b; Hawking & Theischinger 1999	F	-
<i>eboracus</i> (Tillyard, 1913)	Theischinger 1998; Hawking & Theischinger 1999		
<i>griseus</i> (Hagen, 1862)	Tillyard 1917; Theischinger 1998; Hawking & Theischinger 1999		
<i>intermedius</i> (Tillyard, 1913)	Theischinger 1998; Hawking & Theischinger 1999		

Genus / species with larva described	Distribution of genus / reference to larval description	Group	Setae
<i>Heteragrion</i> Selys, 1862	America	B	+
<i>albifrons</i> Ris 1918	Novelo-Gutiérrez 1987		
<i>alienum</i> Williamson, 1919	Novelo-Gutiérrez 1987		
<i>aurantiacum</i> Selys, 1862	Santos 1968		
<i>bariai</i> De Marmels, 1989	De Marmels 2004		
<i>breweri</i> De Marmels, 1989	De Marmels 2004		
<i>chlorotaeniatum</i> De Marmels, 1989	De Marmels 2004		
<i>chrysops</i> Hagen in Selys, 1862	Limongi 1983		
<i>consors</i> Hagen in Selys, 1862	Costa & Santos 1999		
<i>erythrogastrum</i> Selys, 1886	Ramírez 1992		
<i>mitratum</i> Williamson, 1919	De Marmels 2004		
<i>tricellulare</i> Calvert, 1901	Novelo-Gutiérrez 1987		
<i>Heteropodagrion</i> Selys, 1885	America	?	+
No larva described			
<i>Hypolestes</i> Gundlach, 1888	America	B	+
<i>trinitatis</i> Gundlach, 1888	Alayo Soto 1985; Westfall & May 1996		
<i>Megapodagrion</i> Selys, 1885	America	?	+
No larva described			
<i>Mesagrion</i> Selys, 1885	America	?	+
No larva described			
<i>Mesopodagrion</i> MacLachlan, 1896	Mainland Asia	?	+
No larva described			
<i>Miniargiolestes</i> Theischinger, 1998	West Australia	F	–
<i>minimus</i> (Tillyard, 1908)	Theischinger 1998		
<i>Nesolestes</i> Selys, 1891	Madagascar	F	–
sp.	Schütte 2010		
<i>Neurolestes</i> Selys, 1882	West Africa	?	–
No larva described			
<i>Oxystigma</i> Selys, 1862	America	B	+
<i>petiolatum</i> (Selys, 1862)	Geijskes 1943		
<i>Paraphlebia</i> Selys in Hagen, 1861 ⁵	America	B	+/-
<i>zoe</i> Selys in Hagen, 1861	Novelo-Gutiérrez 2008		
<i>Philogenia</i> Selys, 1862	America	B	+
<i>carrillica</i> Calvert, 1907	Ramírez-Ulate & Novelo-Gutiérrez 1994		
<i>cassandra</i> Hagen in Selys, 1862	De Marmels, 1982		
<i>mangosisa</i> Bick & Bick, 1988	Bybee & Tennessen 2008		
<i>peacocki</i> Brooks, 1989	Ramírez-Ulate & Novelo-Gutiérrez 1994		
<i>terraba</i> Calvert, 1907	Ramírez-Ulate & Novelo-Gutiérrez 1994		
<i>Philosina</i> Ris, 1917	Mainland Asia	?	+
No larva described			
<i>Podolestes</i> Selys, 1862	Southeast Asia	F	–
<i>orientalis</i> Selys, 1862	Choong & Orr 2010		
<i>Podopteryx</i> Selys, 1871	Australia, Indonesia, Papua New Guinea	F	–
<i>selysi</i> (Förster, 1899)	Watson & Dyce 1978; Theischinger & Hawking 2006		
<i>Priscagrion</i> Zhou & Wilson, 2001	Mainland Asia	?	+
No larva described			
<i>Protolestes</i> Förster, 1899	Madagascar	F	–
<i>proselytus</i> Liefstinck, 1965 ⁶	Paulian 1958		
<i>Pseudolestes</i> Kirby, 1900	Hainan, China	?	+
No larva described			
<i>Rhinagrion</i> Calvert, 1913	Southeast Asia	T	+
<i>mima</i> (Karsch, 1891)	Liefstinck 1956		

Genus / species with larva described	Distribution of genus / reference to larval description	Group	Setae
<i>philippinum</i> (Selys, 1882)	Needham 1911; Needham & Gyger 1939		
<i>Rhipidolestes</i> Ris, 1912	Mainland Asia, Japan	B	+
<i>aculeatus</i> Ris, 1912	Asahina 1994; Kawai 1985; Sugimura et al. 2001		
<i>asatoi</i> Asahina, 1994	Sugimura et al. 2001		
<i>hiraoui</i> Yamamoto, 1955	Asahina 1994; Kawai 1985; Sugimura et al. 2001		
<i>okinawanus</i> Asahina, 1951	Sugimura et al. 2001		
<i>Sciotropis</i> Racenis, 1959	America	B	+
<i>cyclanthorum</i> Racenis, 1959	De Marmels 2004		
<i>Sinocnemis</i> Wilson & Zhou, 2000	Mainland Asia	?	+
No larva described			
<i>Tatocnemis</i> Kirby, 1889	Madagascar	B	+
<i>malgassica</i> Kirby, 1889	Paulian 1958		
<i>Teinopodagrion</i> De Marmels, 2001	America	L	+
<i>caquetanum</i> De Marmels, 2001	Pérez-Gutiérrez 2007		
<i>decepiens</i> De Marmels, 2001	von Ellenrieder 2006		
<i>meridionale</i> De Marmels, 2001	von Ellenrieder 2006		
<i>oscillans</i> (Selys, 1862)	De Marmels 2001		
<i>vallenatum</i> De Marmels, 2001	Pérez-Gutiérrez 2007		
<i>venale</i> (Hagen in Selys, 1862)	De Marmels 1982		
<i>Thaumatoneura</i> McLachlan, 1897	America	B	+
<i>inopinata</i> McLachlan, 1897	Calvert 1915		
<i>Trineuragrion</i> Ris, 1915	New Caledonia	F	-

1 Identification of larvae based on supposition.

2 The larva of *Caledargiolestes uniseriis* was described and illustrated from a single larva by Lippitt Willey (1955) as an unidentified larva of a megapodagrionid. Liefstinck (1976) redescribed this larva as “Genus et species incert”. In the same paper he gave also a description of the larva he supposed to be *C. uniseriis*. Winstanley (1983) discovered that the “unidentified larva of a megapodagrionid” described by Lippitt Willey (1955) and Liefstinck (1976) in fact belonged to *Caledargiolestes uniseriis* and that the larva described by Liefstinck as *Caledargiolestes uniseriis* belongs to another megapodagrionid-species.

3 *Caledopteryx maculata* had not been discovered when Liefstinck (1976) described the larva of *Caledargiolestes* as *C. sarasini*. Winstanley & Davies (1982) state that Liefstinck used larvae from a locality, where only *C. maculata* has been collected. Liefstinck’s description of *C. sarasini* is therefore believed to pertain to *C. maculata*.

4 Culhane (2005) published pictures of a megapodagrionid larva from Buton Island, Sulawesi. The genus *Celebargiolestes* is widespread and relatively common on Sulawesi while only a single record of *Argiolestes* is known (Kalkman 2007). It is therefore tentatively assumed that the larva in Culhane (2005) belongs to *Celebargiolestes*.

5 Of the three species checked two had a few small setae (*Paraphlebia zoe*, *P. sp. 1*) and one seemed to lack setae (*P. sp. 2*).

6 This larva was described as *Protolestes fickei* Foerster, 1899 but according to Liefstinck (1965) it belongs to *P. proselytus*.

This was partly done based on literature and specimens held by AGO, but mostly based on specimens in the Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH).

For non-megapodagrionid taxa the following arrangements were followed (see table 3).

The species of the monotypic genera *Leptocnemis cyanops* (Selys, 1869), *Oreocnemis phoenix* Pinhey,

1971, and *Thaumatagrion funereum* Liefstinck, 1932 are often placed in Platycnemididae, but are here placed in Coenagrionidae. The original placement of *Thaumatagrion* was doubted by Gassmann (2005), whereas unpublished DNA studies indicate that *Leptocnemis cyanops* and *Oreocnemis phoenix* belong in Coenagrionidae. The placement in Coenagrionidae of the species formerly included in Pseudostigmatidae follows

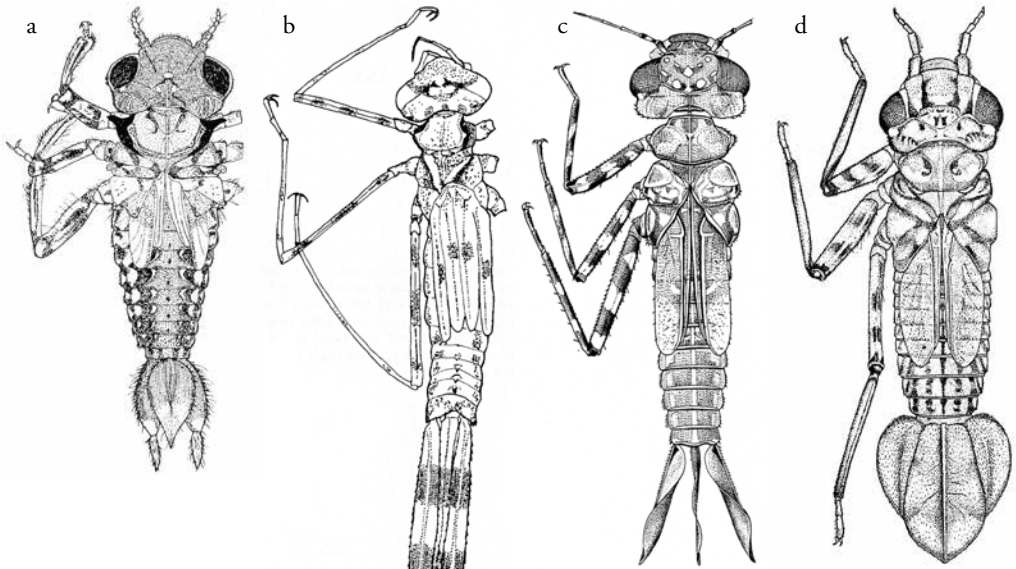


Figure 1. Examples of megapodagrionid larvae with different types of gills – (a) *Sciotropis cyclanthorum* with inflated saccoid gills bearing a terminal filament (Balloon megapods) (from De Marmels 2004); (b) *Teinopodagrion venale* with gills one foliaceous and wider and shorter than the lateral ones (Long-legged megapods) (from De Marmels 2001); (c) *Rhinagrion mima* in which the outer gills in life form a tube folded around the median gill; in preserved specimens these gills present as short thick, vertical laminar forms, similar to the general condition found in most Zygoptera (Tube megapods) (from Liefstinck 1956); (d) *Argiolestes pectitus* with flat horizontal gills (Fan megapods) (from Liefstinck 1956).

the results presented by Carle et al. 2008.

The placement in Coenagrionidae of Protoneuridae s.str. follows the results of Pessacq (2008) who showed that all New World species of the Protoneuridae, including the type genus, fall within Coenagrionidae (Pessacq 2008). The unrelated Old World species of Protoneuridae s.l. are here given as ‘Disparoneurinae’.

Subfamilies thus far defined within Megapodagrionidae have been shown to be of little taxonomic value. For this reason we refrain from using these names and instead have devised descriptive cognomens for definable groups based on the structure of larval gills.

RESULTS

Larvae fell into four definable groups: ‘Balloon megapods’ or species in which the larval gills were

saccoid or balloon-shaped, ‘Long-legged megapods’ for species in which the larvae had flat, often elongate vertical gills, ‘Tube megapods’ for species in which the outer gills formed a tube in life and ‘Fan megapods’ for species in which the larvae have flat horizontal gills. Table 1 gives, for each megapodagrionid genus, a list of described larvae and information on the shape of the gills. In this table also the presence or absence of rows of setae on the sides of the ligula is noted. The distribution of gill types within the family could be summarized as follows:

- (1) Species with inflated saccoid gills bearing a terminal filament (fig. 1a) (Balloon megapods). In some genera the gills were only slightly inflated but then the dorsal, ventral and lateral keels are clearly thickened making the gills three dimensional (triquetral).
 - Africa, Madagascar: *Tatocnemis*
 - Asia west of Huxley’s Line: *Rhipidolestes*

	Fan megapods	Balloon, Long-legged or Tube megapods	Larvae unknown
Setae present	1	10	12
Setae sometimes absent	0	1	0
Setae absent	13	0	3

Family	genera known	Setae present	Setae absent
Amphipterygidae	4	4 (7)	0
Calopterygidae	16	16 (16)	0
Chlorocyphidae	18	0	14 (18)
Coenagrionidae	110+	32	31
Dicteriidae	2	0	1 (1)
'Disparoneurinae'	9	0	7 (17)
Euphacidae	12	9 (20)	2 (2)
Hemiplebiidae	1	1	(1) 0
Isostictidae	12	4 (8) ¹	3 (6) ²
Lestidae	8	0	7 (15)
Lestoideidae	2	2	(3) 0
Perilestidae	3	0	3 (7)
'Philoganga'	1	0	1 (1)
Platynemididae	21	0	17 (20)
Platystictidae	6	6 (34)	0
Polythoridae	7	3 (14)	1 (1) ³
Synlestidae	8	0	7 (12)

- tropical America: *Heteragrion*, *Oxystigma*, *Paraphlebia*, *Philogenia*, *Sciotropis*, *Thaumatoneura*, *Hypolestes*
- (2) Species with gills placed in a vertical plane, the lateral pair long and thickened, each with a median outer ridge along its length, the median one foliaceous and wider and shorter (fig. 1b) (Long-legged megapods).
- tropical America: *Teinopodagrion*
- (3) Species in which the outer gills in life form a tube folded around the median gill; in preserved specimens these gills present as short thick, vertical laminate forms, superficially similar to the general condition found in most Zygoptera (fig. 1c) (Tube megapods). This type of gills is unique to the group and is not found in other Zygoptera.

Table 2. Number of megapodagrionid genera with or without setae on the genital ligula for different larval types.

Table 3. Presence or absence of setae on the genital ligula in families of Zygoptera other than Megapodagrionidae. For each family the following data are included: the total number of genera known worldwide largely based on Kalkman et al. (2008), the number of genera and species (in parentheses) known to possess setae and the number of genera and species (in parentheses) known to lack setae.

- 1 Setae seem present in Australian and New Caledonian genera (*Isosticta* Selys, 1885; *Neosticta* Tillyard, 1913; *Oristicta* Tillyard, 1913; *Rhadinosticta* Watson, 1991).
- 2 Setae seem absent in New Guinean and Solomon Island genera (*Cnemisticta* Donnelly, 1993; *Selysioneura* Förster, 1900; *Tanymercisticta* Liefstinck, 1935).
- 3 *Euthore fasciata* (Hagen in Selys, 1853) is the exception.

- tropical Asia west of Huxley's Line and also the Philippines: *Rhinagrion*
- (4) Species with flat horizontal gills (fig. 1d) (Fan megapods). This structure is unique to the group and is not found in other Zygoptera.
- Africa, Madagascar: *Nesolestes*, *Protolestes*
 - Asia west of Huxley's Line: *Podolestes*
 - Asia east of Huxley's Line (Philippines, eastern Indonesia, Papua New-Guinea Solomons, Australia and New Caledonia): *Archiargiolestes*, *Argiolestes*, *Austroargiolestes*, *Caledargiolestes*, *Caledopteryx*, *Celebargiolestes*, *Griseargiolestes*, *Miniargiolestes*, *Podopteryx*, *Trineuragrion*
 - tropical America: *Dimeragrion*

For four American genera, eight Asian genera and three African megapodagrionid genera no larva

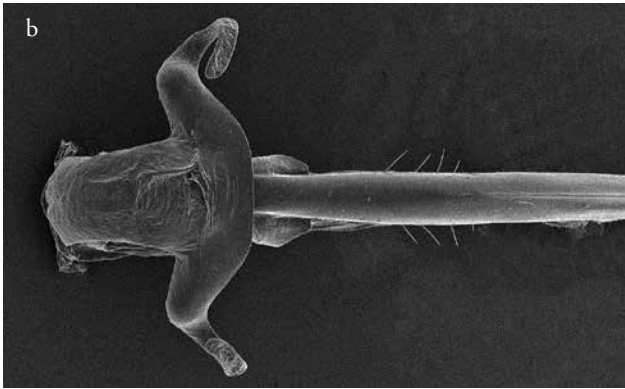
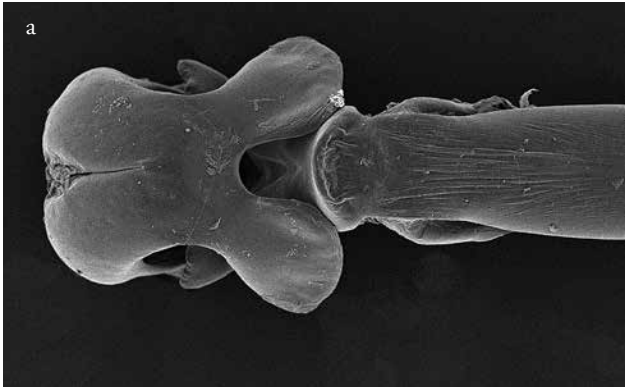


Figure 2. Examples of different structures of the genital ligula in two megapodagrionid species, ventral view – (a) *Neurolestes trinervis* (Selys, 1885) without setae on the ligula; (b) *Oxystigma williamsoni* Geijskes, 1976 with setae on the ligula.

have ever been described. In 13 genera with horizontal gills (Fan megapods) the setae on the genital ligula were absent (fig. 2a). The only exception to this rule is *Dimeragrion* which has horizontal gills and setae on the genital ligula. The setae on the genital ligula were always present in all other genera for which the larvae were known ($n = 10$), with the exception of *Paraphlebia* (fig. 2b). The information on larval gills and the presence of setae on the genital ligula is summarised in table 2. Table 3 provides an overview of the presence or absence of setae on the genital ligula for non-megapodagrionid families of Zygoptera.

DISCUSSION

Within the Zygoptera, the general morphology of the larval gills appears very conservative within

families, and within most families, only one gill-type occurs (Corbet 1999: 77-86). For this reason it is believed that considerable weight can be assigned to this character. The presence or absence of setae on the genital ligula is a seldom-used character. Our analysis of the distribution of this character within families shows it to be fairly consistent within families (table 3) with 13 of the 17 families only exhibiting just one character state. In all families of the Chlorocyphidae, Dictერიადიდაე, ‘Disparoneurinae’, Lestidae, Synlestidae, Perilestidae, ‘*Philoganga*’ and Platycnemididae setae were always absent on the genital ligula. In the families Amphipterygidae, Calopterygidae, Lestoideidae and Platystictidae setae were always present. In Coenagrionidae, Euphaeidae, Isostictidae and Polythoridae both character states were found. However with the exception of Coenagrionidae, no variation was found within genera, and genera with setae form the great majority,

suggesting that in these genera presence of setae is the plesiomorphic character state. In all species with setae studied by us the setae point away from the apex of the genital ligula. This gives the impression that they may function to ‘dock’ the genital ligula in the vagina, and/or perhaps prevent the shaft of the genital ligula from grinding against the wall of the vagina and so protect both from abrasive damage. Males may be capable of erecting the setae slightly. If the setae function in this way, they may provide the genital ligula with the firm grip needed to facilitate freedom of movement by elements of the penis head during insemination and the removal of sperm from other males. If this is true than it seems logical that there would be a link between the development of the setae and the importance of sperm removal in a species. However this topic is outside the scope of this study. Thirteen genera of Megapodagrionidae were found to have horizontal gills and no setae on the genital ligula, whereas setae are present and well developed in 10 genera with other types of gills (table 2). The only exceptions to this general rule are *Dimeragrion* and *Paraplebia*. Of the three species of *Paraplebia* checked two had a few relatively small setae while one lacked setae. *Dimeragrion* is the only genus to have horizontal gills and setae on the genital ligula. As both characters are conservative between families and are not developmentally or selectively associated we consider these results potentially useful in resolving the phylogeny of the megapods. Based on these results Megapodagrionidae fall into four groups:

Balloon megapods This group includes genera from America, *Tatocnemis* from Madagascar and *Rhipidolestes* from Asia. Based on the presence of setae on the genital ligula, all American genera for which the larva have not yet been described, might fall in this group. Based on the same character the Asian genera *Mesopodagrion*, *Priscagrion* and *Sinocnemis* as well as *Agriomorpha*, *Bornargiolestes* and *Burmargiolestes* might also belong in this group. However the former three genera might have completely different and unexpected affinities

while the latter three seem to form a monophyletic group on their own which may or may not fall in Megapodagrionidae. The genus *Pseudolestes* is aberrant in many respects, which led to the establishment of the family Pseudolestidae. However the results of Bybee et al. (2008) suggest that it falls within Megapodagrionidae and is ‘just’ a highly advanced species within this family. The same might be true for *Thaumatoneura inopinata*, which was often placed in its own subfamily, but is now considered, based on adult and larval morphology, to be closely related to *Paraplebia* (Garrison et al. 2010). The genera included here in this group might form a monophyletic clade but could very well be a paraphyletic or polyphyletic group. It must also be noted, in support of the latter suggestions, that this type of gill structure also occurs in Euphaeidae, Lestoideidae, ‘*Philogangá*’, some Isostictidae, some Platystictidae, and in the platycnemidids *Stenocnemis pachystigma* (Selys, 1886) and *Allolestes leucosticta* (Selys, 1863), although the latter lacks the terminal filaments. The Balloon megapods is the least well-defined of our groups, and within any grouping of higher taxa considered the character may represent a symplesiomorphy, or in some cases, homoplasy.

Long-legged megapods This group currently contains only *Teinopodagrion*. According to De Marmels (2001), this genus forms a monophyletic group together with *Allopodagrion* and *Megapodagrion*. Based on adults he gives four ‘possible synapomorphies’ for this group, of which the second ‘legs exceedingly long and spidery’ is in our opinion the most convincing. These long and spidery legs are also prominent in the six larvae that have thus far been described. In addition to this the larvae are further remarkable having dorsal hooks on the abdominal segments, a character not found in other genera of Megapodagrionidae, for which the larvae have been described, and very rare in Zygoptera. The larvae of *Allopodagrion* and *Megapodagrion* are not yet known but are expected to have the same gills as found in *Teinopodagrion*. De Marmels (2002) suggested that the Chinese *Priscagrion* might be related to

the group *Allopodagrion*, *Megapodagrion* and *Teinopodagrion* based on the shape of the apical segment of the genital ligula. *Priscagrion* has like these genera also very long legs, which supports this suggestion.

Tube megapods When describing the larva of *Rhinagrion mima* Lieftinck (1956) remarked that the structure of the caudal gills is 'unlike anything found in other larvae that I know of'. Currently only the genus *Rhinagrion* falls in this group. However, preliminary DNA results suggest that the genus *Philosina*, whose larva is undescribed, is closely related to *Rhinagrion*, which is supported by peculiarities in the morphology of the genital ligula. Neither *Philosina* nor *Rhinagrion* were analysed in Bybee et al. (2008). Preliminary DNA analyses do not show these genera to be closely related to other megapodagrionid genera and they might form a monophyletic group of their own.

Fan megapods In Bybee et al. (2008) six genera with horizontal gills from Australasia are included and these form a monophyletic group at the end of the pectinate Megapodagrionidae branch. Genera with horizontal gills from Africa and Asia are lacking from their analyses. Based on the information on the larva presented here and the absence of setae on the genital ligula we suggest the Madagascan genus *Nesolestes* and the Asian genus *Podolestes* are more closely related to the Australasian genera than to any of the Balloon megapods or Tube megapods. For the genera *Allolestes*, *Amanipodagrion* and *Neurolestes* no larvae have been described. *Allolestes* and especially *Neurolestes* resemble *Nesolestes* (Dijkstra 2003), lack the setae on the genital ligula and are therefore believed to belong to this group. *Amanipodagrion* does not strongly resemble any other megapodagrionid genus. Based on the absence of setae on the genital ligula and unpublished preliminary results of DNA analyses we tentatively suggest that it also belongs in this group. We also provisionally place the Madagascan *Protolestes* within this grouping; we note that, although it has in a general sense horizontal gills, their detailed morphology

may not entirely conform to the typical Fan megapod pattern, and re-examination of fresh larval material is needed to resolve this issue. *Dimeragrion* is the only genus with horizontal gills to occur in South-America. The larva of this genus is described based on one exuvia and it is possible the gills would be inflated in life in which case it would belong to the Balloon megapods. It differs from all other genera with horizontal gills in the respect that it has setae on its genital ligula and that the gills have a terminal filament both better fitting the Balloon megapods than the Fan megapods. If the gills are indeed flat than these characters suggest that either the horizontal gills in *Dimeragrion* have evolved independently or, when considering the presence of setae as a plesiomorphic character, that *Dimeragrion* is basal to the other genera with horizontal gills. In the description of the larva of *Dimeragrion* De Marmels (1999) pointed out the resemblance of the prominent, bilobed median lobe of the labium with that of two species of Fan megapods from New Caledonia: *Argiolestes ochraceus* and a unidentified megapodagrionid larva (Lieftinck 1976) which might be seen as an indication that *Dimeragrion* is more closely related to other Fan megapods. All genera included by us in the Fan megapods, with the possible exception of *Dimeragrion* and *Protolestes*, are believed to form a monophyletic clade.

The present article discusses possible relationships within Megapodagrionidae based on consideration of the thorough phylogenetic work by Bybee et al. (2008) and the interpretation of two highly informative morphological characters. Based on these we consider the Long-legged megapods, the Tube megapods and the Fan megapods, with the possible exception of *Dimeragrion* and *Protolestes*, to be monophyletic groups. Further DNA work on a wider set of megapodagrionid genera is needed to test these hypotheses. There is however also a need for extensive fieldwork in order to understand megapodagrionid taxonomy. Finding and describing the larvae of the 'unknown' genera would be a very valuable contribution. The larvae of four genera or groups are of special interest:

- *Philosina*: Demonstration of tube-like gills in the larva of *Philosina* would confirm its relation with *Rhinagrion*.
- *Pseudolestes*: Demonstration of saccoid gills in larva of this genus would strengthen the suggestion that this aberrant species falls within Megapodagrionidae and is related to species included in the Balloon megapods.
- *Amanipodagrion*: This genus is difficult to place as it has several aberrant characters. Finding the larva might clarify its relationship with the Fan megapods.
- *Agriomorpha*, *Bornargiolestes*, *Burmargiolestes*: This group of seemingly closely related genera might fall in the group of the Balloon megapods.

ACKNOWLEDGEMENTS

Natalia von Ellenrieder, Jürg De Marmels and Rosser Garrison supplied information on the larvae and adults of the American genera. KD Dijkstra did likewise for the African genera. Matti Hämäläinen provided information on setae on the genital ligula of various Caloptera. Neville Yates provided specimens to AGO to examine. Jan van Tol made many SEM images of Platystictidae available for this study. The manuscript benefited greatly from critical comments from Matti Hämäläinen and Günther Theischinger. To all we express our appreciation and thanks.

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4. GENERIC REVISION OF ARGIOLESTIDAE (ODONATA),

WITH FOUR NEW GENERA

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Citation: Kalkman, V.J. & G. Theischinger 2013. Generic revision of Argiolestidae (Odonata), with four new genera. – International Journal of Odonatology 16: 1-52.

The subfamily Argiolestinae is raised to family level to include all zygopteran genera in which the gills of the larvae are flat and held in a horizontal plane. A diagnosis of the family is given and characters for both adults and larvae are presented. The family is divided into two subfamilies based on characters in the genital ligula, with the subfamily Argiolestinae found in Australasia east of Huxley's Line and the subfamily Podolestinae found in Africa and Asia west of Huxley's Line. Four genera are newly described: *Eoargiolestes* (New Caledonia, type species *Sympecma ochracea* Montrouzier, 1864), *Luzonargiolestes* (Philippines, type species *Argiolestes realensis* Gapud & Recuenco, 1993), *Solomonargiolestes* (Bougainville, Papua New Guinea and Malaita, Solomon Islands, type species *Argiolestes bougainville* Kalkman, 2008) and *Pyrhargiolestes* (Papua New Guinea, type species *Argiolestes sidonia* Martin, 1909). In addition *Metagrion* (type species *Argiolestes postnodalis* Selys, 1878) and *Wabnesia* (type species *Argiolestes kirbyi* Förster, 1900), two genera not in use for over 70 years, are reinstated. Based on molecular data the African genera *Neurolestes* and *Nesolestes* have been shown to be good genera and are here treated as such, *Nesolestes nigeriensis* is transferred to *Neurolestes*. All 20 genera included in Argiolestidae are discussed, with type species, key characters of adults, distribution and habitat being given. In addition a diagnosis is presented for each genus and information is given on their identification together with a map of the distribution of the genus and scanning electron microscope images of the genital ligula of most genera. A key to the genera of the Australasian region is presented and keys to the species of *Caledargiolestes*, *Caledopteryx* and *Podopteryx* are given. New distributional records of *Caledargiolestes*, *Caledopteryx*, *Luzonargiolestes*, *Solomonargiolestes* and *Podopteryx* are provided.

INTRODUCTION

Megapodagrionidae sensu lato, with more than 260 species, is the second largest family of Zygoptera. Nearly all species included are tropical or subtropical and most reproduce in running waters and seepages in tropical forest. The taxonomy of the group has long been considered problematic and in the last few years it has slowly become clear that Megapodagrionidae sensu lato comprises several monophyletic groups, some of which are

only distantly related (Bybee et al. 2008, Dumont et al. 2009, Rehn 2003).

Several proposals have been made to divide the family into subfamilies, most of these based on wing venation. The most recent proposals for subfamilies within Megapodagrionidae sensu lato are those of Davies & Tobin (1984) and Bechly (2003); the former was also used by Silsby (2001). These do not however reflect monophyletic groups. Several recent studies of the phylogeny

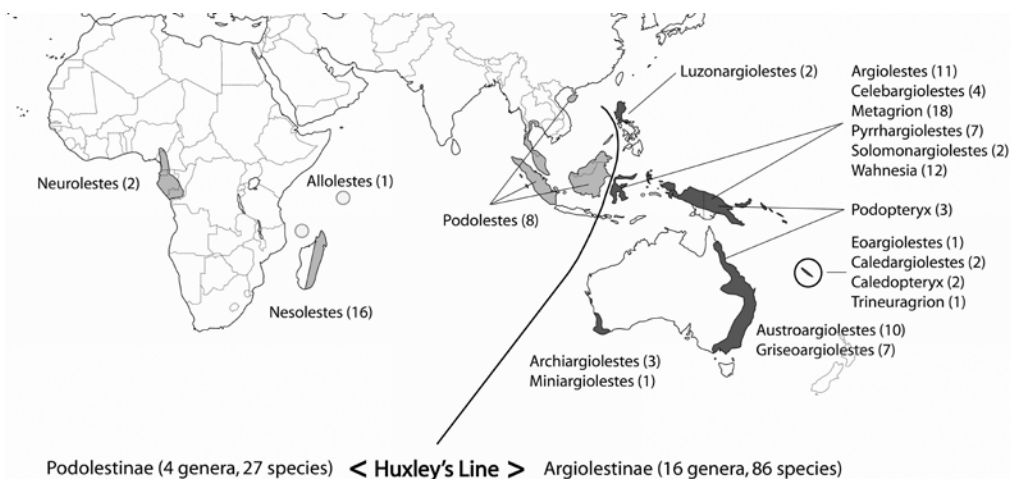


Figure 1. Distribution of the genera included in Argiolestidae, with those belonging to Argiolestinae in dark grey and those belonging to Podolestinae in pale grey. The number of species is shown after the genus names.

of dragonflies based on morphology and/or DNA were only partially successful in dividing Megapodagrionidae *sensu lato* into welldefined monophyletic groups, and a final division of genera included in Megapodagrionidae *sensu lato* into monophyletic groups is still needed (Bybee et al. 2008, Dumont et al. 2009, Rehn 2003). Based on the larval gills Kalkman, Choong et al. (2010) divided Megapodagrionidae *sensu lato* into four groups, three of which were suggested to be monophyletic. One of those groups was nicknamed Fanmegapods because the gills are flat and held in a horizontal plane, a character state not found in any other group of Odonata. Subsequent DNA sequence analysis has shown that the Fan megapods as proposed by Kalkman, Choong et al. (2010) are indeed largely monophyletic and the present paper therefore elevates the subfamily Argiolestinae to family level to contain all species of the Fan megapods with the exclusion of three genera. The three genera originally included in Fan megapods but which molecular work has shown to fall outside the Argiolestidae are *Dimeragrion* Calvert, 1913, *Amanipodagrion* Pinhey, 1962 and *Protolestes* Förster, 1899. The South American genus *Dimeragrion* was included in this group with

some doubts by Kalkman, Choong et al. (2010) because the larva has flat gills which are held in a horizontal plane. Tennesen (2010) argued that the larvae of *Dimeragrion* are different from other genera with fan-shaped gills because they have a terminal filament not present in Fan megapods. This is however not completely correct as some genera (*Archiargiolestes*, *Griseoargiolestes* and *Miniargiolestes*) within Australian genera of Argiolestidae have a filament (Theischinger 1998b). However, in these genera the filaments are articulated at the base, whereas in *Dimeragrion* the terminal filament is unarticulated. Based on the larval characters both Tennesen (2010) and Pérez-Gutiérrez & Montes-Fontalvo (2011) suggested *Dimeragrion* to be more closely related to one of the genera in which the gills are saccoid. This also fits better with the presence of setae on the shaft of the genital ligula in *Dimeragrion* given that these are absent in all other species included in Argiolestidae but present in most other genera of Megapodagrionidae *sensu lato*. *Amanipodagrion* was provisionally placed in the group with larvae having fan shaped gills based on the absence of spines on the shaft of the genital ligula, although its larva was unknown. The adult differs from the adults of Argiolestidae

Table 1. List of species included in Argiolestidae. The species belonging to the new genera were formerly all included in *Argiolestes*. Type species of genera are indicated by a dot.

Family ARGIOLESTIDAE Fraser, 1957	
Subfamily ARGIOLESTINAE Fraser, 1957	
<i>Archiargiolestes</i> Kennedy, 1925	
<i>parvulus</i> (Watson, 1977) – Australia: West Australia	
•	<i>pusillissimus</i> Kennedy, 1925 – Australia: West Australia
	<i>pusillus</i> (Tillyard, 1908) – Australia: West Australia
<i>Argiolestes</i> Selys, 1862	
	<i>alfurus</i> Lieftinck, 1956 – Indonesia: Moluccas
	<i>amphistylus</i> Lieftinck, 1949 – Indonesia: mainland Papua
•	<i>australis</i> (Guérin Meneville, 1830) – Indonesia: mainland Papua, Waigeo
	<i>celebensis</i> Kalkman, 2007 – Indonesia: Sulawesi
	<i>foja</i> Kalkman et al., 2010 – Indonesia: mainland Papua
	<i>macrostylis</i> Ris, 1913 – Indonesia: mainland Papua
	<i>muller</i> Kalkman et al., 2010 – PNG: mainland
	<i>obiensis</i> Lieftinck, 1956 – Indonesia: Moluccas
	<i>pallidistylus</i> Selys, 1878 – Indonesia: mainland Papua
	<i>roon</i> Kalkman et al., 2010 – Indonesia: Roon Island, Mioswaar Island
	<i>tuberculiferus</i> Michalski & Oppel, 2010 – PNG: mainland
<i>Austroargiolestes</i> Kennedy, 1925	
	<i>alpinus</i> (Tillyard, 1913) – Australia: New South Wales
	<i>amabilis</i> (Förster, 1899) – Australia: New South Wales, Queensland
	<i>aureus</i> (Tillyard, 1906) – Australia: Queensland
	<i>brookhousei</i> Theischinger & O'Farrell, 1986 – Australia: New South Wales
	<i>calcaris</i> (Fraser, 1958) – Australia: New South Wales, Victoria
	<i>christine</i> Theischinger & O'Farrell, 1986 – Australia: New South Wales
	<i>chrysoides</i> (Tillyard, 1913) – Australia: Queensland
	<i>elke</i> Theischinger & O'Farrell, 1986 – Australia: Queensland
•	<i>icteromelas</i> (Selys, 1862) – Australia: New South Wales, Victoria, Queensland ssp. – <i>icteromelas</i> (Selys, 1862) syn: – <i>icteromelas nobilis</i> (Tillyard, 1913) ssp. – <i>nigrolabiatius</i> Theischinger & O'Farrell, 1986. Lectotype (of <i>calcaris tenuis</i>) syn: – <i>calcaris tenuis</i> (Fraser, 1959) <i>A. icteromelas nigrolabiatius</i> is nom. nov. for <i>A. calcaris tenuis</i> ; Theischinger & O'Farrell (1986) erroneously designated the lectotype of <i>A. calcaris tenuis</i> as holotype of <i>A. icteromelas nigrolabiatius</i> (Houston & Watson, 1988).
	<i>isabellae</i> Theischinger & O'Farrell, 1986 – Australia: New South Wales
<i>Caledargiolestes</i> Kennedy, 1925	
	<i>janiceae</i> Lieftinck, 1975 – New Caledonia
•	<i>uniseriis</i> (Ris, 1915) – New Caledonia
<i>Caledopteryx</i> Kennedy, 1925	
	<i>maculata</i> Winstanley & Davies, 1982 – New Caledonia
•	<i>sarasini</i> (Ris, 1915) – New Caledonia
<i>Celebargiolestes</i> Kennedy, 1925	
•	<i>cinctus</i> (Selys, 1886) – Indonesia: Sulawesi syn: <i>karnyi</i> (Fraser, 1926)
<i>Eoargiolestes</i> Kalkman & Theischinger, 2012	
•	<i>ochraceus</i> (Montrouzier, 1864) – New Caledonia syn: <i>rouxi</i> (Ris, 1915)
<i>Griseargiolestes</i> Theischinger, 1998	
	<i>albescens</i> (Tillyard, 1913) – Australia: New South Wales, Queensland
	<i>bucki</i> Theischinger, 1998 – Australia: New South Wales
	<i>eboracus</i> (Tillyard, 1913) – Australia: New South Wales, Victoria, Queensland
	<i>fontanus</i> (Tillyard, 1913) – Australia: New South Wales, Queensland
•	<i>griseus</i> (Selys, 1862) – Australia: New South Wales

Table 1. Continued

<p>ssp. – <i>griseus</i> (Selys, 1862) ssp. – <i>subgriseus</i> (Fraser, 1959) ssp. – <i>tenuis</i> (Tillyard, 1913) <i>intermedius</i> (Tillyard, 1913) – Australia: New South Wales, Victoria <i>metallicus</i> (Sjöstedt, 1917) – Australia: Queensland</p>	<p><i>triste</i> (Liefstinck, 1935) – Indonesia: mainland Papua <i>verrucatum</i> (Michalski & Oppel, 2010) – PNG: mainland</p>
<p>Luzonargiolestes Kalkman & Theischinger, 2012 <i>baltazarae</i> (Gapud & Recuenco, 2001) – Philippines: Luzon</p> <ul style="list-style-type: none"> • <i>realensis</i> (Gapud & Recuenco, 1993) – Philippines: Luzon 	<p>Miniargiolestes Theischinger, 1998 <ul style="list-style-type: none"> • <i>minimus</i> (Tillyard, 1908) – Australia: West Australia </p>
<p>Metagrion Calvert, 1913 <i>aurantiacum</i> (Ris, 1898) – PNG: New Britain, New Ireland <i>coartans</i> (Liefstinck, 1956) – Indonesia: Waigeo <i>connectens</i> (Liefstinck, 1956) – Indonesia: mainland Papua <i>convergens</i> (Liefstinck, 1949) – Indonesia: mainland Papua <i>fontinale</i> (Liefstinck, 1956) – Indonesia: mainland Papua <i>fornicatum</i> (Theischinger & Richards, 2007) – PNG: mainland <i>indentatum</i> (Theischinger & Richards, 2006) – PNG: mainland <i>lamprostoma</i> (Liefstinck, 1949) – Indonesia: mainland Papua <i>montivagans</i> (Förster, 1900) – PNG: mainland <i>ochrostoma</i> (Liefstinck, 1949) – Indonesia: Waigeo <i>ornatum</i> (Selys, 1878) – Indonesia: mainland Papua syn: <i>obscurum</i> (Selys, 1878) <i>pectitum</i> (Liefstinck, 1949) – Indonesia: mainland Papua</p> <ul style="list-style-type: none"> • <i>postnodale</i> (Selys, 1878) – Indonesia: mainland Papua, Japan <i>sponsum</i> (Liefstinck, 1956) – Indonesia: mainland Papua <i>subornatum</i> (Liefstinck, 1935) – Indonesia: mainland Papua, Japan <i>trigonale</i> (Theischinger & Richards, 2008) – PNG: mainland 	<p>Podopteryx Selys, 1871 <i>casuarina</i> Liefstinck, 1949 – Indonesia: mainland Papua</p> <ul style="list-style-type: none"> • <i>roseonotata</i> Selys, 1871 – Indonesia: mainland Papua, Salawati, Waigeo, Aru; PNG: mainland <i>selysi</i> (Förster, 1899) – Australia: Queensland; PNG: mainland; Indonesia: mainland Papua
<p>Pyrrhargiolestes Kalkman & Theischinger, 2012 <i>angulatus</i> (Theischinger & Richards, 2007) – PNG: mainland <i>aulicus</i> (Liefstinck, 1949) – Indonesia: mainland Papua; PNG: mainland <i>kula</i> (Englund & Polhemus, 2007) – PNG: mainland <i>lamington</i> Kalkman et al., 2013 – PNG: mainland</p> <ul style="list-style-type: none"> • <i>sidonia</i> (Martin, 1909) – PNG: mainland <i>tenuispinus</i> (Liefstinck, 1938) – PNG: mainland <i>yela</i> Kalkman et al., 2013 – PNG: Rossel Island 	<p>Solomonargiolestes Kalkman & Theischinger, 2012 <ul style="list-style-type: none"> • <i>bougainville</i> (Kalkman, 2008) – PNG: Bougainville <i>malaita</i> (Kalkman, 2008) – Solomon Islands: Malaita </p>
<p>Trineuragrion Ris, 1915 <ul style="list-style-type: none"> • <i>percostale</i> Ris, 1915 – New Caledonia </p>	<p>Wabnesia Förster, 1900 <i>annulipes</i> (Liefstinck, 1956) – PNG: Goodenough Island <i>armeniaca</i> (Liefstinck, 1956) – PNG: Goodenough Island <i>ephippiata</i> (Liefstinck, 1956) – PNG: mainland <i>esuriens</i> (Liefstinck, 1956) – PNG: mainland <i>gizo</i> (Kalkman, 2008) – Solomon Islands: Gizo, Vella Lavella, Rendovo</p>

Table 1. Continued

<ul style="list-style-type: none"> • <i>kirbyi</i> (Förster, 1900) – PNG: mainland <i>luteipes</i> (Liefstinck, 1956) – PNG: mainland <i>microstigma</i> (Liefstinck, 1956) – PNG: mainland <i>prothoracalis</i> (Liefstinck, 1956) – PNG: mainland <i>saltator</i> (Liefstinck, 1956) – PNG: mainland <i>saltuaria</i> (Liefstinck, 1956) – PNG: mainland <i>simplex</i> (Liefstinck, 1949) – Indonesia: mainland Papua <hr/> <p>Subfamily PODOLESTINAE Kalkman & Theischinger, 2012</p> <p><i>Allolestes</i> Selys, 1869</p> <ul style="list-style-type: none"> • <i>maclacblanii</i> Selys, 1869 – Seychelles syn: <i>nigra</i> Martin, 1896 <p><i>Nesolestes</i> Selys, 1891</p> <ul style="list-style-type: none"> <i>albicauda</i> Fraser, 1952 – Madagascar <i>albicolor</i> Fraser, 1955 – Madagascar • <i>alboterminatus</i> Selys, 1891 – Madagascar <i>angydna</i> Schmidt, 1951 – Madagascar <i>drocera</i> Fraser, 1951 – Madagascar <i>elizabethae</i> Liefstinck, 1965 – Madagascar <i>forficuloides</i> Fraser, 1955 – Madagascar <i>mariae</i> Aguesse, 1968 – Madagascar <i>martini</i> Schmidt, 1951 – Madagascar <i>pauliani</i> Fraser, 1951 – Comoros: Mohéli 	<ul style="list-style-type: none"> <i>pulverulans</i> Liefstinck, 1965 – Madagascar <i>radama</i> Liefstinck, 1965 – Madagascar <i>ranavalona</i> Schmidt, 1951 – Madagascar <i>robustus</i> Aguesse, 1968 – Madagascar <i>rubristigma</i> Martin, 1902 – Madagascar <i>tuberculicollis</i> Fraser, 1949 – Madagascar <hr/> <p><i>Neurolestes</i> Selys, 1882</p> <ul style="list-style-type: none"> <i>nigeriensis</i> (Gambles, 1970) – Nigeria • <i>trinervis</i> Selys, 1885 – Cameroon, Equatorial Guinea, Gabon, Republic of Congo <hr/> <p><i>Podolestes</i> Selys, 1862</p> <ul style="list-style-type: none"> <i>atomarius</i> Liefstinck, 1950 – Indonesia: Kalimantan <i>buwaldai</i> Liefstinck, 1940 – Malaysia: Peninsular Malaysia; Indonesia: Sumatra <i>chrysopus</i> Selys, 1889 – Brunei; Malaysia: Sarawak; Indonesia: Kalimantan <i>coomansi</i> Liefstinck, 1940 – Indonesia: Sumatra; Thailand (?) <i>furcifer</i> Liefstinck, 1950 – Indonesia: Kalimantan <i>harrissoni</i> Liefstinck, 1953 – Malaysia: Sarawak • <i>orientalis</i> Selys, 1862 – Brunei; Indonesia: Kalimantan, Sumatra; Malaysia; Singapore <i>pandanus</i> Wilson & Reels, 2001 – China: Hainan
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in lacking supplementary sectors in the tip of the wing and having a dark band in the wing. The larvae of *Protolestes* were shown to have fan-shaped gills, but the adults also lack supplementary sectors in the tip of the wing. Both *Amanipodagrion* and *Protolestes* seem to form separate lines in the evolution of damselflies and do not seem to have close relatives.

In the present paper the former subfamily Argiolestinae is elevated to family level to contain all species of the Fan megapods as discussed above and a definition of this family is given. Table 1 lists all genera and species we propose to include in Argiolestidae. We consider the present family to comprise 20 genera including new genera described here. For eight of these the larvae have not been described and inclusion within this family is

based only on adult morphology and, with the exception of *Solomonargiolestes*, for which DNA-material was not available, supporting molecular data.

The members of Argiolestidae are found in Madagascar and Seychelles (two genera, 17 species), mainland Africa (one genus, two species), mainland SE Asia, Borneo and Sumatra (one genus, eight species) and in the Australasian region from the Philippines, through Sulawesi to the Moluccas, New Guinea, the Solomon Islands, Australia and New Caledonia (16 genera, 83 species) (fig. 1). In the last region the highest diversity is found in Australia, New Caledonia and New Guinea. New Guinea has proven to be exceedingly rich, and in recent years numerous new species have been described from this region

(Englund & Polhemus 2007, Kalkman 2008, Kalkman, Richards et al. 2010, Michalski & Oppel 2010, Theischinger & Richards 2006, 2007, 2008). The genera of Africa, Madagascar, mainland SE Asia, Borneo and Sumatra have always been considered monophyletic in the literature, with only some discussion on whether *Nesolestes* is a synonym of *Neurolestes*. The genera of the Australasian region are more problematic. Those in Australia and most in New Caledonia are relatively well defined partly due to the work of Liefertinck (1975, 1976) and Theischinger (1998a). The 53 species currently placed in the genus *Argiolestes* occurring in the Philippines, Sulawesi, the Moluccas, New Guinea, the Solomons and New Caledonia remain poorly resolved. Earlier attempts to split the genus *Argiolestes* into separate genera resulted in the creation of the genera *Metagrion* Calvert, 1913 and *Wahnesia* Förster, 1900. The description of these genera was poor, partly due to the lack of material, and the characters on which the genera were based were found to be quite variable even within species (Liefertinck 1935a). For this reason these generic names were seldom used after having been established. In Kalkman, Richards et al. (2010) a definition was established for *Argiolestes sensu stricto* in which 10 species were included. In order to accommodate all species of *Argiolestes* excluded from *Argiolestes sensu stricto* we describe four new genera and redefine the genera *Metagrion* and *Wahnesia*. New definitions and a key to all genera included in Argiolestidae are given. For all genera information on key generic characters, identification, habitat and distribution is provided. Our results are based on morphology only but the division proposed here is supported by a molecular study which will be published separately.

METHODS

We examined adults of all genera, 90% of the described species and almost all of the original descriptions. Species for which no material was

studied are *Podolestes pandanus* and 11 species of *Nesolestes* (*albicaudus*, *albicolor*, *angydna*, *drocera*, *elisabethae*, *forficuloides*, *mariae*, *pauliani*, *robustus*, *rubristigma*, *tuberculicollis*). Most studied specimens are present in Naturalis Biodiversity Center, Leiden (RMNH) in which collection nearly all species studied for this revision are available. Additional material, mainly types, has been studied in the BMNH, HNHM and IRSN. Listed material is present in the RMNH unless otherwise noted.

The information on larvae was derived from the literature. Larvae of eight of the 20 genera have not been described (including *Celebargiolestes* for which only an illustration is available) and the larvae of only a small selection of the total number of species have been described (see Kalkman, Choong et al. 2010, for an overview) for four additional genera. Our present study therefore relies largely on adult characters. Morphological terminology largely follows Garrison et al. (2010).

ABBREVIATIONS

BMNH: Natural History Museum, London, UK; HNHM: Hungarian Natural History Museum, Budapest, Hungary; IRSN: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KSP: Koleksi Serangga Papua, Jayapura, Indonesia; PNG: Papua New Guinea; RMNH: Naturalis Biodiversity Centre, Leiden, Netherlands.

SYSTEMATIC PART

Argiolestidae Fraser, 1957 (fig. 1-6)

Unique characters within Zygoptera

Adult. We have found no unequivocally unique character available for adult Argiolestidae. However the row of small dark denticles present on the apex of the cerci (see diagnosis) might have independently evolved in Argiolestidae and could

be regarded as unique although a structure very much reminiscent of this is found in the New World genera *Heteragrion* and *Oxystigma*. Larva. Gills are flat and held in a horizontal plane (shared with *Protolestes* and *Dimeragrion*, see Introduction) (fig. 2).

Diagnosis of adults

Small to large damselflies, all resting with wings open and many lacking bright colours. Venation allows discrimination from most other families with the exception of those formerly placed in Megapodagrionidae (fig. 3): (1) 2, seldom 3 Ax; (2) supplementary sectors between IR1 and RP2 and between RP2 and IR2 present; (3) Pt longer than broad (except in *Caledargiolestes*); and (4) IR2 originating near the subnodus, starting clearly closer to nodus than to arculus. Adults of Argiolestidae can be distinguished from other genera formerly placed in Megapodagrionidae by the absence of setae on the shaft of the genital ligula. The only other genera formerly placed in Megapodagrionidae lacking these setae are *Amanipodagrion* and *Protolestes*; these however lack the supplementary sectors in the wings (character 2 as mentioned above).

The main colour of most species is pale brown to black but many species have some blue or red on the face, thorax and/or legs. The abdomen generally lacks bright colours with the exception of the very strikingly coloured *Eoargiolestes ochraceus*. The following characters found in several genera of Argiolestidae are rare or absent in other damselflies:

- (1) A row of small dark denticles is present on the upper flange of the apex of the cerci (fig. 4). The length of this row varies among genera and its visibility depends partly on the colour of the cerci. Generally the row is easiest to see in less mature specimens as the cerci tend to be paler, whereas the denticles are already black. In some genera the individual denticles merge forming a low undulated ridge which is difficult to detect (for example in *Caledargiolestes* and *Caledopteryx*). The row of denticles

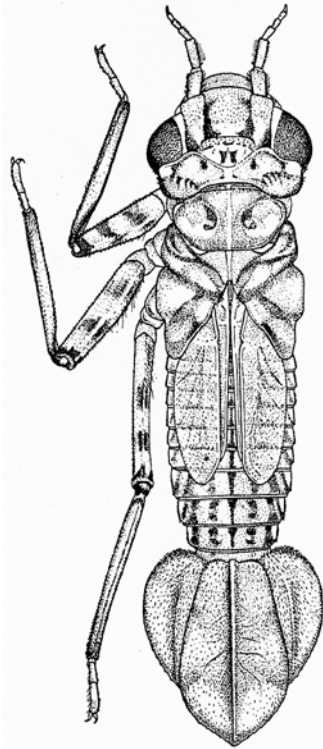


Figure 2. Larva of *Metagrion pectitum* showing the build of Argiolestidae larvae and the distinctive flat horizontal gills. Illustration from Liefstinck (1956).

is present in 16 of the 20 genera but seems to have become lost in *Archargiolestes*, *Austroargiolestes*, *Trineuragrion* and *Pyrrhargiolestes* (except in *P. angulatus*). A single species of the genus *Argiolestes* also lacks the row (*A. tuberculiferus*). Males of only four of the 16 species of *Nesolestes* were studied and only one, *Nesolestes pulverulans*, lacked a row of denticles, suggesting that this row is a prevalent character state within this genus. This row of denticles is absent in most Zygoptera but a similar row is found in some genera of Calopterygidae and some Neotropical genera such as *Heteragrion*, *Oxystigma* and *Heteropodagrion*.

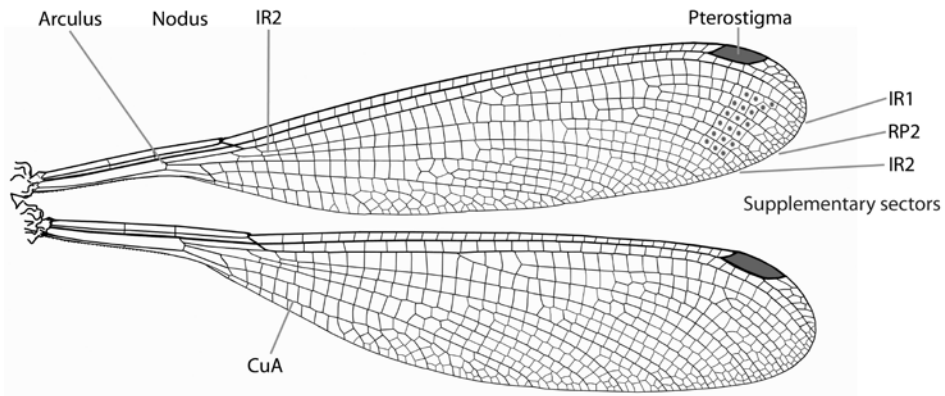


Figure 3. Forewing and hind wing of *Celebargiolestes* sp. showing the general venation found in family Argiolestidae. Drawing by A.G. Orr.

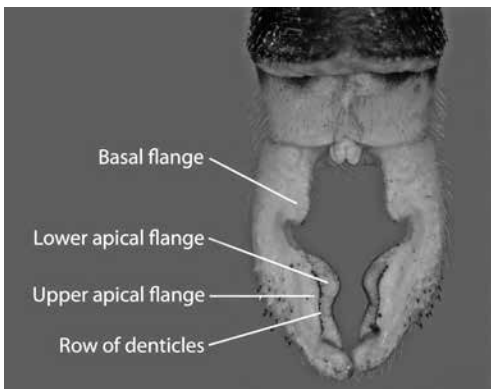


Figure 4. Anal appendages of male *Argiolestes amphistylus* showing the general build of the appendages in Argiolestidae. The white colour of the appendages and the presence of a basal flange are atypical for Argiolestidae and are unique for the genus *Argiolestes*.

- (2) The dorsum of S8-9 is weakly sclerotised (in *Metagrion*, *Wahnesia* and to a lesser extent in *Eoargiolestes* and *Caledopteryx*). This character corresponds with the presence of a dorsal spine or bundle of spines on S10 (*Wahnesia*) (fig. 5e) or with the hind rim of S10 being serrated (*Metagrion*) (fig. 5b).
- (3) The thorax has a fractured pattern with the pale elements on both sides of the humeral suture not aligned (fig. 9c, 9e, 19b, 19d; present

in some species of *Austroargiolestes*, *Caledargiolestes*, *Caledopteryx*, *Griseargiolestes*, *Metagrion*, *Miniargiolestes*, *Nesolestes*, *Podopteryx* and *Solomonargiolestes*). In most other damselfly families the pale pattern either does not cross the humeral suture or is aligned. The taxonomic use of this character is limited as it is often absent simply because the pale pattern is missing either below and/or above the humeral suture.

- (4) Pterostigma of adult females bright white to cream yellow in *Celebargiolestes*, *Eoargiolestes*, *Miniargiolestes* and some species of *Austroargiolestes* and *Griseargiolestes*. In *Podopteryx* the pterostigma of females becomes cream white to yellowish above and brown below.

Subfamilies

We partition the family into two subfamilies, Argiolestinae and Podolestinae. This is based on molecular analyses but is supported by the presence of longitudinal microstriae on the shaft of the ligula in Podolestinae (fig. 26c-f) which are absent in Argiolestinae (eg fig. 7c-d). Species of Podolestinae for which the ligula was studied have the base of the apical segment expanded and scoop-shaped; this is not the case or is present to a lesser extent in Argiolestinae. Two character states prevalent in Podolestinae but rare or absent in Argiolestidae are (1) reduction in of the teeth of the ovipositor with the

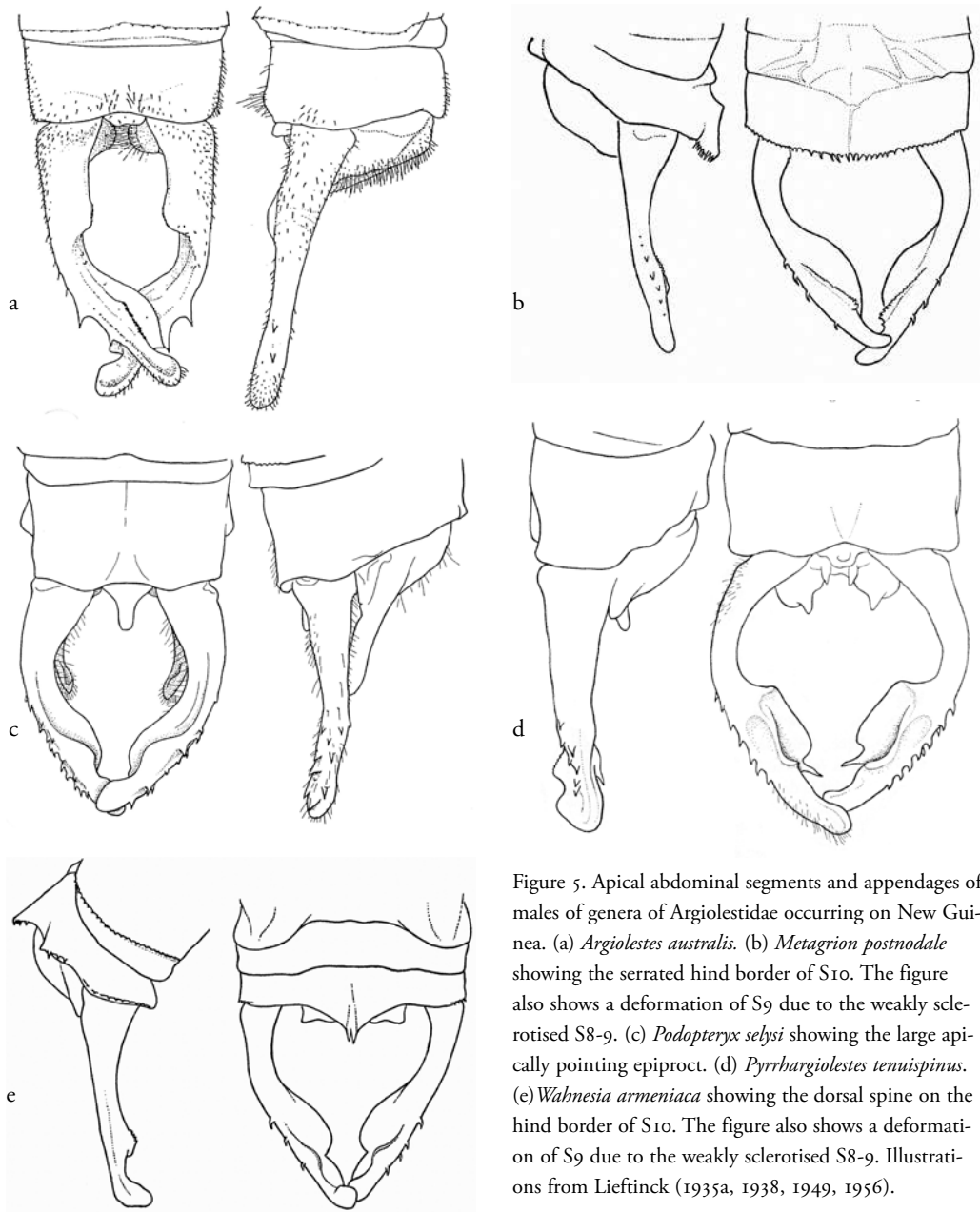


Figure 5. Apical abdominal segments and appendages of males of genera of Argiolestidae occurring on New Guinea. (a) *Argiolestes australis*. (b) *Metagrion postnodale* showing the serrated hind border of S10. The figure also shows a deformation of S9 due to the weakly sclerotised S8-9. (c) *Podopteryx seysi* showing the large apically pointing epiproct. (d) *Pyrrbargiolestes tenuispinus*. (e) *Wabnesia armeniaca* showing the dorsal spine on the hind border of S10. The figure also shows a deformation of S9 due to the weakly sclerotised S8-9. Illustrations from Liefstinck (1935a, 1938, 1949, 1956).

teeth being minute in *Podolestes* and *Allolestes* and absent in *Nesolestes* (fig. 6) (however also present in *Austroargiolestes*); and (2) ovipositor very long and surpassing cerci by at least the length of S10 (present in *Nesolestes*, *Allolestes* and *Podolestes harrisoni*).

Podolestinae includes the four genera found in Africa and Asia west of Huxley's Line while Argiolestinae includes the 16 genera found east of Huxley's Line (fig. 1).

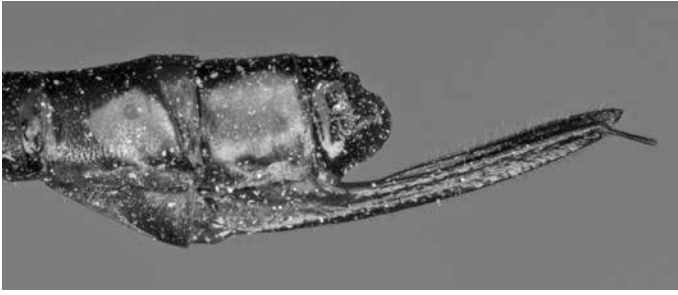


Figure 6. Ovipositor of *Nesolestes ranavalona*.

Argiolestinae Fraser, 1957

Key characters

Adult male. (1) Shaft of ligula smooth, longitudinal microstriae absent.

Adult female. (2) Ovipositor short, not reaching beyond cerci by more than the length of St_1 .

Archiargiolestes Kennedy, 1925 (fig. 7a, b, 8a, 9a)

Unique characters within Argiolestidae

Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Griseargiolestes*, *Miniargiolestes* and *Trineuragrion*).

Male. (2) Interior of base of cerci flattened and beset with long pale hairs. (3) Upper and lower apical flange of cercus merged and together forming a medially directed lobe (relatively small in *A. pusillus*). (4) Terminal fold of genital ligula beset with small spines (fig. 7a, b) (*A. parvulus*; not seen but probably also present in *A. pusillus* and *A. pusillissimus*).

Diagnosis and identification

Adult. The only genus of Argiolestidae with which *Archiargiolestes* overlaps in distribution is *Miniargiolestes*, from which it can be easily separated based on the above-mentioned unique characters. Except from *Miniargiolestes* and the New Caledonian *Trineuragrion percostale*, it can be distinguished from all genera by the completely dark dorsum of the thorax in combination with the sides of the thorax having a well-defined dark (brown to black) and yellow pattern.

A revision of the group including a key to the species, figures of the pattern on the thorax and scanning electron microscope (SEM) images of the cerci is found in Watson (1977). Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of Argiolestidae. Keys to the species can be found in Watson et al. (1991) and Theischinger & Endersby (2009). Theischinger & Hawking (2006) include pictures of all species. *Larva.* A key to distinguish larvae of the genus *Archiargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and in Theischinger & Endersby (2009). Characters to distinguish the individual species of *Archiargiolestes* are not known.

Distribution and habitat

The three species of this genus are limited to the south-western corner of Australia (fig. 8a). Distribution maps of the species can be found in Theischinger & Endersby (2009) and a more detailed map with discussion on their distribution is available in Watson (1977). *Archiargiolestes pusillus* is the most widespread, ranging further inland than *A. parvulus* and *A. pusillissimus*. The distribution of the latter two species falls nearly completely within the distribution of *A. pusillus*. These two have an allopatric distribution, with *A. parvulus* being found at the coastal plain of the west coast, east of the Darling Scarp, while *A. pusillissimus* replaces it on the south coast, south of Busselton. An isolated population of *A. parvulus* is found about 350 km north of its main range at Hutt River, west of Northampton (Watson 1977).

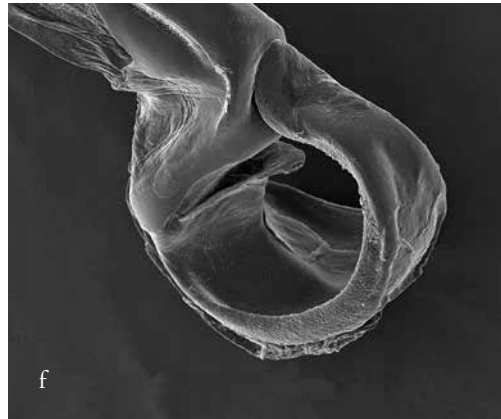
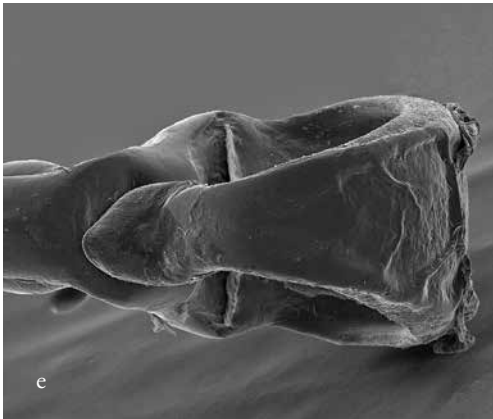
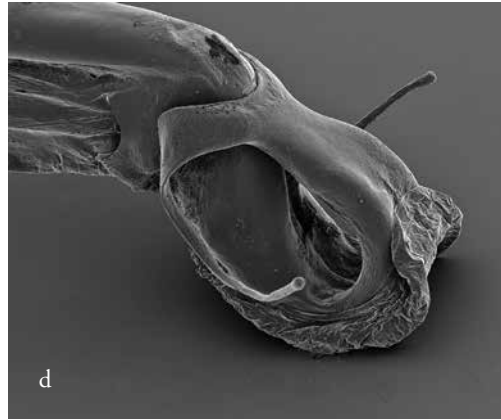
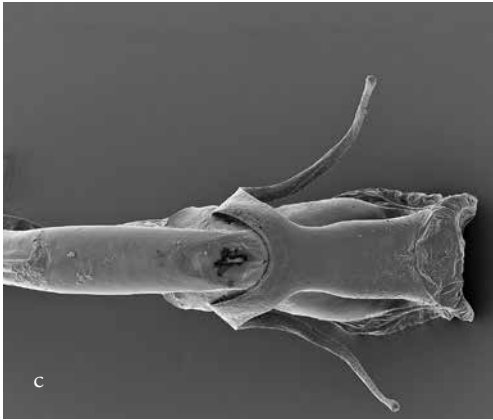
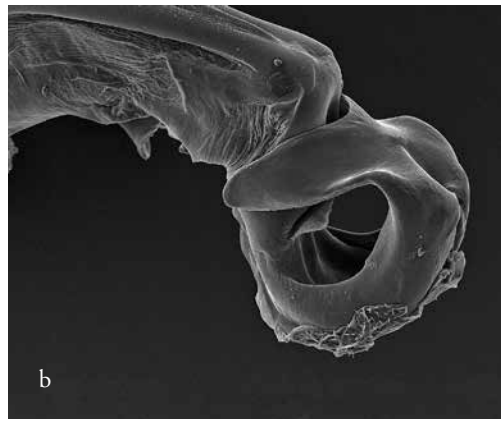
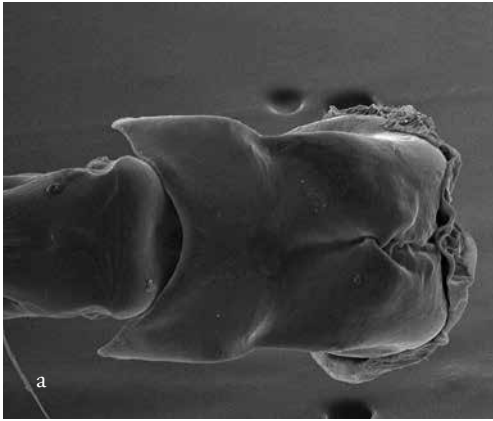


Figure 7. Genital ligula: (a) *Archiargiolestes parvulus*, Australia, West Australia, Gingin, 2010, ventral view; (b) idem, ventrolateral view; (c) *Argiolestes amphistylus*, Indonesia, Papua, Star Mountains, Borme, 2006, ventral view; (d) idem, ventrolateral view; (e) *Austroargiolestes isabellae*, Australia, New South Wales, Barren Ground, 1989, ventral view; (f) idem, ventrolateral view.

Photos: Dirk Gassmann.

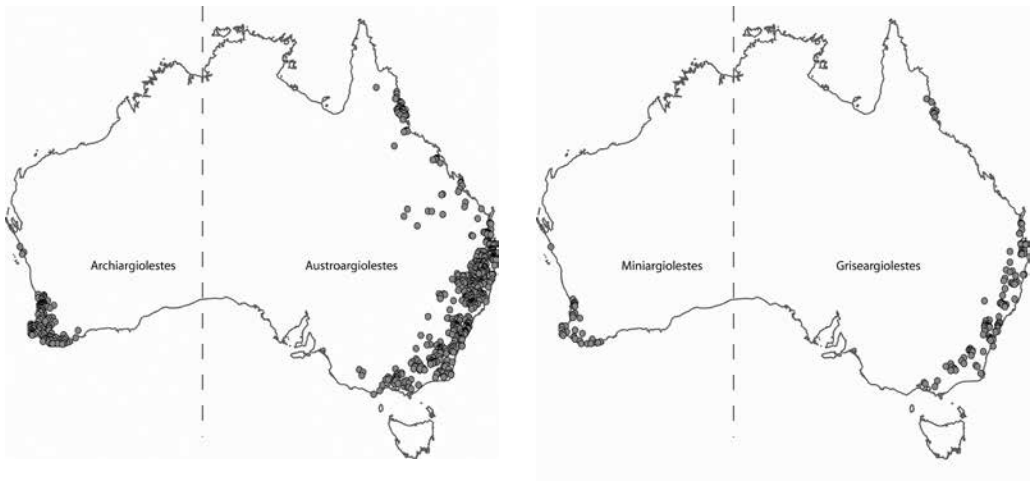


Figure 8. (a) Distribution of *Austroargiolestes* (eastern Australia) and *Archiargiolestes* (western Australia). (b) Distribution of *Griseargiolestes* (eastern Australia) and *Miniargiolestes* (western Australia). Based on records in the Australian Odonata Database.

Watson (1977) described the habitat as shallow, boggy and often seasonal waters, boggy edges of streams and rivers, seepages, marshes and open, shallow, vegetated areas.

***Argiolestes* Selys, 1862**
(fig. 7c, d, 9b, 10, 11a)

Unique characters within Argiolestidae

Male. (1) The two apical lobes of the genital ligula are at least four times as long as broad. (2) Part of S10 and cerci are pale (whitish or blue in life) contrasting with darker S9. This is only visible in fully mature specimens and is more easily seen in living individuals. (3) Base of cercus possesses a basal flange in all species except *A. celebensis* and *A. tuberculiferus* (see illustrations of latter two in Kalkman 2007, Michalski & Oppel 2010).

The sole specimen of *A. celebensis* seems to be sub-adult, which might be the reason that character (2) is not visible in this specimen.

Diagnosis and identification

Adult. The males of the genus have several unique characters, which should facilitate identification.

The pale white or blue S10 should make it possible to recognise members of the genus in the field. Kalkman, Richards et al. (2010) contains a key to the species with field pictures of *A. muller* and *A. roon*.

Larva. Unknown.

Distribution and habitat

The group occurs on New Guinea and adjacent islands, the northern islands of the Moluccas and on Sulawesi (fig. 10). Most species seem to have small ranges and none is known from more than five records. The number of specimens encountered in the field is generally low (Kalkman 2007, Kalkman, Richards et al. 2010, Michalski & Oppel 2010). This is in contrast to some other Papuan genera that are often common when found. The limited information on habitats shows that species of *Argiolestes* are found at small, often shallow, brooks in forest (fig. 11a) (Kalkman, Richards et al. 2010, Michalski & Oppel 2010).



Figure 9. (a) *Archiargiolestes parvulus*, male, Australia, Western Australia, Gingin Brook. Photo by Jan Taylor; (b) *Argiolestes muller*, male, PNG, Western Province. Photo by Steve Richards; (c) *Austroargiolestes alpinus*, male, Australia, New South Wales, Cathedral Rock NP. Photo by Vincent Kalkman; (d) *Caledargiolestes uniseries*, male, New Caledonia, Province Nord. Photo by Steve Richards; (e) *Caledopteryx sarasini*, male, New Caledonia, Province Nord. Photo by Steve Richards; (f) *Caledopteryx sarasini*, male, New Caledonia, Province Nord. Photo by Steve Richards.

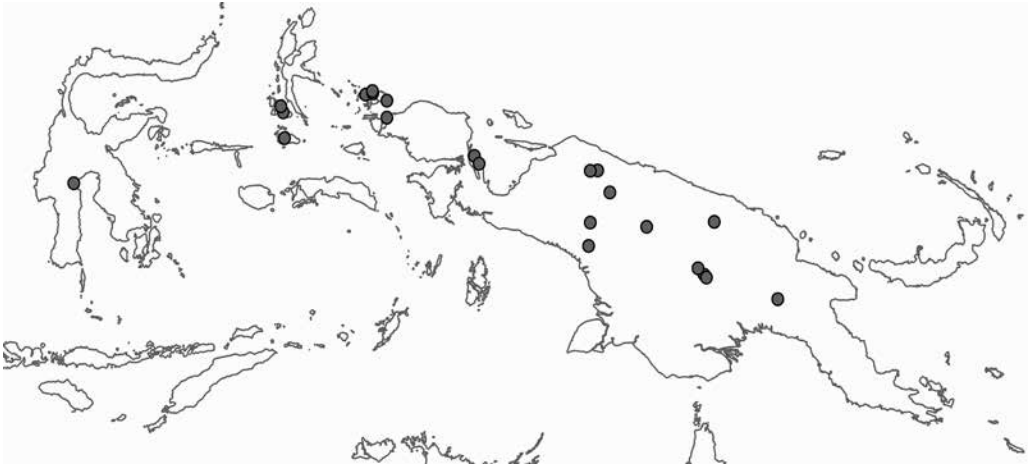


Figure 10. Distribution of *Argiolestes*. Based on record in the Melanesian Odonata Database.

***Austroargiolestes* Kennedy, 1925**
(fig. 7e, f, 8a, 9c)

***Risiolestes* Fraser (1926)**

Unique characters within Argiolestidae

Male. (1) Tip of genital ligula rounded or rounded and widened and never widely bilobed or reduced to a whip-like structure. (2) Sharp ventrally pointing tooth at about two-thirds the length of cerci.

Diagnosis and identification

Adult. Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of Argiolestidae. A key to the species can be found in Theischinger & O'Farrell (1986), Watson et al. (1991) and Theischinger & Endersby (2009). Theischinger & Hawking (2006) include pictures of all species.

Larva. A key to distinguish larvae of the genus *Austroargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and in Theischinger & Endersby (2009). Characters to distinguish the individual species of *Austroargiolestes* are not available.

Distribution and habitat

The 10 species of *Austroargiolestes* are endemic to Eastern Australia, occurring from the Grampians and the surroundings of Melbourne in the south to the Atherton Tableland in the north with their distribution centred on the Great Dividing Range (fig. 8a). *Argiolestes ictromelas* is by far the most widespread species, overlapping with all other species. The ranges of the other species are much smaller. Maps of the species can be found in Theischinger & Endersby (2009). The species inhabit streams and rivers, including streams that dry to pools in summer, rainforest streams and boggy seepages. Often co-occurs with *Griseargiolestes*. Little has been published on the behaviour of the species. Murray (1992) noted that *A. isabellae* oviposited unaccompanied by males. Eggs reared at room temperature hatched after 21 days, whereafter it took another 37 weeks for the adults to emerge (Murray 1992). These observations suggest that their development in natural conditions takes one year. Males are normally encountered in higher numbers than females. This makes a note published by Tillyard (1917) the more remarkable: 'An even more extraordinary result than this was obtained by working three or four small streams in dense palm jungle in Queensland. *Argiolestes amabilis* was to be seen on every rock. In a week

I had taken 195 females, but only a single male! Though I sought for the males high and low, they were not to be found. ' He suggested that the males were probably to be found in the top of the trees.

***Caledargiolestes* Kennedy, 1925**
(fig. 9d, 12a, b)

Unique characters within Argiolestidae

Adult. (1) Pt: costal side subequal to basal side.

Male. (2) Inflated base (“heel”) of apical lobes of genital ligula beset with numerous minute spines in *C. uniseriis* (shared with *Caledopteryx*; genital ligula of *C. janiceae* not described).

Diagnosis and identification

Adult. Endemic to New Caledonia, and males can easily be separated from other New Caledonian Argiolestidae by the absence of blue on the tip of the abdomen, in lacking enlarged distal membranes of S7-9 and in having two, not three, Ax in the wings. A detailed comparison between the males of both species is found in Liefertinck (1976). The males can be identified with the key below.

Larva. Both Willey (1955) and Liefertinck (1976) give a description of *C. uniseriis* as Megapodagrionidae spec. The larva described as *C. uniseriis* by Liefertinck (1976) is in fact *Trineuragion percossale* (Marinov 2012). A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Key to the males of *Caledargiolestes*

- 1. Body without conspicuous long raised hairs. Lower apical flange of cerci ending in a bluntly triangular tooth. Larger: hind wing 23-26 mm *C. uniseriis*
- Body, especially face, thorax and first two abdominal segments, covered with long raised whitish hairs. Lower apical flange of cerci rounded and not ending in a blunt triangular tooth. Smaller: hind wing 18 mm *C. janiceae*

Distribution and habitat

New records of *C. uniseriis*: 2 ♂, 1 ♀: New Caledonia, Yahoue, 17 February 1986, leg. Renevier.

Caledargiolestes uniseriis is common and widespread in New Caledonia, whereas *C. janiceae* seems to be very rare, being known only from the holotype collected on Mount Pouedihi (15 km w of Quenarou Forest Station) and a female specimen from “southern New Caledonia between Nouméa and Yaté” (Davies 2002). *C. uniseriis* has been found from November to April (Davies 2002), whereas the two records of *Caledargiolestes janiceae* are from 5 November 1972 (holotype) and 18 February 1983. Davies (2002) describes the habitat of *C. uniseriis* as “rocky forest streams and their waterfalls on lowground and in mountain areas; exuviae left in abundance on rock ledges and muddy edges at riversides”.

***Caledopteryx* Kennedy, 1925**
(fig. 9e, f, 12c, d)

Unique characters within Argiolestidae

Adult. (1) Blue postocular spots present. (2) Postocular lobes slightly enlarged and crenulated.

Male. (3) Distal membranes of S7-9 enlarged and bright blue. (4) “Heel” of apical lobes of ligula beset with numerous minute spines (shared with *Caledargiolestes*).

Diagnosis and identification

Adult. The blue postocular spots of males and females and the enlarged and bright blue distal membranes of S7-9 of males make this genus easy to recognise. Further distinguished from other genera of Argiolestidae, except *Celebargiolestes*, *Luzonargiolestes* and *Podopteryx*, by its large size (Hw > 32 mm) and by having more than 18 Px (range: 19-28). The two species, both endemic to New Caledonia, are morphologically extremely similar but can be recognised based on size and pattern. The differences between the two were described and illustrated by Winstanley & Davies (1982).

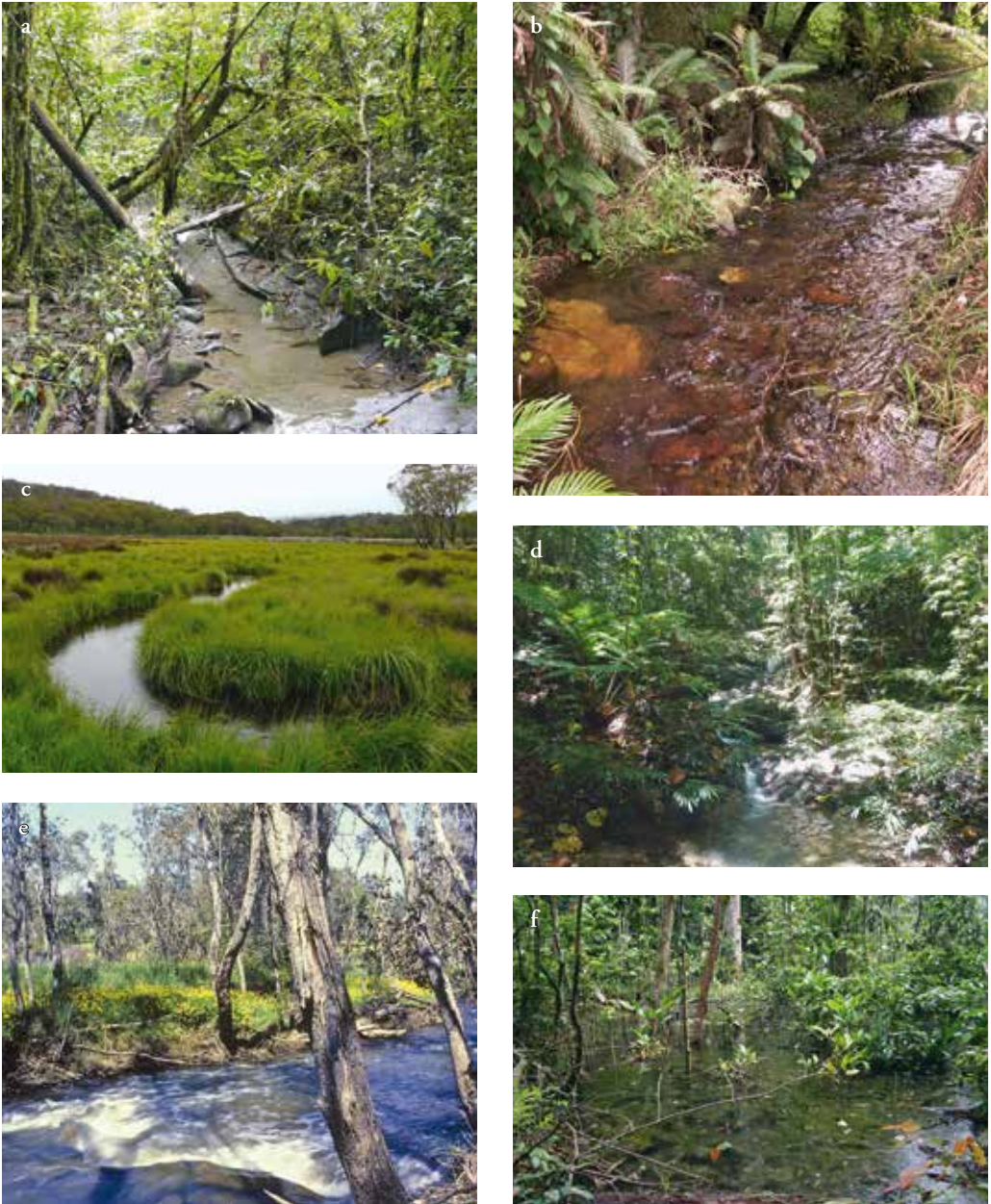


Figure 11. Examples of habitats of genera of Argiolestidae. (a) *Argiolestes muller*, *A. tuberculiferus* and two unidentified species of *Metagrion* (Whip group), PNG, Muller Range, Gugusu Camp. Photo by Vincent Kalkman. (b) *Eoargiolestes ochraceus*, New Caledonia, Thio Province. Photo by Milen Marinov. (c) *Griseargiolestes eboracus*, Polblue Swamp, Australia, New South Wales, Barrington Tops NP. Photo by Vincent Kalkman. (d) *Luzonargiolestes* cf. *baltazarae*, Philippines, Luzon, Cagayan Province, Claveria. Photo by Reagan Villanueva. (e) *Miniargiolestes minimus*, Australia, West Australia, Wooroloo Brook. Photo by Jan Taylor. (f) *Podolestes orientalis*, Malaysia, Selangor, Bangi Forest Reserve. Photo by Chee Yen Choong.

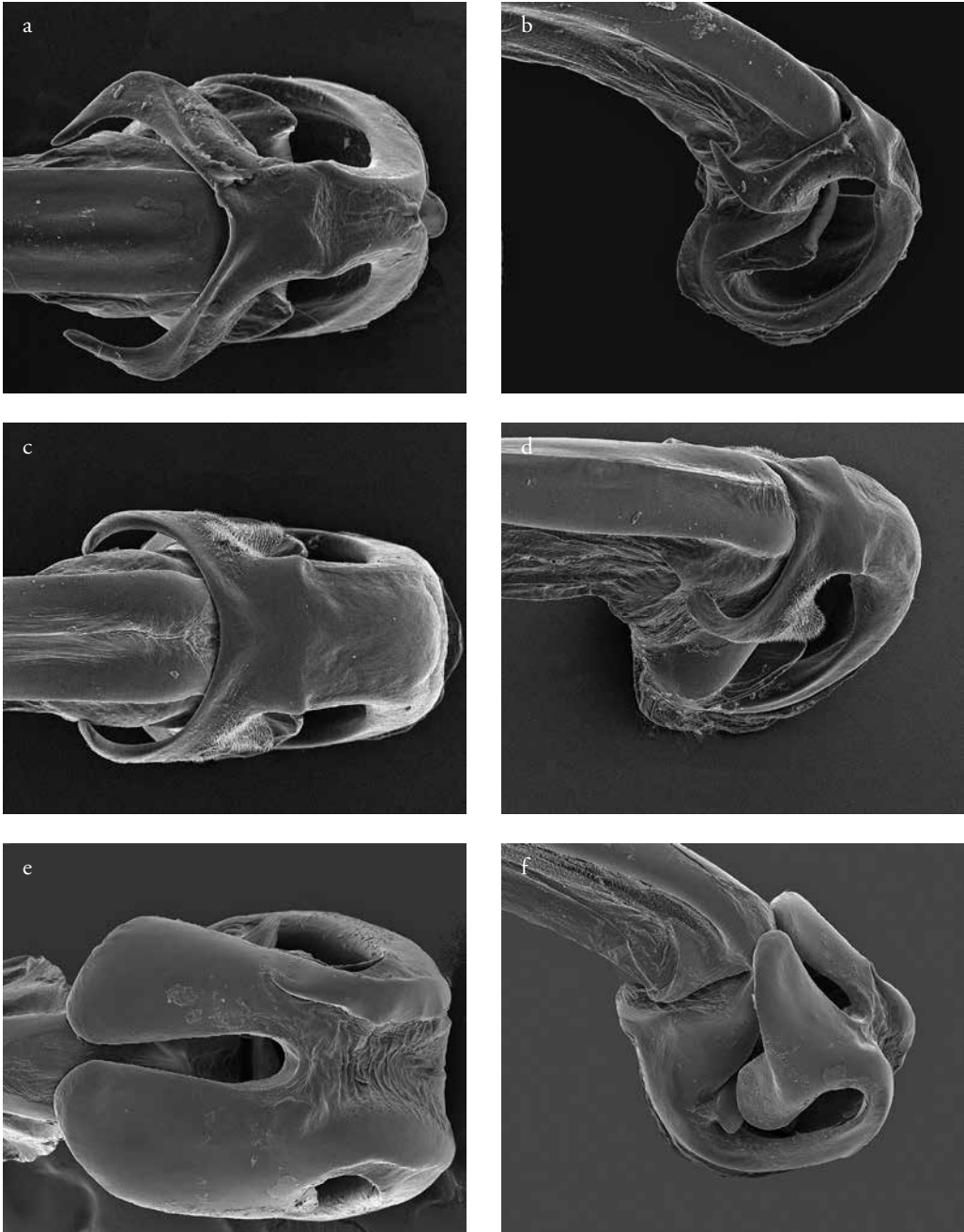


Figure 12. Genital ligula: (a) *Caledargiolestes uniseries*, New Caledonia, Col des Roussettes, 1969, ventral view; (b) idem, ventrolateral view; (c) *Caledopteryx sarasini*, New Caledonia, ventral view; (d) idem, ventrolateral view; (e) *Celebargiolestes cinctus*, Indonesia, Sulawesi, Sulawesi Tengah, 1989, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.



Figure 13. Distribution of *Celebargiolestes*. Based on records in the Melanesian Odonata Database.

Larva. Based on distribution the description of the larva of *C. sarasini* by Lieftinck (1976) probably pertains to the, at that time, undescribed *C. maculata*. The larva of *C. sarasini* is undescribed. A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Key to the males of *Caledopteryx*

1. Dorsum of S9 blue, connecting blue membrane of S8 with that of S9. S2-8 each with a pair of pale lateral spots at posterior border of the segment each covering about one-tenth length of segment *C. maculata*
- Dorsum of S9 black, blue membrane of S8 not connected by blue of S9. S2-8 uniformly dark without pair of pale lateral spots *C. sarasini*

Distribution and habitat

New records of *C. sarasini*, all from New Caledonia: 1 ♂: Valee d’Amoa, 17 February 1963, leg.

N.L.H. Krauss. 2 ♂, 1 ♀: Col de Tendo (near waterfall), 22 November 1985, leg. D.A.L. Davies. New records of *C. maculata*, all from New Caledonia: 2 ♂: Mouirance Pass, 10 February 1962, leg. N.L.H. Krauss. – 2 ♂, 2 ♀: La Captive, 18 February 1983, leg. D.A.L. Davies. – 1 ♂, 2 ♀: Mont Koghi Cascades, 5 February 1983, leg. J. Geijskes. – 1 ♂, 2 ♀: Thi, 9 December 1981, leg. D.A.L. Davies. – 3 ♂: Yate road, no date, leg. D.A.L. Davies.

Both species of *Caledopteryx* are endemic to New Caledonia where they are common at suitable streams (Davies 2002). *Caledopteryx maculata* has mainly been found in the southern tip of New Caledonia and is largely replaced by *C. sarasini* further north although their ranges overlap. Both *C. maculata* and *C. sarasini* have been recorded from November to February. Winstanley & Davies (1982) note that *Caledopteryx* species “generally occur in the steeper sections of forested catchments”. Males were found to settle horizontally on prominent perches at potential oviposition sites. Females were observed to “oviposit directly onto steep rock-faces” and “into a small rivulet flowing over a clay bed, and into a steep hillside seepage area where leaf litter had accumulated”. An exuvia was found “on a rockface approximately 1 m away from the water about halfway up a 3 m waterfall”. They also mention that larvae “were flushed with the point of a stiff leaf from horizontal cracks in the rocks on the faces of waterfalls”.

Celebargiolestes Kennedy, 1925 (fig. 12e, f, 13)

Unique characters within Argiolestidae

Male. (1) Large lateral lobe present at base of each of apical lobes, which is disc-like and covers the lateral “opening” of genital ligula.

Diagnosis and identification

Adult. The genus can be distinguished from all other members of the family by the combination of the following characters: (1) Fw with 25 or more

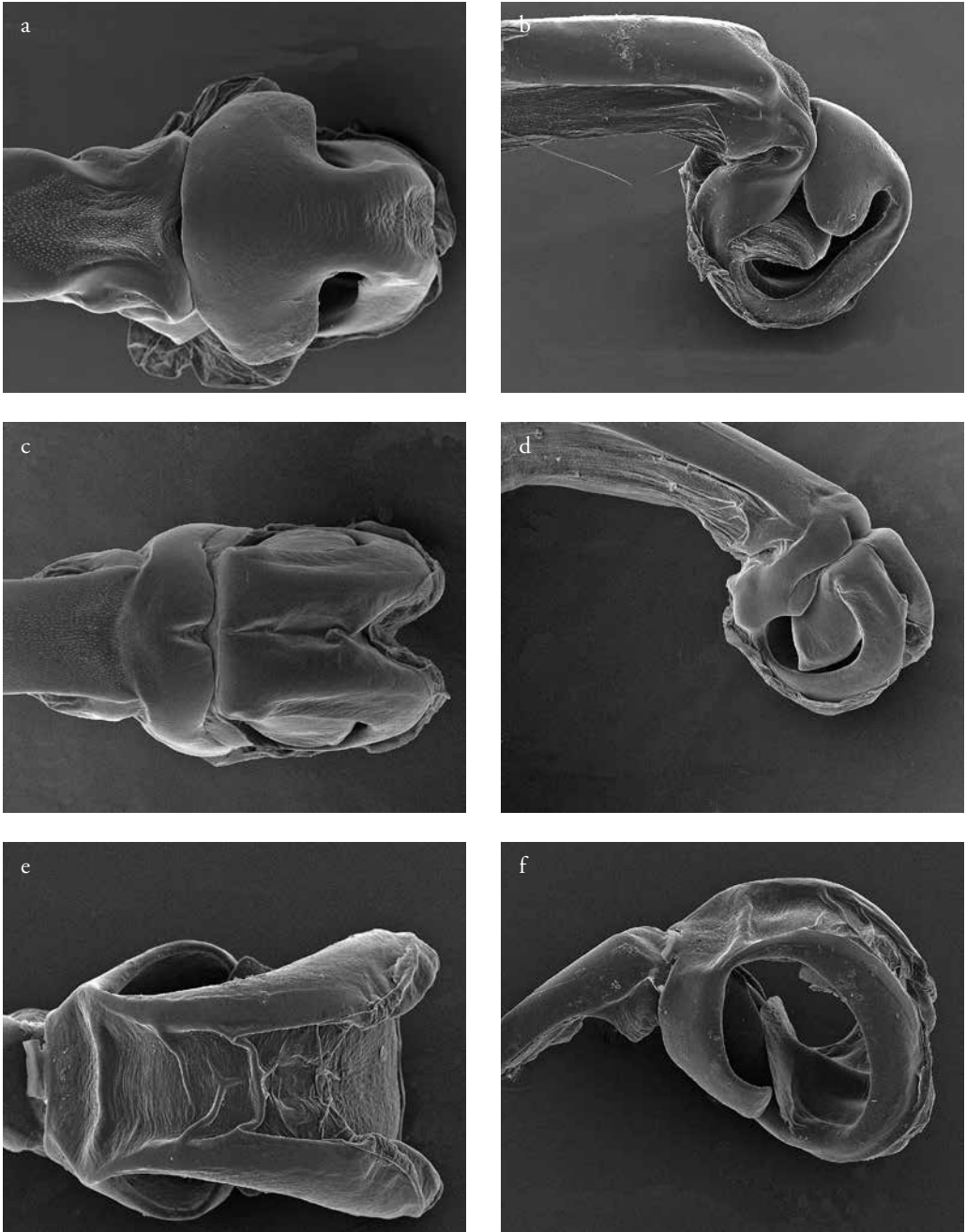


Figure 14. Genital ligula: (a) *Eoargiolestes ochraceus*, New Caledonia, ventral view; (b) idem, ventrolateral view; (c) *Griseargiolestes griseus*, Australia, New South Wales, Wentworth Falls, 2012, ventral view; (d) idem, ventrolateral view; (e) *Luzonargiolestes* cf. *baltazarae*, Philippines, Luzon, Cagayan Province, Claveria, 1997, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

Px; (2) epiproct shorter than one sixth of the length of the cerci; (3) postocular lobes not strongly bulging; and (4) face never with blue. The only other species of Argiolestidae occurring on Sulawesi is *Argiolestes celebensis*. This species is, however, easily distinguished from *Celebargiolestes* by having less than 24 Px and having very long and slender apices of the genital ligula. *Celebargiolestes cincta* is the only species described but descriptions of several new species together with a key by the first author are in preparation.

Larva. No detailed description of the larvae is available. Culhane (2005) published pictures of a megapodagrionid larva from Buton Island which is likely to pertain to *Celebargiolestes* (Kalkman, Choong et al. 2010).

Distribution and habitat

Celebargiolestes is found throughout Sulawesi and the adjacent islands of Sangihe, Peleng and Buton (larva only; Culhane 2005) (fig. 13). Based on the information on the labels of material present in the RMNH the habitat of *Celebargiolestes* is best described as brooks and small rivers in forest. The altitudinal range of the genus extends from 90 to 1500 m. It seems that the species are most common on the lower parts of mountains.

Eoargiolestes gen. nov. (fig. 11b, 14a, b, 15a)

Type species

Sympetma ochracea Montrouzier, 1864 by present designation.

Etymology

The name is composed of “Eo-” and the genus name “Argiolestes”. Eos is ancient Greek for dawn, referring to the bright orange colour on the thorax and abdomen.

Generic characterisation

Adult male. Head black except for pale stripe running from eye to eye across clypeus and small

pale dots between lateral ocelli and sockets of antennae; all pale markings becoming obscured in older specimens. Head slender without prominent postocular lobes. Thorax with ground colour black and with bright orange pattern on sides and on dorsum. Markings on thorax not crossing sutures. Thorax never with pruinosity. Interior of legs not expanded, no strong contrast in colouration between interior and exterior of legs. First pair of legs with one black ring on femora, second and third pair with two black rings. Femora becoming largely blackish with age. S2-6 bright orange, S7-8 black and S9-10 blue. Hw with two rows of cells between CuA and hind border. Discoidal cell of forewing with costal side subequal in length to distal side; Pt in mature males black but strikingly white in immature males. Wings of mature individuals have, especially at base, a distinct orange tinge. Genital valves pointed, longer than broad and gradually tapering towards apex. S9 only weakly sclerotised; S10 without distinct armature. Paraprocts shorter than one half of cerci. In dorsal view distance between cerci subequal to width of cercus at base. Cerci curved inwards from base; dorsally with a knob near apex and 4-6 spines on the outer border. Genital ligula not reduced and with expanded tip; inner fold large and often visible from ventral aspect.

Adult female. Thorax with far less extensive pale pattern than male and lacking bright orange colours; abdomen orange-brown to black lacking bright orange and blue. Pt in adults pale (cream white). Ovipositor short, not surpassing tips of cerci, with dense row of minute spines.

Unique characters within Argiolestidae

Male. (1) S2-6 bright orange. (2) Genital valves about twice as long as broad, gradually tapering towards pointed apex. (3) Wings of mature individuals with distinct orange tinge. Compared to other genera of Argiolestidae the head is relatively slender, with the space behind the lateral ocelli small and both frons and genae steep and not projecting. *Eoargiolestes* shares with *Metagrion* and *Wahnesia* the weakly sclerotised dorsum of S9; this is, however, less expressed in *Eoargiolestes*



Figure 15. (a) *Eoargiolestes ochraceus*, male, New Caledonia, Province Nord, Roche de la Wayem. Photo by Steve Richards. (b) *Griseargiolestes albescens*, male, Australia, Queensland, Springbrook NP. Photo by Vincent Kalkman. (c) *Luzonargiolestes* cf. *baltazarae*, male, Philippines, Luzon, Cagayan Province, Claveria. Photo by Reagan Villanueva. (d) *Metagrion subornatum*, male, Indonesia, Papua Province, Japen Island. Photo by Vincent Kalkman. (e) *Metagrion aurantiacum*, male, Papua New Guinea, New Britain. Photo by Steve Richards. (f) *Metagrion trigonale*, teneral male, Papua New Guinea. Photo by Steve Richards.

and in contrast to these other genera the segment does not appear wrinkled in dead specimens.

Diagnosis and identification

Adult. Monotypic genus, characters as for genus.
Larva. Liefertinck (1976) gives a description of *E. ochraceus*. A larval key to the genera of Argiolestidae occurring on New Caledonia can be found in Marinov (2012).

Distribution and habitat

New records of *E. ochraceus* all from New Caledonia: 1 ♂, 1 ♀: Bourail to Houailou road, March 1959, leg. N.L.H. Krauss. 2 ♀: Sarramca, 12 Feb 1963, leg. N.L.H. Krauss. 1 ♀: 10 km S of Koh, 300 m, 31 January 1963, leg. N.L.H. Krauss. 1 ♂: Mount Koghi, 500 m, January 1963, leg. N.L.H. Krauss.

The monotypic genus *Eoargiolestes* is endemic to New Caledonia where it is common and widespread. Davies (2002) gives the habitat as “shaded streams at edges of forest” (fig. 11b). Liefertinck (1976) provided the following remarks on the eight larvae he studied: “The body cuticle and gills of all specimens are covered throughout with a thin layer of silt and particles of fine sand adhering to the pubescence, so as to conceal most of the colour design. It is evident, therefore, that *A. ochraceus* lives in slow flowing water with a silty bottom”. Recorded from October to March.

Griseargiolestes Theischinger, 1998 (fig. 8b, 11c, 14c, d, 15b)

Unique characters within Argiolestidae

Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Archiargiolestes*, *Miniargiolestes* and *Trineuragrion*).
Male. (2) Genital ligula without inner fold (shared with *Podopteryx*).

Diagnosis and identification

Adult. Theischinger (1998a) gives a definition of the genus based on adult and larval characters and compares it with other Australian genera of

Argiolestidae. Theischinger (1998a, 1998b), and Theischinger & Hawking (2006) include pictures of all species. A key to the species can be found in Theischinger & Endersby (2009). The tip of the genital ligula is strongly curved and at least in the genital ligula of *G. griseus* depicted here, the tip is bent inwards (fig. 14c, d), although this is apparently not the case in all species/specimens (see drawing of genital ligula of *G. griseus*, *G. albescens* and *G. ebonacus* in Theischinger (1998a)).
Larva. A key to distinguish the larvae of the genus *Griseargiolestes* from those of other Australian Argiolestidae, and a key to some of the species can be found in Theischinger & Endersby (2009).

Distribution and habitat

The seven species of *Griseargiolestes* are restricted to eastern Australia, occurring from the surroundings of Melbourne in the south to the Atherton Tableland in the north with their distribution centred on the Great Dividing Range (fig. 8b). Maps for all species can be found in Theischinger & Endersby (2009). Most species are found at boggy seepages, small runnels, springs and streams (fig. 11c). They often co-occur with species of *Austroargiolestes*, but compared to these they are mostly found in the slower flowing and more densely vegetated sections. Adults sit low between the vegetation and rarely sit on the ground or on stones. *Griseargiolestes albescens* has been suggested to occur at dune lakes (Theischinger & Endersby 2009).

Luzonargiolestes gen. nov. (fig. 11d, 14e, f, 15c, 16)

Type species

Argiolestes realensis Gapud & Recuenco, 1993 by present designation.

Etymology The name is composed of a reference to Luzon, referring to the Philippine island where the genus occurs and the genus name “Argiolestes”.

Generic characterisation

Large, bulky species which are largely brownish and lack bright colours.

Adult male. Front of face, including labrum, mandibles, genae, clypeus and sockets of antennae dark brown to black. Postocular lobes bulging. Prothorax and synthorax brown to black without distinct pale pattern and never with pruinosity. Dorsum of synthorax dark brown to black, sides pale brown. Legs pale brown, lacking distinct dark markings and without contrast between interior and exterior; interior of legs not expanded.

S3-6 in all species brown to black with anterior pale mark and smaller posterior pale mark. Wings with two or more rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about three times as long as distal side. Dorsum of S8-9 normal, not weakly sclerotised. Hind rim of S10 without distinct armature, slightly raised in the centre forming low inconspicuous longitudinal crest; hind border slightly concave with epiproct visible in dorsal view. Paraprocts slightly shorter than half the length of cerci. In dorsal view distance between cerci subequal to width of one cercus. Base of cerci without basal flange. Outer border of cerci carrying several medium size spines. Cerci with lower and upper dorsal flange, the latter with row of inconspicuous brown to black denticles. Apical segment of genital ligula well developed with broad apical lobes which are about two to three times as long as wide, whole outer border of genital ligula, up to apex, weakly sclerotised and appearing wrinkled.

Adult female. Pt of adult females black. Ovipositor reaching or surpassing tip of cerci, beset with long yellow hairs and with dense and regularly spaced row of teeth.

Larva. Unknown.

Unique characters within Argiolestidae

Adult. (1) Postocular lobes bulging (shared with *Caledopteryx*, but there lobes are slightly crenulated).

Male. (2) Genital ligula has a distinct morphology which is reminiscent of *Griseargiolestes*: two apical lobes of genital ligula are broad and about two to three times as long as wide, the whole outer border of genital ligula, up to where apical lobes begin, is slightly hollow and appears wrinkled.

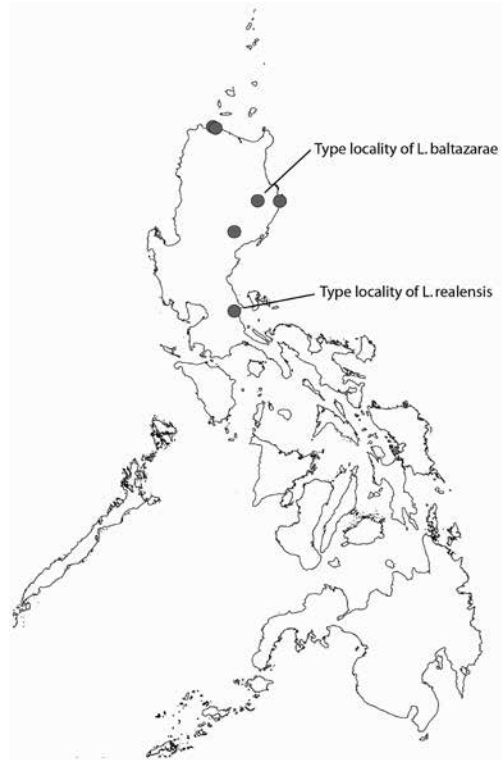


Figure 16. Distribution of *Luzonargiolestes*.

Diagnosis and identification

Adult. The only genus of Argiolestidae occurring in the Philippines. The genus can be easily distinguished from most other members of the family by S8-10 being normally sclerotised (neither weakly sclerotised nor with pale white or blue), the face, thorax and legs lacking blue or red and the thorax lacking a well defined pattern. The genus most resembles *Celebargiolestes* in its large size and the absence of bright colours but can easily be distinguished by its bulging postocular lobes and the shape of the genital ligula.

Information on the identification of the two species can be found in Gapud & Recuenco-Adorada (2001). The material recorded here for the first time was compared with a male from the type locality of *L. realensis* present in the RMNH (Luzon, National Botanical Garden, 14 April 1987, V.P. Gapud). This showed that all new

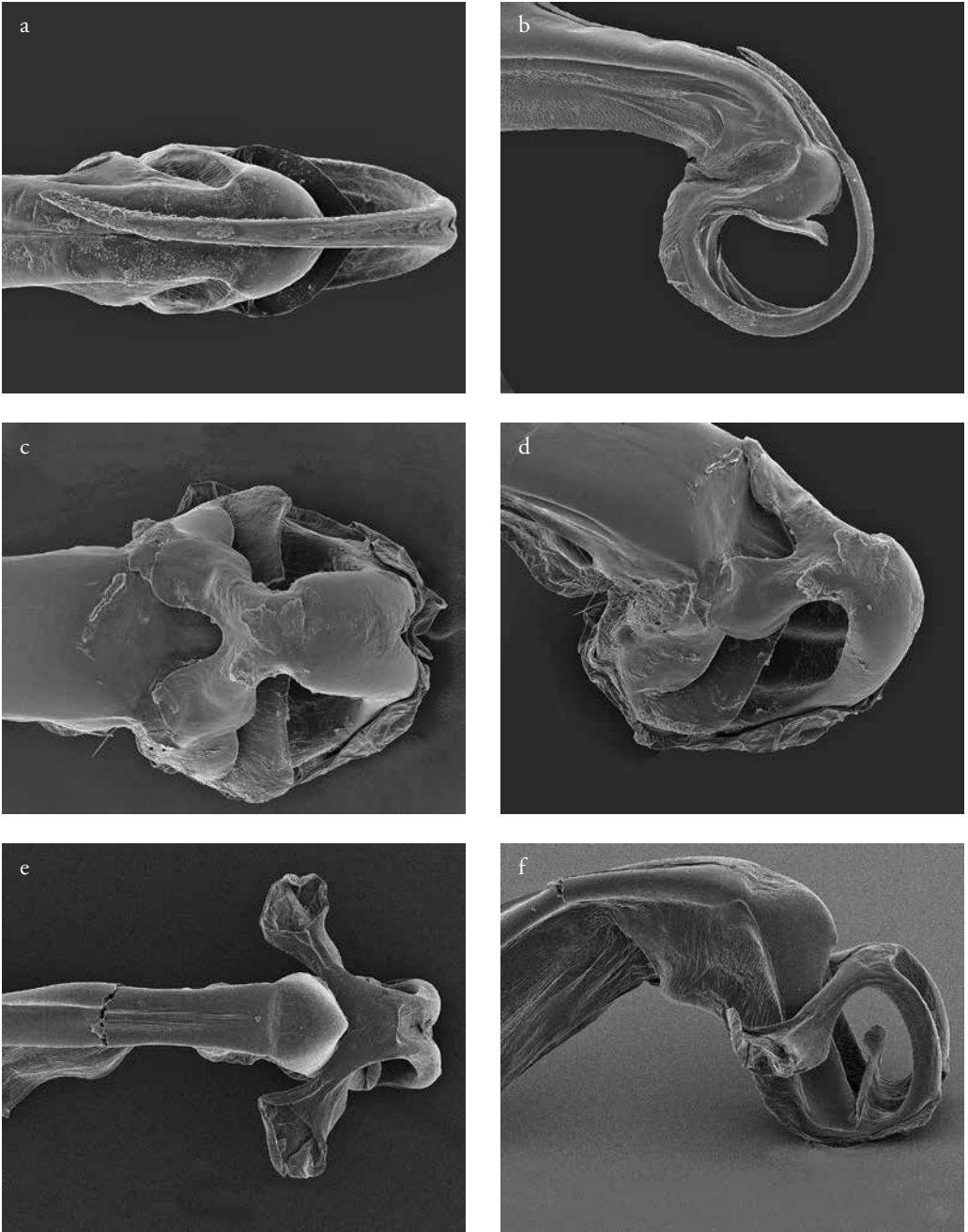


Figure 17. Genital ligula: (a) *Metagrion triste*, Indonesia, Jayapura, Cyclop Mountains, ventral view; (b) idem, lateral view; (c) *Metagrion connectens*, Indonesia, Sorong, 1948, ventral view; (d) idem, lateral view; (e) *Miniargiolestes minimus*, Australia, West-Australia, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

material is different from *L. realensis* and best fits *L. baltazarae* as the Hw has more than two rows of cells between CuA and hind border and the paraprocts are less slender with a less clear constriction halfway. There is however some variation in the shape of the paraprocts between new material from different localities. We do not have material from the type locality of *L. baltazarae* at hand and therefore have chosen to publish these records as *L. cf. baltazarae*.

Larva. Unknown.

Distribution and habitat

New records of *Luzonargiolestes cf. baltazarae*, all from Philippines, Luzon: 1 ♂: Quirino Province, Maddela, Sierra Madre, 15-30 August 1996, 400-600 m, leg. C.M. Nazareno (specimen mentioned as *Argiolestes* sp. n. in Hämäläinen and Müller 1997). – 2 ♂, 1 ♀: Isabela Province, Northern Sierra Madre Natural Park, Dipinantahikan (campsite 1), 300 m, 16°53.398'E 122°20.471'N, 12-20 September 2008, leg. R.J. Villanueva (record without details mentioned in Villanueva et al. 2009). – 15 ♂, 2 ♀: Cagayan Province, Claveria, Barangay Labla-Big, 200-500 m, 20-30 May 1997, leg. C. M. Nazareno. – 34 ♂, 2 ♀: Cagayan Province, Claveria, Barangay Union, 100-500 m, 20-30 May 1997, leg. C.M. Nazareno. The genus *Luzonargiolestes* is known from six localities on Luzon with *Luzonargiolestes realensis* only known from its type locality at the National Botanical Garden and *L. (cf.) baltazarae* known from five widely scattered more northern localities (fig. 16). The mountain regions of Luzon have been insufficiently studied and it seems likely that the genus is present throughout the mountains of Luzon at localities where larger blocks of forest remain at low elevation. Gapud & Recuenco-Adorada (2001) suggest that the species might be absent from the southern part of Luzon (the Bicol region) as it was not encountered there despite several field collections.

Information on habitat is scant. Gapud & Recuenco-Adorada (2001) give the habitat of *Argiolestes baltazarae* as a small stream covered with undergrowth vegetation, although specimens were

also found further away near a river and at a place where the small stream widened into a mountain stream with rock boulders. *Luzonargiolestes cf. baltazarae* was found in deeply shaded and moist forest (R.J. Villanueva, pers. comm.) (fig. 11d). The habitat of the larvae is unknown but observations of *Luzonargiolestes cf. baltazarae* at Isabela Province suggest that they live in seepages and small streams (R.J. Villanueva, pers. comm.).

Metagrion Calvert, 1913

(fig. 5b, 11a, 15d-f, 17a-d, 18)

General

Calvert (1913) created *Metagrion* with *M. postnodalis* as the only species but without studying material of the species. He did not give a separate description of the genus but included it in a venation-based key to the species of the Legion Podagrion (= Megapodagrionidae *sensu lato*). Ris (1915) doubted the validity of the genus and Lieftinck (1935a) studied the specimens and showed that the main character on which the genus was separated from *Argiolestes* (IR2 being distal to the subnodus) varied within the specimens. The genus has subsequently been considered a synonym of *Argiolestes*. Here the genus is reinstated for a group of 18 species all endemic to New Guinea and sharing a serrated hind rim of S10 (character state lost in *M. fornicatum* and *M. verrucatum*).

Generic characterization

Adult male. Labrum in most species either completely pale blue or completely dark metallic. Ground colour of head dark brown to black with three types of pattern: (1) a pale (whitish) line running from eyes to clypeus, and together with pale anteclypeus, forming a pale bar (can become obscured in older specimens; (2) lower part of face, including parts of clypeus and an area along eyes, pale blue; (3) front of face black, lacking clear pale pattern. Ground colour of prothorax and synthorax brown in immature adults, becoming black in fully mature ones. Pale pattern on dorsum of synthorax absent or small and often confined to

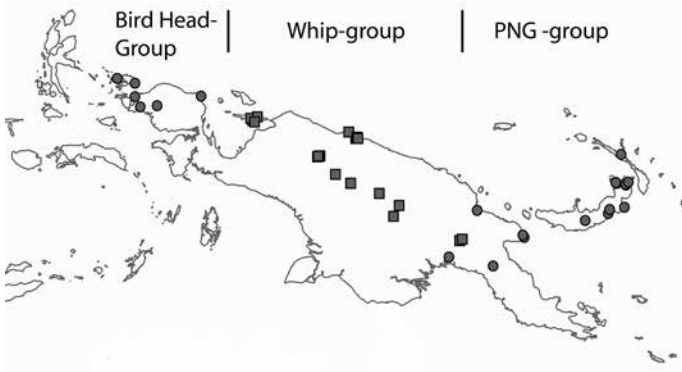


Figure 18. Distribution of *Metagrion*. Based on records in the Melanesian Odonata Database.

anterior corner. Sides of synthorax varying from an extensive blue pattern to completely dark. Legs in most species dark brown but with red on inside or completely red in species of the PNG group. Wings always with at least two and mostly with three rows of cells between the CuA and hind border. Discoidal cell of forewing with costal side 1.5 to 2.2 times as long as distal side. Dorsal surface of S8-9 only very lightly sclerotised, often appearing wrinkled in dead specimens. Hind rim of S10 completely or partially serrated (fig. 5b) (absent in *M. fornicatum* and *M. verrucatum*). Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci is clearly greater than the width of one cercus. Cerci without basal flange but with lower and upper apical flange, the latter with row of sometimes inconspicuous brown to black denticles. Apical segment of genital ligula always slender and in the Whip group reduced to a whip-like structure.

Adult female. Pt of adult females dark brown to black. Ovipositor reaching or slightly surpassing tip of cerci, in some species with dense and regular spaced row of teeth, whereas in others species the teeth are widely and irregularly spaced.

Unique characters within Argiolestidae

Male. (1) S8-S9 weakly sclerotised, often wrinkled in dead specimens (as in *Wabnesia* and to a lesser extent in *Eoargiolestes*). (2) Hind rim of S10 serrated (fig. 5b) (except in *M. fornicatum* and *M. verrucatum*).

Diagnosis and identification

Adult. The above-mentioned unique characters make it easy to recognise the genus. *Metagrion fornicatum* and *M. verrucatum* do not have the serrated S10 but can be recognised by the weakly sclerotised S8 and S9 in combination with a reduced and whip-like apex of the genital ligula. The genus is species-rich with currently 18 described and numerous undescribed species. Together with the relatively small morphological differences this makes identification to species level difficult. No review of the group is available and (re)descriptions of the species must be consulted for identification (Kalkman 2008, Liefertinck 1935a, 1938, 1949, 1956, Michalski & Oppel 2010, Theischinger & Richards 2006, 2007, 2008). Table 2 facilitates identification of the species by dividing them into three groups mainly based on the shape of the ligula. Each of these groups is centred on a different part of New Guinea. Further study is needed to determine if these groups are monophyletic.

Larva. The larvae of *M. fontinale* and *M. pectitum* were described by Liefertinck (1956, 1976).

Distribution and habitat

Metagrion is the most widespread genus of Argiolestidae in New Guinea and occurs throughout the island with exception of the southern lowlands (fig. 18). The PNG group is endemic to Papua New Guinea with *M. aurantiacum* being found on New Britain and New Ireland and the three others occurring in mainland Papua

Table 2. Characters separating the three groups of *Metagrion*.

	PNG group	Whip group	Bird Head group
Included	<i>aurantiacum</i> , <i>montivagans</i> , <i>indentatum</i> , <i>trigonale</i>	<i>fornicatum</i> , <i>lamprostoma</i> , <i>pectitum</i> , <i>sponsum</i> , <i>subornatum</i> , <i>triste</i> , <i>verrucatum</i>	<i>coartans</i> , <i>connectens</i> , <i>convergens</i> , <i>fontinale</i> , <i>ochrostoma</i> , <i>ornatum</i> , <i>postnodale</i>
Colour of legs in life	At least interior of legs orange to red	Never with orange or red	All described species without red, one undes- cribed species known with red legs
Colour of pale parts of thorax in life	Orange to red	Blue or dull yellow	Blue or dull yellow
Inner side of legs	Clearly expanded	Not clearly expanded	Not clearly expanded
Genital ligula	Apex slender with two ort terminal lobes	Head of ligula reduced to a long whip, without terminal lobes (Figure 17a, b)	Apex slender with two short terminal lobes (Figure 17c-d), genital ligula of <i>M. coartans</i> not studied
Labrum	Completely metallic	Varies per species, can be non-metallic, partly metallic or completely metallic	Varies per species, can be non-metallic, partly metallic or completely metallic
Distribution	New Britain and mainland Papua New Guinea	Mainland New Guinea excluding Bird Head Peninsula, Huon Peninsula and the easternmost tip of the mainland	Bird Head Peninsula

New Guinea. The Whip group occurs on mainland New Guinea to the west of the PNG group but is replaced on the Bird Head by the Bird Head group. The latter includes two species endemic to Waigeo, *M. coartans* and *M. ochrostoma*. The species of *Metagrion* are among the more common inhabitants of forest brooks in New Guinea (fig. 11a). They are, less often than species of *Argiolestes* and *Wahnesia*, found at seepages and seem to prefer small, largely shaded brooks although they are sometimes also found at larger rivers. Males sit in the vegetation above or near the water and show little activity. No information is available on territoriality, courtship, mating or oviposition.

***Miniargiolestes* Theischinger, 1998** (fig. 8b, 11e, 17e, f, 19a)

Unique characters within Argiolestidae

Adult. (1) Dark colour of head, thorax and abdomen with distinct metallic sheen (shared with *Archiargiolestes*, *Griseargiolestes* and *Trineuragrion*).
Male. (2) Genital ligula with distinct shape: lateral lobes of genital ligula shaped like trumpets, slender at base but widening towards apex.
(3) Intersegmental annulus of S8 and S9 white, strongly contrasting with the dark segments.

Diagnosis and identification

Adult. The only genus of Argiolestidae with which

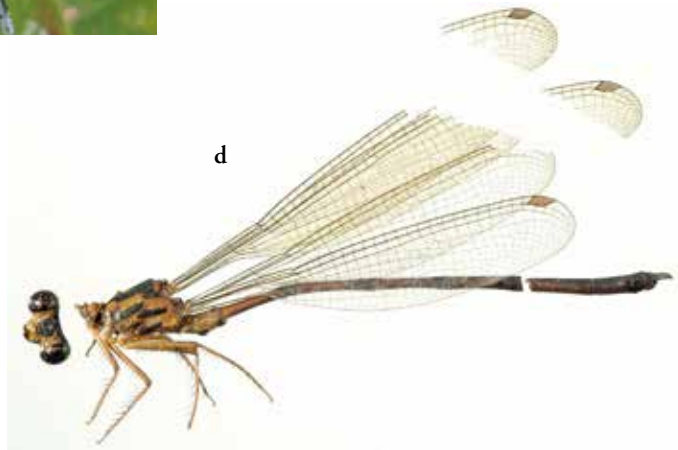


Figure 19. (a) *Miniargiolestes minimus*, male, Australia, Western Australia, Dandalup near Pinjarra. Photo by Jan Taylor. (b) *Podopteryx selysi*, male, Papua New Guinea. Photo by Steve Richards. (c) *Podopteryx selysi*, male, Papua New Guinea. Photo by Steve Richards. (d) *Solomonargiolestes malaita*, male, Solomon Islands, Malaita Island. Photo by Vincent Kalkman. (e) *Wabnesia* spec., male, Papua New Guinea. Photo by Steve Richards.

Miniargiolestes overlaps is *Archiargiolestes*, from which both sexes can be easily separated in the field by having their intersegmental annuli of S8 and S9 white and strongly contrasting with the dark segments. In addition females of *Miniargiolestes* and most males except for very old specimens have a white Pt (in *Archiargiolestes* only white when immature). Illustrations and pictures of the only species, *Miniargiolestes minimus*, can be found in Watson et al. (1991), Theischinger (1998a), Theischinger & Hawking (2006) and Theischinger & Endersby (2009).

Larva. A key to distinguish larvae of the genus *Miniargiolestes* from those of other Australian Argiolestidae can be found in Theischinger (1998a), Theischinger & Hawking (2006) and Theischinger & Endersby (2009).

Distribution and habitat

The only species of the genus, *Miniargiolestes minimus*, is confined to south-western Australia where it overlaps with the three species of *Archiargiolestes* (fig. 8b). *Miniargiolestes minimus* is restricted to streams and rivers (fig. 11e), in contrast to the three species of *Archiargiolestes*, which are also found at boggy seepages and marshes (Watson 1977). The larvae have been found under stones or on submerged sticks (Watson 1977).

Podopteryx Selys, 1871 (fig. 5c, 19b, c, 20a, 21)

Unique characters within Argiolestidae

Male. (1) Genital ligula strongly reduced and consisting of a long and slender whip which is round in basal cross section (fig. 20a). The genital ligula of *Podopteryx* resembles that of the Whip group of *Metagrion* but there the base of the whip is broad, gradually tapering towards the tip and the inner fold on the ligula head is always present. (2) Inner fold on ligula head absent (shared with *Griseargiolestes*) (fig. 20a). (3) Epiproct large and very conspicuous, pointed apically and when seen dorsally, more than twice as long as broad and about one sixth the length of cerci (not so in *P. casuarina*) (fig. 5c). *Female.* (4) Pt brown below but white above.

Diagnosis and identification

Adult. The genus overlaps in range both with genera from New Guinea and with genera occurring in eastern Australia. It can easily be distinguished from all these by its superior size, the large number of Px in Fw (>28), by having four or more rows of cells between the CuA and the hind border of the Hw and by the conspicuous and apically directed epiproct which is about twice as long as broad (except in *P. casuarina*).

The males can be identified with the key below. The characters to distinguish *P. selysi* and *P. roseonotata* based on the pattern and colouration of the thorax given in Liefstinck (1935a) have been found to be incorrect (Liefstinck 1949, 1951), as the colour probably varies with age, whereas the pattern shows individual or possibly regional variation.

Larva. The larva of *P. selysi* was described and illustrated by Watson & Dyce (1978) and Theischinger & Hawking (2006).

Key to the males of Podopteryx

- 1 Paraprocts about half as long as cerci ... *P. selysi*
- Paraprocts less than one fourth as long as cerci 2
- 2 Epiproct conspicuous and about twice as long as broad. Metanepisternum dark with pale marking starting near lower posterior margin then bending towards mesopleural suture. Cerci in lateral view slightly upturned *P. roseonotata*
- Epiproct small, less than twice as long as broad. Metanepisternum dark with pale line running from just above metastigma from posterior margin of metanepisternum towards anterior margin. Cerci in lateral view straight *P. casuarina*

Distribution and habitat

New records of *P. roseonotata*: 1 ♂: Indonesia, Papua, Kabupaten Mimika, Akimuga, Fakafuku, 50 m asl, 2 August 2001, leg. E.M. Rosarianto (KSP).

New records of *P. selysi*: 1 ♂: Indonesia, Papua, Kabupaten, Mamberamo Tengah, Marina Valen,

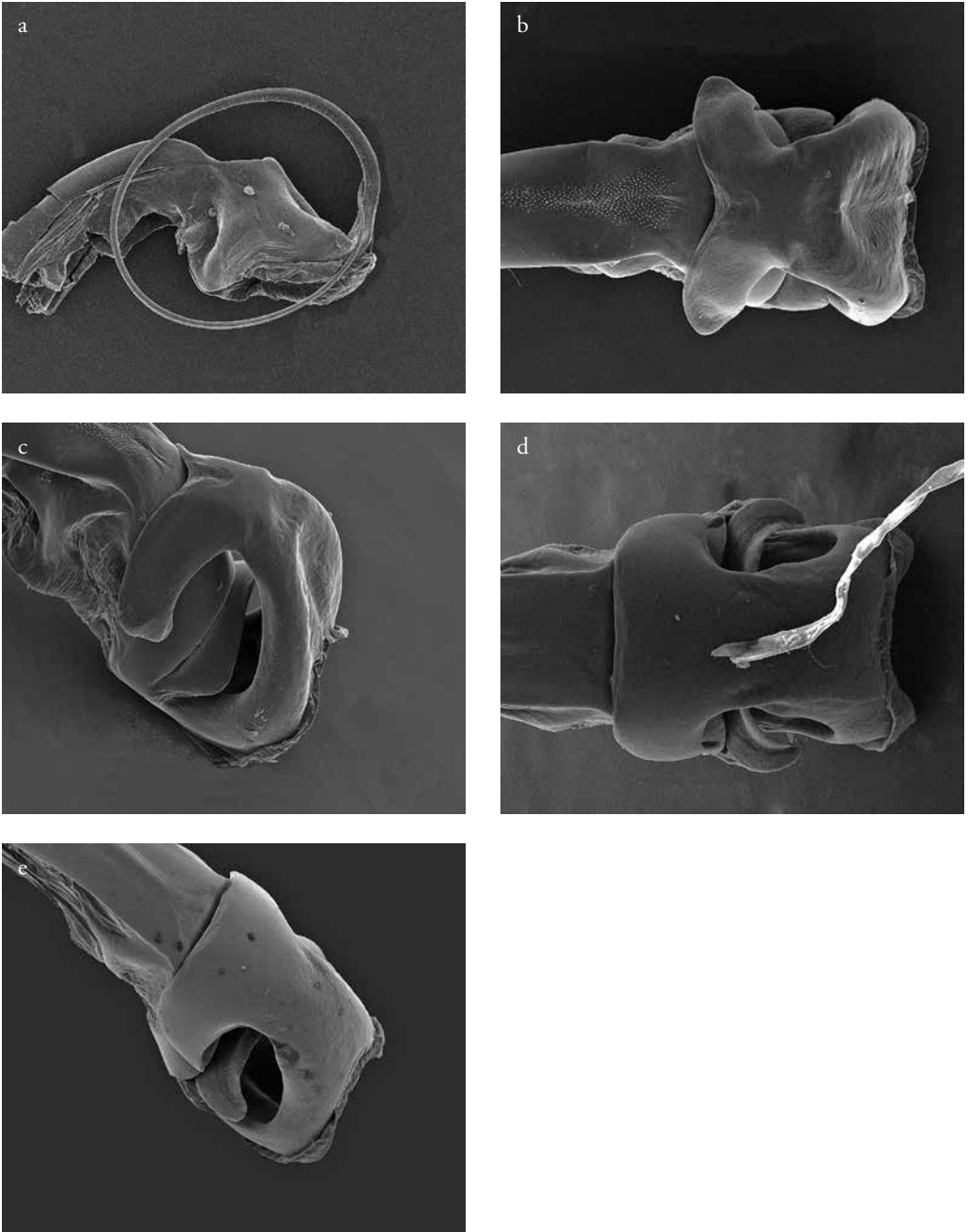


Figure 20. Genital ligula: (a) *Podopteryx selysi*, Indonesia, Jayapura, 1938, lateral view; (b) *Pyrrhargiolestes kula*, Papua New Guinea, Milne Bay Province, Modewa Bay, 1956, ventral view; (c) idem, ventrolateral view; (d) *Trineuragrion percostale*, New Caledonia, Yahoue, 1983, ventral view; (e) idem, ventrolateral view.

Photos: Dirk Gassmann.

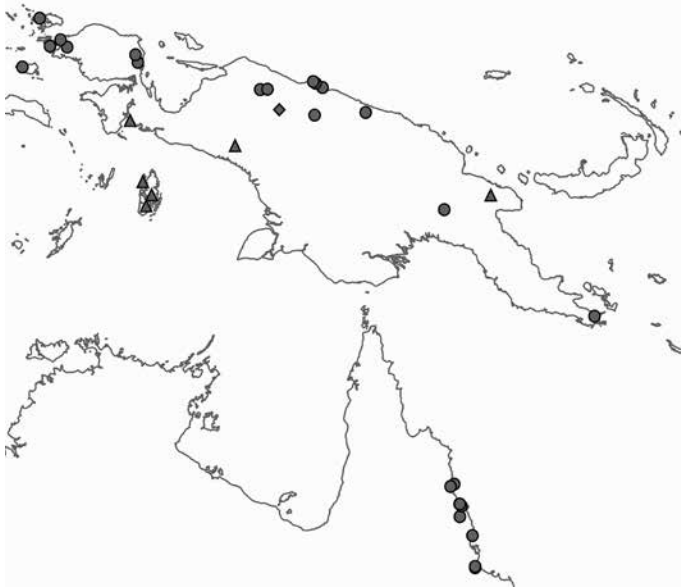


Figure 21. Distribution of *Podopteryx*. *Podopteryx selysi* (dots), *P. roseonotata* (triangles) and *P. casuarina* (diamond). Based on records in the Melanesian Odonata Database and the Australian Odonata Database.

Gunung Acaua, 540 m asl, 17-20 July 2004, leg. H. van Mastrigt (KSP). – 2 ♀ (one adult, 1 immature): Indonesia, Papua Barat, Klamono Oilfields, 18-24 August 1948, leg. M.A. Liefstinck. – 1 ♂: Indonesia, Papua Barat, Misool, Id (w), 0-75 m, 8 September to 20 October 1948, leg. M.A. Liefstinck. – 1 ♀: Indonesia, Papua Barat, Sorong, 26 August 1948, leg. M.A. Liefstinck. – 1 ♀: Indonesia, Papua Barat, Sorong, sea-level forest, 28 August 1948, leg. M.A. Liefstinck. – 1 ♀: Indonesia, Papua Barat, Sorong, forest, 2 September 1948, leg. M.A. Liefstinck. – 2 ♂: Indonesia, Papua, Manokwari, plain of Momi River, 5-10 m, 15-31 August 1948, leg. A.J. Kosterman. – 1 ♂: Indonesia, Papua Barat, Arfak Mts, Angigita, 1800-2000 m, 15-25 October 1948, leg. A.J. Kosterman. – 1 ♂: Papua New Guinea, Kokoda trail, 600 m, 7 December 1971, leg. R. Straatman.

The distribution of the three species of *Podopteryx* is shown in fig. 21. *Podopteryx casuarina* is only known from the male holotype from Bernhard Camp, Papua Province, Indonesia (400 m). *Podopteryx roseonotata* is known from several islands in the Aru Archipelago, from one location on the Huon Peninsula and one hitherto unpublished

record from southern lowland of Papua, Indonesia. *Podopteryx selysi* is the most widespread with records from Australia (Cape York Peninsula, Queensland), mainland New Guinea and the islands of Salawati and Waigeo. One male specimen is labelled “Darwin” in the Northern Territory in Australia. No other records are known from this area and as long as none become known this record is probably in error. Several authors, eg Liefstinck (1935a, 1949, 1951) and Watson (1974), mentioned *P. roseonotata* as occurring in North Queensland, but these records have never been confirmed (Watson & Dyce 1978). All records are from forest, often away from water. Most records are from lowland but *P. selysi* has been recorded from 1650 m in the Foja Mountains and from 1800 m in the Arfak Mountains.

All species appear to be rare and are usually encountered one at a time. Stüber, a collector living in present-day Jayapura (Papua, Indonesia), wrote that all seven specimens of *P. selysi* he collected were found away from water hanging on bushes along paths in forest (cited in Liefstinck 1935a). He also remarked that it was rare, having found only seven specimens in three years of collecting.

Similar observations on *P. selysi* were made near Cairns and on the Atherton Tableland by R. Dobson who noted that “adults of these damselflies occur in forest away from water” (cited in Watson & Dyce 1978). Oppel (2005), who found only three specimens of *P. selysi* at Crater Mountain-Wildlife Management Area (Papua New Guinea) during 112 sampling days, remarked that it was found “generally well away from any water source in sunny clearings of the rainforest”. The text on the envelope of the only specimen of *P. casuarina* states that it was collected in dense tropical forest far away from water. All these observations do not necessarily mean that the species are rare but that they are difficult to find as they are found in forest away from more usual dragonfly habitats. Watson & Dyce (1978) mention that *P. selysi* appears to be not uncommon in the rainforest of North Queensland. The first description of the larva and its biology was published by Watson & Dyce (1978) who recorded two larvae being found in cavities about 60–80 cm above ground in trees bordering a small clearing. Each of these contained 2–3 l water, submerged plant litter and organic sludge. Based on this it seems clear that *P. selysi* is a phytotelmata breeder which explains why the species is found in forest away from visible water. The only other record of larvae of *Podopteryx* is from Kitching (1990) who found one larva “probably of the tree hole genus *Podopteryx*” in a water-filled treehole in Madang (Papua New Guinea). Information on the habitat of the other two species is lacking but it seems likely that they also breed in phytotelmata. As far as is known, *Podopteryx* is the only genus of Argiolestidae breeding in phytotelmata, and in all other genera either larvae have been found in running water or adults are mostly found near running water. It is also the only genus outside Libellulidae, Aeshnidae and Coenagrionidae (including the former Pseudostigmatidae and New World Protoneuridae) to breed in phytotelmata (Corbet 1999). In contrast with other species of Argiolestidae, adults of *Podopteryx* hang with the abdomen held vertically. *Podopteryx selysi* seems to be on the wing throughout the year in New Guinea. In North Queensland the species is found only

in the wet season from the start of October to the start of April (Watson & Dyce 1978; Australian Odonata Database).

***Pyrrhargiolestes* gen. nov.**
(fig. 2ob, c, 22)

Type species

Argiolestes sidonia Martin, 1909 by present designation.

Etymology

The name is composed of the word “pyrrhos” which is the Greek word for flame-like, referring to the bright red-orange colours of many of the species, and the genus name “Argiolestes”.

Generic characterisation

Medium large species with striking orange to red colours on face, legs and thorax.

Adult male. Labrum dark metallic with green or blue gloss, anteclypeus pale (whitish). Mandibles, genae, frons and dorsum of head black with a pale line running from eye-margin to postclypeus and partly continuing on sides of postclypeus, centre of postclypeus dark metallic. Prothorax dark with varying amount of pale pattern on pronotum. Synthorax with mesepisternum, mesepimeron, metepisternum matt black with narrow to broad pale orange band running just above intersegmental suture from near hind border of synthorax to just past metastigma. A short longitudinal orange streak is present on dorsum of synthorax in some species. Lower half of metepimeron dull orange, upper half dirty brown. Legs, including coxae and trochanters, yellow orange in museum specimens but probably bright orange to red in all species when alive. Inner side of femora clearly expanded. Spines orange-brown. Abdomen either dark throughout, or S3–6 pale with a posterior black ring. Wings with one to three rows of cells between CuA and hind border. Discoidal cell of forewing with costal side 1.2 to 1.3 times as long as distal side. S8–9 not weakly sclerotised and S10 lacking spines on dorsum or row of spines on hind

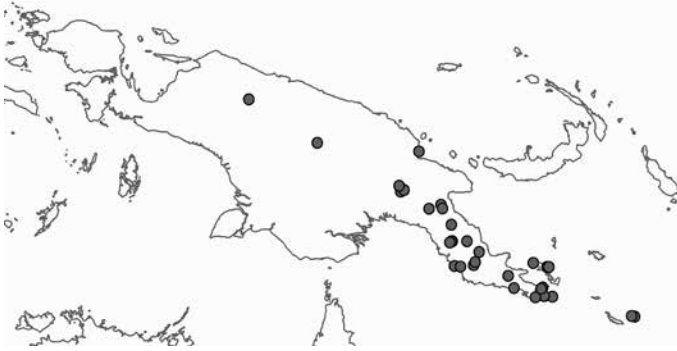


Figure 22. Distribution of *Pyrrhargiolestes*. Based on records in the Melanesian Odonata Database.

margin. Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci subequal to or greater than width of one cercus. No basal flange at base of cerci. Outer border of cerci carrying several medium large spines. Cerci with lower and upper dorsal flange, the latter with or without a row of inconspicuous brown to black denticles. The genital ligula was studied for all species with the exception of *P. angulatus*. All of these have the same general structure, with a well-developed apical segment bearing two apical lobes which are about twice as long as broad. The outer side of the apical segment of ligula is weakly sclerotised up to the point where the apical lobes begin.
Adult female. Pt of adult females black. Ovipositor just reaching or surpassing tip of cerci and with dense row of small and well-developed teeth.

Unique characters within Argiolestidae

Male. (1) Tibiae and femora slightly expanded and orange to red throughout, lacking distinct black marking (shared with some species of *Wahnesia* and *Metagrion*).

Diagnosis and identification

Adult. The species of *Pyrrhargiolestes* are easily recognised as such by having the tibiae and femora orange to red throughout and by lacking modifications on S10. In addition to this the following characters distinguish them from most other species of Argiolestidae occurring on New Guinea: (1) labrum completely dark metallic blue or green; and (2) S8-9 normal (not weakly sclerotised).

A key to the species with description of the species is found in Kalkman et al. (2012).

Larva. Unknown.

Distribution and habitat

Whereas six species are endemic to Papua New Guinea, *P. aulicus* has been recorded in the Indonesian part of the island (fig. 22). A map showing the distribution of all species can be found in Kalkman et al. (2012). The genus is found from sea-level to 1800 m, and in general the species seem to occupy a wide altitudinal range. The species are restricted to seeps and brooks in forest and they seem to have a preference for steeper brooks, waterfalls and seep rheocrenes.

Solomonargiolestes gen. nov. (fig. 19d, 23)

Type species

Argiolestes bougainville Kalkman, 2008 by present designation.

Etymology

The name is composed of a reference to the Solomons, referring to the island group where the genus occurs, and the genus name “Argiolestes”.

Generic characterisation

Adult male. Front of face largely bright blue or orange. Postocular lobes not prominent. Thorax with extensive bold blue or orange pattern.



Figure 23. Distribution of *Wahnesia* (dots) and *Solomonargiolestes* (squares). Based on records in the Melanesian Odonata Database.

Pale markings on thorax cross sutures. Thorax never with pruinosity. Interior of legs not expanded, pale brown or orange and without strong contrast in colouration between interior and exterior. Femora with or without one, clear dark ring. S3-6 brown with apical sixth of each segment dark brown. Wings with two rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about twice as long as distal side. S8-9 not weakly sclerotised and S10 without modification but with the middle of the hind rim slightly depressed and concave. Paraprocts about one fourth to one third the length of cerci. In dorsal view distance between cerci is subequal to width of one cercus. The genital ligula was not studied as only holotypes are available.

Adult female. Unknown.

Unique characters within Argiolestidae

Male. (1) Thorax has a bold orange or blue pattern with markings crossing the sutures. The character of these markings is very distinct although difficult to describe concisely. It is not unlikely that unique characters can be found in the genital ligula but the genital ligula of neither species could be studied.

Diagnosis and identification

Adult. *Solomonargiolestes bougainville* and *S. malaita* can readily be recognised by the combination of

pale brown or orange legs and the face and thorax being largely blue and orange respectively.
Larva. Unknown.

Distribution and habitat

New record of *Solomonargiolestes* spec.: 1 ♀, Solomon Islands, Santa Isabel Island, Hageulu, 400-650 m, 13 September 1964, leg. R. Straatman.

Both species belonging to this genus are known from a single male each. The single specimen of *S. bougainville* was caught on 2 January 1970 on Bougainville without further indication of locality or habitat (fig. 23). The single male *S. malaita* was caught on 27 September 1957 at Tagatalau, E of Auki on the island Malaita at an altitude of 200 m. Bougainville was never thoroughly sampled for dragonflies, and it is difficult to say if *S. bougainville* is genuinely rare or was simply overlooked. *Solomonargiolestes malaita* was not encountered during sampling for aquatic invertebrates at 10 different sites on Malaita between 28 July and 1 August 2005, which indicates that the species is not common (Polhemus et al. 2008). The single female from Hageulu lacks the tip of the abdomen. It can be recognised as *Solomonargiolestes* based on the bold pattern on the thorax resembling that of the two known species. The pattern on the thorax is discoloured but is

probably blue in life. The specimen has 2 Ax and 16-17 Px which is clearly less than the 20-21 and 25-27 Px of the males of *S. malaita* and *S. bougainville*, suggesting that it pertains to an undescribed species.

***Trineuragrion* Ris, 1915**
(fig. 20d, e, 24a, b)

Unique characters within Argiolestidae

Adult. (1) Wings with three Ax, sometimes one or two wings with two Ax (shared with *Neurolestes trinervis*). (2) Dark colour of head, thorax and abdomen has a distinct metallic sheen (shared with *Archiargiolestes*, *Griseargiolestes* and *Miniargiolestes*).

Diagnosis and identification

Adult. *Trineuragrion* shares its range with three other genera of Argiolestidae. Males lack bright blue colours on abdomen and thorax, except for some pruinosity on S9-10, which easily separates them from males of *Eoargiolestes* and *Caledopteryx*. From the two species of *Caledargiolestes* it is separated by the metallic green ground colour of its body and the abdomen being dark throughout. A small number of available photographs suggest that partially mature males and females have the eyes pale blue throughout. These become black in the upper two-thirds and pale greenish in the lower third when mature. The pale blue colour of the eyes is not found in any Argiolestidae, except for and to a lesser extent in the south-western Australian *Miniargiolestes*, and allows easy identification of specimens in life. *Trineuragrion percostale* is the only argiolestine species of which mature adults often sit with their wings closed or partly open. *Larva.* A description of the larva of *Trineuragrion percostale* can be found in Lieftinck (1976: as *Caledargiolestes uniseriis*) and in Marinov (2012). The latter paper also includes a larval key to the genera of Argiolestidae occurring on New Caledonia.

Distribution and habitat

New records of *T. percostale*, all New Caledonia:
1 ♂: Yahoue, 15 February 1983, leg. D.A.L. Davies;

1 ♂: Yahoue, 18 February 1986, leg. D.A.L. Davies.
– 1 ♂: Col de la Pirogue, 13 February 1962, leg. N.L.H. Krauss.

The genus *Trineuragrion* is endemic to New Caledonia. It is widespread but seems to be scarcer than other New Caledonian argiolestids such as *Eoargiolestes ochraceus* and *Caledopteryx maculata*. A record of a male collected on Banks Island, Vanuatu, in November 1929 by Miss L.E. Cheesman published by Kimmins (1936) is the only record outside New Caledonia. This record seems unlikely and is regarded as incorrect as long as no other supportive evidence is available.

Davies (2002) mentions collecting the species from small falls of less than a metre stating that these “will customarily be watched over by a male *Trineuragrion*, perched on the nearest large stone above the pool below, in which the female will be busy ovipositing”. According to Marinov (2012) it mainly inhabits moderate sized rivers up to 5-6 m wide although it was also found at a 20m wide, shallow and rocky river. River banks where the species occurs are typically densely vegetated and fallen tree trunks and branches in the middle course of the river were found to be of great importance for mating and ovipositing (Marinov 2012).

This is the only species of Argiolestidae in which mature specimens regularly have their wings closed when resting (fig. 24a, b). It was estimated that this was the case in 25% of the observed specimens (S. Richards, pers. comm.). Recorded from November to April (Davies 2002).

***Wabnesia* Förster, 1900**
(fig. 5e, 19e, 23, 25a-d, 27c)

General

Förster (1900) described the genus *Wabnesia* based on material of two, at the time undescribed, species (*Wabnesia kirbyi* and *Metagrion montivagans*). *Wabnesia kirbyi* was designated as the type of the



Figure 24. (a) *Trineuragrion percostale*, male, New Caledonia, Province Nord, Roche de la Wayem. Photo by Steve Richards. (b) *Trineuragrion percostale*, female, New Caledonia, Province Nord, Dawenia. Photo by Steve Richards. (c) *Allostes maclachlani*, male, Seychelles, Silhouette Island. Photo by Mike Samways. (d) *Nesoletes ravanalona*, female, Madagascar, Ranomafana NP, Talatakeli. Photo by Julien Renoult. (e) *Neurolestes trinervis*, male, Gabon, Moyabi. Photo by Nicolas Mézière. (f) *Podolestes buwaldai*, male, Malaysia, Pahang. Photo by CheeYen Choong.

genus by Kennedy (1925). Neither Förster (1900) nor Kennedy (1925) presented a full description of these species but Förster (1900) did note characters separating the two species included in his new genus, and this therefore qualifies as a formal description of the species (for details see Garrison et al. 2003). The first proper description of both species was provided by Liefstinck (1935a) who subsequently has sometimes been incorrectly regarded as author of this species (eg Davies & Tobin 1984). Liefstinck (1935a) discussed the genus and its characters and deemed it invalid as it was based on two undescribed (but see above) species whose characters did not warrant the erection of a new genus. The genus has subsequently always been considered a synonym of *Argiolestes*. Here the genus is reinstated to receive all species with weakly sclerotised S8-9 and with the dorsum of S10 having a single spine or a bundle of spines originating from one point. The only species missing the dorsal spine(s) on S10 is *W. saltator*. Based on the weakly sclerotised S8-9 this species belongs to either *Metagrion* or *Wabnesia*. It is here placed in *Wabnesia* as the general shape of the cerci and the pattern on the thorax do not fit *Metagrion* and clearly resemble *Wabnesia*.

Generic characterisation

Small to medium sized species, largely brown to black with, in at least some species, blue pattern on thorax and blue tip of abdomen. More so than in other genera the colour of thorax and legs fade in preserved specimens to such an extent that blue marking on the thorax became pale brownish or greyish and the orange or red markings on legs became yellow-brown. Based on pictures of live specimens of *W. annulipes* (Polhemus et al. 2004) and *W. gizo* (Polhemus et al. 2008) we deem it likely that in all species the pale pattern on face and thorax is pale blue in life, whereas pale parts of legs are orange to red. Additional problems in this genus are caused by the distinct change in pattern and colouration due to age, with the pattern on the thorax and face becoming obscured with age. Many species are known from only a handful of specimens

which, combined with the aforementioned variation, renders members of this genus poorly known.

Adult male. Labrum with outer third to outer two-thirds dark metallic and remainder pale whitish to blue, labrum in *W. simplex* completely metallic. Face and dorsum of head pale brownish in immature specimens, later becoming dark brown to black, with pale (whitish) line running from eyes to clypeus, and together with pale anteclypeus forming pale bar. In older specimens pale line running from eyes to clypeus becomes dark. Postocular lobes not bulging. Ground colour of prothorax and synthorax pale brown in immature adults, becoming black in fully mature individuals. Pattern on synthorax poorly defined, blue in living specimens but becoming pale brownish in preserved specimens. Extent of pattern varies with age and becomes completely obscured (black) with age in at least some species. Colour of legs varies between species and can be dark throughout, dark on the outside and pale (reddish) on the inside, reddish with dark bands on the femora or uniform reddish. Reddish colour becoming yellow-brown in preserved material. S3-6 brown to black with anterior and posterior black annulus. Wings with mostly two, but in some species three, rows of cells between CuA and hind border. Discoidal cell of forewing with costal side about 1.8 to 2.0 times as long as distal side. Dorsal surface of S8-9 only very lightly sclerotised, often appearing wrinkled in preserved specimens. S10 short, about 5 to 6 times as broad as long. Posterior margin of S10 with single large raised spine (fig. 5e) (absent in *W. saltator*); this spine can consist of a tightly packed bundle of smaller spines (*W. kirbyi*). Posterior margin of S10 never serrated. Paraprocts shorter than half the length of cerci. In dorsal view distance between cerci clearly greater than width of one cercus. Cerci without basal flange but with lower and upper dorsal flange, the latter with row of sometimes inconspicuous brown to black denticles. Apical segment of genital ligula well developed with small apical lobes which are about one to two times as long as wide.

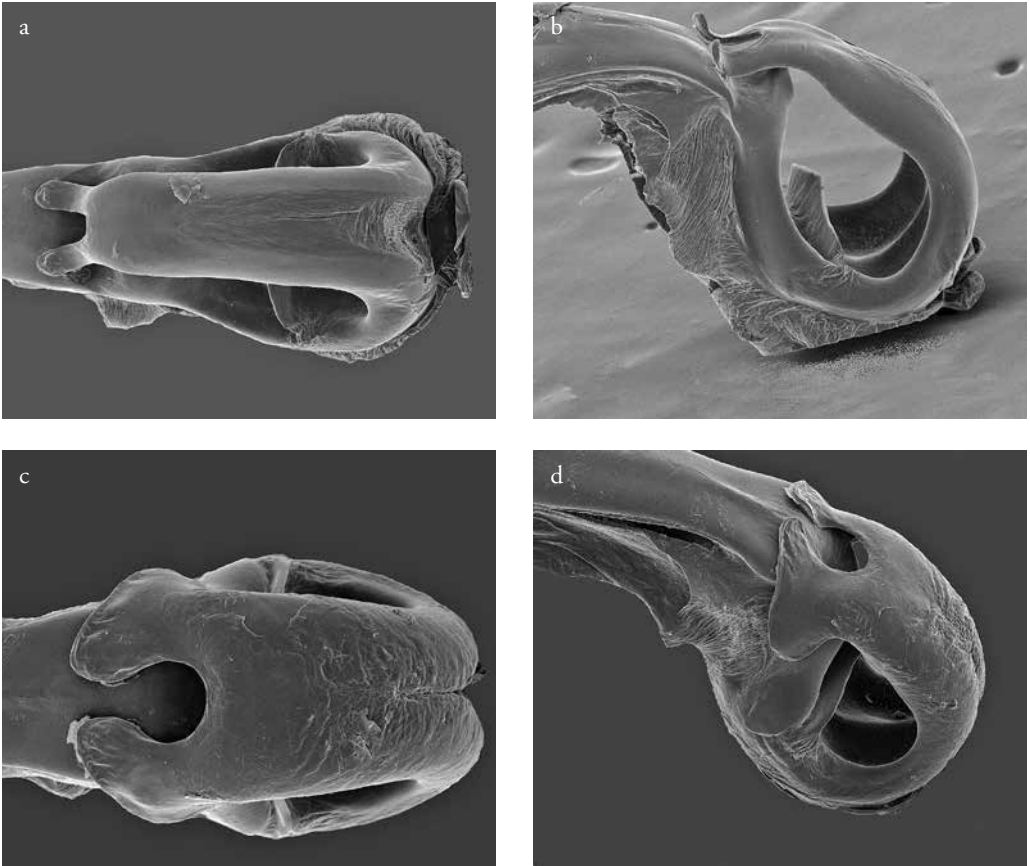


Figure 25. Genital ligula: (a) *Wabnesia armeniaca*, Papua New Guinea, Fergusson Island, ventral view; (b) idem, lateral view; (c) *Wabnesia* spec., Papua New Guinea, Sudest Island, 1956, ventral view; (d) idem, ventrolateral view. Photos: Dirk Gassmann.

Adult female. Pt of adult females black. Ovipositor reaching or surpassing tip of cerci, in some species with dense and regularly spaced row of teeth, whereas in others the teeth are widely and irregularly spaced.

Unique characters within Argiolestidae

Male. (1) S8-S9 weakly sclerotised, often wrinkled in dead specimens (as also in *Metagrion* and to a lesser extent in *Eoargiolestes*). (2) Dorsum of S10 bears near the hind rim a single, often slightly raised, spine (fig. 5e) or, in *W. kirbyi*, a bundle of smaller spines more or less originating from one point (absent in *W. saltator*).

Diagnosis and identification

Adult. With the exception of *W. saltator* all species can easily be recognised as *Wabnesia* based on the above-mentioned unique characters. In *W. saltator* the mid-dorsal spine on S10 is lacking but this species is easily recognised by lacking a row of spines on the posterior margin of S10 and having S8-9 strongly expanded and about twice as broad as S10. Identification to species level is difficult due to the high number of species, the relatively weak morphological differences between species and the large variation of patterns and colouration due to age. A key and illustrations of all species can be found in Michalski (2012).



Figure 26. Genital ligula: (a) *Allolestes maclachlani*, Seychelles, Silhouette, La Pase, 2001, ventral view; (b) idem, ventrolateral view; (c) *Neurolestes trinervis*, Cameroon, Meme District, Ngombo Hills, 1999, ventral view; (d) idem, ventrolateral view; (e) *Podolestes orientalis*, Indonesia, Borneo, Ampah, 1948, ventral view; (f) idem, ventrolateral view. Photos: Dirk Gassmann.

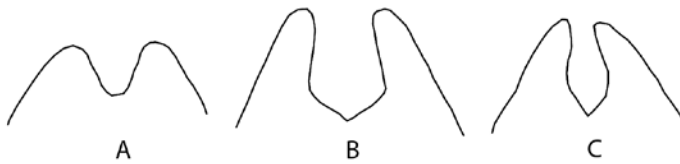


Figure 27. Shape of median cleft of labium: (a) *Allolestes maclachlani*; (b) *Nesolestes ranavalona*; (c) *Wahnesia gizo*.

Distribution and habitat

The genus *Wahnesia* is, with the exception of *W. simplex*, endemic to Papua New Guinea and the Solomon Islands (fig. 23). The highest diversity is found in the eastern part of the Central Mountain Range of Papua New Guinea and the Finisterre Range. To date, 12 species have been described, but a paper with six additional species is in preparation. Only a few specimens of many species are known, suggesting that they have relatively small ranges and are not abundant. This makes it likely that numerous species await discovery and that the genus may well have more than 30 species. *Wahnesia* seems absent from the Bismarck Archipelago but it has reached the d'Entrecasteux Islands, Louisiade Archipelago (undescribed species) and one species, *W. gizo*, occurs on three of the Solomon Islands (Gizo, Vella Lavella, Rendova). The presence of this genus on these island groups suggests that it arrived there wind-borne. *Wahnesia kirbyi* is the only species with a reasonably large range and is seemingly not uncommon within its range. It has been reported as the most common species of Argiolestidae in Crater Mountain Wildlife Management Area (Oppel 2005).

Details on habitat are lacking for most species. *Wahnesia kirbyi* was observed in "all types of shady streams and creeks, with some individuals even occurring along major rivers and others at small temporary seepages" (Oppel 2005). Oppel (2005) furthermore notes that shading is crucial for *W. kirbyi* as the species did not occur along "those streams in Herowana where much of the canopy had been removed". Teneral were observed near a medium-sized boulder creek which was supposed to be their larval habitat. Other species for which some habitat details are known are *W. saltuaria*,

which was found at running waters of different sizes, ranging from large rivers to shady temporary streams, and *W. microstigma*, which was found at small, fully shaded creeks under closed canopy, c. 1-2 m wide with very irregular water flow and a gravel bed (Oppel 2005).

Podolestinae subfam. nov.

Key characters

Adult male. (1) Shaft of genital ligula with longitudinal microstriae. (2) Base of loop (lateral margin of segment 3 of genital ligula distinctly laterally expanded (in *Neurolestes*, *Podolestes* and probably in *Nesolestes*).

Adult female. (3) Ovipositor long, reaching beyond cerci by more than the length of S10 (in *Allolestes*, *Nesolestes* and *Podolestes harrisoni*).

Allolestes Selys, 1869

(fig. 24c, 26a, b, 27a)

Unique characters within Argiolestidae

Adult. (1) Apical corner of discoidal cell surpassing nodus. (2) Only one cell between quadrangle and subnodus. (3) Median cleft of labium shallow, less deep than wide (fig. 27a).

Female. (4) Ovipositor long and surpassing cerci by at least the length of S10 (shared with *Nesolestes* and *Podolestes harrisoni*).

Diagnosis and identification

Adult. Can easily be separated from all other species of the family by the above-mentioned unique characters. In addition the pattern on the abdomen is unique, with S3-7 dark with an anterior pale annulus or mark and the dorsum of S9-10 and

anterior two-thirds to three-fourths of S8 blue. It is the only species of the family occurring on the Seychelles where it can easily be recognised in the field, being the only damselfly to rest with open wings.

Larva. Unknown.

Distribution and habitat

The monotypic genus is endemic to the Seychelles, with its sole species *A. maclachlani* being found on the islands of Mahé, Praslin and Silhouette. The species is restricted to rocky forest streams, and fewer than 10 localities are known. Blackman & Pinhey (1967) state that it is often found below a complete canopy of trees and that it is found at elevations around 300 m, being absent from the coastal lowlands. The species is listed as Endangered on the IUCN red list as forest streams on Mahé and especially Praslin frequently desiccate due to over-extraction of water (Martens 2009).

Nesolestes Selys, 1891 (fig. 6, 24d, 27b)

Taxonomy

The West African *Neurolestes* and the Madagascan *Nesolestes* are closely related and their relationship has repeatedly been discussed (Dijkstra 2003, Fraser 1955, Gambles 1970, Schmidt 1966). *Neurolestes* has been considered a monotypic genus separated from *Nesolestes* by the presence of a third Ax and by having two to five cubito-anal cross veins instead of one. In the publication in which he described *Nesolestes nigeriensis* from Nigeria, Gambles (1970) discusses the differences between the two genera and concludes that with the description of *N. nigeriensis* “the differences between the two genera are reduced to the unusual venational characters of *Neurolestes* (the additional Ax and the extra Cuq), and in general appearance and other detailed characters the new species further bridges the gap”. Although he obviously believed his *nigeriensis* to be more closely related to *Neurolestes* than to *Nesolestes*, he placed it in the latter, retaining the venation-based definition of

both genera. Molecular analysis has shown that the two western African species are clearly more closely related to each other than to the Madagascan species (Kalkman, unpublished). For this reason *Nesolestes nigeriensis* is transferred to *Neurolestes*. The venational characters of *N. trinervis* are therefore considered to have evolved after the western African group became separated from the Madagascan group. The only character known to separate these two genera is the ovipositor, which is remarkably long and reaches beyond the cerci by at least the length of S10 in all six species of *Nesolestes* for which information on the female is available, but is short in the two known species of *Neurolestes*. Relatively little material of these genera was studied and SEM images of the genital ligula of *Nesolestes* could not be made. Further study might therefore very well result in finding additional characters separating the two genera.

Unique characters within Argiolestidae

Female. (1) Ovipositor smooth and long, reaching beyond cerci by at least the length of S10, and in most species by more than the length of S9-10 (fig. 6).

Diagnosis and identification

Adult. This is the only genus of Argiolestidae found on Madagascar and the Comoros, and it can within its range be identified by the venational characters of Argiolestidae. Together with *Tatocnemis* and *Protolestes* it is the only damselfly genus in the region with species sitting with open wings and with the abdomen nearly horizontal. *Tatocnemis* and *Protolestes* however lack the supplementary sectors between IR1 and RP2 and between RP2 and IR2. In addition males of *Tatocnemis* have a red abdomen (never so in *Nesolestes*), whereas the species of *Protolestes* have a clearly more slender head. Fraser (1955) gives a review of the genus and a key and illustrations to the males of all species known at the time (10 of the presently known 16). Nonetheless identification to species level is problematic as many descriptions are brief and based on a limited amount of material so that the variation within the species is poorly known.

Larva. The only description of the larvae available is that of an unidentified larva published by Schütte (2010).

Distribution and habitat

The genus *Nesolestes* contains 16 species, 15 of which are confined to the eastern half of Madagascar while one (*N. pauliani*) is found on Mohéli (Mwali), Comoros. Most species of *Nesolestes* are very poorly known, as females are unknown for half of the species and nine are known only from the type locality. Most species probably have restricted ranges. The absence of the genus in the western part of Madagascar is likely due to the arid conditions there. The scant information available suggests that the genus occupies a broad altitudinal range with some species found at sea level, for instance *N. mariae* which occurs on the coastal island of Santa Maria, and some found in the mountains, such as *N. robustus* at 1300m and both *N. albicolor* and *N. forficuloides* at 1800 m. The latter two species have both been found in the Andohahela National Park, showing that the ranges of species can overlap. Information on the habitat of the species is virtually absent and information on behaviour is not available. Schütte (2009) remarked that species of *Nesolestes* were observed at small running waters in rainforest and littoral forest habitat.

Neurolestes Selys, 1882 (fig. 24e, 26c-d, 28)

Taxonomy

See *Nesolestes*.

Unique characters within Argiolestidae

No unique characters available.

Diagnosis and identification

Adult. *Neurolestes* strongly resembles *Nesolestes* but lacks the long and sword-like ovipositor. The genus does not overlap in range with any other genus of Argiolestidae and can within its range be identified by the venational characters of

Argiolestidae. Together with *Lestes* it is the only damselfly genus in the region with species sitting with open wings but *Neurolestes* sits, in contrast to *Lestes*, with the abdomen near horizontal while *Lestes* perches with body pendent or at a 45° angle to its perch. The two species of the genus can easily be told apart by *N. trinervis* having a third antenodal vein (two in *N. nigeriensis*) and a black with orange anterior synthorax (black, yellow and bluish in *N. nigeriensis*). A detailed comparison of the two species can be found in Gambles (1970).
Larva. Unknown.

Distribution and habitat

The genus currently holds two described, and probably a third undescribed, species. *Neurolestes trinervis* has been recorded from Cameroon, Equatorial Guinea, Gabon and the Republic of Congo (fig. 28). *Neurolestes nigeriensis* is known only from the type locality, the Obudu Plateau in Nigeria, where it has an estimated extent of occurrence of less than 100 km². This species is assessed as Critically Endangered on the IUCN Red List as its forest habitat is expected to deteriorate in the future. Specimens from adjacent Cameroon might be conspecific with *N. nigeriensis* or might belong to an undescribed species (Piney 1974). *Neurolestes trinervis* is found along cool streams in submontane (above 700 m) rainforest and *N. nigeriensis* is found in rainforest where it probably occurs in streams (Clausnitzer & Dijkstra 2010).

Podolestes Selys, 1862 (fig. 11f, 24f, 26e, f, 29)

Unique characters within Podolestinae

No unique characters known.

Diagnosis and identification

Adult. *Podolestes* is the only representative of Argiolestidae occurring in Sundaland and mainland South-East Asia. *Podolestes* resembles *Nesolestes* and *Neurolestes* in general morphology but has, in contrast to these two genera, but in accordance with most other genera of Argio-

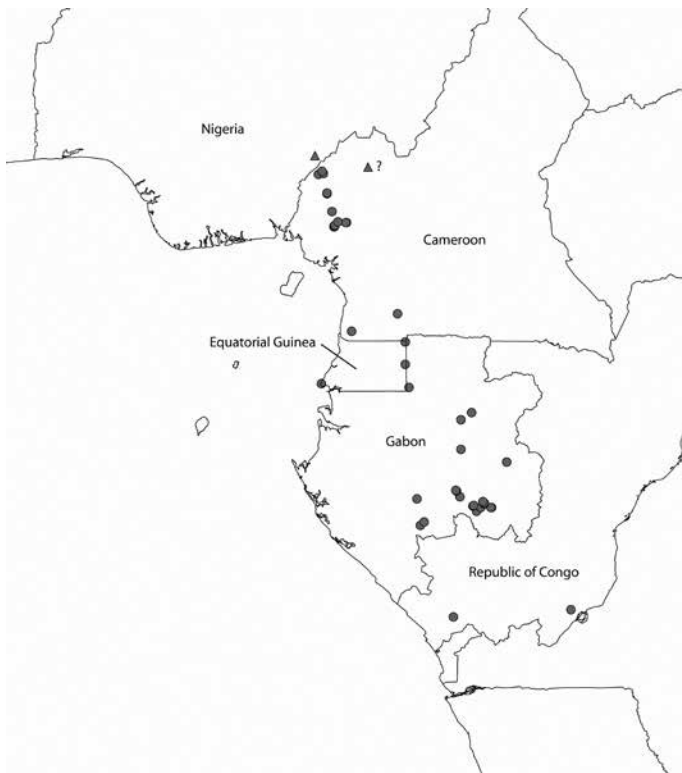


Figure 28. Distribution of *Neurolestes*. *Neurolestes trinervis* (dots) and *N. nigeriensis* (triangle). The triangle with question mark refers to the locality of a possibly third species close to *N. nigeriensis*. Largely based on records in the Odonata Database Africa.

lestidae, a serrated ovipositor. Although there are no clear characters setting it apart from *Nesolestes* and *Neurolestes* it is easily distinguished from these two by the general pattern and colouration of thorax and abdomen. The genus does not overlap with other genera of Argiolestidae and can, within its range, be recognised by the venational characters of the family. Within its range it is, together with the far more colourful *Rhinagrion*, the only damselfly genus including species sitting with open wings and with the abdomen near horizontal. A review of the genus is not available and identification should be based on the descriptions and redescrptions provided by Lieftinck (1935b, 1940, 1950, 1953) and Wilson & Reels (2001).

Larva. The only larva described thus far is that of *P. orientalis* (Choong & Orr 2010). The remark on the microhabitat of the larvae of *P. atomarius* by Lieftinck (1954) suggests that he collected larvae but for some reason never described them.

Distribution and habitat

Seven of the eight species of *Podolestes* are found in Borneo, Sumatra and Peninsular Malaysia (fig. 29). Of these *P. orientalis* has the widest distribution, being relatively common throughout the region. The islands of the Sunda Shelf have, at least at the genus level, largely the same fauna and it is therefore surprising that the genus has not been recorded from Java. The discovery in 1999 of *Podolestes pandanus*, endemic to the Chinese province of Hainan (Wilson & Reels 2001), was rather surprising as the genus was at the time not known to occur in Thailand, Cambodia, Laos or Vietnam. From 2008 on a *Podolestes* species close to the Sumatran *P. coomansi* has been recorded from two provinces in Central and South Thailand (R. Ruan-grong, O. Kosterin, pers. comm.), making it likely that the genus also occurs in Cambodia and Vietnam, which would close the gap with *P. pandanus*. The species of *Podolestes* are confined to swamp forest in lowland where they are found mostly

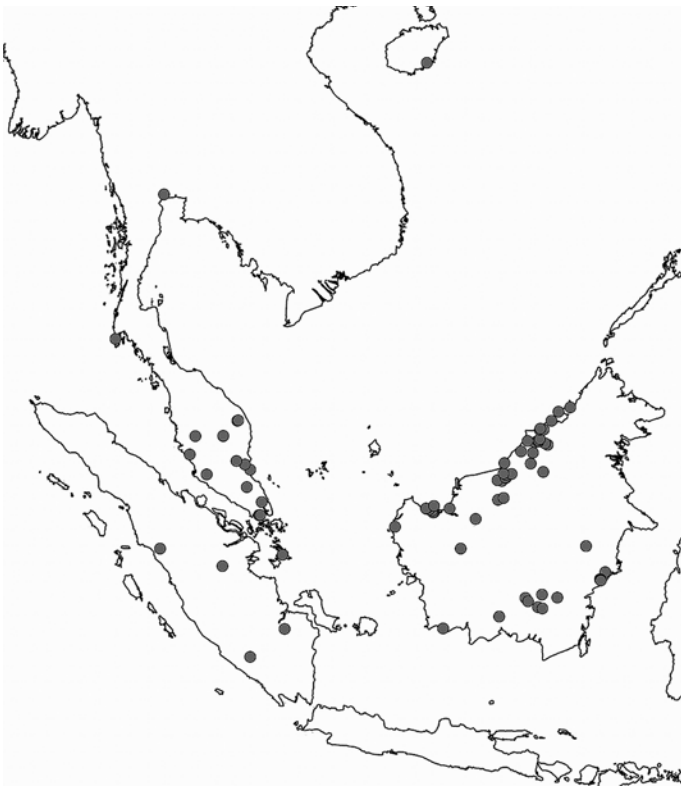


Figure 29. Distribution of *Podolestes*. Based on records in the Melanesian Odonata Database, including unpublished records by Rory Dow.

near shallow pools and slow, sluggish streams (Lieftinck 1954) (fig. 11f). Lieftinck (1954) mentions that *P. atomarius* from Borneo breeds in rain puddles and shallow marshes and that the larvae are found among root-masses and decaying vegetable matter. The larvae of *P. orientalis* were found in a shallow, leafy, forest pool where they lived among submerged or semi-submerged leaves and sticks at the shallow edge of the pools, down to 10 cm depth (Choong & Orr 2010). Females of *Podolestes orientalis* oviposit in leaf stalks above puddles of water. During oviposition the female is guarded by the male (Tang et al. 2010).

KEY TO GENERA FOR MALES OF AUSTRALASIAN ARGIOLESTIDAE

1 S1-6 bright orange, S7-8 black and S9-10 and posterior fifth of S8 blue (fig. 15a) *Eoargiolestes*

- Pattern and colouration on abdomen different, never with a combination of blue and orange 2
- 2 Dorsum of head with blue postocular spots (fig. 9e, f). Annulus between S8 and S9 and between S9 and S10 conspicuously blue (fig. 9e) *Caledopteryx*
- Dorsum of head without blue postocular spots. Annulus between S8 and S9 and between S9 and S10 not enlarged and never blue 3
- 3 Dorsal surface of S8-9 only very lightly sclerotised (fig. 5b, e), often appearing wrinkled in dead specimens. Most species with either a single large raised spine on S10 or with posterior margin of S10 serrated 4
- Dorsal surface of S8-9 normal, as strongly sclerotised as lateral and ventral surfaces. S10 without distinct armature 5

- 4 Posterior margin of S10 with single large raised spine or a tightly packed bundle of smaller spines (fig. 5e). Posterior margin of S10 never serrated. The spine is absent in *W. saltator* but in this species S8-9 are expanded and about twice as broad as S10, a condition never found in *Metagrion* *Wahnesia*
- Posterior margin of S10 never with single raised spine. Posterior margin of S10 serrated, forming a series of teeth (fig. 5b). The serrations on S10 are absent in *M. fornicatum* and *M. verrucatum* but these have the apex of the genital ligula reduced to a whip-like structure lacking apical lobes, while in *Wahnesia* the apical lobes are always present ..
..... *Metagrion*
- 5 Postocular lobes strongly bulging, clearly extending beyond level of compound eyes; head, thorax and abdomen never with bright blue, red or orange colours *Luzonargiolestes*
- Postocular lobes not strongly bulging and not extending beyond level of compound eyes ... 6
- 6 Cerci and apical half of S10 whitish and contrasting with darker S9 (fig. 4, 9b); two apical lobes of genital ligula at least four times as long as broad *Argiolestes*
- Cerci and S10 dark, not contrasting with S9, two apical lobes of genital ligula absent or less than four times as long as broad 7
- 7 Large species. Fw with 28 (rarely 25) or more Px 8
- Medium to small species. Fw with fewer than 28 Px 9
- 8 Hw with up to three rows of cells between CuA and hind border. Terminal segment of genital ligula not reduced to a long whip (fig. 12e, f) *Celebargiolestes*
- Hw with four or more rows of cells between CuA and hind border. Terminal segment of genital ligula reduced to a long whip that is round in basal cross section (fig. 20a)
..... *Podopteryx*
- 9 Cerci with ventrally pointing spur. Generally three or more cells in discoidal field between discoidal cell and level of subnodus.....
..... *Austroargiolestes*
- Cerci never with large ventrally pointing spur. Generally one or two, sometimes three (*Podopteryx*), cells in discoidal field between discoidal cell and level of subnodus 10
- 10 Paraprocts more than half as long as cerci ... 11
- Paraprocts less than half as long as cerci 12
- 11 Ground colour of body metallic green (fig. 24a, b). Wings with 3 Ax, sometimes one or two wings with 2 Ax. Lateral horns of ligula without distinct inflated base (“heel”) (fig. 20d, e) *Trineuragrion*
- Ground colour of body brown to black, not metallic (fig. 9d). Wings with 2 Ax. Lateral horns of ligula with inflated base (“heel”) armed with minute spines (fig. 12a, b)
..... *Caledargiolestes*
- 12 Legs and thorax without bright orange, red or blue colours 13
- Legs and thorax with bright orange, red or occasionally blue colours 15
- 13 Hind rim of S8-9 with conspicuous white annulus (fig. 19a) *Miniargiolestes*
- Hind rim of S8-9 without conspicuous white annulus 14
- 14 Interior of base of cerci flattened and beset with long pale hairs. Dorsum of thorax without or with very small pale stripe
..... *Archiargiolestes*
- Interior of base of cerci not flattened or beset with long pale hairs. Dorsum of thorax with pale stripe along humeral suture for at least half the length of thorax *Griseargiolestes*
- 15 Labrum deeply metallic throughout. Dorsum of synthorax dark *Pyrrhargiolestes*
- Labrum not metallic. Dorsum of synthorax with orange or blue pattern *Solomonargiolestes*

DISCUSSION

Taxonomy

The classification presented here forms a thorough framework for the family Argiolestidae and at present it does not seem likely that further genera are needed in this family. Possible exceptions are the genera *Metagrion*, of which future taxonomic work might show that it should be further divided, and the genus *Argiolestes* where *A. tuberculiferus* stands apart both on morphology and molecular characters. The morphology of the larvae has contributed strongly to the recognition of this group as a family on its own, yet the larvae of many genera are still unknown (*Allolestes*, *Argiolestes*, *Luzonargiolestes*, *Neurolestes*, *Wahnesia*, *Pyrrhargiolestes*), whereas in some other genera (eg *Nesolestes*, *Metagrion*, *Podolestes*, *Podopteryx*) only the larvae of a few of the species have been described or only pictures are available (*Celebargiolestes*). Probably all species occurring in Australia and New Caledonia have been described. It is however likely that in the other areas several dozens of species still await description. At present at least half a dozen undescribed species belonging to each of *Metagrion* and *Wahnesia* are available in the RMNH. Other genera in which new species are likely to be found are *Argiolestes*, *Nesolestes*, *Podolestes*, *Pyrrhargiolestes* and probably also *Neurolestes* and *Luzonargiolestes*. It seems likely that the family holds between 150 and 180 species.

Distribution

Argiolestidae is confined to the eastern hemisphere and is found on Madagascar, the Comoros and the Seychelles (two genera, 17 species), mainland West Africa (one genus, two species), South-East Asia and Borneo and Sumatra (one genus, eight species) and in the Australasian region from the Philippines, over Sulawesi, the Moluccas, New Guinea, the Solomon Islands to Australia and New Caledonia (16 genera and 83 species) (fig. 1). The distribution of all genera is reasonably well known and the maps presented here are likely to give a proper estimate of the true distribution of the genera. The distribution of many species is

poorly known and many species, especially on New Guinea and Madagascar, are known from one or two records only. A review of the biogeography of the family will be published elsewhere.

Life history

It is remarkable how little has been published on the life history of the species belonging to Argiolestidae. For most species only some general information on habitat is available. Detailed notes on territoriality, aggressive behaviour, courtship, mating and oviposition are not available for any species. The species belonging to Argiolestidae generally tend to show very little behaviour, with adults sitting motionless most of time. Many of the species have striking patterns on the face or brightly coloured legs and in some genera males can widen their abdominal tip (eg *Wahnesia*, *Metagrion*, *Eoargiolestes*) all of which suggests that courtship and aggressive behaviour do take place regularly. As far as is known, all species are limited or largely limited to running waters or seepages. The only marked exception is the genus *Podopteryx* with probably all of its species breeding in phytotelmata. To our knowledge this is the only example of an odonate genus belonging to a running-water dependent family which has become adapted to phytotelmata. Information on larval behaviour and larval microhabitat is likewise scarce, with a more detailed account only available for *Podolestes* (Choong & Orr 2010). The suggestion by Liefstinck (1976) that the horizontal position of the gills “probably serve to anchor the insect to rocks” still remains to be tested. A basic study on the life history of one of the Australian species or of *Podolestes* would provide a valuable framework for further data collection on the life history.

ACKNOWLEDGEMENTS

The following persons provided information or ideas for this study: KD Dijkstra, Rory Dow, Ian Endersby, Heinrich Fliedner, Rosser Garrison, Bert Orr, Jan van Tol, and Reagan Villanueva. Specimens and DNA samples were received from

Rory Dow, KD Dijkstra, Andre Gunther, René Hoess, Milen Marinov, Henk van Mastrigt, John Michalski, Steffen Oppel, Steve Richards, Kay Schütte and Jan Taylor. Pictures of species and habitats were kindly provided by Milen Marinov, Nicolas Mézière, Julien Renoult, Steve Richards, Mike Samways, Jan Taylor, Reagan Villanueva and Chee Yen Choong. Jens Kipping provided the records from *Neurolestes* held in the Odonata Database Africa. The SEM images included in this paper were all made by Dirk Gassmann. Rosser Garrison, Jan van Tol and Dan Polhemus critically reviewed the paper. Fieldwork in Australia and New Guinea was made possible due to grant of the Uyttenboogaart-Eliassen Stichting and Schure-Beijerinck-Popping Fonds (KNAW).

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5. REDEFINING THE DAMSELFLY FAMILIES: A COMPREHENSIVE MOLECULAR PHYLOGENY OF ZYGOPTERA (ODONATA)

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Citation: Dijkstra, K.-D.B., V.J. Kalkman, R.A. Dow, F.R. Stokvis & J. van Tol 2013. Redefining the damselfly families: the first comprehensive molecular phylogeny of Zygoptera (Odonata). – *Systematic Entomology*, DOI: 10.1111/syen.12035

An extensive molecular phylogenetic reconstruction of the suborder Zygoptera of the Odonata is presented, based on mitochondrial (16S, COI) and nuclear (28S) data of 59% of the 310 genera recognized and all (suspected) families except the monotypic Hemiphlebiidae. A partial reclassification is proposed, incorporating morphological characters. Many traditional families are recovered as monophyletic, but reorganization of the superfamily Coenagrionoidea into three families is proposed: Isostictidae, Platynemididae and Coenagrionidae. *Archboldargia* Lieftinck, *Hylaeargia* Lieftinck, *Palaiargia* Förster, *Papuargia* Lieftinck and *Onychargia* Selys are transferred from Coenagrionidae to Platynemididae, and *Leptocnemis* Selys, *Oreocnemis* Pinhey and *Thaumatagrion* Lieftinck from Platynemididae to Coenagrionidae. Each geographically well-defined clade of Platynemididae is recognized as a subfamily, and thus Disparoneurinae (i.e. Old World ‘Protoneuridae’) is incorporated, Calicnemiinae is restricted, and Allocnemidinae (type genus: *Allocnemis* Selys) subfam.n., Idiocnemidinae (type genus: *Idiocnemis* Selys) subfam.n. and Onychargiinae (type genus: *Onychargia* Selys) subfam.n. and Coperini trib.n. (type genus: *Copera* Kirby) are described. Half of Coenagrionidae belongs to a well-supported clade incorporating *Coenagrion* Kirby and the potential subfamilies Agriocnemidinae, Ischnurinae and Pseudagrioninae. The remainder is less well defined, but includes the Pseudostigmatidae and New World Protoneuridae that, with Argiinae and Teinobasinae, may prove valid subfamilies with further evidence. Ninety-two per cent of the genera formerly included in the polyphyletic Amphipterygidae and Megapodagrionidae were studied. Pentaphebiidae, Rimanellidae and Devadattidae fam.n. (type genus: *Devadatta* Kirby) are separated from Amphipterygidae, and Argiolestidae, Heteragrionidae, Hypolestidae, Philogeniidae, Philosinidae and Thaumatooneuridae from Megapodagrionidae. Eight further groups formerly placed in the latter are identified, but are retained as *incertae sedis*; the validity of Lestoideidae, Philogangidae and Pseudolestidae is confirmed. For some families (e.g. Calopterygidae, Chlorocyphidae) a further subdivision is possible; Protostictinae subfam.n. (type genus: *Protosticta* Selys) is introduced in Platystictidae. Numerous new combinations are proposed in the Supporting Information. Many long-established families lack strong morphological apomorphies. In particular, venation is incongruent with molecular results, stressing the need to review fossil Odonata taxonomy: once defined by the reduction of the anal vein, Protoneuridae dissolves completely into six clades from five families.

INTRODUCTION

Odonata are among the most ancient of winged insects, dating from the Permian (Grimaldi & Engel 2005). Extant Odonata are considered monophyletic (e.g. Davis et al. 2011) and include two suborders of almost 3000 species each, the Zygoptera or damselflies and the Anisoptera or true dragonflies, and a third suborder, the Anisozygoptera or damselfly dragons with only four species (Kalkman et al. 2008, Dijkstra et al. 2013). Although wing venation guided classification of Odonata, rampant homoplasy (convergence) obscures relationships, as has been demonstrated in Anisoptera (e.g. Dijkstra & Vick 2006, Ware et al. 2007, Pilgrim & von Dohlen 2008, Fleck et al. 2008a, Blanke et al. 2013). The same applies, perhaps more so, in Zygoptera (O'Grady & May 2003, Carle et al. 2008, Pessacq 2008), in which systematic challenges remain in groups with the most simplified venation (mostly Coenagrionoidea) and those characterized by the potentially highly homoplasious insertion of supplementary longitudinal veins (mostly Megapodagrionidae).

Although the phylogeny of the Anisoptera has been reasonably well studied and its classification is fairly settled (e.g. Ware et al. 2007, Fleck et al. 2008b), recent studies of Zygoptera rely on rather incomplete molecular datasets (Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010) and one extensive morphological study (Rehn 2003), although the family Calopterygidae has been studied in detail (Dumont et al. 2005, 2007). Our taxon sampling is the most extensive thus far in Zygoptera, including members of 59% of the 310 genera currently recognized and all (suspected) families, except for the monotypic Hemiphlebiidae. To optimize sampling breadth versus phylogenetic depth, our approach targeted two variable mitochondrial markers [16S, cytochrome c oxidase I (COI)] and a more conserved nuclear one (28S) for many species, rather than more markers for a limited selection. These are among the most commonly applied markers in Odonata and generally provide well resolved and supported trees, at least

from species to family level (Hasegawa & Kasuya 2006, Ballare & Ware 2011). Moreover, a relatively long section of 28S was sequenced and the combined total extent of 28S+16S is comparable (84–145%) to several studies with three or more markers (Ware et al. 2007, Bybee et al. 2008, Pilgrim & von Dohlen 2008, Fleck et al. 2008a, b) and 75% of two studies using four nuclear markers only (Dumont et al. 2005, 2010). For 83% of the studied taxa, COI was sequenced and available sequences surpass previous studies (121–210% and 108%). We focus on the phylogenetic and taxonomic implications of the newly available data (cf. Dijkstra & Kalkman 2012), particularly for the definition of the families, using Silsby (2001) as the basis of the 'traditional' classification (Dijkstra et al. 2013).

METHODS

Specimen acquisition

The study relies on collections assembled in recent years at the Naturalis Biodiversity Center, Leiden, the Netherlands (formerly the National Museum of Natural History and the Netherlands Centre for Biodiversity Naturalis), by the authors, supplemented with donations from our international network (see the Acknowledgements section). Specimens included in the analysis were collected from 43 countries and from all continents, excluding Antarctica. In 34% of cases, one or two legs were removed from a live sample and preserved in 96% ethanol; the specimen was retained as an acetone-dried voucher. In the remaining cases, legs were removed from a specimen previously preserved either in 96% ethanol or by drying with acetone.

DNA extraction and amplification

Genomic DNA was extracted from legs using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Venlo, The Netherlands). Elution was performed in 100 µL elution buffer. Fragments of the nuclear 28S rRNA gene (1346–1532 bp) and the mitochondrial 16S rRNA (522–542 bp) and COI genes

(658 bp) were amplified using primer combinations developed with Primer3 (Rozen & Skaletsky 2000) (Table S1). Twenty-five microlitres of PCR reaction mixes for 16S and COI contained 2.5 µL of 10× CoralLoad PCR Buffer (Qiagen), 1 µL of each primer (10 pM), 1.25U of Taq DNA Polymerase (Qiagen), 0.5 µL of dNTPs and 1 µL of DNA template. Five microlitres of Qsolution (Qiagen) were added to the reaction mix for 28S. The amplification protocol consisted of 3 min at 94°C followed by 40–50 cycles of 15 s at 94°C, 30 s at 60°C to 35°C and 40 s at 72°C, and a final 5 min at 72°C. Direct sequencing was performed at MacroGen Europe on an ABI 3730XL sequencer (Applied Biosystems, Carlsbad, CA).

Data analysis

Sequences were edited with sequencher 4.10.1 (Gene Codes Corporation, Ann Arbor, MI) and assembled using bioedit 7.0.9.0 (Hall 1999), geneious pro 5.6.4 (Biomatters Ltd, Auckland, New Zealand) (Drummond et al. 2011) was used to check for stop codons. All sequence data and additional geographic and ecological data as well as photographs of the specimens were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham & Hebert 2007). Sequences were also deposited in GenBank. Barcode index numbers (BINs) and GenBank accession numbers are provided in Table S2. The number of unique site patterns was 635 for 28S, 452 for 16S and 359 for COI.

Phylogenetic analyses

Multiple sequence alignments were performed using mafft (Katoh et al. 2009) under default parameters. After exploration of all molecular data with neighbour joining analysis using mafft, a selection was made for in-depth analysis of specimens for which both 16S and 28S sequences were available. As a rule, we included two individuals per genus, preferably representing distant species, or two for each distinct clade if the genus appeared not to be monophyletic. The subset included 356 specimens, representing at least 322 species placed in 184 genera. For 295 of these specimens, COI sequences are available as well. Maximum parsimo-

ny (MP), maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the individual datasets of 28S (additional taxa: *Amazoneura*, *Dolonagrion*, *Megapodagrion*) and 16S (adding *Coeliccia dinoceras* Laidlaw, *Xiphiagrion*), as well as the combined 28S+16S and 28S+16S+COI datasets. MP analyses were performed in tnt (Goloboff et al. 2008) by heuristic search with 10 000 random-taxonaddition replicates, TBR branch swapping, maxtrees set to 1000 with auto-increase. All characters were treated as equal and unordered. Gaps were treated as missing data. Node support was established with a bootstrap analysis of 500 replicates. ML analyses were run with raxml (Stamatakis et al. 2008) using a Gamma model of rate heterogeneity, with each fragment treated as a separate partition. For the BI, the best-fitting nucleotide substitution model for each of the individual fragments was assessed using hierarchical likelihood ratio tests in mmodeltest 2.3 (Nylander 2004). For 28S and 16S, a general time reversal (GTR + I + G) model (nst=6) was selected, whereas for COI the Hasegawa-Kishino-Yano model (nst=2) was used, all with a proportion of invariable sites and a gamma distribution for rates across sites (rates = invgamma). For each dataset, two independent Monte Carlo Markov Chain simulations were run in mrbayes 3.2.1 (Huelsenbeck & Ronquist 2001) with four chains, for 4 000 000 generations and a sample frequency of 2000 at a temperature of 0.05, providing >10 000 trees for the consensus after an average standard deviation of split frequencies <0.01 had been reached. Several anisopteran were tested as outgroup, leading to similar topologies, and thus only results using *Aeshna juncea* (Linnaeus) of Aeshnidae are shown.

Morphology

Specimens in the Naturalis Biodiversity Center (Leiden) and University Museum of Zoology (Cambridge) and numerous publications (e.g. Bechly 1996, O'Grady & May 2003, Rehn 2003, Gassmann 2005, Bybee et al. 2008, Pessacq 2008, van Tol et al. 2009, Garrison et al. 2010, Yu & Bu 2011b) were examined for morphological

characters of the lineages identified by molecular analysis.

RESULTS

The phylogenies reconstructed on the 28S+16S and 28S+ 16S+COI datasets are presented in figures 1-3. Support for important clades is summarized in Table S3 and, where relevant, is discussed for separate partitions in the following sections. Of the generally accepted families, many were recovered as monophyletic with good support in (almost) all analyses: Calopterygidae, Chlorocyphidae, Euphaeidae, Isostictidae, Lestidae, Lestoideidae, Platystictidae and Polythoridae. Coenagrionidae was monophyletic if the Pseudostigmatidae and New World Protoneuridae were included, as was Platycnemididae if the Old World Protoneuridae were included, although seven genera had to be moved between the two families (see Discussion for details). Amphipterygidae and Megapodagrionidae were found to be highly polyphyletic, although the latter revealed several large and sometimes well-supported groups of genera. The remaining families are either monogeneric (Philogangidae, Pseudolestidae) or nearly so with only one taxon sampled (Dicteriidae). Perilestidae and Synlestidae were paraphyletic in many analyses but in BI/ML 28S+16S+COI, the two combined were monophyletic with low support and a well-supported monophyletic Perilestidae was embedded in Synlestidae.

Although family-level clades often were well supported and the internal topology of these clades was frequently resolved, generally limited support was found for family interrelationships. However, the clade combining Coenagrionidae, Platycnemididae, Pseudostigmatidae and the entire Protoneuridae was well supported. BI/ML 28S+16S recovered Isostictidae as their sister group, but with low support. Lestoidea (including Lestidae, Perilestidae and Synlestidae) was well supported consistently as the sister group of all remaining Zygoptera, as was Platystictidae as the sister group

of the remainder. No nearest relatives could be identified for the families Calopterygidae, Chlorocyphidae, Philogangidae, Polythoridae and Pseudolestidae, as well as for the clades that formerly constituted Amphipterygidae and Megapodagrionidae. Only Euphaeidae and Lestoideidae appeared consistently as sister groups with good support, but their further relationships remained unclear. The results and their implications are detailed in the following section for each family and/or well-supported clade.

DISCUSSION

Molecular and morphological studies indicate that Zygoptera are monophyletic (Bechly 1996, Rehn 2003, Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010), although Trueman (1996, 2007) questioned this based on an analysis of wing venation. Given our focus on that suborder and the often low support of higher-level relationships found within it, our dataset is unsuited for this issue. Our analyses supported the prevailing family classification for 72% of all genera and 80% of all species of Zygoptera. Therefore recognition at the family level of equally well-supported but previously unrecognized clades, particularly within the 'family' Megapodagrionidae, should be considered. Proposed taxonomic consequences are discussed in the following sections, starting with the relatively well defined smaller sister groups of remaining Zygoptera (the superfamilies Lestoidea and Platystictoidea), followed by the 'crown' radiation of the Coenagrionoidea, which encompasses three-fifths of all damselfly species. The discussion concludes with the problematic remainder, grouped strictly for convenience in the probably paraphyletic 'Calopterygoidea'.

The suggested reclassification of Zygoptera based on this discussion is provided in Appendix 1, including the authorities for all genus- and family-group names. Diagnoses of new or revised family groups are given in Appendix 2 and a summary of proposed taxonomic changes, including new combinations, is given in Table S4.

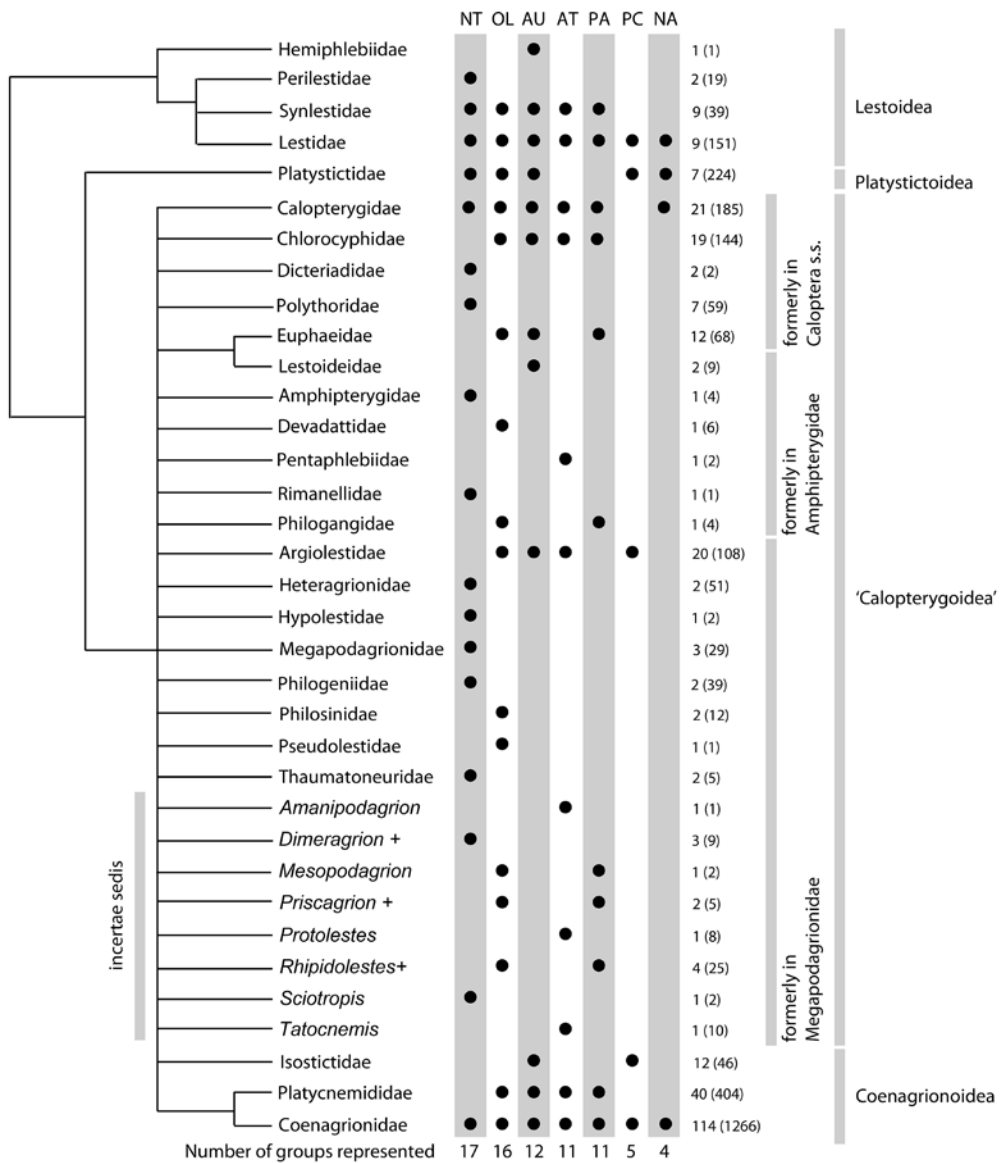


Figure 1. Summary of Zygoptera phylogeny, based on figures 2, 3 and the Discussion section. Only reasonably supported dichotomies are shown. The classification follows Appendix 1 (see for other genera placed near *Dimeragrion*, *Priscagrion* and *Rhipidolestes*) and the fate of some traditional taxa is indicated. For each recognized damselfly lineage, the known numbers of genera and species (in brackets) are shown, as is their occurrence in the Afrotropical (AT), Australasian (AU), Nearctic (NA), Neotropical (NT), Oriental (OL), Pacific (PC) and Palearctic (PA) regions.

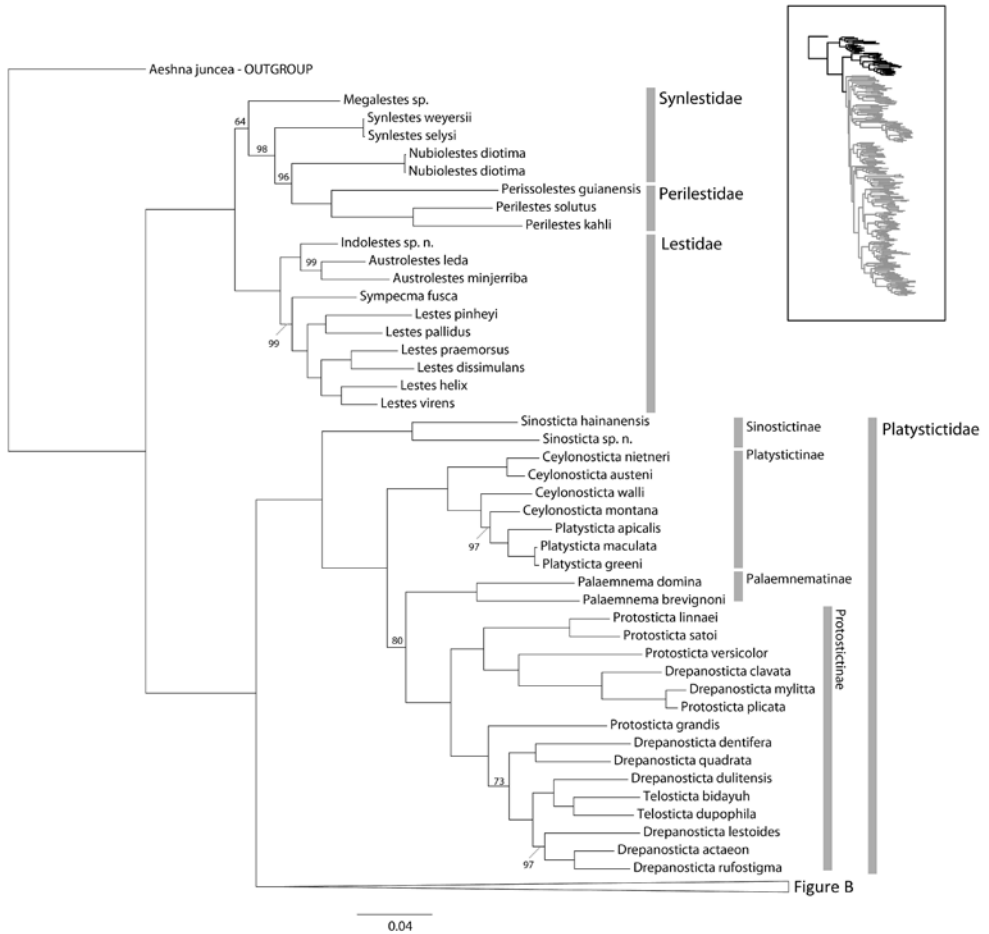


Figure 2a. Phylogenetic reconstruction for 295 specimens from the combined Bayesian analysis of 28S, 16S and COI. Posterior probabilities are shown (as percentages) only if below 100%. Species names and classification as proposed are shown. (a) Lestoidea and Platysticticoidea; (b, c) various groups; (d) Platycnemididae; (e) Coenagrionidae.

Superfamily Lestoidea

All analyses confirmed that the over 200 species of Lestoidea (not to be confused with the unrelated genus *Lestoidea*) form the sister group of all the other 93% of damselflies (cf. Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010, Davis et al. 2011). Contrary to Rehn (2003), the position of the superfamily Lestoidea suggests that the narrowed external edge of the labial palp is an apomorphy of remaining Zygoptera, rather than that the expanded edge arose convergently in Lestoidea and Anisoptera. With the exception of *Hemiphlebia*,

Lestoidea possesses distinctly modified secondary genitalia with a reduced apex of the genital ligula (the functional penis) and triangular anterior hamules (Rehn 2003, Garrison et al. 2010). The monotypic Hemiphlebiidae from southeastern Australia and Tasmania was not studied, but is the sister group of remaining Lestoidea according to previous studies (Rehn 2003, Dumont et al. 2010, Davis et al. 2011).

Just over a quarter of the Lestoidea species are placed currently in the Perilestidae and Synlestidae.

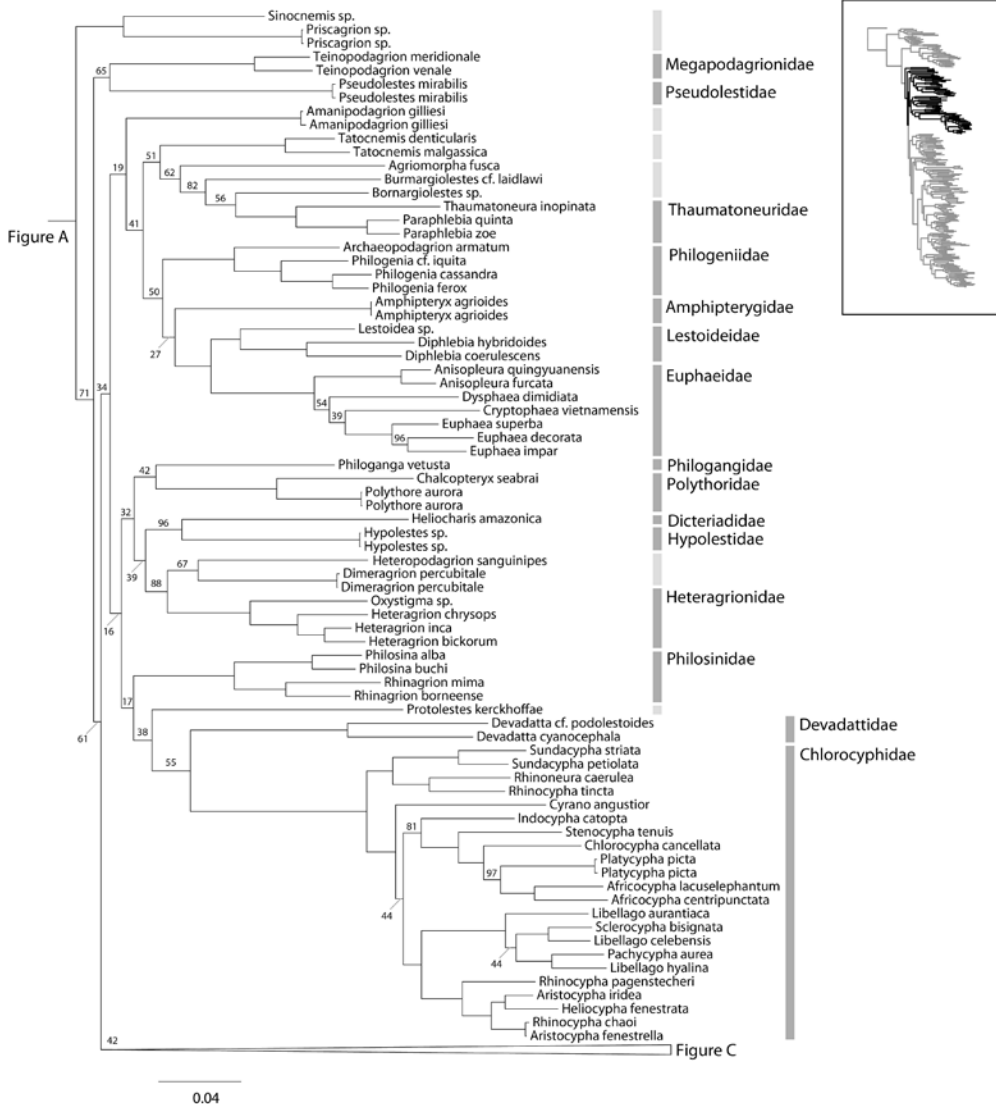


Figure 2b. Continued.

We found no support for the monophyly of the latter family, but in BI/ML 28S+16S+COI the two combined were monophyletic with low support, as was Perilestidae with high support. The last is expected given the morphological similarity of the Neotropical *Perilestes* and *Perissolestes*. The monotypic *Nubiolestes* from central Africa has been considered the only non-American perilestid, but

formed the sister group of the American genera only in BI/ML 28S+16S+COI, although with low support. However, we had difficulty amplifying COI for many synlestids and BI, ML and MP of 28S and 28S+16S recovered *Nubiolestes* as the sister group of the southern African *Chlorolestes*. Neotropical Perilestidae share mid-dorsal spines on the larval abdomen, a two-toothed ovipositor,

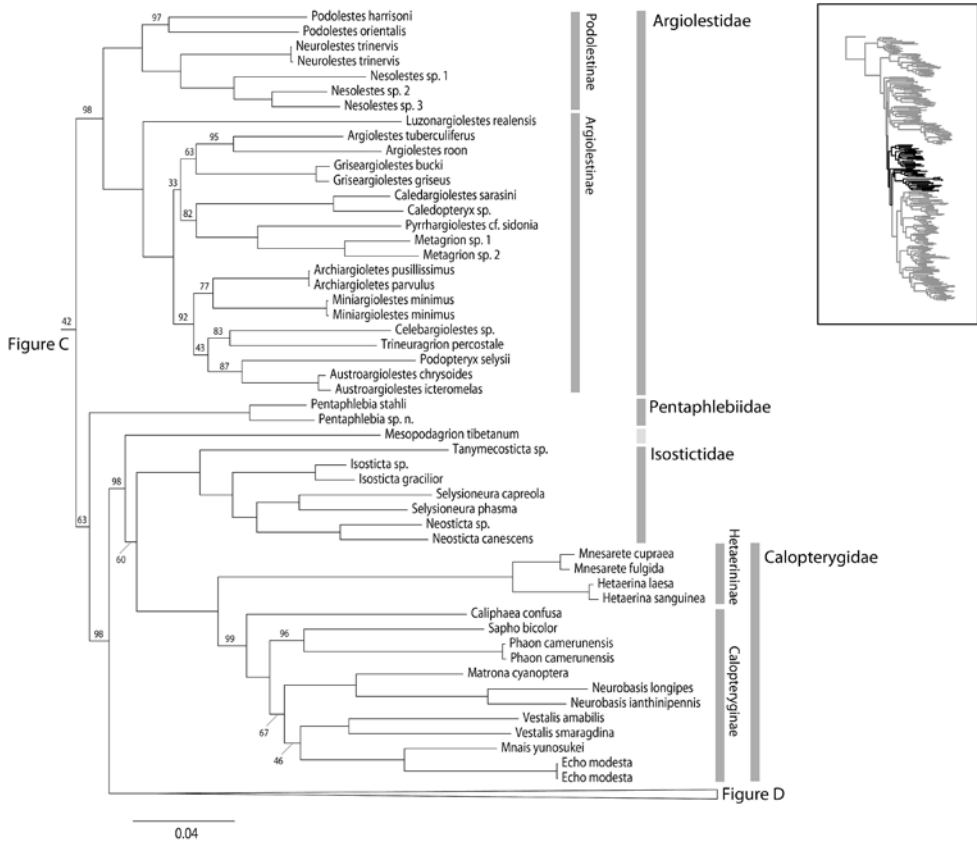


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very short pterostigmata, anal veins reduced basally (or shifted distally) allowing the quadrilateral cells to reach the wing margins, and a distinctive layout of markings and appendages (Garrison et al. 2010). The anal vein and ovipositor dentition of *Nubiolestes* are intermediate to *Chlorolestes* and other features are closer to the latter. Interestingly, the Synlestidae from South Africa (*Chlorolestes*, *Ecchlorolestes*) never grouped together, nor did those from Australia (*Episyntlestes*, *Syntlestes*). We did not sample the problematic genera *Phylolestes* from Hispaniola, *Sinolestes* from China and *Chorismagrion* from Australia. The last, sometimes placed in the Chorismagrionidae (Bechly 1996), was recovered within Synlestidae by Bybee et al. (2008) and Dumont et al. (2010). May et al.

(unpublished data in Dijkstra et al. 2013) found Synlestidae to be monophyletic if *Nubiolestes* was included, but morphological apomorphies for the group remain to be identified. Given the discussed problems, we retain Perilestidae and Synlestidae as currently recognized, only transferring *Nubiolestes*, although Synlestidae may still prove not be monophyletic and the two families might eventually be merged or divided. Lestidae was monophyletic in all analyses (cf. Rehn 2003, Bybee et al. 2008, Dumont et al. 2010). *Austrolestes* and *Indolestes* are sister groups, but were never monophyletic with *Sympecma*, which also closes its wings at rest, and thus no support for the subfamily Sympecmatinae was found. *Sympecma* was recovered in *Lestes* in ML 28S+16S: over half the species of Lestidae are

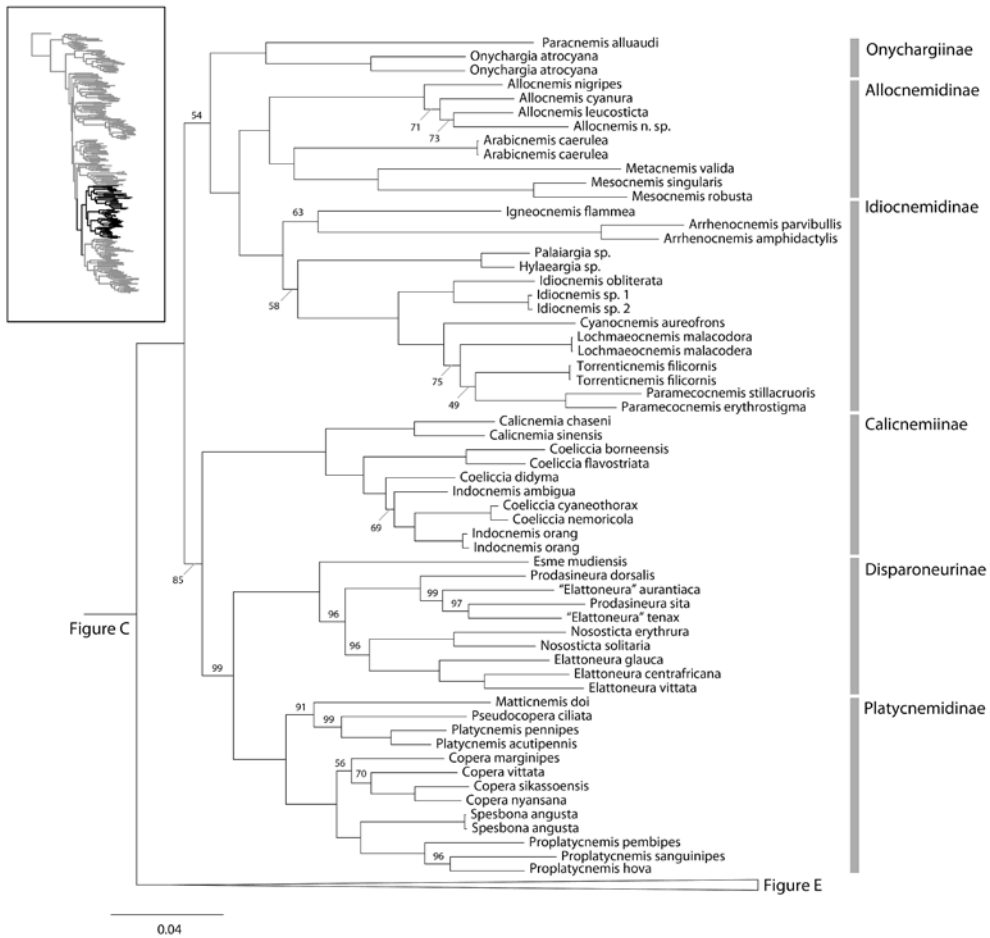


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currently placed in *Lestes* and this heterogeneous and cosmopolitan genus is likely to be subdivided in the future.

Superfamily Platystictoidea and family Platystictidae

Platystictidae is monophyletic in all analyses and the sister group of all Zygoptera, excluding Lestoidea, in BI and ML of 28S+16S and 28S+16S+COI (cf. Bybee et al. 2008, van Tol et al. 2009, Dumont et al. 2010, Davis et al. 2011). The group possesses a peculiar combination of venation characters, including a reduced anal vein abutting (when

present) the quadrilateral cell, a supplementary basal cross-vein and a very basally positioned node, and is also characterized by the ridges on the occiput and postgenae (Rehn 2003, Garrison et al. 2010). Currently the over 220 species are placed in just seven genera, a higher ratio than in any other family. This is due to the highly polyphyletic nature of the Oriental genera *Protosticta* and *Drepanosticta* (van Tol et al. 2009). The recently described genus *Telosticta* is monophyletic, but further generic revision is required (Dow & Orr 2012). Wilson (1997) erected the subfamily Sinostictinae for the distinct genus *Sinosticta* from

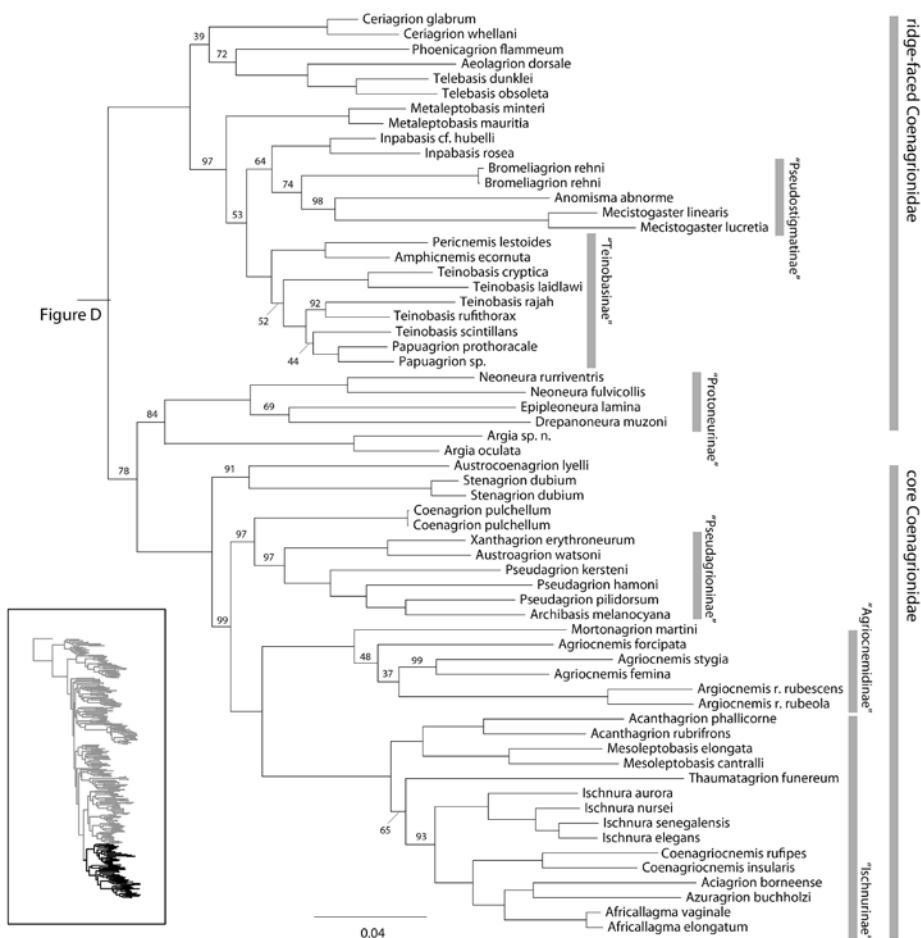


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southern China, which was the sister group of remaining Platystictidae with high support. The Sri Lankan Platystictidae were found to be the sister group of all platystictids except *Simosticta* in BI 28S+16S and BI/ML 28S+16S+COI, and of the Neotropical genus *Palaemnema* (sole member of the subfamily Palaemnematinae) in BI/ML 28S and ML 28S+16S, making the Oriental Platystictinae paraphyletic. Therefore we limit Platystictinae to the Sri Lankan group and erect Protostictinae subfam.n. for the remaining Asian Platystictidae. The genus *Ceylonosticta* is reinstated for the Sri Lankan species placed in the mainland genus

Drepanosticta, although this genus appears paraphyletic relative to the endemic *Platysticta* and must be revised (Table S4).

Superfamily Coenagrionoidea

A monophyletic group including Coenagrionidae, Platycnemididae, Protoneuridae and Pseudostigmatidae *sensu* Silsby (2001), was well supported by BI/ML 28S+16S/ 28S+16S+COI (cf. Bybee et al. 2008, Carle et al. 2008). Isostictidae is the sister group of this assemblage according to Bybee et al. (2008), a relationship we recovered only with low support in BI/ML 28S+16S. All aforementioned

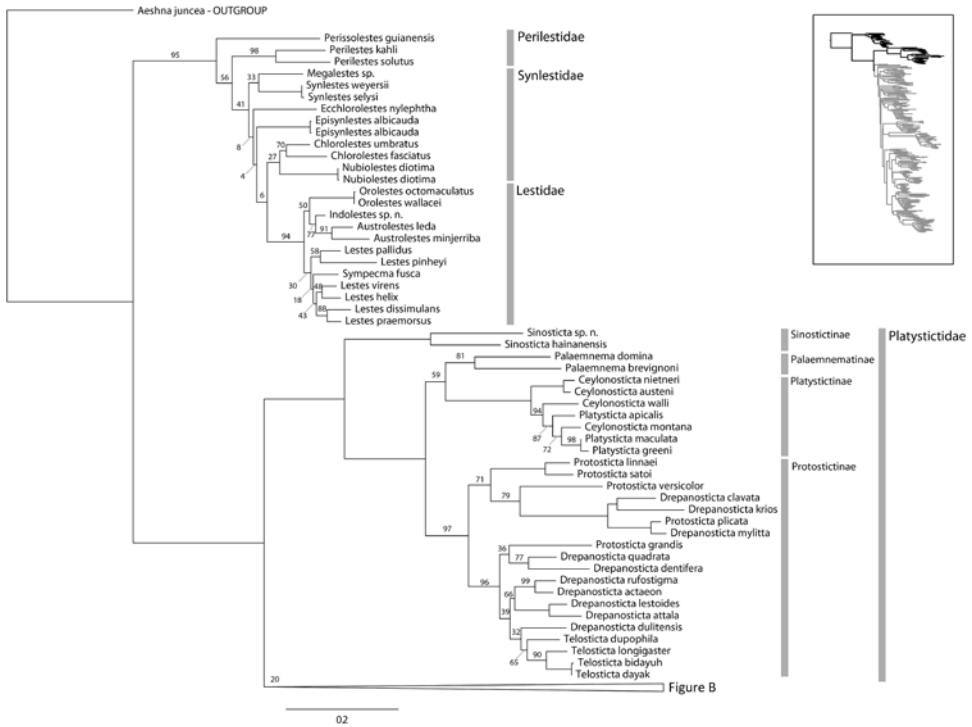
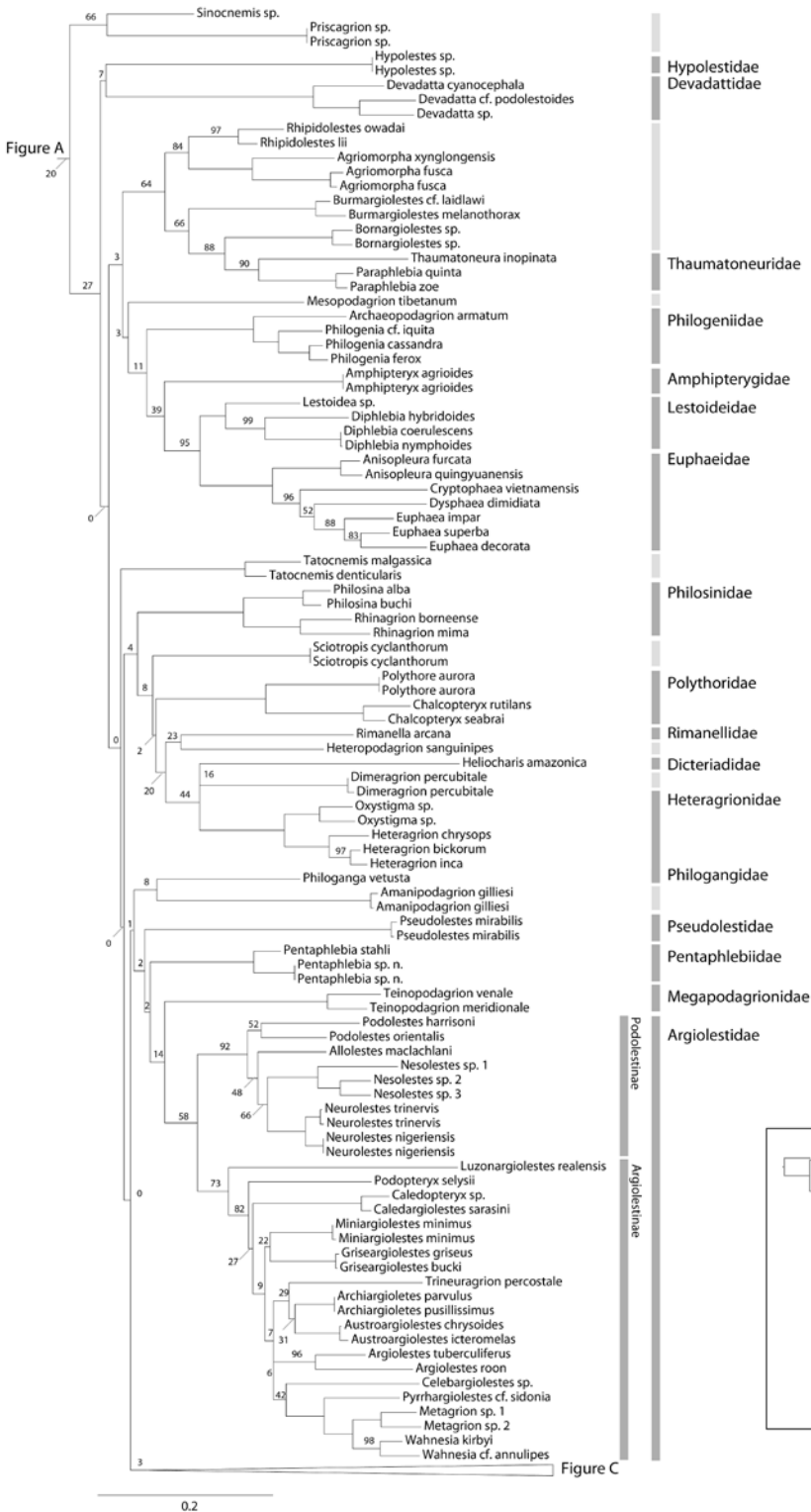


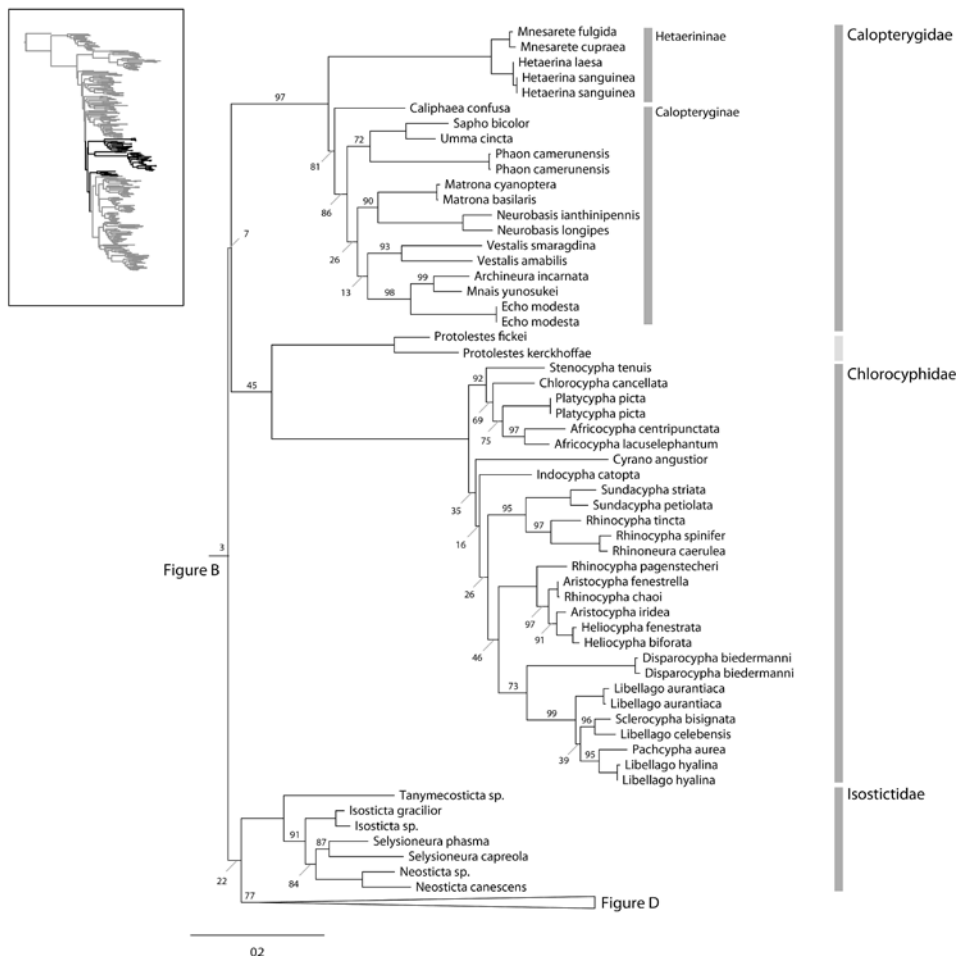
Figure 3a. Phylogenetic reconstruction for 356 specimens from the combined maximum likelihood analysis of 28S and 16S. Bootstrap values are shown only if below 100. Species names and classification as proposed are shown. (a) Lestoidea and Platystictioidea; (b, c) various groups; (d) Platycnemididae; (e) Coenagrionidae.

families are retained in the superfamily Coenagrionoidea, including almost three-fifths of all damselfly species. They are characterized by the larval prementum, which has an (almost) entire anterior border and palps bearing setae, although palpal setae also occur in the Lestidae (Bechly 1996, Rehn 2003).

Coenagrionoid classification has been unsettled by the discovery of non-monophyly of its long-recognized families. As detailed in the following, our extensive sampling allows reconfiguration of the superfamily into three families, of which Isocticidae includes less than 3% of species and Platycnemididae 24%. The Old World 'protoneurids' (Disparoneuridae in Kalkman & Orr 2012) are not closely related to the true New World Proto-

neuridae (Pessacq 2008), being either the sister group of Platycnemididae (Bybee et al. 2008, van Tol et al. 2009, Dumont et al. 2010) or falling within that family (Rehn 2003, Carle et al. 2008). In BI/ML 16S/28S+16S/28S+16S+COI, Platycnemididae forms the sister group of remaining Coenagrionoidea (excluding Isocticidae) and Disparoneuridae is the sister group of its subfamily Platycnemidinae. The remaining Platycnemididae (previously considered as subfamily Calicnemidinae) are paraphyletic, as demonstrated previously based on morphology (Gassmann 2005). Our analyses show that they form several geographically well-defined clades. Stability is served by expanding the family to incorporate the Disparoneuridae and recognizing each of these clades as a subfamily. The latter family-group name is favoured over





Caconeuridae, introduced simultaneously (Fraser 1957), because *Caconeura* belongs to a distinctive southern Indian radiation, while *Disparoneura* has more in common with the widespread elements of this group. The complex systematics of the remaining 73% of Coenagrionoidea is discussed under Coenagrionidae.

Family Isostictidae

All analyses confirmed that Isostictidae is monophyletic, although its position is problematic and it may not belong in Coenagrionoidea (cf. Bybee

et al. 2008, Carle et al. 2008). The family incorporates less than 50 damselfly species confined to Australia, New Guinea, New Caledonia and neighbouring islands. Larvae have unique gills that are strongly constricted medially and somewhat swollen basally in most genera. Adults are peculiar with laterally compressed heads, recalling some Coenagrionidae such as *Amphicnemis*, *Ceriagrion* and *Neoneura*, with wide and deep labial clefts, and have rather forcipate and often toothed or serrate cerci, lack bright colours and are generally very slender.

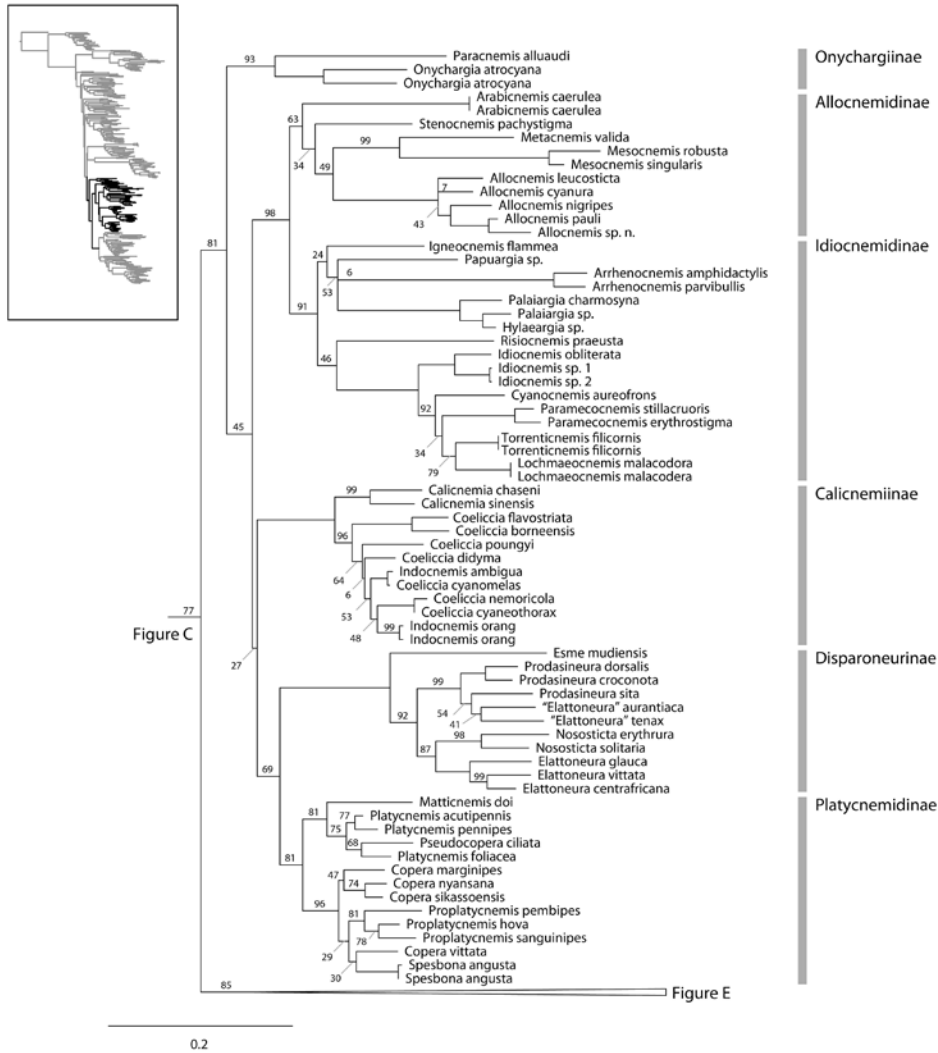


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Family Platycnemididae

Incorporating Disparoneuridae, this family includes over 400 species confined to the Old World, mostly to tropical streams and rivers. Despite being long recognized as a family and genetically well defined, no clear morphological apomorphies are known, although the species always lack spines on the genital ligula shaft (Pessacq 2008, Kalkman et al. 2010), while these are present in at least 53% of 103 examined coenagrionid genera. Adults

often have laterally expanded heads (with usually shallow labial cleft and no trace of postfrontal suture) and tibiae with dense long spines (Rehn 2003, Carle et al. 2008). A consistently recovered clade comprised the small Oriental genus *Onychargia* and the Madagascan *Paracnemis*: we consider this as the subfamily Onychargiinae subfam.n. It was the sister group of remaining Platycnemididae in ML 28S+16S/28S+16S+COI, but of the combined African and Papuan clades (see later) in

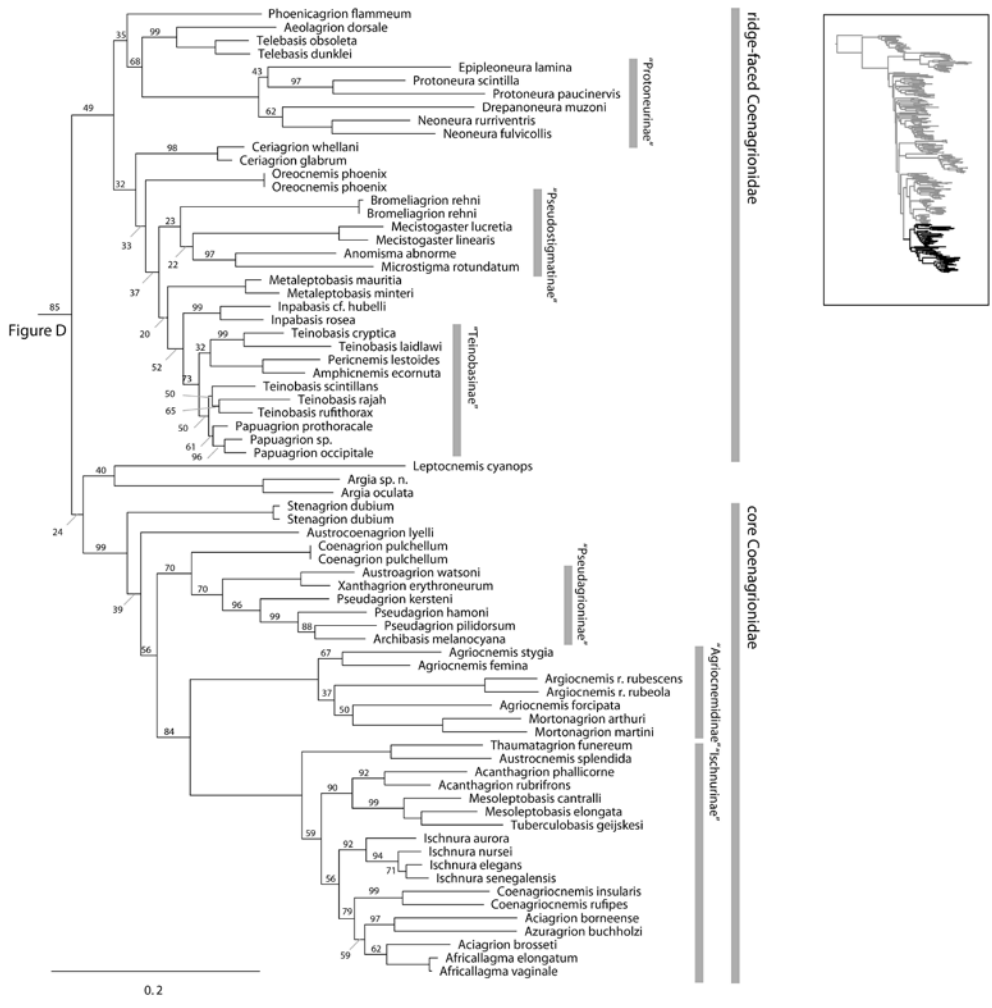


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BI 28S+16S/28S+16S+COI. *Onychargia* was placed previously in Coenagrionidae, but its spineless genital ligula, long leg spines, markings (most notably the transverse pale band across vertex) and cerci with long internal tooth (concealed in tenth tergite) fit Platycnemididae better. The two genera have quite similar markings and share notably short cerci, as well as their swampy habitats (K. Schütte, *in litt.*), which is unusual for the family. *Paracnemis* is monotypic, although '*Metacnemis*' *secundaris* Aguesse (known only from the holotype from Madagascar) is unlike that South African genus

and closer to *Paracnemis*, most notably by markings, and is placed there until its rediscovery allows a better assessment (Table S4).

Another clade represents almost 30 species restricted to tropical mainland Africa (*Allocnemis*, *Mesocnemis*, *Metacnemis*, *Stenocnemis*) plus the endemic monotypic genus from adjacent Arabia *Arabincnemis*, which we consider as the subfamily Allocnemidinae subfam.n. Although this group is well defined geographically, their morphology is heterogeneous, the robust *Mesocnemis* and

Metacnemis having been previously associated with 'argiine' Coenagrionidae. Distinguished only by the relative length of the anal vein, the genera *Allocnemis*, *Chlorocnemis* Selys and *Isomecoccnemis* Cowley (the latter two were formerly in Protoneuridae for this reason) are intermixed and all species should be treated under the first name (Table S4). *Metacnemis* should be restricted to *M. valida* (Hagen in Selys), as both species added to that genus later appear not to be related (see discussion both earlier and later in this paper). This African clade is the sister group of one of about 100 platycnemidid species occurring east of Huxley's Line. The studied New Guinean genera with crenulated wingtip margins (*Cyanocnemis*, *Idiocnemis*, *Lochmaecocnemis*, *Paramecoccnemis*, *Torrenticnemis*) form a well-supported monophyletic subgroup. Based on this and other morphology, *Rhyacocnemis* from New Guinea and *Lieftinckia* and *Salomocnemis* from the Solomon Islands belong here too (Gassmann 2005). This subfamily, to be called Idiocnemidinae subfam.n., also includes New Guinean genera with absent or reduced wingtip crenulation: *Arrhenocnemis* was placed previously in Megapodagrionidae but shown to belong here by Gassmann (2005) and Orr & Kalkman (2010). *Palaiargia* and *Papuargia* (as well as presumably *Archboldargia*) were considered previously as 'argiine' Coenagrionidae, based on their venation and lacking the lateral expansion of the head (Lieftinck 1949). *Hylaeargia* was found to fall within *Palaiargia* although the male appendages are rather different; better taxon sampling is needed before a decision can be made on its status. The Philippine genus *Risioecnemis* was recovered here consistently. The positions of the morphologically well-defined subgenera (cf. Gassmann & Hämäläinen 2002) varied by analysis, but they were never recovered as sister groups and this warrants recognizing *Ignecocnemis* as a genus (Table S4). The gills of *Hylaeargia*, *Lieftinckia* and *Palaiargia* larvae form a unique three-dimensional ruff (Lieftinck 1957, Corbet 1999). Whether this is an apomorphy of Idiocnemidinae is unclear, as no other larvae have been described.

Calicnemiinae is limited to the Oriental genera *Calicnemia*, *Coelliccia* and *Indocnemis* in our analyses, which together have about 85 species. Within the family, these genera are notable for possessing distinct elongate pale spots on the posterior border of the postocular lobes (Gassmann 2005). *Indocnemis* makes *Coelliccia* paraphyletic. That genus probably requires further subdivision and more species may be placed in *Indocnemis*, so synonymizing it now would be confusing. Moreover, the sister group of remaining *Coelliccia*, Dow's (2010) *borneensis* group from Borneo, shares some characters with *Coelliccia lieftincki* Laidlaw from Java and *Coelliccia* species from the Philippine islands Mindoro, Mindanao and Palawan. The Philippine species are especially close to the Palawan genus *Asthenocnemis*, 16S data groups *Coelliccia dinoceras* from Mindanao firmly with the *borneensis* group. *Asthenocnemis* may make *Coelliccia* paraphyletic and major generic reclassification of the subfamily is needed.

Disparoneurinae includes distinct African, Asian and Papua- Australian clades (representing over 25, 45 and 55 species, respectively) that together form the largest platycnemidid radiation. This includes all platycnemidids with a largely or entirely reduced anal vein, except some *Allocnemis*, and typically rather short and high male appendages. The Papua- Australian clade conforms to the genus *Nososticta*, but species currently assigned to *Elattonaura* and *Prodasineura* are mixed in both the African and Asian clades. The slightly less reduced anal vein that supposedly separates *Elattonaura* from *Prodasineura* is obviously not reliable. Nonetheless, most species can be assigned to the correct continent by their combination of coloration (e.g. blue is frequent in Asia, but absent in Africa), venation (complete reduction anal vein only in Asia) and paraproct shape, the distal border of which is rather vertical in Africa, but tends to slope in Asia (Dijkstra 2007). As the type-species of *Elattonaura* is African and that of *Prodasineura* is Asian, all African species should be placed in *Elattonaura* (Table S4). The situation in Asia is more complicated, as the species now

placed in *Elattonneura* may not be closely related to the type of *Prodasineura* and the entire group requires revision. The Arabian *Arabineura* and Indian *Disparoneura* presumably belong to this clade too, as both have appendages nearest *Prodasineura*. Ten ‘caconeurine’ species are endemic to southern India, but although morphologically very distinctive as a group, the four genera (*Caconeura*, *Esme*, *Melanoneura*, *Phylloneura*) are almost identical. We retrieved *Esme* as the sister group of all other Disparoneurinae sampled, but Dumont et al. (2010) retrieved *Caconeura* within *Prodasineura*. The latter study had a narrow taxon-sampling, and while Bybee et al. (2008) confirmed that *Phylloneura* is disparoneurine, they only had *Nososticta* to compare. As with the Allocnemidinae and Idiocnemidinae, the African *Elattonneura* and Papua-Australian *Nososticta* were retrieved mostly as sister groups of each other, rather than of the Oriental *Prodasineura*, a pattern worthy of closer investigation and supported by the generally vertical profile of their paraprocts.

The subfamily Platycnemidinae as previously known, defined by feather-like tibiae (expanded, coloured) in males, is a monophyletic assemblage of nearly 40 species, including the family’s only notable Malagasy and Palaearctic radiations. It consists of two well-supported clades, both of which contain species presently classified in *Platycnemis* and *Copera*. The clade with the generotypic *Copera marginipes* (Rambur), which we recognize as the tribe Coperini trib.n., has a unique larval character (gills with frilled borders) and adult males often have barred eyes, colourful legs (white, yellow, orange, red, blue) and an internal tooth on the cerci. Aside from the true Oriental *Copera* species, it includes all Afrotropical species until now placed in *Platycnemis*. The name *Proplatycnemis* is available for the Malagasy species (Table S4), which have a distinctive genital ligula shape; *Proplatycnemis pembipes* (Dijkstra et al.) from the Tanzanian island Pemba belongs here (Dijkstra et al. 2007). The continental African species group with the morphologically similar true *Copera*, and are best transferred accordingly

(Table S4). The South African genus *Spesbona* is the sister group of *Proplatycnemis*; its sole species *Spesbona angusta* (Selys) was previously placed in *Metacnemis* but is distantly related to the type of the genus, *M. valida* (Dijkstra 2013). The species’ markings, genital ligula and appendages are close to those of *Proplatycnemis*. Its tibiae, however, are black and not widened, which prevented an earlier association with its true relatives. This and the bulging postocular lobes, pointed pterostigmata and deep blue colour are unique within the subfamily (Dijkstra 2013). The tribe Platycnemidini has smooth-bordered gills and males always have white legs and no cercal tooth. It consists of the Palaearctic *Platycnemis* species (including the generotype) and the black-and-white species placed formerly in *Copera*, which extend from Japan to Java. The genus *Platycnemis* should be limited to the Palaearctic species, and for its probable sister group of ‘false’ *Copera* species the name *Pseudocopera* is available (Table S4). The recently described *Matticnemis doi* (Hämäläinen) is the sister group of these two genera (Hämäläinen 2012, Dijkstra 2013).

Family Coenagrionidae

Encompassing almost 1300 species, remaining Coenagrionoidea represents the greatest damselfly radiation. Earlier subdivisions are generally unsupported by morphology (O’Grady & May 2003), but molecular studies are revealing some notable groups. We sampled 45 of 115 genera and, and with data published for another 17, these groups are becoming increasingly well supported. As detailed in the following, two major groups can be distinguished, both of which are cosmopolitan and contain over 600 species, but only the group including *Coenagrion* is unquestionably monophyletic. This group is generally defined by well-developed postocular spots and dominates in the Holarctic and Palaetropics, representing over 80% of species diversity in the Palaearctic and Afrotropics and just 30% (ischnurines only) in the Neotropics. The remainder rarely possesses postocular spots, but is characterized by a ridged frons in most species, although the large genus

Argia is the notable exception for both characters. This half is richest in the Neotropics with 70% of species, including Pseudostigmatidae and true Protoneuridae. It also has a notable Palaeotropical presence, e.g. teinobasines and *Ceriagrion*, representing over 40% of species in the Oriental, Australian and Pacific regions.

We treat all this diversity within a massively expanded Coenagrionidae. Such an inclusive approach serves stability, although given the size of this group (about 30% larger than any other odonate family), applying the family rank to more manageable units might seem appropriate when better phylogenetic support is obtained. The oldest name available for the non-core genera is Pseudostigmatidae Kirby 1890, applied for over 120 years to just a score of peculiar species. It seems counterintuitive to apply that name to about 30 times as many generally 'ordinary' damselflies. Given its long history in a polyphyletic sense, using Protoneuridae Jakobson & Bianchi 1905 for almost 500 species never known by that name may also cause confusion. Both 'families' as currently known are apophyletic groups (i.e. their distinctness resulted in an exaggerated taxonomic rank; see O'Grady & May 2003), defined by the extreme expansion and reduction of their venation, respectively. Although taxonomic names are governed by rules, they are applied by consensus. We expect these names will continue to signify only these damselflies for most users, even if only in a colloquial sense, as they have for over a century. The family-group name Teinobasidae Tillyard 1917 has been applied for most of the former Coenagrionidae in the ridge-faced group (De Marmels 2007), yet is sufficiently unfamiliar to most users to be neutral. *Teinobasis* and other 'Teinobasinae' are characterized by all features defining the group. We believe that if the monophyly of the whole group is resolved and a name for it is required, this one would be carried best by the odonatological community. Prioritizing it would, however, require a ruling of the International Commission on Zoological Nomenclature. The data suggest that Agriocnemidinae, Ischnurinae and Pseuda-

grioninae constitute distinct groups within core Coenagrionidae, as may Argiinae, Protoneurinae, Pseudostigmatinae and Teinobasinae among the remainder. Thus a taxonomic solution in which most familiar names can be conserved as subfamilies is conceivable and therefore perhaps preferable. However, sampling and support are still insufficient for a comprehensive subdivision and thus, for now, we apply these names only in a vernacular sense.

Core Coenagrionidae

The monophyly of this group representing over 650 species is well supported in our and all previous molecular analyses (Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010). Three well-supported clades conforming to previously named subfamilies are recovered within it, which together appear to contain almost nine-tenths of the species. The largest clade represents just over half and conforms to the cosmopolitan Ischnurinae, including all genera that possess a vulvar spine in the female, although it is occasionally absent: *Acanthagrion*, *Aciagrion*, *Africallagma*, *Austrocnemis*, *Azuragrion*, *Coenagriocnemis*, *Dolonagrion* (based on 28S only), *Ischnura*, *Mesoleptobasis* (with *Tuberculobasis* within it) and *Xiphiagrion* (16S only). The formerly 'platycnemid' *Thaumatagrion* is closely related to *Austrocnemis*, also a dark-bronzy long-legged Papua-Australian genus, which is supported by its spiny genital ligula (Gassmann 2005). Hovmöller (2006) previously investigated the group's monophyly, adding *Amphiallagma*, *Cyanallagma*, *Homeoura* and *Oxyagrion*, while *Amphiagrion*, *Enallagma*, *Hesperagrion* and *Proischnura* belong here as well (Carle et al. 2008, Dumont et al. 2010), all possessing the vulvar spine. Based on this character and/or similarity to other ischnurines, the genera *Acanthallagma*, *Andinagrion*, *Argentagrion*, *Austroallagma*, *Denticulobasis* (denticulate vulvar plate is assumed homologous), *Enacantha*, *Leptobasis*, *Leucobasis*, *Mesamphiagrion*, *Millotagrion*, *Oreagrion*, *Oreiallagma*, *Oxyallagma*, *Pinheyagrion*, *Protallagma*, *Tigriagrion* and *Zoniagrion* can be added. *Amorphostigma* Fraser, *Boninagrion* Asahina, *Rhodischnura* Laidlaw and probably *Pacificagrion*

must be subsumed into *Ischnura* (O'Grady & May 2003, Hovmöller 2006, Karube et al. 2012). *Anisagrion*, *Apanisagrion* and *Calvertagrion* lack the vulvar spine, but form a largely Central American, probably monophyletic, group with the spined *Hesperagrion* (De Marmels 2002a).

The clade incorporating *Agriocnemis*, *Argiocnemis* and *Mortonagrion* conforms to the Palaeotropical Agriocnemidinae of about 55 species. The first appears paraphyletic, but all three genera require redefinition (Dow 2011). It is the only coenagrionid subfamily supported by the morphological analysis of O'Grady & May (2003), the arculus being shifted considerably distal to the second antenodal cross-vein. The clade of *Archibasis*, *Austroagrion*, *Pseudagrion* and *Xanthagrion* conforms to the mostly Palaeotropical Pseudagrioninae, including almost 200 species. The Asian *Pseudagrion* species sampled was closer to the Asian *Archibasis* than to the two African species studied. As the type of *Pseudagrion* is African, this indicates that the Asian taxa may have to be reclassified. Earlier results suggest that the Palaearctic *Erythromma* and Oriental *Paracercion* and *Stenagrion* are related (Carle et al. 2008, Dumont et al. 2010), as may be the Antipodean *Caliagrion* and *Xanthocnemis*, but we found no clear relationship for *Stenagrion*. Also the Australian *Austrocoenagrion* and Holarctic *Coenagrion* were not recovered with any specific subgroup, although their genetic distinctiveness confirms their separation as genera (Dijkstra & Kalkman 2012). Jordan et al. (2003) could not resolve the origin of the Hawaiian *Megalagrion* radiation; Dumont et al. (2010) recovered it between agriocnemidines and ischnurines.

An apomorphy of all genera discussed earlier is the usual presence of well-developed postocular spots (cf. De Marmels 1984). Although variable in their extent and development, the spots are typically positioned centrally on the postocular lobes and enclosed by dark coloration. In *Austrocnemis*, *Thaumatagrion*, most *Amphiagrion* and occasional species of other genera (e.g. *Erythromma*), the head is so dark to have obliterated them, while in

Andinagrion and *Oxyallagma*, the head and thorax are uniformly reddish, and in *Tigriagrion* the spots are partially obliterated by a dark pattern. Postocular spots are absent in 89% of the remaining coenagrionoid genera, discussed later. Where markings occur, these usually differ in their shape and position, e.g. a pale occipital bar may expand laterally and/or posteriorly onto the postocular lobes. None of the core Coenagrionidae members have an angularly ridged frons, which is present in 75% of remaining genera. Although extremely plastic, the male appendages of core Coenagrionidae often show typical features, with notably swollen paraproct bases and terminally branched cerci, both branches often being hooked and bearing a soft pad between them. The distal segment of the genital ligula often has a well-developed pair of median lobes. The discussed characters suggest that *Himalagrion* and *Neoerythromma* are core Coenagrionidae too.

Remaining Coenagrionidae

The relationships of the remaining genera are much less resolved than for the core Coenagrionidae. Generally we retrieved them as the monophyletic sister group of core Coenagrionidae, but with weak support and different groups (sometimes combined) excluded in certain analyses: *Argia* and *Leptocnemis* in ML 28S+16S, *Argia* and Proto-neuridae in BI 28S+16S+COI, and *Argia* only in ML 28S+16S+COI, probably because COI was unavailable for *Leptocnemis*. *Argia* and *Leptocnemis* together were the sister group of all other Coenagrionidae in BI 28S+16S. Carle et al. (2008) retrieved them as monophyletic, including *Argia* and the protoneurid *Neoneura*, although their taxon sampling was limited and excluded *Leptocnemis*. Separate ML 28S+16S of a wider coenagrionid sampling (outgroup: *Platycnemis*) recovered all non-core genera together, except for *Leptocnemis*, which was the sister group of all other Coenagrionidae. Although the entire group may yet prove to be monophyletic, further analysis is needed, especially of the monotypic genus *Leptocnemis* from the Seychelles and the American genus *Argia*. The latter is the only remaining genus of Argiinae,

now that all Old World ‘argiines’ (*Mesocnemis*, *Onychargia*, *Palaiargia* and relatives) have been confirmed as Platycnemididae. It is probably the largest odonate genus, with at least 130 species, and differs from most taxa discussed in the following (but is similar to core coenagrionids) in having a rounded frons and prominent postocular spots (Garrison et al. 2010). *Leptocnemis* was regarded as platycnemidid but lacks features of that family, possessing a spiny genital ligula (Gassmann 2005). It also has a rounded frons and peculiar postocular spots shifted towards the vertex.

As in core Coenagrionidae, three notable clades are apparent in the remaining assemblage, although we estimate that together these represent less than half of over 600 species involved. All investigated genera of true Protoneuridae form a well-supported clade (*Amazoneura* based on 28S only, *Drepanoneura*, *Epipleoneura*, *Neoneura*, *Protoneura*, *Psaironeura*) in all analyses. Its position varied, being recovered with reasonable support with *Aeolagrion* and *Telebasis* within the complex of remaining genera in BI/ML 28S+16S, but forming the sister group of all those genera in ML 28S+16S+COI or falling outside the complex together with *Argia* in BI 28S+16S+COI with only moderate support. However, as discussed in the following, ‘protoneurid’ morphology is very consistent with non-core Coenagrionidae and its position well inside that family is certain.

Earlier molecular studies focused exclusively on the charismatic but small ‘family’ Pseudostigmatidae (Groeneveld et al. 2007, Ingley et al. 2012). Adults are substantially larger than other damselflies, have highly modified venation and pterostigmata (from which their name derives), a genital ligula with distal segment modified to form a very long single flagellum, feed mostly on orb-weaving spiders and their prey, and breed in phytotelmata. We found only moderate support for the group’s monophyly. It was represented by *Anomisma*, *Mecistogaster* and *Microstigma*, but also includes *Megaloprepus*, *Pseudostigma* and possibly the eastern African *Coryphagrion*, which would be the only

non-Neotropical representative and lacks the flagellum. Our study and earlier molecular work suggest that the smaller-bodied American genera *Bromeliagrion*, *Diceratobasis* and *Leptagrion* are close or should be included too (Groeneveld et al. 2007, Carle et al. 2008, Ingley et al. 2012). The latter genera lack modified wings, although they are still comparatively large-bodied and also breed in phytotelmata. This reproductive habitat is not unique to the group, however, also occurring occasionally in the third well-supported clade, represented in our dataset by the (principally) Malesian genera *Amphicnemis*, *Papuaagrion*, *Pericnemis* and *Teinobasis*. De Marmels (2007) considered these four genera as Teinobasinae (subfamily of Coenagrionidae) with a cercal spur, an articulated ventral process at the appendage base that is typically directed posteriorly.

De Marmels (2007) also treated *Bromeliagrion*, *Chromagrion*, *Melanesobasis*, *Nehalennia*, *Plagulibasis*, *Pyrrhosoma* and *Tepuibasis* as Teinobasinae with a cercal spur, to which *Aceratobasis* and *Diceratobasis* can be added (Garrison et al. 2010). Such a structure is not found in any core Coenagrionidae, but a potentially homologous (but seldom articulated) basal process occurs in about half the remaining genera, including the ‘pseudostigmatid’ *Microstigma* (near which the spurred *Bromeliagrion* and *Diceratobasis* have been recovered) and many ‘protoneurids’, e.g. *Epipleoneura*, *Forcepsioneura*, *Idioneura*, *Microneura*, *Neoneura*, *Peristicta*, *Phasmononeura*, *Protoneura* and *Psaironeura*. Given its plasticity, we doubt this structure (also when articulated) defines a monophyletic group and hence no strict delimitation of the subgroup nearest *Teinobasis* can presently be made. We suspect it is an Indo-Pacific complex, including also *Melanesobasis* and *Plagulibasis*, which have a cercal spur, and *Nesobasis* and *Vanuatubasis*, which do not, but it is apparent from the paraphyly of *Teinobasis* and the recent separation of *Luzonobasis*, *Pandanobasis* and *Sangabasis* from Philippine *Amphicnemis* (Villanueva 2012) that generic revision is needed. The precise positions of genera listed by De Marmels (2007) as Teinobasinae lacking the

spur (*Aeolagrion*, *Ceriagrion*, *Inpabasis*, *Metaleptobasis*, *Phoenicagrion* and *Telebasis*; only *Hylaeonympha*, *Leptagrion* and *Minagrion* were unavailable for our study) varied by analysis, but were always recovered near the ‘protoneurid’, ‘pseudostigmatid’ and ‘teinobasine’ clades (cf. Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010), as was the monotypic genus *Oreocnemis* from Mt Mulanje in Malawi. Although described in Platycnemididae, the last lacks all features associated with that family and possesses a spiny genital ligula. Carle et al. (2008) and Dumont et al. (2010) retrieved *Chromagrion*, *Nehalennia* and *Pyrrhosoma* here as well (cf. De Marmels 2007).

Aside from the general lack of postocular spots and the frequently present cercal spur, 83% of the non-core coenagrionid genera for which there is molecular evidence possess an angularly ridged frons. Other ridge-faced coenagrionids are *Aceratobasis*, *Angelagrion*, *Antiagrion*, *Leptagrion*, *Melanesobasis* and *Minagrion*. The ridge is variably present in species of *Tepuibasis*, as in the sampled genus *Phoenicagrion*. Of the Protoneuridae not sampled only *Junix*, *Phasmoneura* and *Proneura* lack the ridge, although *Amazonaura* and some *Proneura* species also lack it. Another potentially informative character is the female’s deeply or entirely divided 10th tergite (O’Grady & May 2003, Garrison et al. 2010) in *Aeolagrion*, *Amphicnemis*, *Antiagrion*, *Argia*, *Ceriagrion*, *Chromagrion*, *Hylaeonympha*, *Leptocnemis*, *Minagrion*, *Nehalennia*, *Papuagrion*, *Pyrrhosoma*, *Teinobasis* and *Telebasis*, although it sometimes occurs in the core coenagrionid *Pseudagrion*. Extensive metallic coloration in genera as disparate as *Amphicnemis*, *Epipleoneura* and *Nehalennia*, as well as a prominently modified epiproct, also appears to occur in this group but not in core Coenagrionidae. Although *Schistobos* and *Telagrion* have a rounded frons and somewhat spot-like postocular markings, their appendages and setose genital ligula suggest a relationship to *Aceratobasis*. The metallic coloration and genital ligula of *Tukanobasis* imply it also belongs near the ridge-faced genera despite a rounded frons.

The mysterious monotypic genera *Argiagrion* Selys and *Moroagrion* Needham & Gyger also have features of the group, but have been found to be synonyms of *Leptagrion* and *Pyrrhosoma*, respectively (Dijkstra & Kalkman 2013).

Superfamily ‘Calopterygoidea’

With the superfamilies Lestoidea, Platystictioidea and Coenagrionoidea reasonably defined, the position of the remaining 27% of damselfly diversity (almost 800 species) is left uncertain. Thus far, the superfamily name ‘Calopterygoidea’ and the more colloquial ‘Caloptera’ have been used for about three-fifths of this diverse assemblage. Rehn (2003) limited it to the most densely veined families Calopterygidae, Chlorocyphidae, Dicteriidae, Euphaeidae and Polythoridae, whereas Bechly (1996) included Amphipterygidae and the genera *Diphlebia*, *Philoganga*, *Pseudolestes* and *Thaumato-neura* as well. This leaves only the genus *Lestoidea* (not to be confused with the unrelated superfamily) and heterogeneous Megapodagrionidae ‘in limbo’. There is no convincing evidence for the combined monophyly of all (or any combination) of these groups, although Bybee et al. (2008) found weak support in some analyses, as did Carle et al. (2008) if Isostictidae was included, although that was also unstable. ‘Calopterygoidea’, by almost any definition, may ultimately prove paraphyletic, requiring the creation of further superfamilies. In the following sections we discuss all well-supported groups within this complex.

Family Calopterygidae

With almost a quarter of the species, Calopterygidae is the largest and most widespread family in the complex. Despite their distinctive appearance, good morphological apomorphies are unclear, although they probably exist in the shape of the larval prementum and antennae. Our results are broadly congruent with those of Dumont et al. (2005, 2007, 2010) based on a different set of (exclusively nuclear) markers. The strictly American Hetaerinae (including *Mnesarete* and presumably *Bryoplathanon* and *Ormenophlebia*; see Garrison et al. 2010), with about a third of the species, is

confirmed as the sister group of the remaining Calopterygidae. Dumont et al. (2010) prefer to treat this group as a family, but as Calopterygidae is monophyletic (cf. Rehn 2003, Bybee et al. 2008) stability is served by retaining the present ranks and separating the distinct clades within Calopterygidae as tribes. The distinctness of ranks is subjective: classifying all lineages as one family best communicates their common ancestry. Three tribes are largely Oriental: Vestalini (*Vestalaria*, *Vestalis*), Calopterygini (*Atrocalopteryx*, *Matrona*, *Matronoides*, *Neurobasis*, with only *Calopteryx* extending across the Holarctic) and Mnaisini (*Archineura*, *Echo*, *Mnais*, *Psolodesmus*). Dumont et al. (2010) recovered the last clade but retained the genera in Calopterygini. However, Vestalini variably form the sister group of Calopterygini s.s. or Mnaisini in our and Dumont's analyses, and Mnaisini can thus best be separated. Saphoini is strictly Afrotropical (*Phaon*, *Sapho*, *Umma*). The distinctive Oriental genera *Caliphaea* and *Noguchiphaea* each represents a monogeneric tribe, as does the only South American calopterygine, *Iridictyon* (Dumont et al. 2010).

Family Chlorocyphidae

The more than 140 Palaeotropical species are unique by the adult's expanded eyes and clypeus, short abdomen, and the larva's spike-like paraprocts and reduced epiproct (Bechly 1996). Our results confirm their monophyly (cf. Rehn 2003, Bybee et al. 2008, Dumont et al. 2010) and show reasonable congruence with Bechly's (1996) classification. Subfamilies could be recognized, but because two of the available names (*Disparocyphinae* and *Libellaginae*) are older than the family name in prevailing use, we refrain from applying them formally until the nomenclatory conundrum is resolved (see Dijkstra et al. 2013). Four Afrotropical genera form the monophyletic 'Chlorocyphinae'. The analyses indicate that '*C. centripunctata* Gambles, which also shares details of markings and extended paraprocts with *A. lacuselephantum* (Karsch), should be transferred to *Africocypha* (Table S4). *Stenocypha* is the sister group of the remaining African genera and

formerly made up the *gracilis* group of *Chlorocypha*, making that genus paraphyletic (Dijkstra 2013). Only BI/ML 28S and ML 28S+16S suggest that the clear-winged Africans are the sister group of the entire Asian radiation, in which marked wings predominate. Two consistently well-supported clades include *Rhinocypha* species and would constitute Bechly's (1996) 'Rhinocyphinae', but their combined monophyly was not recovered. One clade is predominantly continental and also includes *Aristocypha* and *Heliocypha* (often treated as subgenera of *Rhinocypha*) and all species with a brightly coloured mid-dorsal wedge on the thorax and/or wing markings with clear fields within the dark pattern. The second clade is largely insular and includes the type species of *Rhinocypha*, *Rhinoneura* and *Sundacypha*. Major generic revision is required, including the probably related genera *Calocypha*, *Heterocypha* and *Paracypha*. 'Libellaginae' is well supported and its main constituent genus *Libellago* also consists of two clades differing in wing markings: those with dark tips (including *Sclerocypha* and presumably *Melanocypha* and *Watuwila*) and those without, including *Pachycypha*. Wing markings are thus unexpectedly informative about relationships within the group: the clear-winged genera *Cyrano* (Philippines) and *Indocypha* (south Asia), and the Sulawesi *Disparocypha*, with its narrow wings and a distally broadened pterostigmata, stand apart from the major Asian radiations in all analyses, probably representing monogeneric subfamilies.

Families Euphaeidae and Lestoideidae

All analyses recovered the Asian family Euphaeidae of almost 70 species as monophyletic with good support (cf. Rehn 2003, Bybee et al. 2008, Dumont et al. 2010), and identified *Diphlebia* plus *Lestoidea* as its sister group (cf. Bybee et al. 2008, Carle et al. 2008). The most notable apomorphy of Euphaeidae is that the larvae possess lateral gills on the eighth abdominal segment as well as on the six preceding segments (Bechly 1996). The close relation of the superficially dissimilar Australian genera *Diphlebia* and *Lestoidea* was suggested by Novelo-Gutiérrez (1995), based on their similar

larvae and venation ground plan, although no shared apomorphies are known: the genera differ only in venation density, *Lestoidea* lacking numerous cross-veins and most of the anal vein. As family-group names are available, each of these distinctive genera could also be treated as a family. However, as genus- and family-group names that refer to the same group of species seem rather redundant, and distinctiveness is subjective, classifying these lineages together in the family Lestoideidae to communicate their common ancestry is preferred.

Family Polythoridae

Our limited sampling shows this Neotropical family to be monophyletic (cf. Rehn 2003, Bybee et al. 2008, Dumont et al. 2010). The almost 60 species share several notable larval characters, such as lateral gills on the second to seventh abdominal segments, dorsal abdominal spines or knobs (shared with *Teinopodagrion* in Megapodagrionidae) and swollen gills with angular or finger-like projections (Garrison et al. 2010). The apical projection of the genital ligula is also distinctive. The family has been considered close to the Euphaeidae, because the larvae share lateral abdominal gills (e.g. Bechly 1996), but no support has been found in any molecular studies.

Family Megapodagrionidae

The greatest systematic challenge in Zygoptera is classifying the over 300 species currently or formerly associated with Amphipterygidae and Megapodagrionidae. Their heterogeneity has long been recognized, as is apparent from the fact that many family-group names reinstated below are over half a century old. Previous studies showed that so-called ‘megapods’ are not monophyletic, containing at least five or six lineages that are richest in tropical America, Madagascar, South-east Asia, New Guinea and Australia (Rehn 2003, Bybee et al. 2008, van Tol et al. 2009, Dumont et al. 2010, Kalkman et al. 2010). Until now, however, no comparative phylogenetic data were available for the majority of genera. We obtained molecular data for 92% of the 51 genera involved,

most of which are morphologically well defined (e.g. Garrison et al. 2010, Kalkman & Theischinger 2013), and the results indicate that Megapodagrionidae includes between eight and 15 distinct (potentially family-level) clades and Amphipterygidae includes four. No 16S data were available for the family’s type genus, the monotypic Amazonian *Megapodagrion*. In BI/ML 28S it was the sister group of the Andean *Teinopodagrion*, represented by two species with complete sequences in our dataset. These two genera, together with the southern Brazilian *Allopodagrion*, were already recognized to be a monophyletic group by De Marmels (2001). In comparison to other formerly ‘megapod’ genera, both the adults and larvae have very long legs. The latter have long triquetral paraprocts and long antennae with an elongated first segment (De Marmels 2001, Kalkman et al. 2010, Neiss et al. 2011, Fleck et al. 2012). Fleck et al. (2012) noted a close resemblance between *Allopodagrion*, *Megapodagrion* and *Teinopodagrion* larvae and those of Calopterygidae and Dictyriidae, but our dataset provides no support for a relationship with these groups. *Megapodagrion* and *Teinopodagrion* were not recovered close to any other ‘megapods’, and as they possess distinct morphology, Megapodagrionidae should be restricted to just these three genera.

Family Argiolestidae

Over 100 ‘megapod’ species form a well-supported clade confined to the Old World tropics in all analyses. Separated as the family Argiolestidae, it comprises two subfamilies divided by Huxley’s Line (Kalkman & Theischinger 2013). This group includes all ‘megapod’ genera entirely lacking spines on the shaft of the genital ligula (Kalkman et al. 2010) except for *Amanipodagrion* and *Protolestes*, which do not seem to be closely related (see later). They differ from all other Zygoptera by the larval gills forming a horizontal fan (Kalkman et al. 2010). The only other damselflies described as having such gills are the Madagascan *Protolestes* and South American *Dimeragrion*. Our analyses implied these are not related to Argiolestidae, which is supported by other details of the larval

gills and adult morphology (Tennesen 2010, Pérez-Gutiérrez & Montes-Fontalvo 2011, Kalkman & Theischinger 2013). Another apomorphy is a central ridge of tubercles on the male cerci, which is present in all genera and absent only secondarily in a few species. It seems absent from all other Zygoptera, although *Heteragrion*, *Oxystigma* and *Heteropodagrion* possess something similar. The subfamily Argiolestinae makes up almost three-quarters of the family's species diversity, restricted largely to Australia, New Guinea and New Caledonia, with some isolated species in Sulawesi and the Philippines. Podolestinae includes *Podolestes* in South-east Asia, *Allolestes* in the Seychelles, *Nesolestes* in Madagascar and the Comores, and *Neurolestes* in Central Africa.

Family Philosinidae

The Oriental *Philosina* and *Rhinagrion* are similar in morphology both in the adult stage, sharing the general shape of the genital ligula with notably long and dense setae on its shaft, and in the larval stage, with the larval paraprocts forming a unique tube around the epiproct (Kalkman & Villanueva 2011, Zhang et al. 2011). Their sister group relationship is highly supported in all analyses and together they are recognized as Philosinidae, encompassing only 12 known species, but no near relatives were identified.

Family Thaumtoneuridae

The Central American *Paraphlebia* and *Thaumtoneura* were recovered consistently as sister genera, sharing details of genital ligula, venation and larval morphology. They are also the only 'megapod' genera with dimorphic males in some species, the wings being either distinctly marked or completely clear (Garrison et al. 2010). All analyses except BI/ML 28S retrieved these two combined with the Asian genera *Agriomorpha*, *Bornargiolestes*, *Burmargiolestes* and *Rhipidolestes* as monophyletic, with *Bornargiolestes* as the Americans' sister group, but while support was good in BI/ML 28S+16S it was poor in BI/ML 28S+16S+COI. The Oriental genera are similar in general morphology, but no apomorphies are known for them or for this

possible subtropical group as a whole. They include some of the few 'megapods' with distinct wing markings or that perch with closed wings. *Agriomorpha* and *Paraphlebia* share very hairy larval gills and all genera have notably dense venation towards the wing margins, but all these tendencies require further study. We combine the two American genera into the family Thaumtoneuridae, but leave the rest as *incertae sedis*. *Burmargiolestes xinglongensis* Wilson & Reels is nearer to *Agriomorpha* than to the other *Burmargiolestes* and is transferred to that genus (Table S4).

Remaining Neotropical 'megapods' and family Dictyriidae

The status of the remaining Neotropical 'megapods' is only partly resolved, but we retrieved three notable groups. Firstly, a well-supported relationship was found between *Philogenia* (35 species) and the small Ecuadorian genus *Archaeopodagrion* in all analyses. These genera are rather distinct morphologically, but share the presence of very long coiled flagella on the genital ligula. Secondly, the large genus *Heteragrion* (over 50 species) and smaller *Oxystigma* were recovered together with high support in all analyses. These genera resemble each other closely in the shape of the male appendages, genital ligula and markings. A probable apomorphy is the inflated larval gills, which bear rows of strongly curved spines (Geijskes 1943, De Marmels 2004). Thirdly, the localized *Dimeragrion* (Guiana Shield) and *Heteropodagrion* (northern Andes) were sister groups in MP 28S+16S and BI/ML 28S+16S+COI. Based on their closed wings at rest (except *Dimeragrion*), angulate frons (found also in *Heteragrion*) and especially the adult female's uniquely divided eighth tergite (Garrison et al. 2010), we assume the monotypic Colombian *Mesagrion* belongs here too.

Heliocharis and *Hypolestes* were recovered as sister groups with moderate support in all analyses except BI/ML 28S/28S+16S. *Heliocharis* forms the Amazonian family Dictyriidae with the also monotypic *Dictyrias*, while *Hypolestes* is endemic with three species to the Greater Antilles.

Dicteriid adults are peculiar among Zygoptera for their anteriorly widened postclypeus, drawn-out palpal hooks and almost bare legs. *Hypolestes* differs considerably from other ‘megapods’ by venation, genital ligula and appendages, but the two groups bear no obvious morphological resemblance, making this result rather inexplicable (Garrison et al. 2010). The Venezuelan *Sciotropis* shares the presence of several basal cross-veins with Polythoridae, but not with other ‘megapod’ genera except for the occasional *Dimeragrion* (N. von Ellenrieder, *in litt.*), and a general similarity of the male appendages and genital ligula can be seen (cf. Garrison et al. 2010). However, this genus was resolved as the sister group of Polythoridae, with negligible support only in MP 28S+16S (COI unavailable).

Although some of these groups grouped together in some analyses – sometimes also with other Neotropical taxa such as *Rimanella* and Polythoridae – good support for further relationships was not found. Therefore the complex taxonomy cannot be resolved definitively at present, also because the oldest name available (Hypolestidae) is connected to one of the more disparate taxa. However, considering the results and keeping nomenclatorial stability in mind, we tentatively propose to divide this group. Such a solution at least progresses from the previous situation, in which most genera were included in a clearly polyphyletic Megapodagrionidae. Dictერიადიდაე should be retained for *Dictérias* and *Heliocharis*, while the family-group name Philogeniidae is available for *Archaeopodagrion* and *Philogenia*, Heteragrionidae for *Heteragrion* and *Oxystigma*, and Hypolestidae for *Hypolestes*. While *Dimeragrion*, *Heteropodagrion* and *Mesagrion* may form another group, no name is available and these genera are considered *incertae sedis*, as is *Sciotropis*.

Families Philogangidae, Pseudolestidae and the ‘amphipterygid’ complex

Novelo-Gutiérrez (1995) removed the Papua-Australian *Diphlebia* and Oriental *Philoganga* from Amphipterygidae, restricting the family to four

small and geographically disjunct genera with larvae possessing gill tufts: *Amphipteryx* in Central America and *Devadatta* in South-east Asia forming the subfamily Amphipteryginae, and *Pentaplebia* in central Africa and *Rimanella* in northern South America constituting Rimanellinae. Rehn’s (2003) morphological analysis confirmed this classification, but molecular studies recovered the group as polyphyletic (Bybee et al. 2008, Dumont et al. 2010). The larva of *Pseudolestes mirabilis* Kirby from the Chinese island Hainan also possess tufts (Yu & Bu 2011a), but with sufficiently distinct morphology to consider Pseudolestidae a monotypic family. As discussed earlier, the affinities of *Diphlebia* are with the genus *Lestoidea* and Euphaeidae, whereas no support for relationships of *Amphipteryx*, *Devadatta*, *Philoganga*, *Pentaplebia*, *Pseudolestes* and *Rimanella* with each other or with any damselfly genera could be found. Although the molecular evidence cannot disprove the relationship, the morphological grounds to retain any except *Amphipteryx* in Amphipterygidae are weak. For example, *Pseudolestes* has gill tufts but was never placed in that family, while *Philoganga* and *Diphlebia* do not have gill tufts but were long considered amphipterygids. Other larval features, especially of the paraprocts and epiproct, differ strongly between the genera. While the genera were grouped for possessing numerous postnodal cross-veins that are not aligned with adjacent veins, they differ in number and alignment of the antenodal crossveins, the position of the radial sectors and the shape of the quadrangles, but all these characters are probably homoplasious (Rehn 2003). As each genus has distinctive adult and larval morphology (see Appendix 2) and family-group names are available (except for Devadattidae fam.n.), all can be considered best as monogeneric families. Even if any of these genera were sister groups, the phylogenetic and geographic distance between them is great and recognizing them as highly localized families seems the most convenient and stable solution.

Remaining Palaeotropical ‘megapods’

After the reclassification of most ‘megapod’ genera, six from tropical Asia, Madagascar and Africa

remain unassigned. The Chinese *Priscagrion* and *Sinocnemis* are recovered as sister groups in all analyses with reasonable support. Based on morphology, both De Marmels (2002b) and Yu & Bu (2011b) suggested *Priscagrion* was close to Argiolestidae, but molecular data indicate this is unlikely. *Sinocnemis* has a more simplified venation, but these characters are highly homoplasious. The two genera appear similar, most strikingly in the shape of the genital ligula and the modification of its internal fold. This is long and tapering in at least one *Sinocnemis* species and even drawn out and filamentlike in one *Priscagrion* species (Yu & Bu 2011b). The similar appearance of *Sinocnemis* to the sympatric genus *Mesopodagrion* was noted by Kalkman (2008), but their very different genital ligulae and our molecular data imply there is no close relationship. Both *Mesopodagrion* species have the terminal rim of the 10th tergite distinctively extended between the cerci (Yu & Bu 2009), although something similar occurs in the coenagrionid genus *Inpabasis*.

No close relatives could be identified for the monotypic *Amanipodagrion* from the East Usambara Mountains in Tanzania, or for *Protolestes* and *Tatocnemis* from Madagascar. Each possesses a combination of adult characters that fits none of the recognized groups. *Amanipodagrion* has a hanging resting posture and banded wings, creating a superficial resemblance to the unrelated *Chlorolestes*, and lacks spines on the genital ligula shaft. *Tatocnemis* has crenulated wingtips, shared with idiocnemidine Platycnemididae, but is not close otherwise. *Protolestes* has a broadened head recalling many Platycnemididae, but supposedly has fan-like larval gills found otherwise only in Argiolestidae and possibly *Dimeragrion* (Kalkman et al. 2010). None of these genera appears to have close relatives and future work is likely to show that they constitute five separate families, assuming a close relation between *Priscagrion* and *Sinocnemis*. Study of the unknown and poorly known (*Tatocnemis* and *Protolestes*) larvae is likely to confirm these groups' isolated positions. Pending further study these genera are regarded as *incertae sedis*.

OUTLOOK

Altogether, our phylogenetic reconstruction is largely congruent with the traditional classification of Zygoptera. Nonetheless, we reinstate, raise and create 11 damselfly families, bringing the total to 27, with at least another seven likely to be separated in the near future. While this seems radical, most changes are in smaller groups and the family affiliation of only one in five damselfly species changes. Also, we believe the revised classification will prove to be stable: further splits are considered more likely than the reemerging of groups. Furthermore, we have refrained from subjectively recognizing 'distinctive' families (e.g. Diphlebiidae, Disparoneuridae, Hetaerinidae, Sinostictidae) for which there was no phylogenetic imperative. Most of the 'new' names have existed for over half a century, constituting taxonomic 'hunches' for which no decisive evidence was available (or accepted) at the time of introduction.

Consensus for the suggested reclassification must be found, as attained for the better-known Anisoptera (Dijkstra et al. 2013), but we feel separating well-supported groups is more consistent than retaining unsupported groups for tradition's sake. All 11 (re-)instated families come from only two former families composed mostly of geographically isolated groups. These families were 'waste baskets' for equally unusual taxa, which persisted in stable but isolated areas, with no or only very distant relatives surviving elsewhere. Although better support for relationships between families may be obtained with more sequence data and morphological evidence (especially of larvae and genitalia), our expectations are modest, as the most challenging groups are so isolated phylogenetically, and morphologically so simplified, that comparable groups may not be identifiable with the available methods.

Finally, two general observations about the phylogeny and taxonomy of damselflies must be made. First, almost all larger genera for which multiple species were sampled (e.g. *Drepanosticta*, *Libellago*,

Rhinocypha, *Coeliccia*, *Agriocnemis*, *Pseudagrion*, *Teinobasis*) are not monophyletic and thus extensive revision of the suborder must take place. Secondly, many identified clades lack strong morphological apomorphies, and this also applies to many long-established families, such as Calopterygidae, Euphaeidae and Platycnemididae, even prior to molecular investigations. Characters of venation, in particular, show little congruence with our molecular results. The most poignant example is Protonneuridae, characterized by the absence or reduction of the anal vein. The family dissolves completely and in its broadest historic definition is seen to include six clades from five families: all Platystictidae, *Lestoidea* in Lestoideidae, all Isostictidae, most *Allocnemis* species and all Disparoneurinae in Platycnemididae, and true 'Protonneurinae' in Coenagrionidae. This result challenges the current taxonomy for fossil Odonata which is based almost entirely on venation, and stresses the importance of a review of fossil data in the light of molecular results.

ACKNOWLEDGEMENTS

Our thanks go first and foremost to those who supplied crucial samples from all over the world or provided valuable comments: Christine Apodaca, Matjaž Bedjanič, Evan Bowen-Jones, Seth Bybee, Viola Clausnitzer, Jürg De Marmels, Henri Dumont, Tim Faasen, Rosser Garrison, Dirk Gassmann, Justin Gerlach, Enrique González-Soriano, Andre Günther, Matti Hämäläinen, John Kaize, Haruki Karube, Walter Keding, Milen Marinov, Mike May, Nyegang Megan, Nicolas Mézière, Kees Mostert, C.M. Nazareno, Yong Foo Ng, Mike Parr, Dan Polhemus, Bert Orr, Graham Reels, Andy Rehn, Bob Reimer, Steve Richards, Richard Rowe, Wolfgang Schneider, Kai Schütte, John Simaika, Andy Skinner, Harry Smit, John Smit, Luke Southwell, Stephen Stone, Warwick Tarboton, Jan Taylor, Ken Tennesen, Günther Theischinger, John Trueman, Reagan Villanueva, Gert Veurink, Jessica Ware, Marcel Wasscher, Natalia von Ellenrieder, Wen-Chi Yeh and

Haomiao Zhang. Yvonne van Nierop helped in the collection at Naturalis. Kevin Beentjes, Camiel Doorenweerd, Ullasa Kodandaramaiah and Rutger Vos advised on analyses.

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APPENDIX I:

CLASSIFICATION OF THE SUBORDER ZYGOPTERA

The proposed classification follows Dijkstra et al. (2013). Superfamilies and families are provided for all genera, subfamilies and tribes for selected ones (see text). For convenience, groups of (presumably) related genera within Coenagrionidae also are indicated (see text). The order of superfamilies and families is phylogenetic (smallest sister group first), while that of lower ranks and ‘calopterygoid’ families is alphabetical. Sampled genera are indicated with an asterisk. Three widely accepted family names are outdated by older names, although these have, at most, 15% of usage (Google search): Libellaginidae Yakobson & Bianchi, 1905 and Disparocyphidae Munz, 1919 for Chlorocyphidae, Heliocharitidae Tillyard & Fraser, 1939 for Dictyriidae, and Epallagidae Needham, 1903 for Euphaeidae. An application to the International Commission on Zoological Nomenclature for the suppression of the older names will be prepared (Dijkstra et al. 2013). Because of this problem, groups within Chlorocyphidae are listed informally.

SUPERFAMILY LESTOIDEA CALVERT, 1901

Family Hemiphlebiidae Kennedy, 1920

(*Hemiphlebia* Selys, 1869)

Family Perilestidae Kennedy, 1920 (**Perilestes*

Hagen, 1862, **Perissolestes* Kennedy, 1941)

Family Synlestidae Tillyard, 1917 (**Chlorolestes*

Selys, 1862, *Chorismagrion* Morton, 1914,

**Ecchlorolestes* Barnard, 1937, **Episynlestes*

Kennedy, 1920, **Megalestes* Selys, 1862,

**Nubiolestes* Fraser, 1945, *Phylolestes* Christian-

sen, 1948, *Sinolestes* Needham 1930, **Synlestes*

Selys, 1868)

Family Lestidae Calvert, 1901 (*Archilestes* Selys,

1862, **Austrolestes* Tillyard, 1913, *Chalcolestes*

Kennedy, 1920, **Indolestes* Fraser, 1922,

**Lestes* Leach, 1815, **Orolestes* McLachlan, 1895,

Platylestes Selys, 1862, *Sinhalestes* Fraser, 1951,

**Sympetma* Burmeister, 1839)

SUPERFAMILY PLATYSTICTOIDEA KENNEDY, 1920

Family Platystictidae Kennedy, 1920

Subfamily Palaemnematinae Tillyard &

Fraser, 1938 (**Palaemnema* Selys, 1860)

Subfamily Platystictinae Kennedy, 1920

(**Ceylonosticta* Fraser, 1931, **Platysticta* Selys,

1860) Subfamily Protostictinae subfam.n.

(**Drepanosticta* Laidlaw, 1917, **Protosticta*

Selys, 1885, *Sulcosticta* van Tol, 2005,

**Telosticta* Dow & Orr, 2012)

Subfamily Sinostictinae Wilson, 1997

(**Sinosticta* Wilson, 1997)

SUPERFAMILY ‘CALOPTERYGOIDEA’ SELYS, 1850

Family Amphipterygidae Tillyard, 1917

(**Amphipteryx* Selys, 1853)

Family Argiolestidae Fraser, 1957

Subfamily Argiolestinae Fraser, 1957

(**Archiargiolestes* Kennedy, 1925, **Argiolestes*

Selys, 1862, **Austroargiolestes* Kennedy, 1925,

**Caledargiolestes* Kennedy, 1925, **Caledo-*

pteryx Kennedy, 1925, **Celebargiolestes*

Kennedy, 1925, *Eoargiolestes* Kalkman &

Theischinger, 2013, **Griseargiolestes* Thei-

schinger, 1998, **Luzonargiolestes* Kalkman

& Theischinger, 2013, **Metagrion* Calvert,

1913, **Miniargiolestes* Theischinger, 1998,

**Podopteryx* Selys, 1871, **Pyrrhargiolestes*

Kalkman & Theischinger, 2013, *Solomonar-*

giolestes Kalkman & Theischinger, 2013,

**Trineuragrion* Ris, 1915, **Wahnesia* Förster,

1900)

Subfamily Podolestinae Kalkman & Thei-

schinger, 2013 (**Allolestes* Selys, 1869,

**Nesolestes* Selys, 1891, **Neurolestes* Selys,

1882, **Podolestes* Selys, 1862)

Family Calopterygidae Selys, 1850

Subfamily Calopteryginae Selys, 1850

Tribe Caliphacini Fraser, 1929

(**Caliphaea* Hagen, 1859)

- Tribe Calopterygini Selys, 1850
(Atrocalopteryx Dumont et al. 2005,
 **Calopteryx* Leach, 1815, **Matrona* Selys,
 1853, *Matronoides* Foerster, 1897,
 **Neurobasis* Selys, 1853)
- Tribe Iridictyonini Dumont et al. 2005
(Iridictyon Needham & Fisher, 1940)
- Tribe Mnaisini Ishida, 1996 (**Archineura*
 Kirby, 1894, **Echo* Selys, 1853, **Mnais*
 Selys, 1853, *Psolodesmus* McLachlan,
 1870)
- Tribe Noguchiphaeini Dumont et al.
 2005 (*Noguchiphaea* Asahina, 1976)
- Tribe Saphoini Dumont et al. 2005
 (**Phaon* Selys, 1853, **Sapho* Selys, 1853,
 **Umma* Kirby, 1890)
- Tribe Vestalini Needham, 1903 (*Vesta-*
laria May, 1935, **Vestalis* Selys, 1853)
- Subfamily Hetaeriniinae Tillyard & Fraser,
 1939 (*Bryoplathanon* Garrison, 2006,
 **Hetaerina* Hagen, 1853, **Mnesarete* Cowley,
 1934, *Ormenophlebia* Garrison, 2006)
- Family Chlorocyphidae Cowley, 1937**
 ‘Chlorocyphinae’ (**Africocypha* Pinhey,
 1961, **Chlorocypha* Fraser, 1928, **Platycypha*
 Fraser, 1949, **Stenocypha* Dijkstra, 2013)
 ‘Disparocyphinae’ (**Disparocypha* Ris, 1916)
 ‘Libellagininae’ (**Libellago* Selys, 1840,
Melanocypha Fraser, 1949, **Pachycypha*
 Lieftinck, 1950, **Sclerocypha* Fraser, 1949,
Watuwila van Tol, 1998)
 ‘Rhinocyphinae’ (**Aristocypha* Laidlaw,
 1950, *Calocypha* Fraser, 1928, **Heliocypha*
 Fraser, 1949, *Heterocypha* Laidlaw, 1950,
Paracypha Fraser, 1949, **Rhinocypha*
 Rambur, 1842, **Rhino-neura* Laidlaw, 1915,
 **Sundacypha* Laidlaw, 1950)
 Incertae sedis (**Cyrano* Needham & Gyger,
 1939, **Indocypha* Fraser, 1949)
- Family Devadattidae fam.n.** (**Devadatta*
 Kirby, 1890)
- Family Dictერიადიე Montgomery, 1959**
(Dicteria Selys, 1853, **Heliocharis* Selys, 1853)
- Family Euphaeidae Jakobson & Bianchi, 1905**
 (**Anisopleura* Selys, 1853, *Bayadera* Selys, 1853,
 **Cryptophaea* Hämäläinen, 2002, *Cyclophaea*
 Ris, 1930, **Dysphaea* Selys, 1853, *Epallage*
 Charpentier, 1840, **Euphaea* Selys, 1840,
Heterophaea Cowley, 1934, *Schmidtphaea*
 Asahina, 1978)
- Family Heteragrionidae Ráčenis, 1959**
 (**Heteragrion* Selys, 1862, **Oxytigma* Selys,
 1862)
- Family Hypolestidae Fraser, 1938** (**Hypolestes*
 Gundlach, 1888)
- Family Lestoideidae Munz, 1919**
 Subfamily Diphlebiinae Heymer, 1975
 (**Diphlebia* Selys, 1869)
 Subfamily Lestoideinae Munz, 1919
 (**Lestoidea* Tillyard, 1913)
- Family Megapodagrionidae Calvert, 1913**
(Allopodagrion Förster, 1910, **Megapodagrion*
 Selys, 1885, **Teinopodagrion* De Marmels, 2001)
- Family Pentaplebiidae Novelo-Gutiérrez, 1995**
 (**Pentaplebia* Förster, 1909)
- Family Philogangidae Kennedy, 1920 (**Philo-*
ganga Kirby, 1890)
- Family Philogeniidae Ráčenis, 1959** (**Archaeop-*
odagrion Kennedy, 1939, **Philogenia* Selys, 1862)
- Family Philosinidae Kennedy, 1925** (**Philosina*
 Ris, 1917, **Rhinagrion* Calvert, 1913)
- Family Polythoridae Munz, 1919** (**Chalcop-*
teryx Selys, 1853, *Chalcothore* De Marmels,
 1985, *Cora* Selys, 1853, *Euthore* Selys, 1869,
Miocora Calvert, 1917, **Polythore* Calvert, 1917,
Stenocora Kennedy, 1940)
- Family Pseudolestidae Fraser, 1957** (**Pseudo-*
lestes Kirby, 1900)
- Family Rimanellidae Davies & Tobin, 1984**
 (**Rimanella* Needham, 1934)
- Family Thaumatoneuridae Fraser, 1938**
 (**Paraplebia* Selys, 1861, **Thaumatonaura*
 McLachlan, 1897)
- Incertae sedis group 1:** **Agriomorpha* May,
 1933, **Bornargiolestes* Kimmins, 1936,
 **Burmargiolestes* Kennedy, 1925, **Rhipidolestes*
 Ris, 1912; **group 2:** **Amanipodagrion* Pinhey,
 1962; **group 3:** **Dimeragrion* Calvert, 1913,
 **Heteropodagrion* Selys, 1885, *Mesagrion* Selys,
 1885; **group 4:** **Mesopodagrion* McLachlan,
 1897; **group 5:** **Priscagrion* Zhou & Wilson,
 2001, **Sinocnemis* Wilson & Zhou, 2000;

group 6: **Protolestes* Förster, 1897; **group 7** (= 'Tatocnemidinae Rácenis, 1959'): **Tatocnemis* Kirby, 1889; **group 8:** **Sciotropis* Rácenis, 1959

SUPERFAMILY COENAGRIONOIDEA
KIRBY, 1890

Family Isostictidae Fraser, 1955 (*Austrosticta* Tillyard, 1908, *Cnemisticta* Donnelly, 1993, *Eurysticta* Watson, 1969, **Isosticta* Selys, 1885, *Labidiosticta* Watson, 1991, *Lithosticta* Watson, 1991, **Neosticta* Tillyard, 1913, *Oristicta* Tillyard, 1913, *Rhadinosticta* Watson, 1991, **Selysioneura* Förster, 1900, **Tanymecosticta* Liefstinck, 1935, *Titanosticta* Donnelly, 1993)

Family Platycnemididae Yakobson & Bianchi, 1905

Subfamily Allocnemidinae subfam.n. (**Allocnemis* Selys, 1863, **Arabincnemis* Waterston, 1984, **Mesocnemis* Karsch, 1891, **Metacnemis* Hagen, 1863, **Stenocnemis* Karsch, 1899)

Subfamily Calicnemiinae Fraser, 1957 (*Asthenocnemis* Liefstinck, 1949, **Calicnemia* Strand, 1928, **Coelliccia* Kirby, 1890, **Indocnemis* Laidlaw, 1917)

Subfamily Disparoneurinae Fraser, 1957 (*Arabineura* Schneider & Dumont, 1995, *Caconeura* Kirby, 1890, *Disparoneura* Selys, 1860, **Elatoneura* Cowley, 1935, **Esme* Fraser, 1922, *Melanoneura* Fraser, 1922, **Nososticta* Hagen, 1860, *Phylloneura* Fraser, 1922, **Prodasineura* Cowley, 1934)

Subfamily Idiocnemidinae subfam.n. (*Archboldargia* Liefstinck, 1949, **Arrhenocnemis* Liefstinck, 1933, **Cyanocnemis* Liefstinck, 1949, **Hylaeargia* Liefstinck, 1949, **Idiocnemis* Selys, 1878, **Ignocnemis* Hämäläinen, 1991, *Liefstinckia* Kimmins, 1957, **Lochmaeocnemis* Liefstinck, 1949, **Palatargia* Förster, 1903, **Papuargia* Liefstinck, 1938, **Paramecocnemis* Liefstinck, 1932, *Rhyacocnemis* Liefstinck, 1956, **Risiocnemis* Cowley, 1934, *Salomocnemis* Liefstinck, 1987, **Torrenticnemis* Liefstinck, 1949)

Subfamily Onychargiinae subfam.n.

(**Onychargia* Selys, 1865, **Paracnemis* Martin, 1902) Subfamily Platycnemidinae Yakobson & Bianchi, 1905

Tribe Coperini trib.n. (**Copera* Kirby, 1890, **Proplatycnemis* Kennedy, 1920, **Spesbona* Dijkstra, 2013)

Tribe Platycnemidini Yakobson & Bianchi, 1905 (**Matticnemis* Dijkstra, 2013, **Platycnemis* Burmeister, 1839, **Pseudocopera* Fraser, 1922)

Family Coenagrionidae Kirby, 1890

Core Coenagrionidae [genera associated with *Agriocnemis* ('Agriocnemidinae Fraser, 1957'): **Agriocnemis* Selys, 1877, **Argiocnemis* Selys, 1877, **Mortonagrion* Fraser, 1920; genera associated with *Ischnura* ('Ischnurinae Fraser, 1957'): **Acanthagrion* Selys, 1976, *Acanthallagma* Williamson & Williamson, 1924, **Aciagrion* Selys, 1891, **Africallagma* Kennedy, 1920, *Amphiagrion* Selys, 1876, *Amphiallagma* Kennedy, 1920, *Andinagrion* Bulla, 1973, *Anisagrion* Selys, 1876, *Apanisagrion* Kennedy, 1920, *Argentagrion* Fraser, 1948, *Austroallagma* Liefstinck, 1953, **Austrocnemis* Tillyard, 1913, **Azuragrion* May, 2002, *Calvertagrion* St Quentin, 1960, **Coenagrionocnemis* Fraser, 1949, *Cyanallagma* Kennedy, 1920, *Denticulobasis* Machado, 2009, **Dolonagrion* Garrison & von Ellenrieder, 2008, *Enacantha* Donnelly & Alayo, 1966, *Enallagma* Charpentier, 1840, *Hesperagrion* Calvert, 1902, *Homeoura* Kennedy, 1920, **Ischnura* Charpentier, 1840, *Leptobasis* Selys, 1877, *Leucobasis* Rácenis, 1959, *Mesamphiagrion* Kennedy, 1920, **Mesoleptobasis* Sjöstedt, 1918, *Millotagrion* Fraser, 1953, *Oreagrion* Ris, 1913, *Oreiallagma* von Ellenrieder & Garrison, 2008, *Oxyagrion* Selys, 1876, *Oxyallagma* Kennedy, 1920, *Pacificagrion* Fraser, 1926, *Pinheyagrion* May, 2002, *Proischnura* Kennedy, 1920, *Protallagma* Kennedy, 1920, **Thaumatagrion* Liefstinck, 1932, *Tigriagrion* Calvert, 1909, **Tuberculobasis* Machado, 2009, **Xiphiagrion* Selys, 1876, *Zoniagrion* Kennedy, 1917;

genera associated with *Pseudagrion* ('Pseudagrioninae Tillyard, 1917'): **Archibasis* Kirby, 1890, **Austroagrion* Tillyard, 1913, **Caliagrion* Tillyard, 1913, **Erythromma* Charpentier, 1840, **Paracercion* Weekers & Dumont, 2004, **Pseudagrion* Selys, 1876, **Xanthagrion* Selys, 1876, **Xanthocnemis* Tillyard, 1913; remaining genera: **Austrocoenagrion* Kennedy, 1920, **Coenagrion* Kirby, 1890, **Himalagrion* Fraser, 1920, **Megalagrion* McLachlan, 1883, **Neoerythromma* Kennedy, 1920, **Senagrion* Laidlaw, 1915]

Ridge-faced complex [genera associated with *Protoneura* ('Protoneurinae Yakobson & Bianchi, 1905'): **Amazona* Machado, 2004, **Drepanoneura* von Ellenrieder & Garrison, 2008, **Epipleoneura* Williamson, 1915, **Epipotoneura* Williamson, 1915, **Forcepsioneura* Lencioni, 1999, **Idioneura* Selys, 1860, **Junix* Rácenis, 1968, **Lamproneura* De Marmels, 2003, **Microneura* Hagen, 1886, **Neoneura* Selys, 1860, **Peristicta* Hagen, 1860, **Phasmoneura* Williamson, 1916, **Proneura* Selys, 1889, **Protoneura* Selys, 1857, **Psaironeura* Williamson, 1915, **Roppa* Santos, 1966; genera associated with *Pseudostigma* ('Pseudostigmatinae Kirby, 1890'): **Anomisma* McLachlan, 1877, **Bromeliagrion* De Marmels, 2005, **Coryphagrion* Morton, 1924, **Diceratobasis* Kennedy, 1920,

**Leptagrion* Selys, 1876, **Mecistogaster* Rambur, 1842, **Megaloprepus* Rambur, 1842, **Microstigma* Rambur, 1842, **Pseudostigma* Selys, 1860; genera associated with *Teinobasis* ('Teinobasinae Tillyard, 1917'): **Amphicnemis* Selys, 1863, **Luzonobasis* Villanueva, 2012, **Melanesobasis* Donnelly, 1984, **Nesobasis* Selys, 1891, **Pandanobasis* Villanueva, 2012, **Papuagrion* Ris, 1913, **Pericnemis* Selys, 1863, **Plagulibasis* Lieftinck, 1949, **Sangabasis* Villanueva, 2012, **Teinobasis* Kirby, 1890, **Vanuatubasis* Ober & Staniczek, 2009; remaining genera: **Aceratobasis* Kennedy, 1920, **Aeolagrion* Williamson, 1917, **Angelagrion* Lencioni, 2008, **Antigrion* Ris, 1904, **Ceriagrion* Selys, 1876, **Chromagrion* Needham, 1903, **Hylaeonympha* Rácenis, 1968, **Inpabasis* Santos, 1961, **Metaleptobasis* Calvert, 1907, **Minagrion* Dos Santos, 1965, **Nehalennia* Selys, 1850, **Oreocnemis* Pinhey, 1971, **Phoenicagrion* von Ellenrieder, 2008, **Pyrrhosoma* Charpentier, 1840, **Schistolobos* von Ellenrieder & Garrison, 2008, **Telagrion* Selys, 1876, **Telebasis* Selys, 1865, **Tepuibasis* De Marmels, 2007, **Tukanobasis* Machado, 2009]

Undetermined [**Argia* Rambur, 1842 (= 'Argiinae Tillyard, 1917'), **Leptocnemis* Selys, 1886]

APPENDIX 2:

DIAGNOSES OF NEW AND REVISED FAMILY-GROUP NAMES

Alloknemidinae subfam.n. (type genus: *Alloknemis* Selys, 1863 by present designation) – small damselflies separated within range (Africa and Arabia) from other genera with two antenodal cross-veins (Ax), no spines on shaft of genital ligula, long leg spines, rounded frons and no postocular spots by combination of arculus clearly proximal to Ax2, which often converges posteriorly with Ax1; cubital cross-vein distal to origin of anal vein by about three times its length (by about its length in *Stenocnemis*); often more than three cells between quadrilateral and subnode (two in *Arabicnemis* and *Stenocnemis*). *Alloknemis* differs from similar genera in range by combination of R4 originating closer to subnode than IR3 (Tillyard & Fraser terminology); cubital cross-vein at origin of anal vein; wings often stained yellow. Male cerci in all genera are triangular (broad base and pointed tip) and usually with ventral process near base; paraprocts simple, often rather pointed or elongate.

Amphipterygidae (type genus: *Amphipteryx* Selys, 1853) – large damselflies with seven to eight Ax, two to three in subcostal space; arculus near Ax3; quadrangle without cross-veins; IR3 (Tillyard & Fraser terminology) originating at level of quadrangle, much closer to arculus than to nodus. Wings clear and closed at rest. Thorax and abdomen black with blue pattern on thorax and tip of abdomen but without metallic shine. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts roundish in cross-section but not balloon-shaped, broadest at approximately one-fifth of their base from where they gradually taper to a single point, as well as two filamentous gills tufts located beneath them.

Argiolestidae (type genus: *Argiolestes* Selys, 1862) – medium-sized to large damselflies with two (rarely three) Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear

and held open at rest. Most species largely brown to black, often with blue, orange or red pattern on face, thorax, legs and/or tip of abdomen. Shaft of genital ligula without setae. Larvae with epiproct and paraprocts broad and flat, lying in a horizontal plane.

Coperini trib.n. (type genus: *Copera* Kirby, 1890 by present designation) – small damselflies featuring typical characters of subfamily Platycnemidinae, characterized by feather-like tibiae, which are dilated and bright white, yellow, orange, red or blue, and used in display; only entirely black and not widened in *Spesbona angusta* (Selys). Differs from tribe Platycnemidini by: caudal lamellae of larvae with frilled border (unique character among Odonata); inner side of the male cerci with a tooth- or branch-like process, but tiny in *C. sikassoensis* (Martin) and *C. vittata* (Selys), and reduced completely in *C. marginipes* (Rambur); male tibiae often not white.

Devadattidae fam.n. (type genus: *Devadatta* Kirby, 1890 by present designation) – large damselflies with seven to 12 Ax, four to five in subcostal space; arculus between Ax4 and Ax6; quadrangle with two to three cross-veins; IR3 originating at level of quadrangle, much closer to arculus than to nodus. Wings clear except for brown spot at the tips; closed at rest. Thorax and abdomen dull, without metallic shine or bright colours. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts sturdy and pyramidal, widest subbasally and terminating in single (paraprocts) or triple (epiproct) points, as well as two filamentous gills tufts located beneath them.

Heteragrionidae (type genus: *Heteragrion* Selys, 1862) – medium-sized to large damselflies with two Ax and several intercalated veins distally in radial fields; IR3 originating near the subnodus, clearly closer to nodus than to arculus. Wings clear and held open at rest. Body of many species marked with bright orange or red. Genital ligula with setae on shaft and distal segment with paired laterally directed apical flagella. Larvae with epiproct and paraprocts inflated and triangular in cross-section, bear-

ing a filament at tip; basal part with dorsal rib carrying a row of strongly curved spines.

Hypolestidae (type genus: *Hypolestes* Gundlach, 1888) – medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR₃ originating somewhat distal to quadrangle, much closer to arculus than to nodus. Wings clear and held open at rest. Body dark brown or black with pale yellow pattern; mature males with extensive light grey pruinosity on head, thorax and ninth and 10th abdominal segments. Genital ligula with setae on shaft and distal segment with paired lateral and apical flagella. Larvae with epiproct and paraprocts inflated, constricted in the middle and ending in a long and sharply pointed filament.

Idiocnemidinae subfam.n. (type genus: *Idiocnemis* Selys, 1878 by present designation) – small to medium-sized damselflies with two Ax; the arculus at Ax₂; pterostigma with costal side subequal to distal side; anal vein terminates in distal half of wing; shaft of genital ligula without spines; spines on legs long. Margins of wing tips crenulated (not in *Archboldargia*, *Hylaeargia*, *Palaiargia*, *Papuargia*, and weakly developed in *Rhyacocnemis*; similar character state acquired independently, but weakly developed, in *Tatocnemis*). Larvae with epiproct and paraprocts forming a unique three-dimensional ruff (described only for *Hylaeargia*, *Liefinckia* and *Palaiargia*).

Megapodagrionidae (type genus: *Megapodagrion* Selys, 1885) – small to medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR₃ originating near the subnodus, clearly closer to nodus than to arculus. Wings clear and held open at rest. Shaft of genital ligula with setae. First antennal segment in both larvae and adults long, usually similar to slender second segment; legs also very long, with hind femur reaching anterior margin of third abdominal segment or beyond. Larvae with paraprocts long and thickened, each with a median outer ridge along their length, and foliaceous, wider and shorter epiproct.

Onychargiinae subfam.n. (type genus: *Onychargia* Selys, 1865 by present designation) – small damselflies with two Ax; arculus at Ax₂; pterostigma with costal side subequal to its distal side; anal vein terminates in distal half of wing; shaft of genital ligula without spines; spines on legs long. Head not laterally expanded, frons not angulate, dorsum black and lacking postocular spots but often with a pale line running from eye to eye across the lateral ocelli (sometimes partly broken). Margins of wing tips not crenulated. Male cerci distinctly shorter than 10th abdominal segment and subequal to paraprocts.

Pentaphlebiidae (type genus: *Pentaphlebia* Förster, 1909) – large damselflies with four to six Ax, two in subcostal space; arculus close to Ax₂; quadrangle without cross-veins; IR₃ originating at level of quadrangle, much closer to arculus than to nodus. Wings clear to smoky with darkened falcate tips and very long pterostigmata; closed at rest. Adult male is rather dark and plain, with reddish to black thorax and abdomen. Shaft of genital ligula with setae. Second antennal segment distinctly elongated, thin in adults and swollen in larvae. Larvae with blade-like paraprocts, expanded laterally near base and shorter than abdomen, short trifid epiproct, as well as two filamentous gills tufts located beneath them.

Philogangidae (type genus: *Philoganga* Kirby, 1890) – very large damselflies with 11–13 Ax, 14–17 in subcostal space; arculus close to Ax₂; quadrangle without cross-veins; IR₃ originating distal to quadrangle, closer to arculus than to nodus. Wings clear with long pterostigmata; held open at rest. Thorax and abdomen black, boldly marked with yellow or orange. Shaft of genital ligula without or with a few setae. Larvae with epiproct and paraprocts similar, inflated at base and tapering to finely pointed tips, without filamentous gills tufts.

Philogeniidae (type genus: *Philogenia* Selys, 1862) – medium-sized to large damselflies with 2 Ax and several intercalated veins distally in radial fields; IR₃ originating near the subnodus, clearly closer to

nodus than to arculus. Wings clear or with brownish tips; held open at rest. Body dark brown to black with yellow, blue or green pattern and blue pruinosity on dorsum of abdomen in males. Genital ligula with setae on shaft; distal segment with paired long and slender spiral-shaped apical flagella. Larvae with epiproct and paraprocts inflated, constricted in the middle and ending in a filament.

Philosinidae (type genus: *Philosina* Ris, 1917) – medium-sized to large damselflies with two Ax and several intercalated veins distally in radial fields; IR₃ originating near the subnodus, clearly closer to nodus than to arculus. Wings clear (except for diffuse dark spot at tips in *Philosina buchi* Ris) and held open at rest. Head, thorax and abdomen in most species with bold pattern of yellow, orange, red or blue; partly covered with pruinosity in *Philosina*; dorsum of tip of abdomen weakly sclerotized in males allowing them to expand their abdomen. Shaft of genital ligula with dense long setae. Larvae with paraprocts thick and undulating, longer than thinner and foliaceous epiproct; in life the paraprocts form a tube folded around the epiproct.

Protostictinae subfam.n. (type genus: *Protosticta* Selys, 1885 by present designation) – small to moderately large damselflies, with venation characteristic of family, i.e. node at about one-quarter of wing length from base, and a cross-vein in the postcubital space closer to wing base than to the level of the proximal Ax. Distinctive combination of characters: IR₃ arising distal to subnode (typically at level of subnode in other genera of family); CuP vein meeting hind margin of forewing at level of R₃, or even proximal to it; anal bridge vein present (*Drepanosticta*) or absent (*Protosticta*); R₄₊₅ at or distal to subnode (as in Platystictinae s.s.). Male appendages very diverse in form; genital ligula with squarish cleft (rather than triangular as in *Sinosticta* and *Palaemnema*) and long horns (short in *Platysticta*).

Pseudolestidae (type genus: *Pseudolestes* Kirby, 1900) – medium-sized damselflies with two Ax and several intercalated veins distally in radial fields; IR₃

originating near the subnodus, clearly closer to nodus than to arculus. Wings held open at rest, forewing clear; hind wing shorter than forewing, broadened in apical half and slightly falcate at tip, dark with bright orange patches (male) or clear with a broad iridescent subapical black band (female). Adult male has blue face and a black body with yellow lines on thorax. Shaft of genital ligula with setae. Larvae with epiproct and paraprocts inflated and sack-like, each as broad as the abdomen itself and ending a short nipple-like filament, as well as two filamentous gills tufts located beneath them.

Rimanellidae (type genus: *Rimanella* Needham, 1934) – large damselflies with two Ax; arculus at Ax₂; quadrangle without cross-veins; IR₃ originating somewhat distal to quadrangle, much closer to arculus than to nodus. Wings clear with long pterostigmata; closed at rest. Adult male is colourful with blue pattern on head, yellowish green thorax with dark stripes and red to reddish brown abdomen. Sternum of 10th abdominal segment in both sexes forms a concave semicircular plate, delimited by lateral carinae from tergum. Shaft of genital ligula with setae. Larvae with whip-like paraprocts that are jointed near base and longer than abdomen, short trifold epiproct, as well as two filamentous gills tufts located beneath them.

Thaumatoneuridae (type genus: *Thaumatoneura* McLachlan, 1897) – medium-sized to large damselflies with two to four Ax (only two in subcostal space) and several intercalated veins distally in radial fields; IR₃ originating near the subnodus, clearly closer to nodus than to arculus. Wings broad, with numerous intercalated veins in posterior portion and one to two accessory cross-veins distal to the cubital cross-vein, posterior to quadrangle. Several species with dimorphic males, i.e. wings either clear or with broad black band; wings closed at rest. Shaft of genital ligula with setae; distal segment with pair of broad lateral lobes. Larvae with epiproct and paraprocts inflated, strongly constricted in middle and ending in a filament, both inflated base and filament covered with stout stiff setae.

SUPPORTING INFORMATION (SI)

Supporting Information Table S1. Primers used.

Primer name Target Direction Sequence (5' to 3')

ODO_28S_f2_2	28S	F	CCCGGCCGGTCCCCGACGGT
ODO_28S_r2_p3	28S	R	TTACACACTCCTTAGCGGATTC
ODO_28S_f3	28S	F	ACCATGAAAGGTGTTGGTTG
ODO_28S_r3_p3	28S	R	ATCTCCCTGCGAGAGGATTC
ODO_12852F	16S	F	AGAAACCGACCTGGCTTAAA
ODO_13393R	16S	R	CGCCTGTTTATCAAAAACAT
ODO_LCOI490d	COI	F	TTTCTACWAACCAYAAAGATATTGG
ODO_HCO2198d	COI	R	TAAACTTCWGGRTGTCCAAARAATCA

Supporting Information Table S2*. List of analysed samples. GenBank Accession numbers are provided for 16S, 28S and COI: a blank space thus indicates the marker was not available for analysis.

Family	Species	Authority	Year	Collector	Repository
Aeshnidae	<i>Aeshna juncea</i>	(Linnaeus)	1758		RMNH
Amphipterygidae	<i>Amphipteryx agrioides</i>	Selys	1853	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Amphipterygidae	<i>Amphipteryx agrioides</i>	Selys	1853	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Argiolestidae	<i>Allolestes maclachlani</i>	Selys	1869	Gerlach, J.	RMNH
Argiolestidae	<i>Archiargiolestes parvulus</i>	(Watson)	1977	Taylor, J.	RMNH
Argiolestidae	<i>Archiargiolestes pusillissimus</i>	(Kennedy)	1925	Taylor, J.	RMNH
Argiolestidae	<i>Argiolestes roon</i>	Kalkman, Richards & Polhemus	2010	Polhemus, D.A.	BPBM
Argiolestidae	<i>Argiolestes tuberculiferus</i>	Michalski & Oppel	2010	Kalkman, V.J.	RMNH
Argiolestidae	<i>Austroargiolestes chrysoides</i>	(Tillyard)	1913	Kalkman, V.J.	RMNH
Argiolestidae	<i>Austroargiolestes icteromelas</i>	(Selys)	1862	Kalkman, V.J.	RMNH
Argiolestidae	<i>Caledopteryx sarasini</i>	(Ris)	1915	Marinov, M. & Richards, S.	RMNH
Argiolestidae	<i>Caledopteryx</i> sp.			Marinov, M.	RMNH
Argiolestidae	<i>Celebargiolestes</i> sp.			Gunther, A. & Randow, F.	RMNH
Argiolestidae	<i>Griseargiolestes bucki</i>	Theischinger	1998	Kalkman, V.J.	RMNH
Argiolestidae	<i>Griseargiolestes griseus</i>	(Selys)	1862	Kalkman, V.J.	RMNH
Argiolestidae	<i>Luzonargiolestes baltazarae</i>	(Gapud & Recuenca)	2001	Nazareno, C.M.	RMNH
Argiolestidae	<i>Metagrion</i> sp.			Kaize, J.	RMNH
Argiolestidae	<i>Metagrion</i> sp.			Kalkman, V.J.	RMNH
Argiolestidae	<i>Miniargiolestes minimus</i>	(Tillyard)	1908	Taylor, J.	RMNH
Argiolestidae	<i>Miniargiolestes minimus</i>	(Tillyard)	1908	Taylor, J.	RMNH
Argiolestidae	<i>Nesolestes nigriensis</i>	Gambles	1970	Parr, M.J.	RMNH
Argiolestidae	<i>Nesolestes nigriensis</i>	Gambles	1970	Parr, M.J.	RMNH
Argiolestidae	<i>Nesolestes</i> sp.			Schütte, K.	RMNH
Argiolestidae	<i>Nesolestes</i> sp.			Schütte, K.	RMNH
Argiolestidae	<i>Neurolestes trinervis</i>	(Selys)	1885	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Argiolestidae	<i>Podolestes harrisoni</i>	Lieftinck	1953	Dow, R.A.	RMNH
Argiolestidae	<i>Podolestes orientalis</i>	Selys	1862	Dow, R.A.	RMNH
Argiolestidae	<i>Podopteryx selysi</i>	(Förster)	1899	Richards, S.	RMNH
Argiolestidae	<i>Pyrrhargiolestes</i> cf <i>sidonia</i>	(Martin)	1909	Richards, S.	RMNH
Argiolestidae	<i>Trineuragrion percostale</i>	Ris	1915	Marinov, M.	RMNH
Argiolestidae	<i>Wahnesia</i> cf <i>annulipes</i>	(Lieftinck)	1956	Polhemus, D.A.	BPBM
Argiolestidae	<i>Wahnesia kirbyi</i>	(Lieftinck)	1935	Gassmann, D.	RMNH
Calopterygidae	<i>Archineura incarnata</i>	(Karsch)	1891	Kalkman, V.J.	RMNH
Calopterygidae	<i>Caliphaea confusa</i>	Hagen in Selys	1859	Hämäläinen, M.	RMNH
Calopterygidae	<i>Echo modesta</i>	Laidlaw	1902	Dow, R.A.	RMNH
Calopterygidae	<i>Echo modesta</i>	Laidlaw	1902	Dow, R.A.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
The Netherlands		228912	25925401	KF369596	KF369992	KF369278	ODOPH001-13
Mexico	Oaxaca State	504314	30104157	KF369616	KF370014	KF369296	ODOPH002-13
Mexico	Oaxaca State	504313	25919417	KF369615	KF370013	KF369295	ODOPH003-13
Seychelles	Mahe	500397	25925674	KF369611	KF370007		ODOPH004-13
Australia	Western Australia	502085	25924878	KF369623	KF370021	KF369303	ODOPH005-13
Australia	Western Australia	502082	25924781	KF369624	KF370022	KF369304	ODOPH006-13
Indonesia	West Papua Province, Roon Island	500848	25925591	KF369631	KF370029	KF369310	ODOPH007-13
Papua New Guinea		501972	25924702	KF369632	KF370030	KF369311	ODOPH008-13
Australia	Queensland	505271	30102316	KF369638	KF370036	KF369317	ODOPH009-13
Australia	New South Wales	504912	30102330	KF369639	KF370037	KF369318	ODOPH010-13
New Caledonia	Grand Terre	503406	25924883	KF369651	KF370049	KF369328	ODOPH011-13
New Caledonia		500855	25925671	KF369652	KF370050	KF369329	ODOPH012-13
Indonesia	Sulawesi	500856	25925448	KF369656	KF370054	KF369333	ODOPH013-13
Australia	New South Wales	504888	30102304	KF369723	KF370122	KF369390	ODOPH014-13
Australia	New South Wales	504927	30102334	KF369724	KF370123	KF369391	ODOPH015-13
Philippines	Luzon	502091	25924671	KF369769	KF370168	KF369431	ODOPH016-13
Indonesia	Papua Barat	502075	25924734	KF369783	KF370182	KF369445	ODOPH017-13
Indonesia	Papua	500542	25924698	KF369782	KF370181	KF369444	ODOPH018-13
Australia	Western Australia	502080	25924879	KF369787	KF370186	KF369448	ODOPH019-13
Australia	Western Australia	502078	25924904	KF369788	KF370187	KF369449	ODOPH020-13
Nigeria	Obudu Plateau	229198	25925528	KF369800	KF370199		ODOPH021-13
Nigeria	Obudu Plateau	229199	25925540	KF369799	KF370198		ODOPH022-13
Madagascar	Apasy	228875	25925463	KF369801	KF370200	KF369458	ODOPH023-13
Madagascar	Sainte Luce	228871	25925439	KF369802	KF370201	KF369459	ODOPH024-13
Gabon	Haut-Ogooué	502482	25924903	KF369805	KF370204	KF369462	ODOPH025-13
Malaysia	Sarawak	501278	25924193	KF369855	KF370254	KF369504	ODOPH026-13
Malaysia	Sarawak	503423	25924229	KF369856	KF370255	KF369505	ODOPH027-13
Papua New Guinea		504973	30102343	KF369857	KF370256	KF369506	ODOPH028-13
Papua New Guinea		543750	30102337	KF369883	KF370282	KF369530	ODOPH029-13
New Caledonia		500854	25925588	KF369936	KF370335	KF369575	ODOPH030-13
Papua New Guinea	Milne Bay Province	500852	25925446	KF369941	KF370340		ODOPH031-13
Papua New Guinea	Morobe Province	500857	25925400	KF369942	KF370341		ODOPH032-13
China	Guǎngxī	500707	30104131	KF369626	KF370024		ODOPH033-13
Vietnam	Lao Cai	502054	25924866	KF369655	KF370053	KF369332	ODOPH034-13
Malaysia	Terengganu	503924	30102260	KF369709	KF370108	KF369378	ODOPH035-13
Malaysia	Terengganu	503928	30102262	KF369710	KF370109	KF369379	ODOPH036-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Calopterygidae	<i>Hetaerina laesa</i>	Hagen in Selys	1853	Wasscher, M.	RMNH
Calopterygidae	<i>Hetaerina sanguinea</i>	Selys	1853	Faasen, T.	RMNH
Calopterygidae	<i>Hetaerina sanguinea</i>	Selys	1853	Faasen, T.	RMNH
Calopterygidae	<i>Matrona basilaris</i>	(Selys)	1853	Kalkman, V.J.	RMNH
Calopterygidae	<i>Matrona cyanoptera</i>	Hämäläinen & Yeh	2000	Yeh, C.	RMNH
Calopterygidae	<i>Mnais yunosukei</i>	Asahina	1990	Hämäläinen, M.	RMNH
Calopterygidae	<i>Mnesarete cupraea</i>	(Selys)	1853	Wasscher, M.	RMNH
Calopterygidae	<i>Mnesarete fulgida</i>	(Selys)	1879	Faasen, T.	RMNH
Calopterygidae	<i>Neurobasis ianthinipennis</i>	Lieftinck	1849	Kalkman, V.J.	RMNH
Calopterygidae	<i>Neurobasis longipes</i>	Hagen	1887	Dow, R.A.	RMNH
Calopterygidae	<i>Phaon camerunensis</i>	Sjöstedt	1899	Dijkstra, K.-D.B.	RMNH
Calopterygidae	<i>Phaon camerunensis</i>	Sjöstedt	1899	Dijkstra, K.-D.B., Kipping, J. & Schütte, K.	RMNH
Calopterygidae	<i>Sapho bicolor</i>	(Selys)	1853	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Calopterygidae	<i>Umma cincta</i>	(Hagen in Selys)	1853	Dijkstra, K.-D.B.	RMNH
Calopterygidae	<i>Vestalis amabilis</i>	Lieftinck	1965	Teo, J.	RMNH
Calopterygidae	<i>Vestalis smaragdina</i>	Selys	1879	Hämäläinen, M.	RMNH
Chlorocyphidae	<i>Africocypha lacuselephantum</i>	(Karsch)	1899	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Chlorocyphidae	<i>Aristocypha fenestrella</i>	(Rambur)	1842	Dow, R.A.	RMNH
Chlorocyphidae	<i>Aristocypha iridea</i>	(Selys)	1891	Hämäläinen, M.	RMNH
Chlorocyphidae	<i>Chlorocypha cancellata</i>	(Selys)	1879	Dijkstra, K.-D.B., Kipping, J. & Schütte, K.	RMNH
Chlorocyphidae	<i>Chlorocypha centripunctata</i>	Gambles	1975	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Chlorocyphidae	<i>Cyrano angustior</i>	Hämäläinen	1989	Villanueva, R.J.T.	RMNH
Chlorocyphidae	<i>Disparocypha biedermanni</i>	Ris	1916	Günther, Andre	RMNH
Chlorocyphidae	<i>Disparocypha biedermanni</i>	Ris	1916	Günther, Andre	RMNH
Chlorocyphidae	<i>Helicypha biforata</i>	(Selys)	1859	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Chlorocyphidae	<i>Helicypha fenestrata cornelli</i>	(Lieftinck)	1947	Günther, Andre	RMNH
Chlorocyphidae	<i>Indocypha catopta</i>	Zhang, Hämäläinen & Tong	2010	Zhang, H.	RMNH
Chlorocyphidae	<i>Libellago aurantiaca</i>	Selys	1859	Dow, R.A.	RMNH
Chlorocyphidae	<i>Libellago aurantiaca</i>	Selys	1859	Kalkman, V.J., Dijkstra, K.-D.B., Dingermanse, N.J. & Goudsmits, K.	RMNH
Chlorocyphidae	<i>Libellago celebensis orientalis</i>	van Tol	2007	Günther, Andre	RMNH
Chlorocyphidae	<i>Libellago hyalina</i>	Selys	1859	Hämäläinen, M.	RMNH
Chlorocyphidae	<i>Libellago hyalina</i>	Selys	1859	Dow, R.A.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Suriname	Sipaliwini	504753	30102348	KF369728	KF370127	KF369394	ODOPHO37-13
Peru	Tamshiyacu-Tahuayo Reserve	501933	30104122	KF369730	KF370129	KF369395	ODOPHO38-13
Peru	Tamshiyacu-Tahuayo Reserve	501872	25924874	KF369729	KF370128		ODOPHO39-13
China	Guāngxī	500702	30104130	KF369770	KF370169	KF369432	ODOPHO40-13
Taiwan	Taipei County	505773	30104141	KF369771	KF370170	KF369433	ODOPHO41-13
Thailand	Chiang Mai	505746	30104134	KF369789	KF370188	KF369450	ODOPHO42-13
Suriname	Sipaliwini	505200	30102289	KF369790	KF370189	KF369451	ODOPHO43-13
Peru	Tamshiyacu-Tahuayo Reserve	501910	30104121	KF369791	KF370190	KF369452	ODOPHO44-13
Indonesia	Papua	500612	30104124	KF369803	KF370202	KF369460	ODOPHO45-13
Malaysia	Pahang	501097	25925908	KF369804	KF370203	KF369461	ODOPHO46-13
Democratic Republic of Congo	Province Orientale	502115	25924828	KF369838	KF370237	KF369488	ODOPHO47-13
Cameroon	Centre Province	500146	25924787	KF369839	KF370238	KF369489	ODOPHO48-13
Gabon	Haut-Ogooué	502474	25924246	KF369896	KF370295	KF369539	ODOPHO49-13
Democratic Republic of Congo	Province Orientale	502320	25924259	KF369938	KF370337		ODOPHO50-13
Malaysia	Sarawak	503483	25924707	KF369939	KF370338	KF369576	ODOPHO51-13
Thailand	Chiang Mai	505747	30104135	KF369940	KF370339	KF369577	ODOPHO52-13
Cameroon	Southwest Province	229119	25925362	KF369600	KF369996	KF369282	ODOPHO53-13
Malaysia	Terengganu	503911	30102258	KF369633	KF370031	KF369312	ODOPHO54-13
Thailand	Chiang Mai	505756	25919438	KF369634	KF370032	KF369313	ODOPHO55-13
Cameroon	South Province	229139	25925636	KF369665	KF370063	KF369341	ODOPHO56-13
Cameroon	Northwest Province	229140	25925374	KF369599	KF369995	KF369281	ODOPHO57-13
Philippines	Luzon	500682	25919436	KF369684	KF370082	KF369356	ODOPHO58-13
Indonesia	Sulawesi	505705	30104112	KF369693	KF370091		ODOPHO59-13
Indonesia	Sulawesi	505708	30104114	KF369694	KF370092		ODOPHO60-13
Thailand	Nakhon Ratchasima	229185	25925413	KF369726	KF370125		ODOPHO61-13
Indonesia	Bali	505711	30104116	KF369727	KF370126	KF369393	ODOPHO62-13
China	Guizhou	502066	30104142	KF369745	KF370144	KF369410	ODOPHO63-13
Malaysia	Sarawak	503497	25924149	KF369762	KF370161	KF369426	ODOPHO64-13
Brunei Darussalam	Belait	500799	25924715	KF369763	KF370162		ODOPHO65-13
Indonesia	Sulawesi	505707	30104113	KF369764	KF370163	KF369427	ODOPHO66-13
Thailand	Phangnga	505697	30104105	KF369765	KF370164	KF369428	ODOPHO67-13
Malaysia	Sarawak	228958	25925275	KF369766	KF370165		ODOPHO68-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Chlorocyphidae	<i>Pachycypha aurea</i> cf	Lieftinck	1950	Dow, R.A.	RMNH
Chlorocyphidae	<i>Platycypha picta</i>	(Pinhey)	1962	Mézière, N.	RMNH
Chlorocyphidae	<i>Platycypha picta</i>	(Pinhey)	1962	Mézière, N.	RMNH
Chlorocyphidae	<i>Rhinocypha chaoi</i>	Wilson	2004	Dijkstra, K.-D.B.	RMNH
Chlorocyphidae	<i>Rhinocypha pagenstecheri</i>	Förster	1897	Günther, Andre	RMNH
Chlorocyphidae	<i>Rhinocypha spinifer</i>	Laidlaw	1931	Dow, R.A.	RMNH
Chlorocyphidae	<i>Rhinocypha tincta</i>	Rambur	1842	Kalkman, V.J.	RMNH
Chlorocyphidae	<i>Rhinoneura caerulea</i>	Kimmins	1936	Reels, G.T.	RMNH
Chlorocyphidae	<i>Sclerocypha bisignata</i>	(McLachlan)	1870	Günther, Andre	RMNH
Chlorocyphidae	<i>Stenocypha tenuis</i>	(Longfield)	1936	Apodaca, C.	RMNH
Chlorocyphidae	<i>Sundacypha petiolata</i>	(Selys)	1859	Dow, R.A.	RMNH
Chlorocyphidae	<i>Sundacypha striata</i>	Orr	1999	Dijkstra K.-D.B. & Kalkman, V.J.	RMNH
Coenagrionidae	<i>Acanthagrion phallicorne</i>	Leonard	1977	Faasen, T.	RMNH
Coenagrionidae	<i>Acanthagrion rubrifrons</i>	Leonard	1977	Wasscher, M.	RMNH
Coenagrionidae	<i>Aciagrion borneense</i>	Ris	1911	Dow, R.A.	RMNH
Coenagrionidae	<i>Aciagrion brosetti</i>	Legrand	1982	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Aeolagrion dorsale</i>	(Burmeister)	1839	Faasen, T.	RMNH
Coenagrionidae	<i>Africallagma elongatum</i>	(Martin)	1907	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Africallagma vaginale</i>	(Sjöstedt)	1917	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Coenagrionidae	<i>Agriocnemis femina</i>	(Brauer)	1868	Dow, R.A.	RMNH
Coenagrionidae	<i>Agriocnemis forcipata</i>	Le Roi	1915	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Coenagrionidae	<i>Agriocnemis stygia</i>	(Fraser)	1954	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Amphicnemis ecornuta</i>	Selys	1889	Dow, R.A.	RMNH
Coenagrionidae	<i>Anomisma abnorme</i>	McLachlan	1877	Faasen, T.	RMNH
Coenagrionidae	<i>Archibasis melanocyana</i>	(Selys)	1877	Dow, R.A.	RMNH
Coenagrionidae	<i>Argia oculata</i>	Hagen in Selys	1865	Wasscher, M.	RMNH
Coenagrionidae	<i>Argia</i> sp.			Wasscher, M.	RMNH
Coenagrionidae	<i>Argiocnemis rubescens rubeola</i>	Selys	1877	Dow, R.A.	RMNH
Coenagrionidae	<i>Argiocnemis rubescens rubescens</i>	Selys	1877	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Austroagrion watsoni</i>	Lieftinck	1982	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Austrocnemis splendida</i>	(Martin)	1901	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Austrocoenagrion lyelli</i>	(Tillyard)	1913	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Azuragrion buchholzi</i>	(Pinhey)	1971	Mézière, N.	RMNH
Coenagrionidae	<i>Bromeliagrion rebni</i>	Garrison	2005	Faasen, T.	RMNH
Coenagrionidae	<i>Bromeliagrion rebni</i>	Garrison	2005	Faasen, T.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Malaysia	Sarawak	501002	25925799	KF369818	KF370217	KF369471	ODOPHO69-13
Gabon	Haut-Ogooué	502649	25924907	KF369850	KF370249	KF369499	ODOPHO70-13
Gabon	Haut-Ogooué	502610	25924861	KF369851	KF370250	KF369500	ODOPHO71-13
China	Guangdong	229240	25925437	KF369886	KF370285	KF369533	ODOPHO72-13
Indonesia	Lombok	505712	30104117	KF369887	KF370286	KF369534	ODOPHO73-13
Malaysia	Sarawak	503488	30104097	KF369888	KF370287	KF369535	ODOPHO74-13
Indonesia	Papua	500674	30104128	KF369889	KF370288	KF369536	ODOPHO75-13
Malaysia	Sarawak	503485	25919425	KF369890	KF370289	KF369537	ODOPHO76-13
Indonesia	Sulawesi	505706	25919429	KF369899	KF370298	KF369540	ODOPHO77-13
Uganda	Kibale NP	229154	25918278	KF369910	KF370309	KF369550	ODOPHO78-13
Malaysia	Sarawak	504000	30102270	KF369911	KF370310	KF369551	ODOPHO79-13
Brunei Darussalam	Belait	229245	25919414	KF369912	KF370311	KF369552	ODOPHO80-13
Peru	Tamshiyacu-Tahuayo Reserve	501719	25924109	KF369591	KF369987	KF369273	ODOPHO81-13
Suriname	Sipaliwini	504755	30102347	KF369592	KF369988	KF369274	ODOPHO82-13
Malaysia	Sarawak	503596	25918240	KF369593	KF369989	KF369275	ODOPHO83-13
Democratic Republic of Congo	Province Orientale	502280	25924062	KF369594	KF369990	KF369276	ODOPHO84-13
Peru	Tamshiyacu-Tahuayo Reserve	501723	25924051	KF369595	KF369991	KF369277	ODOPHO85-13
Tanzania	Tanga Region	504230	30104082	KF369597	KF369993	KF369279	ODOPHO86-13
Gabon	Haut-Ogooué	502448	25924075	KF369598	KF369994	KF369280	ODOPHO87-13
Malaysia	Sarawak	501242	25924204	KF369601	KF369997	KF369283	ODOPHO88-13
Gabon	Haut-Ogooué	50285	30104123	KF369602	KF369998	KF369284	ODOPHO89-13
Democratic Republic of Congo	Province Orientale	502179	25924112	KF369794	KF370193	KF369454	ODOPHO90-13
Malaysia	Sarawak	503580	30104100	KF369614	KF370012	KF369294	ODOPHO91-13
Peru	Tamshiyacu-Tahuayo Reserve	501709	25924846	KF369619	KF370017	KF369299	ODOPHO92-13
Malaysia	Sarawak	228996	25925353	KF369625	KF370023	KF369305	ODOPHO93-13
Suriname	Sipaliwini	504761	30102282	KF369627	KF370025	KF369306	ODOPHO94-13
Suriname	Sipaliwini	504749	30102278	KF369628	KF370026	KF369307	ODOPHO95-13
Malaysia	Selangor	500068	25925624	KF369629	KF370027	KF369308	ODOPHO96-13
Indonesia	Papua, Japen	500599	25924625	KF369630	KF370028	KF369309	ODOPHO97-13
Australia	Queensland	505304	30102326	KF369637	KF370035	KF369316	ODOPHO98-13
Australia	Queensland	505255	30102321	KF369640	KF370038		ODOPHO99-13
Australia	New South Wales	504852	30102308	KF369641	KF370039	KF369319	ODOPHI00-13
Gabon	Haut-Ogooué	502620	30104143	KF369644	KF370042	KF369322	ODOPHI01-13
Peru	Tamshiyacu-Tahuayo Reserve	501856	25924868	KF369648	KF370046	KF369326	ODOPHI02-13
Peru	Tamshiyacu-Tahuayo Reserve	501718	25924849	KF369647	KF370045	KF369325	ODOPHI03-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Coenagrionidae	<i>Ceriatrion glabrum</i>	(Burmeister)	1839	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Coenagrionidae	<i>Ceriatrion whellani</i>	Longfield	1952	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Coenagriocnemis insularis</i>	(Selys)	1872	Skinner, A.	RMNH
Coenagrionidae	<i>Coenagriocnemis rufipes</i>	(Rambur)	1842	Skinner, A.	RMNH
Coenagrionidae	<i>Coenagrion pulchellum</i>	(Vander Linden)	1825	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Coenagrion pulchellum</i>	(Vander Linden)	1825	Smit, J.	RMNH
Coenagrionidae	<i>Dolonagrion fulvellum</i>	(Selys)	1876	Wasscher, M.	RMNH
Coenagrionidae	<i>Drepanoneura muzoni</i>	von Ellenrieder & Garrison	2008	Faasen, T.	RMNH
Coenagrionidae	<i>Epipleoneura lamina</i>	Williamson	1915	Faasen, T.	RMNH
Coenagrionidae	<i>Episynlestes albicauda</i>	(Tillyard)	1913	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Episynlestes albicauda</i>	(Tillyard)	1913	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Inpabasis hubelli</i> cf	Santos	1961	Faasen, T.	RMNH
Coenagrionidae	<i>Inpabasis rosea</i>	(Selys)	1877	Wasscher, M.	RMNH
Coenagrionidae	<i>Ischnura aurora</i>	(Brauer)	1865	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Ischnura elegans</i>	(Vander Linden)	1820	Van Tol, J.	RMNH
Coenagrionidae	<i>Ischnura nursei</i>	Morton	1907	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Ischnura senegalensis</i>	(Rambur)	1842	Dow, R.A.	RMNH
Coenagrionidae	<i>Leptocnemis cyanops</i>	(Selys)	1869	Gerlach, J.	RMNH
Coenagrionidae	<i>Mecistogaster linearis</i>	(Fabricius)	1777	Faasen, T.	RMNH
Coenagrionidae	<i>Mecistogaster lucretia</i>	(Drury)	1773	Faasen, T.	RMNH
Coenagrionidae	<i>Mesoleptobasis cantralli</i>	Santos	1961	Faasen, T.	RMNH
Coenagrionidae	<i>Mesoleptobasis elongata</i>	Garrison & von Ellenrieder	2009	Wasscher, M.	RMNH
Coenagrionidae	<i>Metaleptobasis mauritia</i>	Williamson	1915	Wasscher, M.	RMNH
Coenagrionidae	<i>Metaleptobasis minteri</i>	Daigle	2003	Faasen, T.	RMNH
Coenagrionidae	<i>Microstigma rotundatum</i>	(Selys)	1860	Faasen, T.	RMNH
Coenagrionidae	<i>Mortonagrion arthuri</i>	Fraser	1942	Dow, R.A.	RMNH
Coenagrionidae	<i>Mortonagrion martini</i>	(Ris)	1900	Richards, S.	RMNH
Coenagrionidae	<i>Neoneura fulvicollis</i>	Selys	1886	Wasscher, M.	RMNH
Coenagrionidae	<i>Neoneura rurriventris</i>	(Selys)	1860	Faasen, T.	RMNH
Coenagrionidae	<i>Oreocnemis phoenix</i>	Pinhey	1971	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Oreocnemis phoenix</i>	Pinhey	1971	Dijkstra, K.-D.B.	RMNH

Country	Location	Voucher	Extract	1S	2S	COI	Barcode Index
Gabon	Haut-Ogooué	502549	25924844	KF369657	KF370055	KF369334	ODOPHI04-13
Democratic Republic of Congo	Katanga	505470	30104088	KF369658	KF370056	KF369335	ODOPHI05-13
Mauritius		504477	30102297	KF369675	KF370073	KF369347	ODOPHI06-13
Mauritius		504475	30102295	KF369676	KF370074	KF369348	ODOPHI07-13
Nederland	Leiden	504320	25919418	KF369678	KF370076	KF369350	ODOPHI08-13
Ukraine		504321	30104158	KF369677	KF370075	KF369349	ODOPHI09-13
Suriname	Tapatso	505024	30102285		KF370093	KF369364	ODOPHI10-13
Peru	Tamshiyacu-Tahuayo Reserve	501759	30104165	KF369695	KF370094	KF369365	ODOPHI11-13
Peru	Tamshiyacu-Tahuayo Reserve	501870	25924899	KF369716	KF370115	KF369385	ODOPHI12-13
Australia	Queensland	505246	30102319	KF369717	KF370116		ODOPHI13-13
Australia	Queensland	505303	30102324	KF369718	KF370117		ODOPHI14-13
Peru	Tamshiyacu-Tahuayo Reserve	501754	25924106	KF369747	KF370146	KF369412	ODOPHI15-13
Suriname	Sipaliwini	504751	30102279	KF369748	KF370147	KF369413	ODOPHI16-13
Australia	New South Wales	504855	30102310	KF369749	KF370148	KF369414	ODOPHI17-13
Netherlands		228277	25925473	KF369750	KF370149	KF369415	ODOPHI18-13
India	Maharashtra	500482	30104145	KF369893	KF370292	KF369538	ODOPHI19-13
Malaysia	Sarawak	501241	25924216	KF369751	KF370150	KF369416	ODOPHI20-13
Seychelles	Mahe	500398	25925618	KF369754	KF370153		ODOPHI21-13
Peru	Tamshiyacu-Tahuayo Reserve	501850	25924887	KF369773	KF370172	KF369435	ODOPHI22-13
Peru	Tamshiyacu-Tahuayo Reserve	501805	30104167	KF369774	KF370173	KF369436	ODOPHI23-13
Peru	Tamshiyacu-Tahuayo Reserve	501848	30104168	KF369778	KF370177	KF369440	ODOPHI24-13
Suriname	Sipaliwini	505203	30102290	KF369779	KF370178	KF369441	ODOPHI25-13
Suriname	Sipaliwini	504747	30102277	KF369784	KF370183	KF369446	ODOPHI26-13
Peru	Tamshiyacu-Tahuayo Reserve	501701	25924083	KF369785	KF370184	KF369447	ODOPHI27-13
Peru	Tamshiyacu-Tahuayo Reserve	501735	25924860	KF369786	KF370185		ODOPHI28-13
Singapore	Pulau Ubin	503516	25924169	KF369792	KF370191		ODOPHI29-13
Papua New Guinea		504969	30104080	KF369793	KF370192	KF369453	ODOPHI30-13
Suriname	Marowijne	504744	30102275	KF369795	KF370194	KF369455	ODOPHI31-13
Peru	Tamshiyacu-Tahuayo Reserve	501845	25924862	KF369796	KF370195	KF369456	ODOPHI32-13
Malawi	Southern Region	229209	25925435	KF369812	KF370211		ODOPHI33-13
Malawi	Southern Region	229208	25925459	KF369813	KF370212		ODOPHI34-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Coenagrionidae	<i>Papuagrion occipitale</i>	(Selys)	1877	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Papuagrion prothoracale</i>	Lieftinck	1935	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Perinemis lestoides</i>	(Brauer)	1868	Villanueva, R.J.T.	RMNH
Coenagrionidae	<i>Phoenicagrion flammeum</i>	(Selys)	1876	Faasen, T.	RMNH
Coenagrionidae	<i>Protoneura paucinervis</i>	Selys	1886	Faasen, T.	RMNH
Coenagrionidae	<i>Protoneura scintilla</i>	Gloyd	1939	Faasen, T.	RMNH
Coenagrionidae	<i>Pseudagrion hamoni</i>	Fraser	1955	Tarboton, W.	RMNH
Coenagrionidae	<i>Pseudagrion kersteni</i>	Gerstaecker	1869	Dijkstra, K.-D.B.	RMNH
Coenagrionidae	<i>Pseudagrion pilidorsum</i>	(Brauer)	1868	Dow, R.A.	RMNH
Coenagrionidae	<i>Stenagrion dubium</i>	(Laidlaw)	1912	Dow, R.A.	RMNH
Coenagrionidae	<i>Stenagrion dubium</i>	(Laidlaw)	1912	Hämäläinen, M.	RMNH
Coenagrionidae	<i>Teinobasis cryptica</i>	Dow	2010	Megan, N.	RMNH
Coenagrionidae	<i>Teinobasis laidlawi</i>	Kimmins	1936	Kebing, W.	RMNH
Coenagrionidae	<i>Teinobasis rajah</i>	Laidlaw	1912	Kalkman, V.J., Dijkstra, K.-D.B., Dingermanse, N.J. & Goudsmits, K.	RMNH
Coenagrionidae	<i>Teinobasis rufithorax</i>	(Selys)	1877	Smit, H.	RMNH
Coenagrionidae	<i>Teinobasis scintillans</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Telebasis dunklei</i>	Bick & Bick	1995	Faasen, T.	RMNH
Coenagrionidae	<i>Telebasis obsoleta</i>	(Selys)	1876	Faasen, T.	RMNH
Coenagrionidae	<i>Thaumatagrion funereum</i>	Lieftinck	1932	Richards, S.	RMNH
Coenagrionidae	<i>Tuberculobasis geijskesi</i>	Machado	2009	Wasscher, M.	RMNH
Coenagrionidae	<i>Xanthagrion erythroneurum</i>	(Selys)	1876	Kalkman, V.J.	RMNH
Coenagrionidae	<i>Xiphiagrion cyanomelas</i>	Selys	1876	Reels, G.T.	RMNH
Coenagrionidae	<i>Xiphiagrion cyanomelas</i>	Selys	1876	Dow, R.A.	RMNH
Devadattidae	<i>Devadatta cyanocephala</i>	Hämäläinen, Sasamota & Karube	2006		RMNH
Devadattidae	<i>Devadatta</i> sp.			Dow, R.A.	RMNH
Devadattidae	<i>Devadatta</i> sp.			Kalkman, V.J., Dijkstra, K.-D.B., Dingermanse, N.J. & Goudsmits, K.	RMNH
Dicteriadidae	<i>Heliocharis amazonica</i>	Selys	1853	Wasscher, M.	RMNH
Euphaeidae	<i>Anisopleura furcata</i>	Selys	1891	Hämäläinen, M.	RMNH
Euphaeidae	<i>Anisopleura quingyuanensis</i>	Zhou	1982	Kalkman, V.J.	RMNH
Euphaeidae	<i>Cryptophaea vietnamensis</i>	(van Töl & Rozendaal)	1995	Hämäläinen, M.	RMNH
Euphaeidae	<i>Dysphaea dimidiata</i>	(Selys)	1853	Dijkstra K.-D.B. & Kalkman, V.J.	RMNH
Euphaeidae	<i>Euphaea decorata</i>	Hagen in Selys	1853	Dijkstra, K.-D.B.	RMNH
Euphaeidae	<i>Euphaea impar</i>	Selys	1859	Dow, R.A.	RMNH
Euphaeidae	<i>Euphaea superba</i>	Kimmins	1936	Kalkman, V.J.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Indonesia	Papua, Japen	500554	25924649	KF369824	KF370223		ODOPH135-13
Indonesia	Papua, Japen	229213	25925280	KF369825	KF370224	KF369476	ODOPH136-13
Philippines	Mindanao	500872	25925449	KF369834	KF370233	KF369484	ODOPH137-13
Peru	Tamshiyacu-Tahuayo Reserve	501728	25923076	KF369846	KF370245	KF369496	ODOPH138-13
Peru	Tamshiyacu-Tahuayo Reserve	501963	30104153	KF369871	KF370270	KF369519	ODOPH139-13
Peru	Tamshiyacu-Tahuayo Reserve	501961	25924850	KF369872	KF370271		ODOPH140-13
South Africa	Limpopo	500376	25924848	KF369877	KF370276	KF369524	ODOPH141-13
Liberia	Nimba County	503080	25923008	KF369878	KF370277	KF369525	ODOPH142-13
Malaysia	Sarawak	228961	25925205	KF369879	KF370278	KF369526	ODOPH143-13
Malaysia	Sarawak	228951	25925217	KF369908	KF370307	KF369549	ODOPH144-13
Malaysia	Sabah	505760	30104137	KF369907	KF370306	KF369548	ODOPH145-13
Malaysia	Sarawak	503885	30104090	KF369919	KF370318	KF369559	ODOPH146-13
Malaysia	Sarawak	503565	30104101	KF369920	KF370319	KF369560	ODOPH147-13
Brunei Darussalam	Belait	500747	25924668	KF369921	KF370320	KF369561	ODOPH148-13
Indonesia	Papua	504970	30104081	KF369922	KF370321	KF369562	ODOPH149-13
Indonesia	Papua	229289	25925342	KF369923	KF370322	KF369563	ODOPH150-13
Peru	Tamshiyacu-Tahuayo Reserve	501793	25923001	KF369926	KF370325	KF369566	ODOPH151-13
Peru	Tamshiyacu-Tahuayo Reserve	501855	30104144	KF369927	KF370326	KF369567	ODOPH152-13
Papua New Guinea		501979	25924818	KF369932	KF370331	KF369571	ODOPH153-13
Suriname	Para	505022	30102286	KF369937	KF370336		ODOPH154-13
Australia	New South Wales	504854	30102309	KF369943	KF370342	KF369578	ODOPH155-13
Malaysia	Sarawak	228954				KF369579	ODOPH156-13
Malaysia	Sarawak	228983				KF369580	ODOPH157-13
Vietnam	Central Vietnam	229256	25925508	KF369685	KF370083	KF369357	ODOPH158-13
Malaysia	Sarawak	503484	25924203	KF369686	KF370084	KF369358	ODOPH159-13
Brunei Darussalam	Temburong	500720	25924633	KF369687	KF370085	KF369359	ODOPH160-13
Suriname	Sipaliwini	505205	30102291	KF369725	KF370124	KF369392	ODOPH161-13
Thailand	Chiang Mai	505757	30104136	KF369617	KF370015	KF369297	ODOPH162-13
China	Guǎngxī	229123	25925575	KF369618	KF370016	KF369298	ODOPH163-13
Vietnam	Northern Vietnam	229255	25925505	KF369682	KF370080	KF369354	ODOPH164-13
Brunei Darussalam	Temburong	229164	25925442	KF369707	KF370106	KF369377	ODOPH165-13
China	Hong Kong	229182	25925526	KF369720	KF370119	KF369387	ODOPH166-13
Malaysia	Sarawak	504004	30102272	KF369721	KF370120	KF369388	ODOPH167-13
China	Guǎngxī	229184	25925270	KF369722	KF370121	KF369389	ODOPH168-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Heteragrionidae	<i>Heteragrion bickorum</i>	Daigle	2005	Garrison, R.W. & Ellenrieder, N. von	RMNH
Heteragrionidae	<i>Heteragrion chrysops</i>	Hagen in Selys	1862	Demarmels, J.	RMNH
Heteragrionidae	<i>Heteragrion inca</i>	Calvert	1909	Faasen, T.	RMNH
Heteragrionidae	<i>Oxystigma</i> sp.				RMNH
Heteragrionidae	<i>Oxystigma</i> sp.			Dijkstra, K.-D.B.	RMNH
Hypolestidae	<i>Hypolestes</i> sp.			Veurink, G.	RMNH
Hypolestidae	<i>Hypolestes</i> sp.			Veurink, G.	RMNH
Incertae sedis	<i>Agriomorpha fusca</i>	May	1933	Van Tol, J.	RMNH
Incertae sedis	<i>Agriomorpha fusca</i>	May	1933	Reels, G.T.	RMNH
Incertae sedis	<i>Agriomorpha xynglongensis</i>	Wilson & Reels	2001	Reels, G.T.	RMNH
Incertae sedis	<i>Amanipodagrion gilliesi</i>	Pinhey	1962	Clausnitzer, V.	RMNH
Incertae sedis	<i>Amanipodagrion gilliesi</i>	Pinhey	1962	Clausnitzer, V.	RMNH
Incertae sedis	<i>Bornargiolestes</i> sp.			Reels, G.T.	RMNH
Incertae sedis	<i>Bornargiolestes</i> sp.			Dow, R.A.	RMNH
Incertae sedis	<i>Burmargiolestes laidlawi</i> cf	Lieftinck	1960	Hämäläinen, M.	RMNH
Incertae sedis	<i>Burmargiolestes melanothorax</i>	(Selys)	1891	Hämäläinen, M.	RMNH
Incertae sedis	<i>Dimeragrion percubitale</i>	Calvert	1913	Demarmels, J.	RMNH
Incertae sedis	<i>Dimeragrion percubitale</i>	Calvert	1913	Demarmels, J.	RMNH
Incertae sedis	<i>Heteropodagrion sanguinipes</i>	Selys	1885	Tennessen, K.	RMNH
Incertae sedis	<i>Mesopodagrion tibetanum</i>	McLachlan	1896	Hämäläinen, M.	RMNH
Incertae sedis	<i>Priscagrion</i> sp.			Bowen-Jones, E.	RMNH
Incertae sedis	<i>Priscagrion</i> sp.			Bowen-Jones, E.	RMNH
Incertae sedis	<i>Protolestes fickei</i>	Förster	1899	Schütte, K.	RMNH
Incertae sedis	<i>Protolestes kerckhoffae</i>	Schmidt in Fraser	1949	Schütte, K.	RMNH
Incertae sedis	<i>Rhipidolestes lii</i>	Zhou	2003	Zhang, H.	RMNH
Incertae sedis	<i>Rhipidolestes owadai</i>	Asahina	1997	Hämäläinen, M.	RMNH
Incertae sedis	<i>Sciotropis cyclamborum</i>	Racenis	1959	Demarmels, J.	RMNH
Incertae sedis	<i>Sciotropis cyclamborum</i>	Racenis	1959	Demarmels, J.	RMNH
Incertae sedis	<i>Smocnemis</i> sp.			Zhang, H.	RMNH
Incertae sedis	<i>Tatocnemis denticularis</i>	Aguesse	1968	Schütte, K.	RMNH
Incertae sedis	<i>Tatocnemis malgassica</i>	Kirby	1889	Schütte, K.	RMNH
Isostictidae	<i>Isosticta gracilior</i>	Lieftinck	1975	Marinov, M.	RMNH
Isostictidae	<i>Isosticta</i> sp.			Marinov, M.	RMNH
Isostictidae	<i>Neosticta canescens</i>	Tillyard	1913	Kalkman, V.J.	RMNH
Isostictidae	<i>Neosticta</i> sp.			Kalkman, V.J.	RMNH
Isostictidae	<i>Selysioneura capreola</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Isostictidae	<i>Selysioneura phasma</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Isostictidae	<i>Tanymecosticta</i> sp.			Kalkman, V.J.	RMNH
Lestidae	<i>Austrolestes leda</i>	(Selys)	1862	Kalkman, V.J.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Ecuador	Orenella	502100	25924759	KF369731	KF370130	KF369396	ODOPH169-13
Venezuela	Aragua	502036	25924806	KF369732	KF370131	KF369397	ODOPH170-13
Peru	Tamshiyacu-Tahuayo Reserve	501859	25924723	KF369733	KF370132	KF369398	ODOPH171-13
Suriname		500842	25924655	KF369816	KF370215	KF369469	ODOPH172-13
Suriname	Paramaribo	228855	25925560	KF369817	KF370216	KF369470	ODOPH173-13
Dominican Republic		503672	30104091	KF369736	KF370135	KF369401	ODOPH174-13
Dominican Republic		503671	25919415	KF369737	KF370136	KF369402	ODOPH175-13
Vietnam	Vinh Phu	228706	25918280	KF369603	KF369999	KF369285	ODOPH348-13
China	Hainan	228938	25925519	KF369604	KF370000		ODOPH349-13
China	Hainan	228941	25925496	KF369605	KF370001		ODOPH350-13
Tanzania	Usumbara Mountains	229121	25925555	KF369612	KF370008	KF369290	ODOPH189-13
Tanzania	Usumbara Mountains	229120	25925543	KF369613	KF370009	KF369291	ODOPH190-13
Malaysia	Sarawak	500005	25924765	KF369646	KF370044	KF369324	ODOPH351-13
Malaysia	Sarawak	501245	25924209	KF369645	KF370043	KF369323	ODOPH352-13
Vietnam	Thua Thien Hue	502086	25924789	KF369649	KF370047	KF369327	ODOPH353-13
Thailand	Chiang Mai	228104	25925579	KF369650	KF370048		ODOPH354-13
Venezuela	Pijianaus-BO	502032	25924693	KF369689	KF370087	KF369361	ODOPH176-13
Venezuela	Pijianaus-BO	502033	25924705	KF369688	KF370086	KF369360	ODOPH177-13
Ecuador	Santo Domingo de los Tsachilas	501970	25924894	KF369734	KF370133	KF369399	ODOPH178-13
Vietnam	Lao Cai	502079	25924783	KF369780	KF370179	KF369442	ODOPH179-13
China	Fujian	501994	25924760	KF369860	KF370259	KF369509	ODOPH180-13
China	Fujian	504323	25919416	KF369861	KF370260	KF369510	ODOPH181-13
Madagascar	Apasy	228865	25925568	KF369869	KF370268	KF369517	ODOPH182-13
Madagascar	Malio	228866	25925580	KF369870	KF370269	KF369518	ODOPH183-13
China	Guizhou	502063	25924784	KF369891	KF370290		ODOPH357-13
Laos	Bolikhamsai	502089	25924718	KF369892	KF370291		ODOPH358-13
Venezuela	Aragua	502029	25924725	KF369898	KF370297		ODOPH184-13
Venezuela	Aragua	502028	25924808	KF369897	KF370296		ODOPH185-13
China	Guizhou	502059	25924696	KF369902	KF370301	KF369543	ODOPH186-13
Madagascar	Tolongoina	228858	25925545	KF369917	KF370316	KF369557	ODOPH187-13
Madagascar	Amboavola	228861	25925569	KF369918	KF370317	KF369558	ODOPH188-13
New Caledonia		503408	25924826	KF369752	KF370151	KF369417	ODOPH193-13
New Caledonia		503409	25924822	KF369753	KF370152	KF369418	ODOPH194-13
Australia	Queensland	505269	30102327	KF369797	KF370196	KF369457	ODOPH191-13
Australia		502016	25924689	KF369798	KF370197		ODOPH192-13
Indonesia	Papua	500515	25924685	KF369900	KF370299	KF369541	ODOPH195-13
Indonesia	Papua	229242	25925292	KF369901	KF370300	KF369542	ODOPH196-13
Indonesia	Papua	500651	25924799	KF369916	KF370315	KF369556	ODOPH197-13
Australia	New South Wales	504856	30102311	KF369642	KF370040	KF369320	ODOPH198-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Lestidae	<i>Austrolestes minjerriba</i>	Watson	1979	Kalkman, V.J.	RMNH
Lestidae	<i>Indolestes</i> sp.			Kalkman, V.J.	RMNH
Lestidae	<i>Lestes dissimulans</i>	Fraser	1955	Dijkstra, K.-D.B.	RMNH
Lestidae	<i>Lestes helix</i>	Ris	1918	Faasen, T.	RMNH
Lestidae	<i>Lestes pallidus</i>	Rambur	1842	Dijkstra, K.-D.B.	RMNH
Lestidae	<i>Lestes pinheyi</i>	Fraser	1955	Dijkstra, K.-D.B.	RMNH
Lestidae	<i>Lestes praemorsus decipiens</i>	Kirby	1894	Dow, R.A.	RMNH
Lestidae	<i>Lestes virens</i>	(Charpentier)	1825		RMNH
Lestidae	<i>Orolestes octomaculatus</i>	Martin	1902	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Lestidae	<i>Orolestes wallacei</i>	(Kirby)	1889	Dow, R.A.	RMNH
Lestidae	<i>Sympetma fusca</i>	(Vander Linden)	1820	Dijkstra, K.-D.B.	RMNH
Lestoideidae	<i>Dipblebia coerulescens</i>	Tillyard	1913	Kalkman, V.J.	RMNH
Lestoideidae	<i>Dipblebia hybridoides</i>	Tillyard	1912	Kalkman, V.J.	RMNH
Lestoideidae	<i>Dipblebia nymphoides</i>	Tillyard	1912	Kalkman, V.J.	RMNH
Lestoideidae	<i>Lestoidea</i> sp.			Kalkman, V.J.	RMNH
Megapodagrionidae	<i>Teinopodagrion meridionale</i>	De Marmels	2001	Ellenrieder, N. von & Lozano, F.	RMNH
Megapodagrionidae	<i>Teinopodagrion venale</i>	(Hagen in Selys)	1862	Demarmels, J.	RMNH
Pentaplebiidae	<i>Pentaplebia</i> n. sp.			Dijkstra, K.-D.B. & Vanappelghem, C.	RMNH
Pentaplebiidae	<i>Pentaplebia</i> n. sp.			Dijkstra, K.-D.B. & Vanappelghem, C.	RMNH
Pentaplebiidae	<i>Pentaplebia stabli</i>	Förster	1909	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Perilestidae	<i>Perilestes kabli</i>	Williamson & Williamson	1924	Wasscher, M.	RMNH
Perilestidae	<i>Perilestes solutus</i>	Williamson & Williamson	1924	Wasscher, M.	RMNH
Perilestidae	<i>Perisselestes guianensis</i>	Williamson & Williamson	1924	Wasscher, M.	RMNH
Philogangidae	<i>Philoganga vetusta</i>	Ris	1912	Van Tol, J.	RMNH
Philogeniidae	<i>Archaeopodagrion armatum</i>	Tennesen & Johnson	2009	Tennesen, K. & Johnson, J.T.	RMNH
Philogeniidae	<i>Philogenia cassandra</i>	Hagen in Selys	1862	Demarmels, J.	RMNH
Philogeniidae	<i>Philogenia ferox</i>	Racenis	1959	Demarmels, J.	RMNH
Philogeniidae	<i>Philogenia iquita</i> cf	Dunkle	1990	Faasen, T.	RMNH
Philosinidae	<i>Philosina alba</i>	Wilson	1999	Zhang, H.	RMNH
Philosinidae	<i>Philosina buchi</i>	Ris	1917	Kalkman, V.J.	RMNH
Philosinidae	<i>Rhinagrion borneense</i>	(Selys)	1886	Stone, S.	RMNH
Philosinidae	<i>Rhinagrion mimia</i>	(Karsch)	1891	Hämäläinen, M.	RMNH
Platycnemididae	<i>“Elattonewra” aurantiaca</i>	(Selys)	1886	Dow, R.A.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Australia	Queensland	505287	30102350	KF369643	KF370041	KF369321	ODOPH199-13
Indonesia	Papua	500625	30104094	KF369746	KF370145	KF369411	ODOPH200-13
Ghana	Eastern Region	500228	25924697	KF369755	KF370154	KF369419	ODOPH201-13
Peru	Tamshiyacu-Tahuayo Reserve	501919	25924896	KF369756	KF370155	KF369420	ODOPH202-13
Democratic Republic of Congo	Katanga	505583	30104087	KF369757	KF370156	KF369421	ODOPH203-13
Democratic Republic of Congo	Katanga	505433	30104084	KF369758	KF370157	KF369422	ODOPH204-13
Malaysia	Sarawak	503590	25924185	KF369759	KF370158	KF369423	ODOPH205-13
Europe		228913	25925414	KF369760	KF370159	KF369424	ODOPH206-13
Thailand	Krabi	229210	25925426	KF369814	KF370213		ODOPH207-13
Malaysia	Pahang	500060	25924811	KF369815	KF370214		ODOPH208-13
Nederland	Leiden	504319	25919419	KF369913	KF370312	KF369553	ODOPH209-13
Australia	Queensland	505268	30102322	KF369690	KF370088	KF369362	ODOPH210-13
Australia		501976	25924630	KF369691	KF370089	KF369363	ODOPH211-13
Australia	New South Wales	504876	30102313	KF369692	KF370090		ODOPH212-13
Australia		502014	25924642	KF369761	KF370160	KF369425	ODOPH213-13
Argentina	Salta	502087	25924675	KF369924	KF370323	KF369564	ODOPH214-13
Venezuela	Aragua	502035	25924761	KF369925	KF370324	KF369565	ODOPH215-13
Gabon	Haut-Ogooué	502559	25924867	KF369831	KF370230	KF369482	ODOPH216-13
Gabon	Haut-Ogooué	502562	25924891	KF369832	KF370231		ODOPH217-13
Cameroon	Southwest Province	500108	25924812	KF369833	KF370232	KF369483	ODOPH218-13
Suriname	Brokopondo	505207	30102293	KF369835	KF370234	KF369485	ODOPH219-13
Suriname	Sipaliwini	504759	30102281	KF369836	KF370235	KF369486	ODOPH220-13
Suriname	Sipaliwini	504762	30102346	KF369837	KF370236	KF369487	ODOPH221-13
Vietnam	Dak Lak	228428	25925572	KF369840	KF370239	KF369490	ODOPH222-13
Ecuador	Zamora Chinchipe	501971	25924741	KF369622	KF370020	KF369302	ODOPH223-13
Venezuela	Aragua	502038	25924795	KF369841	KF370240	KF369491	ODOPH224-13
Venezuela	Cumbre de Choroni	502040	25924892	KF369842	KF370241	KF369492	ODOPH225-13
Peru	Tamshiyacu-Tahuayo Reserve	501714	25924890	KF369843	KF370242	KF369493	ODOPH226-13
China	Hainan	502061	25924724	KF369844	KF370243	KF369494	ODOPH227-13
China	Guǎngxī	229215	25925552	KF369845	KF370244	KF369495	ODOPH228-13
Malaysia	Sarawak	500942	25925690	KF369884	KF370283	KF369531	ODOPH229-13
Thailand	Ranong	502101	25924772	KF369885	KF370284	KF369532	ODOPH230-13
Malaysia	Pahang	503648	25924910	KF369711	KF370110	KF369380	ODOPH231-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Platycnemididae	<i>Elatoneura tenax</i>	(Hagen in Selys)	1860	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Allocnemis cyanura</i>	(Förster)	1909	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	RMNH
Platycnemididae	<i>Allocnemis leucosticta</i>	(Selys)	1863	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Allocnemis</i> n. sp. <i>near pauli</i>			Dijkstra, K.-D.B., & K. Schütte	RMNH
Platycnemididae	<i>Allocnemis nigripes</i>	(Selys)	1886	Mézière, N.	RMNH
Platycnemididae	<i>Allocnemis pauli</i>	(Longfield)	1936	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Amazona ephippigera</i>	(Selys)	1886	Faasen, T.	RMNH
Platycnemididae	<i>Amazona ephippigera</i>	(Selys)	1886	Faasen, T.	RMNH
Platycnemididae	<i>Arabicnemis caerulea</i>	Waterston	1984	Schneider, W.	RMNH
Platycnemididae	<i>Arabicnemis caerulea</i>	Waterston	1984	Schneider, W.	RMNH
Platycnemididae	<i>Arrhenocnemis amphidactylis</i>	Lieftinck	1949	Kalkman, V.J.	RMNH
Platycnemididae	<i>Arrhenocnemis parvibullis</i>	Orr & Kalkman	2010	Kalkman, V.J.	RMNH
Platycnemididae	<i>Calicnemia chaseni</i>	(Laidlaw in Campion & Laidlaw)	1928	Dow, R.A.	RMNH
Platycnemididae	<i>Calicnemia sinensis</i>	Lieftinck	1984	Kalkman, V.J.	RMNH
Platycnemididae	<i>Coelliccia borneensis</i>	(Selys)	1886	Southwell, L.	RMNH
Platycnemididae	<i>Coelliccia cyaneothorax</i>	Kimmins	1936	Dow, R.A.	RMNH
Platycnemididae	<i>Coelliccia cyanomelas</i>	Ris	1912	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Coelliccia didyma</i>	(Selys)	1863	Dow, R.A.	RMNH
Platycnemididae	<i>Coelliccia dinoceras</i>	Laidlaw	1925	Van Tol, J.	RMNH
Platycnemididae	<i>Coelliccia flavostriata</i>	Laidlaw	1918	Dow, R.A.	RMNH
Platycnemididae	<i>Coelliccia nemoricola</i>	Laidlaw	1912	Dow, R.A.	RMNH
Platycnemididae	<i>Coelliccia poungyi</i>	Fraser	1924	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Platycnemididae	<i>Copera marginipes</i>	(Rambur)	1842	Dow, R.A.	RMNH
Platycnemididae	<i>Copera nyansana</i>	(Förster)	1916	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Copera sikassoensis</i>	(Martin)	1912	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Copera vittata</i>	(Selys)	1863	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Platycnemididae	<i>Cyanocnemis aureofrons</i>	Lieftinck	1949	Richards, S.	RMNH
Platycnemididae	<i>Elatoneura centrafricana</i>	Lindley	1976	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Elatoneura glauca</i>	(Selys)	1860	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Elatoneura vittata</i>	(Selys)	1886	Dijkstra, K.-D.B., Kipping, J. & Schütte, K.	RMNH
Platycnemididae	<i>Esme mudiensis</i>	Fraser	1931	Bedjanič, M.	RMNH
Platycnemididae	<i>Hylaeargia</i> sp.			Richards, S.	RMNH
Platycnemididae	<i>Idiocnemis obliterata</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Platycnemididae	<i>Idiocnemis</i> sp.			Kalkman, V.J.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Sri Lanka	Kitulgala	229264	25925262	KF369714	KF370113	KF369383	ODOPH232-13
Gabon	Haut-Ogooué	502478	25924876	KF369606	KF370002	KF369286	ODOPH233-13
South Africa	Prince Albert	228210	25925498	KF369607	KF370003	KF369287	ODOPH234-13
Cameroon	Northwest Province	229129	25925616	KF369609	KF370005	KF369289	ODOPH235-13
Gabon	Haut-Ogooué	502653	25924809	KF369608	KF370004	KF369288	ODOPH236-13
DR Congo	Orientale	229133	25925422	KF369610	KF370006		ODOPH237-13
Peru	Tamshiyacu-Tahuayo Reserve	501694	25924829		KF370011	KF369293	ODOPH238-13
Peru	Tamshiyacu-Tahuayo Reserve	501967	25924870		KF370010	KF369292	ODOPH239-13
Yemen	Wadi Dau'an System	505846	30104156	KF369620	KF370018	KF369300	ODOPH240-13
Yemen	Wadi Dau'an System	505845	30104155	KF369621	KF370019	KF369301	ODOPH241-13
Indonesia	Papua	229253	25925675	KF369635	KF370033	KF369314	ODOPH242-13
Papua New Guinea		501977	25924785	KF369636	KF370034	KF369315	ODOPH243-13
Malaysia	Pahang	500057	25924754	KF369653	KF370051	KF369330	ODOPH244-13
China	Hong Kong	229127	25925564	KF369654	KF370052	KF369331	ODOPH245-13
Malaysia	Sarawak	503469	25924164	KF369668	KF370066	KF369342	ODOPH246-13
Malaysia	Sarawak	501314	25924158	KF369669	KF370067	KF369343	ODOPH247-13
China	Guangdong	228208	25925491	KF369670	KF370068		ODOPH248-13
Malaysia	Terengganu	503926	30102261	KF369671	KF370069	KF369344	ODOPH249-13
Philippines	Mindanao	226847					ODOPH250-13
Malaysia	Sarawak	501225	25925484	KF369672	KF370070	KF369345	ODOPH251-13
Malaysia	Sarawak	503632	30104095	KF369673	KF370071	KF369346	ODOPH252-13
Thailand	Chiang Mai	229162	25925570	KF369674	KF370072		ODOPH253-13
Malaysia	Pahang	501092	25925932	KF369679	KF370077	KF369351	ODOPH254-13
Democratic Republic of Congo	Province Orientale	502195	25924877	KF369680	KF370078	KF369352	ODOPH255-13
Liberia	Nimba County	503091	25924819	KF369681	KF370079	KF369353	ODOPH256-13
Thailand	Khao Yai National Park	229163	25925511	KF369715	KF370114	KF369384	ODOPH257-13
Papua New Guinea		501995	25924750	KF369683	KF370081	KF369355	ODOPH258-13
Democratic Republic of Congo	Orientale	229169	25919412	KF369712	KF370111	KF369381	ODOPH259-13
South Africa	Mpumalanga/ KwaZulu Natal	229171	25925514	KF369713	KF370112	KF369382	ODOPH260-13
Cameroon	South Province	229233	25925613	KF369865	KF370264	KF369513	ODOPH261-13
India		502041	30104083	KF369719	KF370118	KF369386	ODOPH262-13
Papua New Guinea		502071	25924855	KF369735	KF370134	KF369400	ODOPH263-13
Indonesia	Papua	500639	25924791	KF369738	KF370137	KF369403	ODOPH264-13
Papua New Guinea		502018	25924762	KF369740	KF370139	KF369405	ODOPH265-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Platycnemididae	<i>Idiocnemis</i> sp.			Kalkman, V.J.	RMNH
Platycnemididae	<i>Igneocnemis flammea</i>	(Selys)	1882	Kalkman, V.J. & J. van Tol	RMNH
Platycnemididae	<i>Indocnemis ambigua</i>	(Asahina)	1997	Van Tol, J.	RMNH
Platycnemididae	<i>Indocnemis orang</i>	(Förster in Förster & Laidlaw)	1907	Dow, R.A.	RMNH
Platycnemididae	<i>Indocnemis orang</i>	(Förster in Förster & Laidlaw)	1907	Van Tol, J.	RMNH
Platycnemididae	<i>Lochmaeocnemis malacodora</i>	Lieftinck	1949	Kalkman, V.J.	RMNH
Platycnemididae	<i>Lochmaeocnemis malacodora</i>	Lieftinck	1949	Kalkman, V.J.	RMNH
Platycnemididae	<i>Maticnemis doi</i>	(Hämäläinen)	2012	Hämäläinen, M.	RMNH
Platycnemididae	<i>Mesocnemis robusta</i>	(Selys)	1886	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Mesocnemis singularis</i>	Karsch	1891	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Metacnemis valida</i>	(Hagen in Selys)	1863	Tarboton, W.	RMNH
Platycnemididae	<i>Nososticta erythrura</i>	(Lieftinck)	1932	Kalkman, V.J.	RMNH
Platycnemididae	<i>Nososticta solitarius</i>	(Tillyard)	1906	Kalkman, V.J.	RMNH
Platycnemididae	<i>Onychargia atrocyana</i>	(Selys)	1865	Dow, R.A.	RMNH
Platycnemididae	<i>Onychargia atrocyana</i>	(Selys)	1865	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Palaiargia charmosyna</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Platycnemididae	<i>Palaiargia</i> sp.			Kalkman, V.J.	RMNH
Platycnemididae	<i>Palaiargia</i> sp.			Richards, S.	RMNH
Platycnemididae	<i>Paracnemis alluaudi</i>	Martin	1902	Schütte, K.	RMNH
Platycnemididae	<i>Paramecocnemis erythrostroma</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Platycnemididae	<i>Paramecocnemis stillacruoris</i>	Lieftinck	1956	Kalkman, V.J.	RMNH
Platycnemididae	<i>Platycnemis acutipennis</i>	Selys	1841	Mostert, Kees	RMNH
Platycnemididae	<i>Platycnemis foliacea</i>	Selys	1886	Karube, H.	RMNH
Platycnemididae	<i>Platycnemis pennipes</i>	(Pallas)	1771	Tol, J, Van	RMNH
Platycnemididae	<i>Prodasineura croconota</i>	(Ris)	1916	Dijkstra, K.-D.B.	RMNH
Platycnemididae	<i>Prodasineura dorsalis</i>	(Selys)	1860	Dow, R.A.	RMNH
Platycnemididae	<i>Prodasineura sita</i>	(Kirby)	1894	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Platycnemididae	<i>Proplatycnemis hova</i>	(Selys in Martin)	1908	Schütte, K.	RMNH
Platycnemididae	<i>Proplatycnemis pembipes</i>	(Dijkstra, Clausnitzer & Martens)	2007	Clausnitzer, V.	RMNH
Platycnemididae	<i>Proplatycnemis sanguinipes</i>	(Schmidt)	1951	Schütte, K.	RMNH
Platycnemididae	<i>Pseudocopera ciliata</i>	(Selys)	1863	Ng, Y.F.	RMNH
Platycnemididae	<i>Risocnemis praeusta</i>	Hämäläinen	1991	Villanueva, R.J.T.	RMNH
Platycnemididae	<i>Spesbona angusta</i>	(Selys)	1863	Simaika, J.	RMNH
Platycnemididae	<i>Spesbona angusta</i>	(Selys)	1863	Simaika, J.	RMNH
Platycnemididae	<i>Stenocnemis pachystigma</i>	(Selys)	1886	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Platycnemididae	<i>Torrenticnemis filicornis</i>	Lieftinck	1949	Kalkman, V.J.	RMNH
Platycnemididae	<i>Torrenticnemis filicornis</i>	Lieftinck	1949	Kalkman, V.J.	RMNH
Platystictidae	<i>Ceylonosticta austeni</i>	Lieftinck	1940	Bedjanič, M.	RMNH
Platystictidae	<i>Ceylonosticta montana</i>	(Hagen in Selys)	1860	Bedjanič, M.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Papua New Guinea		502020	25924774	KF369739	KF370138	KF369404	ODOPH266-13
Philippines	Mindanao	500686	25924629	KF369741	KF370140	KF369406	ODOPH267-13
Vietnam	Vinh Phu	228684	25925561	KF369742	KF370141	KF369407	ODOPH268-13
Malaysia	Pahang	501077	25925956	KF369744	KF370143	KF369409	ODOPH269-13
Vietnam	Dak Lak	228399	25925573	KF369743	KF370142	KF369408	ODOPH270-13
Indonesia	Papua	229271	25925630	KF369767	KF370166	KF369429	ODOPH271-13
Indonesia	Papua	229193	25925539	KF369768	KF370167	KF369430	ODOPH272-13
Vietnam	Lang Son	506232	30104160	KF369772	KF370171	KF369434	ODOPH273-13
Egypt	Nile Valley	500908	25925600	KF369776	KF370175	KF369438	ODOPH274-13
South Africa	DhluMudhluMu Mountains	228202	25925516	KF369777	KF370176	KF369439	ODOPH275-13
South Africa	Eastern Cape	500866	25925551	KF369781	KF370180	KF369443	ODOPH276-13
Indonesia	Papua, Japen	229202	25925538	KF369806	KF370205	KF369463	ODOPH277-13
Australia		502015	30104103	KF369807	KF370206	KF369464	ODOPH278-13
Malaysia	Sarawak	500022	25924624	KF369811	KF370210	KF369468	ODOPH279-13
China	Hong Kong	229207	25925563	KF369810	KF370209	KF369467	ODOPH280-13
Indonesia	Papua	500580	25924652	KF369821	KF370220	KF369474	ODOPH281-13
Indonesia	Papua	500627	25924636	KF369823	KF370222	KF369475	ODOPH282-13
Papua New Guinea		502070	25924901	KF369822	KF370221		ODOPH283-13
Madagascar		229282	25925559	KF369826	KF370225	KF369477	ODOPH284-13
Indonesia	Papua	229283	25925654	KF369827	KF370226	KF369478	ODOPH285-13
Indonesia	Papua	500610	25924664	KF369828	KF370227	KF369479	ODOPH286-13
France		228906	25925571	KF369847	KF370246	KF369497	ODOPH287-13
Japan		228191	25925477	KF369848	KF370247		ODOPH288-13
Netherlands	Drentsche Aa	228274	25925393	KF369849	KF370248	KF369498	ODOPH289-13
China	Hong Kong	229235	25925281	KF369862	KF370261		ODOPH290-13
Malaysia	Sarawak	501332	25924184	KF369863	KF370262	KF369511	ODOPH291-13
Sri Lanka	Colombo	229286	25925215	KF369864	KF370263	KF369512	ODOPH292-13
Madagascar		228196	25925440	KF369866	KF370265	KF369514	ODOPH293-13
Tanzania	Pemba Island	228169	25925465	KF369867	KF370266	KF369515	ODOPH294-13
Madagascar		228197	25925429	KF369868	KF370267	KF369516	ODOPH295-13
Malaysia	Pahang	501165	25925872	KF369880	KF370279	KF369527	ODOPH296-13
Philippines	Dinagat Island	500878	25925418	KF369895	KF370294		ODOPH297-13
South Africa		229272	25925523	KF369906	KF370305	KF369547	ODOPH298-13
South Africa		229273	25925535	KF369905	KF370304	KF369546	ODOPH299-13
Cameroon	Southwest Province	229244	25925666	KF369909	KF370308		ODOPH300-13
Indonesia	Papua	500622	25924660	KF369935	KF370334	KF369574	ODOPH301-13
Indonesia	Papua	229291	25925678	KF369934	KF370333	KF369573	ODOPH302-13
Sri Lanka	Uva	229757	25925644	KF369659	KF370057	KF369336	ODOPH303-13
Sri Lanka	Uva Province	229778	25925609	KF369660	KF370058	KF369337	ODOPH304-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Platystictidae	<i>Ceylonosticta nietneri</i>	Fraser	1931	Bedjanič, M.	RMNH
Platystictidae	<i>Ceylonosticta walli</i>	(Fraser)	1931	Bedjanič, M.	RMNH
Platystictidae	<i>Drepanosticta actaeon</i>	Laidlaw	1934	Kebing, W.	RMNH
Platystictidae	<i>Drepanosticta attala</i>	Lieftinck	1934	Dow, R.A.	RMNH
Platystictidae	<i>Drepanosticta clavata</i>	Lieftinck	1932	Kalkman, V.J.	RMNH
Platystictidae	<i>Drepanosticta dentifera</i>	Kimmins	1936	Tateh, O.	RMNH
Platystictidae	<i>Drepanosticta dulitensis</i>	Kimmins	1936	Dow, R.A.	RMNH
Platystictidae	<i>Drepanosticta krios</i>	van Tol	2005	Van Tol, J. & Kalkman, V.J.	RMNH
Platystictidae	<i>Drepanosticta lestoides</i>	(Brauer)	1868	Van Tol, J. & Kalkman, V.J.	RMNH
Platystictidae	<i>Drepanosticta myliitta</i>	Cowley	1936	Villanueva, R.J.T.	RMNH
Platystictidae	<i>Drepanosticta quadrata</i>	(Selys)	1860	Dow, R.A.	RMNH
Platystictidae	<i>Drepanosticta rufostigma</i>	(Selys)	1886	Kalkman, V.J., Dijkstra, K.-D.B., Dingermans, N.J. & Goudsmits, K.	RMNH
Platystictidae	<i>Palaemnema brevignoni</i>	Machet	1990	Wasscher, M.	RMNH
Platystictidae	<i>Palaemnema domina</i>	Calvert	1903	Gonzalez-Soriano, E.	RMNH
Platystictidae	<i>Platysticta apicalis</i>	Kirby	1894	Bedjanič, M.	RMNH
Platystictidae	<i>Platysticta greeni</i>	Kirby	1891	Bedjanič, M.	RMNH
Platystictidae	<i>Platysticta maculata</i>	Selys	1860	Bedjanič, M.	RMNH
Platystictidae	<i>Protosticta grandis</i>	Asahina	1985	Van Tol, J.	RMNH
Platystictidae	<i>Protosticta linnaei</i>	van Tol	2008	Van Tol, J.	RMNH
Platystictidae	<i>Protosticta plicata</i>	van Tol	2005		RMNH
Platystictidae	<i>Protosticta satoi</i>	Asahina	1997	Van Tol, J.	RMNH
Platystictidae	<i>Protosticta versicolor</i>	Laidlaw	1913	Dow, R.A.	RMNH
Platystictidae	<i>Smosticta hainanense</i>	Wilson & Reels	2001		RMNH
Platystictidae	<i>Smosticta</i> sp.				RMNH
Platystictidae	<i>Telosticta bidayuh</i>	Dow & Orr	2012	Dow, R.A.	RMNH
Platystictidae	<i>Telosticta dayak</i>	Dow & Orr	2012	Dow, R.A.	RMNH
Platystictidae	<i>Telosticta dupophila</i>	Lieftinck	1933	Dow, R.A.	RMNH
Platystictidae	<i>Telosticta longigaster</i>	Dow & Orr	2012	Dow, R.A.	RMNH
Polythoridae	<i>Chalcopteryx rutilans</i>	(Rambur)	1842	Smit, J.	RMNH
Polythoridae	<i>Chalcopteryx seabrai</i>	Santos & Machado	1961	Wasscher, M.	RMNH
Polythoridae	<i>Polythore aurora</i>	(Selys)	1879	Faasen, T.	RMNH
Polythoridae	<i>Polythore aurora</i>	(Selys)	1879	Faasen, T.	RMNH
Pseudolestidae	<i>Pseudolestes mirabilis</i>	Kirby	1900	Reels, G.T.	RMNH
Pseudolestidae	<i>Pseudolestes mirabilis</i>	Kirby	1900	Reels, G.T.	RMNH
Rimanellidae	<i>Rimanella arcana</i>	(Needham)	1933	Demarmels, J.	
Synlestidae	<i>Chlorolestes fasciatus</i>	(Burmeister)	1839	Dijkstra, K.-D.B.	RMNH
Synlestidae	<i>Chlorolestes umbratus</i>	Hagen in Selys	1862	Dijkstra, K.-D.B.	RMNH

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
Sri Lanka	Sabaragamuwa Province	229772	25925633	KF369661	KF370059	KF369338	ODOPH305-13
Sri Lanka	Central Province	503239	25925646	KF369662	KF370060	KF369339	ODOPH306-13
Malaysia	Sarawak	503455	25924230	KF369696	KF370095	KF369366	ODOPH307-13
Malaysia	Sarawak	503447	25924200	KF369697	KF370096	KF369367	ODOPH308-13
Indonesia	Papua, Japen	228097	25925517	KF369698	KF370097	KF369368	ODOPH309-13
Malaysia	Sarawak	501317	25924159	KF369699	KF370098	KF369369	ODOPH310-13
Malaysia	Sarawak	500011	25924764	KF369700	KF370099	KF369370	ODOPH311-13
Philippines	Mindanao	226901	25925506	KF369701	KF370100	KF369371	ODOPH312-13
Philippines	Mindanao	228849	25925518	KF369702	KF370101	KF369372	ODOPH313-13
Philippines	Dinagat Island	228843	25925530	KF369703	KF370102	KF369373	ODOPH314-13
Singapore	Nee Soon	501013	25925785	KF369704	KF370103	KF369374	ODOPH315-13
Brunei Darussalam	Belait	500823	25924680	KF369705	KF370104	KF369375	ODOPH316-13
Suriname	Brokopondo	505198	30102288	KF369819	KF370218	KF369472	ODOPH317-13
Mexico		228084	25924701	KF369820	KF370219	KF369473	ODOPH318-13
Sri Lanka	Uva Province	229762	25925596	KF369852	KF370251	KF369501	ODOPH319-13
Sri Lanka	Central Province	229765	25925670	KF369853	KF370252	KF369502	ODOPH320-13
Sri Lanka	Central Province	229760	25925611	KF369854	KF370253	KF369503	ODOPH321-13
Vietnam	Dak Lak	228386	25925631	KF369873	KF370272	KF369520	ODOPH322-13
Vietnam	Dak Lak	228353	25925500	KF369874	KF370273	KF369521	ODOPH323-13
Philippines	Cebu	228842	25925578	KF369875	KF370274	KF369522	ODOPH324-13
Vietnam	Vinh Phu	228714	25925536	KF369876	KF370275	KF369523	ODOPH325-13
Malaysia	Sarawak	501032	25925789	KF369706	KF370105	KF369376	ODOPH326-13
China	Hainan	228939	25925541	KF369903	KF370302	KF369544	ODOPH327-13
China	Hainan	228935	25925553	KF369904	KF370303	KF369545	ODOPH328-13
Malaysia	Sarawak	503627	25924160	KF369928	KF370327	KF369568	ODOPH329-13
Malaysia	Sarawak	503637	25924213	KF369929	KF370328	KF369569	ODOPH330-13
Malaysia	Sarawak	504051	30102273	KF369930	KF370329	KF369570	ODOPH331-13
Malaysia	Sarawak	503509	25924225	KF369931	KF370330		ODOPH332-13
Peru	Tamshiyacu-Tahuayo Reserve	505717	30104154	KF369663	KF370061		ODOPH333-13
Suriname	Sipaliwini	505197	30102287	KF369664	KF370062	KF369340	ODOPH334-13
Peru	Tamshiyacu-Tahuayo Reserve	501729	25924842	KF369859	KF370258	KF369508	ODOPH335-13
Peru	Tamshiyacu-Tahuayo Reserve	501969	25924885	KF369858	KF370257	KF369507	ODOPH336-13
China	Hainan	228942	25925509	KF369882	KF370281	KF369529	ODOPH337-13
China	Hainan	228943	25925521	KF369881	KF370280	KF369528	ODOPH338-13
Venezuela	Sierra De Lema		r_1023_R	KF369894	KF370293		ODOPH339-13
South Africa	border of Mpumalanga and KwaZulu Natal	229156	25925293	KF369666	KF370064		ODOPH340-13
South Africa	border of Western and Eastern Cape	229158	25925210	KF369667	KF370065		ODOPH341-13

Table S2 - Continued

Family	Species	Authority	Year	Collector	Repository
Synlestidae	<i>Ecchlorolestes nylephtha</i>	(Barnard)	1937	Dijkstra, K.-D.B.	RMNH
Synlestidae	<i>Megalestes</i> sp.			Kalkman, V.J.	RMNH
Synlestidae	<i>Nubiolestes diotima</i>	(Fraser)	1944	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Synlestidae	<i>Nubiolestes diotima</i>	(Fraser)	1944	Dijkstra, K.-D.B. & Schütte, K.	RMNH
Synlestidae	<i>Synlestes selysi</i>	Tillyard	1917	Kalkman, V.J.	RMNH
Synlestidae	<i>Synlestes weyersii</i>	Selys	1869	Kalkman, V.J.	RMNH
Thaumatoneuridae	<i>Paraplebia quinta</i>	Calvert	1901	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Thaumatoneuridae	<i>Paraplebia zoe</i>	Hagen	1861	Dijkstra, K.-D.B. & Kalkman, V.J.	RMNH
Thaumatoneuridae	<i>Thaumatoneura inopinata</i>	McLachlan	1897	Esquivel, C.	RMNH

Supplementary Information Table S3. Support in analyses for proposed classification of Zygoptera.

Support for each group presented in the classification is provided for the maximum likelihood (ML) and Bayesian inference (BI) analyses for the combined 28S and 16S (and COI) datasets, as bootstrap values (ML) and percentages of posterior probabilities (BI). Support values are not applicable (n.a.) for groups for which no or only one species was available.

Group	ML 28S+16S	BI 28S+16S	ML 28S+ 16S+COI	BI 28S+ 16S+COI	Support for monophyly and classification
Superfamily Lestoidea Calvert, 1901	95	100	98	100	very high support
Family Hemiplebiidae Kennedy, 1920	n.a.	n.a.	n.a.	n.a.	monotypic; see Davis et al. (2011) and others
Family Perilestidae Kennedy, 1920	0	0	84	100	high support for 28S+16S+COI
Family Synlestidae Tillyard, 1917	0	0	0	0	no support, convenience; see May et al. (pers. comm.) in Dijkstra et al. (2013)
Family Lestidae Calvert, 1901	94	100	99	100	very high support
Superfamily Platystictioidea Kennedy, 1920	100	100	100	100	complete support
Family Platystictidae Kennedy, 1920	100	100	100	100	complete support
Subfamily Palaemnematinae Tillyard & Fraser, 1938	81	100	100	100	very high support
Subfamily Platystictinae Kennedy, 1920	100	100	100	100	complete support
Subfamily Protostictinae subfam. nov.	97	100	100	100	very high support
Subfamily Sinostictinae Wilson, 1997	100	100	100	100	complete support
Superfamily 'Calopterygoidea' Selys, 1850	0	0	0	0	no support, convenience; see Bybee et al. (2008)
Family Amphipterygidae Tillyard, 1917	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Argiolestidae Fraser, 1957	58	100	85	98	good support
Subfamily Argiolestinae Fraser, 1957	73	99	98	100	high support
Subfamily Podolestinae Kalkman & Theischinger, 2013	92	100	94	100	very high support

Country	Location	Voucher	Extract	16S	28S	COI	Barcode Index
South Africa	Eastern Cape	229165	25925502	KF369708	KF370107		ODOPH342-13
China	Guāngxī	229194	25925492	KF369775	KF370174	KF369437	ODOPH343-13
Cameroon	Southwest Province	500110	25924728	KF369809	KF370208	KF369466	ODOPH344-13
Cameroon	Southwest Province	229206	25925249	KF369808	KF370207	KF369465	ODOPH345-13
Australia	Queensland	505293	30102325	KF369914	KF370313	KF369554	ODOPH346-13
Australia	New South Wales	504868	30102312	KF369915	KF370314	KF369555	ODOPH347-13
Mexico	Oaxaca State	504317	25919420	KF369829	KF370228	KF369480	ODOPH355-13
Mexico	Veracruz State	504309	25919421	KF369830	KF370229	KF369481	ODOPH356-13
Costa Rica	San José	501982	25924773	KF369933	KF370332	KF369572	ODOPH359-13

Table S3 - Continued

Group	ML	BI	ML 28S+	BI 28S+	Support for monophyly and classification
	28S+16S	28S+16S	16S+COI	16S+COI	
Family Calopterygidae Selys, 1850	97	100	96	100	very high support
Subfamily Calopteryginae Selys, 1850	81	58	93	99	good support
Tribe Caliphaeini Fraser, 1929	n.a.	n.a.	n.a.	n.a.	monogeneric; see Dumont et al. (2010)
Tribe Calopterygini Selys, 1850	90	100	99	100	very high support
Tribe Iridictyonini Dumont et al., 2005	n.a.	n.a.	n.a.	n.a.	monogeneric; see Dumont et al. (2010)
Tribe Mnaisini Ishida, 1996	98	100	100	100	complete support
Tribe Noguchiphaeini Dumont et al., 2005	n.a.	n.a.	n.a.	n.a.	monogeneric; see Dumont et al. (2010)
Tribe Saphoini Dumont et al., 2005	72	95	64	96	good support
Tribe Vestalini Needham, 1903	93	100	81	100	high support
Subfamily Hetaeriniinae Tillyard & Fraser, 1939	100	100	100	100	complete support
Family Chlorocyphidae Cowley, 1937	100	100	100	100	complete support
possible subfamily Chlorocyphinae	92	100	98	100	very high support
possible subfamily Disparocyphinae	n.a.	n.a.	n.a.	n.a.	monogeneric
possible subfamily Libellaginae	99	100	100	100	complete support
possible subfamily Rhinocyphinae	0	0	0	0	no support
Family Devadattidae fam. nov.	n.a.	n.a.	n.a.	n.a.	monogeneric, no near relatives
Family Dictyeriidae Montgomery, 1959	n.a.	n.a.	n.a.	n.a.	two very close genera, no near relatives
Family Euphaeidae Yakobson & Bianchi, 1905	100	100	100	100	complete support
Family Heteragrionidae Ráčenis, 1959	100	100	100	100	complete support
Family Hypolestidae Fraser, 1938	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Lestoideidae Munz, 1919	100	100	100	100	complete support
Subfamily Diphlebiinae Heymer, 1975	n.a.	n.a.	n.a.	n.a.	monogeneric, name available

Table S3 - Continued

Group	ML	BI	ML 28S+	BI 28S+	Support for monophyly and classification
	28S+16S	28S+16S	16S+COI	16S+COI	
Subfamily Lestoideinae Munz, 1919	n.a.	n.a.	n.a.	n.a.	monogeneric, name available
Family Megapodagrionidae Calvert, 1913	100	100	100	100	complete support
Family Pentaplebiidae Novelo-Gutiérrez, 1995	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Philogangidae Kennedy, 1920	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Philogeniidae Rácenis, 1959	100	100	100	100	complete support
Family Philosinidae Kennedy, 1925	100	100	100	100	complete support
Family Polythoridae Munz, 1919	100	100	100	100	complete support
Family Pseudolestidae Fraser, 1957	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Rimanelidae Davies & Tobin, 1984	n.a.	n.a.	n.a.	n.a.	monogeneric, name available, no near relatives
Family Thaumatonneuridae Fraser, 1938	90	100	96	100	very high support
group 1 (<i>Rhipidolestes</i> + related genera) + Thaumatonneuridae	64	100	28	62	some support
group 2: <i>Amanipodagrion</i>	n.a.	n.a.	n.a.	n.a.	no near relatives
group 3: <i>Dimeragrion</i> + <i>Heteropodagrion</i>	0	0	48	67	some support in 28S+16S+COI
group 4: <i>Mesopodagrion</i>	n.a.	n.a.	n.a.	n.a.	no near relatives
group 5: <i>Priscagrion</i> + <i>Sinocnemis</i>	66	100	86	100	good support
group 6: <i>Protolestes</i>	n.a.	n.a.	n.a.	n.a.	no near relatives
group 7: <i>Tatocnemis</i>	n.a.	n.a.	n.a.	n.a.	no near relatives
group 8: <i>Sciotropis</i>	n.a.	n.a.	n.a.	n.a.	no near relatives
Superfamily Coenagrionoidea Kirby, 1890	22	57	0	0	low support in 28S+16S; see Bybee et al. (2008)
Family Isostictidae Fraser, 1955	100	100	99	100	complete support
Family Platycnemididae Jakobson & Bianchi, 1905	81	100	82	100	high support
Subfamily Allocnemidinae subfam. nov.	63	59	91	100	good support
Subfamily Calicnemiinae Fraser, 1957	100	100	100	100	complete support
Subfamily Disparoneurinae Fraser, 1957	100	100	100	100	complete support
Subfamily Idiocnemidinae subfam. nov.	91	100	100	100	very high support
Subfamily Onychargiinae subfam. nov.	93	100	83	100	high support
Subfamily Platycnemidinae Jakobson & Bianchi, 1905	81	97	96	100	high support
Tribe Coperini trib. nov.	96	100	98	100	very high support
Tribe Platycnemidini Jakobson & Bianchi, 1905	81	98	91	91	high support
Family Coenagrionidae Kirby, 1890	85	100	77	100	high support
Core Coenagrionidae	99	100	100	100	complete support
possible subfamily Agriocnemidinae	100	100	100	100	complete support
possible subfamily Ischnurinae	100	100	100	100	complete support

Table S3 - Continued

Group	ML	BI	ML 28S+	BI 28S+	Support for monophyly and classification
	28S+16S	28S+16S	16S+COI	16S+COI	
possible subfamily Pseudagrioninae	70	90	61	97	good support
Ridge-faced complex	49	55	43	0	low support
possible subfamily Protoneurinae	100	100	100	100	complete support
possible subfamily Pseudostigmatinae (incl. <i>Bromeliagrion</i>)	23	79	27	74	some support
possible subfamily Teinobasinae	73	100	66	100	good support

Supplementary Information Table S4. Summary of proposed taxonomic changes, including new combinations.

Genera *incertae sedis* not listed, see Classification in main text.

Genus	Former family*	Proposed family
<i>Nubiolestes</i> Fraser, 1945	Perilestidae	Synlestidae*
<i>Devadatta</i> Kirby, 1890	Amphipterygidae	Devadattidae
<i>Pentaplebia</i> Förster, 1909	Amphipterygidae	Pentaplebiidae
<i>Rimanella</i> Needham, 1934	Amphipterygidae	Rimanellidae
<i>Heteragrion</i> Selys, 1862	Megapodagrionidae	Heteragrionidae
<i>Oxy stigma</i> Selys, 1862	Megapodagrionidae	Heteragrionidae
<i>Hypolestes</i> Gundlach, 1888	Megapodagrionidae	Hypolestidae
<i>Archaeopodagrion</i> Kennedy, 1939	Megapodagrionidae	Philogeniidae
<i>Philogenia</i> Selys, 1862	Megapodagrionidae	Philogeniidae
<i>Philosina</i> Ris, 1917	Megapodagrionidae	Philosinidae
<i>Rhinagrion</i> Calvert, 1913	Megapodagrionidae	Philosinidae
<i>Paraplebia</i> Selys, 1861	Megapodagrionidae	Thaumtoneuridae
<i>Thaumtoneura</i> McLachlan, 1897	Megapodagrionidae	Thaumtoneuridae
<i>Archboldargia</i> Lief tinck, 1949	Coenagrionidae	Platycnemididae
<i>Hylaeargia</i> Lief tinck, 1949	Coenagrionidae	Platycnemididae
<i>Onychargia</i> Selys, 1865	Coenagrionidae	Platycnemididae
<i>Palaiargia</i> Förster, 1903	Coenagrionidae	Platycnemididae
<i>Papuargia</i> Lief tinck, 1938	Coenagrionidae	Platycnemididae
<i>Leptocnemis</i> Selys, 1886	Platycnemididae	Coenagrionidae
<i>Oreocnemis</i> Pinhey, 1971	Platycnemididae	Coenagrionidae
<i>Thaumtagrion</i> Lief tinck, 1932	Platycnemididae	Coenagrionidae

* following Dijkstra et al. (2013)

Platystictidae

The Sri Lankan Platystictidae is either the sister-group of all platystictids except *Simosticta* or of the Neotropical subfamily Palaemnematinae, making the Oriental Platystictinae *s.l.* paraphyletic. We limit Platystictinae to the Sri Lankan group and reinstate the genus *Ceylonosticta* for the Sri Lankan species placed in the mainland genus *Drepanosticta*. These species agree with Platystictinae *s.s.* in the vein CuP meeting the hind margin of the fore wing at the origin of R₃, rather than proximal to it.

Table S4 - Continued

Family / Former combination	Proposed new combination
<i>Drepanosticta adami</i> (Fraser, 1933)	<i>Ceylonosticta adami</i> Fraser, 1933
<i>Drepanosticta anamia</i> Bedjanič, 2010	<i>Ceylonosticta anamia</i> (Bedjanič, 2010)
<i>Drepanosticta austeni</i> Liefstinck, 1940	<i>Ceylonosticta austeni</i> (Liefstinck, 1940)
<i>Drepanosticta bine</i> Bedjanič, 2010	<i>Ceylonosticta bine</i> (Bedjanič, 2010)
<i>Drepanosticta brincki</i> Liefstinck, 1971	<i>Ceylonosticta brincki</i> (Liefstinck, 1971)
<i>Drepanosticta digna</i> (Hagen in Selys, 1860)	<i>Ceylonosticta digna</i> (Hagen in Selys, 1860)
<i>Drepanosticta hilaris</i> (Hagen in Selys, 1860)	<i>Ceylonosticta hilaris</i> (Hagen in Selys, 1860)
<i>Drepanosticta lankanensis</i> (Fraser, 1931)	<i>Ceylonosticta lankanensis</i> Fraser, 1931
<i>Drepanosticta mojca</i> Bedjanič, 2010	<i>Ceylonosticta mojca</i> (Bedjanič, 2010)
<i>Drepanosticta montana</i> (Hagen in Selys, 1860)	<i>Ceylonosticta montana</i> (Hagen in Selys, 1860)
<i>Drepanosticta nietneri</i> (Fraser, 1931)	<i>Ceylonosticta nietneri</i> Fraser, 1931
<i>Drepanosticta submontana</i> (Fraser, 1933)	<i>Ceylonosticta submontana</i> Fraser, 1933
<i>Drepanosticta subtropica</i> (Fraser, 1933)	<i>Ceylonosticta subtropica</i> Fraser, 1933
<i>Drepanosticta tropica</i> (Hagen in Selys, 1860)	<i>Ceylonosticta tropica</i> (Hagen in Selys, 1860)
<i>Drepanosticta walli</i> (Fraser, 1931)	<i>Ceylonosticta walli</i> Fraser, 1931

incertae sedis

Genetically *B. xinglongensis* is nearer *Agriomorpha fusca* May, 1933 than to the other *Burmargiolestes*. Its general coloration and markings, including the dorsally pale eighth to tenth abdominal segments, and the nearly straight CuA reaching halfway the nodus and pterostigma are also shared with that species but not with any *Burmargiolestes*.

Burmargiolestes xinglongensis Wilson & Reels, 2001 *Agriomorpha xinglongensis* (Wilson & Reels, 2001)

Chlorocyphidae

C. centripunctata is genetically closer to *Africocypha lacuselephantum* (Karsch, 1899) than to *Chlorocypha*: its extended paraprocts, black tenth tergite and other details of markings are also shared with that species but not with any *Chlorocypha*.

Chlorocypha centripunctata Gambles, 1975 *Africocypha centripunctata* (Gambles, 1975)

Platycnemididae

Chlorocnemis and *Isomecocnemis* were separated from *Allocnemis* and placed in a separate family (Protoneuridae) only for the reduction of the anal vein, and distinguished from each other by the degree of that reduction. This character is not congruent with the genetic data. All species in Africa that combine R₄ originating closer to subnode than IR₃, Cux at origin of anal vein and often yellow-stained wings are considered congeneric.

<i>Chlorocnemis abbotti</i> (Calvert, 1892)	<i>Allocnemis abbotti</i> (Calvert, 1892)
<i>Chlorocnemis contraria</i> Schmidt, 1951	<i>Allocnemis contraria</i> (Schmidt, 1951)
<i>Isomecocnemis cyanura</i> (Förster, 1909)	<i>Allocnemis cyanura</i> (Förster, 1909)
<i>Chlorocnemis eisentrauti</i> Pinhey, 1974	<i>Allocnemis eisentrauti</i> (Pinhey, 1974)
<i>Chlorocnemis elongata</i> Hagen in Selys, 1863	<i>Allocnemis elongata</i> (Hagen in Selys, 1863)
<i>Chlorocnemis flavipennis</i> Selys, 1863	<i>Allocnemis flavipennis</i> (Selys, 1863)
<i>Chlorocnemis interrupta</i> Legrand, 1984	<i>Allocnemis interrupta</i> (Legrand, 1984)

Table S4 - Continued

Family / Former combination	Proposed new combination
<i>Chlorocnemis maccleeryi</i> Pinhey, 1969	<i>Allocnemis maccleeryi</i> (Pinhey, 1969)
<i>Chlorocnemis marshalli</i> Ris, 1921	<i>Allocnemis marshalli</i> (Ris, 1921)
<i>Chlorocnemis montana</i> St. Quentin, 1942	<i>Allocnemis montana</i> (St. Quentin, 1942)
<i>Chlorocnemis nigripes</i> Selys, 1886	<i>Allocnemis nigripes</i> (Selys, 1886)
<i>Chlorocnemis pauli</i> Longfield, 1936	<i>Allocnemis pauli</i> (Longfield, 1936)
<i>Isomecocnemis subnodalis</i> (Selys, 1886)	<i>Allocnemis subnodalis</i> (Selys, 1886)
<i>Chlorocnemis superba</i> Schmidt, 1951	<i>Allocnemis superba</i> (Schmidt, 1951)
<i>Chlorocnemis wittei</i> Fraser, 1955	<i>Allocnemis wittei</i> (Fraser, 1955)

All continental African species placed formerly in *Platycnemis* have features typical of the tribe Coperini (caudal lamellae of larvae with filled borders, male cerci with tooth- or branchlike inner process; male tibiae not white). They share with Asian *Copera* – type species *C. marginipes* (Rambur, 1842) – a genital ligula that is unique in the subfamily by its rounded apex without branches.

<i>Platycnemis congolensis</i> Martin, 1908	<i>Copera congolensis</i> (Martin, 1908)
<i>Platycnemis guttifera</i> Fraser, 1950	<i>Copera guttifera</i> (Fraser, 1950)
<i>Platycnemis nyansana</i> Förster, 1916	<i>Copera nyansana</i> (Förster, 1916)
<i>Platycnemis rufipes</i> (Selys, 1886)	<i>Copera rufipes</i> (Selys, 1886)
<i>Platycnemis sikassoensis</i> (Martin, 1912)	<i>Copera sikassoensis</i> (Martin, 1912)

The slightly less reduced anal vein is not reliable to separate *Elatoneura* from *Prodasineura*. All African species placed in *Prodasineura* are closer to the type species *Elatoneura glauca* (Selys, 1860) than to true *Prodasineura* by coloration (e.g. never blue, often pruinose), venation (anal vein never completely lost) and rather vertical distal border of the paraproct.

<i>Prodasineura flavifacies</i> Pinhey, 1981	<i>Elatoneura flavifacies</i> (Pinhey, 1981)
<i>Prodasineura incerta</i> Pinhey, 1962	<i>Elatoneura incerta</i> (Pinhey, 1962)
<i>Prodasineura odzala</i> (Aguesse, 1966)	<i>Elatoneura odzala</i> (Aguesse, 1966)
<i>Prodasineura perisi</i> Compte Sart, 1964	<i>Elatoneura perisi</i> (Compte Sart, 1964)
<i>Prodasineura villiersi</i> Fraser, 1948	<i>Elatoneura villiersi</i> (Fraser, 1948)
<i>Prodasineura vittata</i> (Selys, 1886)	<i>Elatoneura vittata</i> (Selys, 1886)

The morphologically well-defined subgenera *Igneocnemis* and *Risioicnemis* were never recovered as sister-groups. All species listed below possess the characters of *Igneocnemis*: arculus at Ax2, wing tips only smoothly crenulated, pedicel of antenna subequal to scape, male postclypeus distinctly angulate, and female pronotal hindlobe not divided into three lobes (Gassmann & Hämäläinen, 2002).

<i>Risioicnemis antoniae</i> Gassmann & Hämäläinen, 2002	<i>Igneocnemis antoniae</i> (Gassmann & Hämäläinen, 2002)
<i>Risioicnemis atripes</i> (Needham & Gyger, 1941)	<i>Igneocnemis atripes</i> (Needham & Gyger, 1941)
<i>Risioicnemis atropurpurea</i> (Brauer, 1868)	<i>Igneocnemis atropurpurea</i> (Brauer, 1868)
<i>Risioicnemis calceata</i> Hämäläinen, 1991	<i>Igneocnemis calceata</i> (Hämäläinen, 1991)
<i>Risioicnemis flamma</i> (Selys, 1882)	<i>Igneocnemis flamma</i> (Selys, 1882)
<i>Risioicnemis fuligifrons</i> Hämäläinen, 1991	<i>Igneocnemis fuligifrons</i> (Hämäläinen, 1991)

Table S4 - Continued

Family / Former combination	Proposed new combination
<i>Risioenemis haematopus</i> (Selys, 1882)	<i>Igneocnemis haematopus</i> (Selys, 1882)
<i>Risioenemis ignea</i> (Brauer, 1868)	<i>Igneocnemis ignea</i> (Brauer, 1868)
<i>Risioenemis incisa</i> Kimmins, 1936	<i>Igneocnemis incisa</i> (Kimmins, 1936)
<i>Risioenemis kaiseri</i> Gassmann & Hämäläinen, 2002	<i>Igneocnemis kaiseri</i> (Gassmann & Hämäläinen, 2002)
<i>Risioenemis melanops</i> Hämäläinen, 1991	<i>Igneocnemis melanops</i> (Hämäläinen, 1991)
<i>Risioenemis nigra</i> Gassmann & Hämäläinen, 2002	<i>Igneocnemis nigra</i> (Gassmann & Hämäläinen, 2002)
<i>Risioenemis odobeni</i> Hämäläinen, 1991	<i>Igneocnemis odobeni</i> (Hämäläinen, 1991)
<i>Risioenemis pistor</i> Gassmann & Hämäläinen, 2002	<i>Igneocnemis pistor</i> (Gassmann & Hämäläinen, 2002)
<i>Risioenemis plebeja</i> Hämäläinen, 1991	<i>Igneocnemis plebeja</i> (Hämäläinen, 1991)
<i>Risioenemis polilloensis</i> Hämäläinen, 1991	<i>Igneocnemis polilloensis</i> (Hämäläinen, 1991)
<i>Risioenemis rubricercus</i> Gassmann & Hämäläinen, 2002	<i>Igneocnemis rubricercus</i> (Gassmann & Hämäläinen, 2002)
<i>Risioenemis rubripes</i> (Needham & Gyger, 1939)	<i>Igneocnemis rubripes</i> (Needham & Gyger, 1939)
<i>Risioenemis siniae</i> Hämäläinen, 1991	<i>Igneocnemis siniae</i> (Hämäläinen, 1991)
<i>Risioenemis tendipes</i> (Needham & Gyger, 1941)	<i>Igneocnemis tendipes</i> (Needham & Gyger, 1941)
<i>M. secundaris</i> is known only from the holotype from Madagascar. It is closer to <i>Paracnemis</i> , most notably by markings and distribution, than to the South African generotype <i>M. valida</i> (Hagen in Selys, 1863).	
<i>Metacnemis secundaris</i> Aguesse, 1968	<i>Paracnemis secundaris</i> (Aguesse, 1968)
All Malagasy and Comoro species placed formerly in <i>Platycnemis</i> have features typical of the tribe Coperini (caudal lamellae of larvae with frilled borders, male cerci with tooth- or branchlike inner process; male tibiae often not white) and a genital ligula with a pair of lobe-like apical branches, creating a marked apical notch between them, and a more basal pair of slender lateral branches. The latter pair is unique in the subfamily, but reduced in <i>P. sanguinipes</i> . <i>P. hova</i> (Martin, 1908) is the type species of <i>Proplatycnemis</i> Kennedy, 1920. <i>P. pembipes</i> from Pemba also belongs here (Dijkstra et al., 2007).	
<i>Platycnemis agrioides</i> Ris, 1915	<i>Proplatycnemis agrioides</i> (Ris, 1915)
<i>Platycnemis alatipes</i> (McLachlan, 1872)	<i>Proplatycnemis alatipes</i> (McLachlan, 1872)
<i>Platycnemis aurantipes</i> Lieftinck, 1965	<i>Proplatycnemis aurantipes</i> (Lieftinck, 1965)
<i>Platycnemis hova</i> Martin, 1908	<i>Proplatycnemis hova</i> (Martin, 1908)
<i>Platycnemis longiventris</i> Schmidt, 1951	<i>Proplatycnemis longiventris</i> (Schmidt, 1951)
<i>Platycnemis malgassica</i> Schmidt, 1951	<i>Proplatycnemis malgassica</i> (Schmidt, 1951)
<i>Platycnemis melana</i> Aguesse, 1968	<i>Proplatycnemis melana</i> (Aguesse, 1968)
<i>Platycnemis pembipes</i> Dijkstra et al., 2007	<i>Proplatycnemis pembipes</i> (Dijkstra et al., 2007)
<i>Platycnemis protostictoides</i> Fraser, 1953	<i>Proplatycnemis protostictoides</i> (Fraser, 1953)
<i>Platycnemis pseudalatipes</i> Schmidt, 1951	<i>Proplatycnemis pseudalatipes</i> (Schmidt, 1951)
<i>Platycnemis sanguinipes</i> Schmidt, 1951	<i>Proplatycnemis sanguinipes</i> (Schmidt, 1951)

Table S4 - Continued

Family / Former combination	Proposed new combination
<p>All black-and-white species placed formerly in <i>Copera</i> have features typical of the tribe Platycnemidini (caudal lamellae of larvae with smooth borders, male cerci without tooth- or branchlike process; male tibiae always white) and a genital ligula with short and lobe-like apical branches. The name <i>Pseudocopera</i> Fraser, 1922 is available for these 'false' <i>Copera</i> (type species <i>P. arachnoides</i> Fraser, 1922 is a synonym of <i>C. ciliata</i>). <i>C. superplatypes</i> is tentatively placed here due to similarities with <i>P. ciliata</i>, but its penis is unknown and it may belong to <i>Platycnemis</i>.</p>	
<i>Copera annulata</i> (Selys, 1863)	<i>Pseudocopera annulata</i> (Selys, 1863)
<i>Copera ciliata</i> (Selys, 1863)	<i>Pseudocopera ciliata</i> (Selys, 1863)
<i>Copera superplatypes</i> Fraser, 1927	<i>Pseudocopera superplatypes</i> (Fraser, 1927)
<i>Copera tokyoensis</i> Asahina, 1948	<i>Pseudocopera tokyoensis</i> (Asahina, 1948)

Part 3

Biogeography

6. THE AUSTRALIAN MONSOON TROPICS AS A BARRIER FOR EXCHANGE OF DRAGONFLIES (INSECTA: ODONATA) BETWEEN NEW GUINEA AND AUSTRALIA

Vincent J. Kalkman & Albert G. Orr

Citation: Kalkman, V.J. & A.G. Orr 2012. The Australian monsoon tropics as a barrier for exchange of dragonflies (Insecta: Odonata) between New Guinea and Australia. – *Hydrobiologia* 693: 55-70.

Recent studies show a remarkable scarcity of faunal exchange events between Australia and New Guinea in the Pleistocene despite the presence of a broad land connection for long periods. This is attributed to unfavourable conditions in the connecting area associated with the long established northern Australian Monsoon Climate. This would be expected to have impacted strongly on freshwater faunas with the following results: (1) limited overlap in species, (2) most higher taxonomic groups present in both areas sharing no species or even genera and (3) shared species dominated by lentic species with high dispersal capacity. Testing these predictions for dragonflies showed the turnover in the family, genus and species composition between Australia and New Guinea to be higher than anywhere in the world with only 50% of families and subfamilies, 33% of the genera and 8% of the species being shared. Only one of the 53 shared species favors lotic waters compared with 64% of the 652 combined Australian-New Guinean species. These results agree with our predictions and indicate that the dragonfly fauna of Australia and New Guinea have effectively been separated during the Pleistocene probably due to the prolonged unfavourable climatic conditions in the intervening areas.

INTRODUCTION

New Guinea forms the northern edge of the Australian continental plate. Geologically relatively recent tectonic events shaped the island into its present form consisting of a flat southern lowland over 200 Ma old, a central mountain range uplifted in the Eocene to Late Miocene (55-5 Ma) and a northern lowland consisting partly of accreted islands still recognisable as mountain ranges such as the mountains of Foja, Cyclops, Adelbert and Finisterre (Polhemus 2007). The southern lowlands of New Guinea are separated from Australia by the Arafura Sea and Torres Strait. These might seem formidable obstacles for the exchange of flora and

fauna but these seas are relatively shallow and the Arafura Shelf that lies between emerged as dry land during periods of low sea level. In the past 250,000 years, this happened several times broadly connecting Australia and New Guinea for approximately 17% of the time (Voris 2000) (fig. 1). At least during the last Pleistocene Glacial Maximum this land bridge is thought to have been an extensive plain with rivers, open woodland and riparian gallery forest (Macqueen et al. 2010). Part of this plain was the large freshwater to brackish Lake Carpentaria which received water from rivers originating from both Australia and New Guinea (Reeves et al. 2007) and it has been suggested that it formed a connection between the

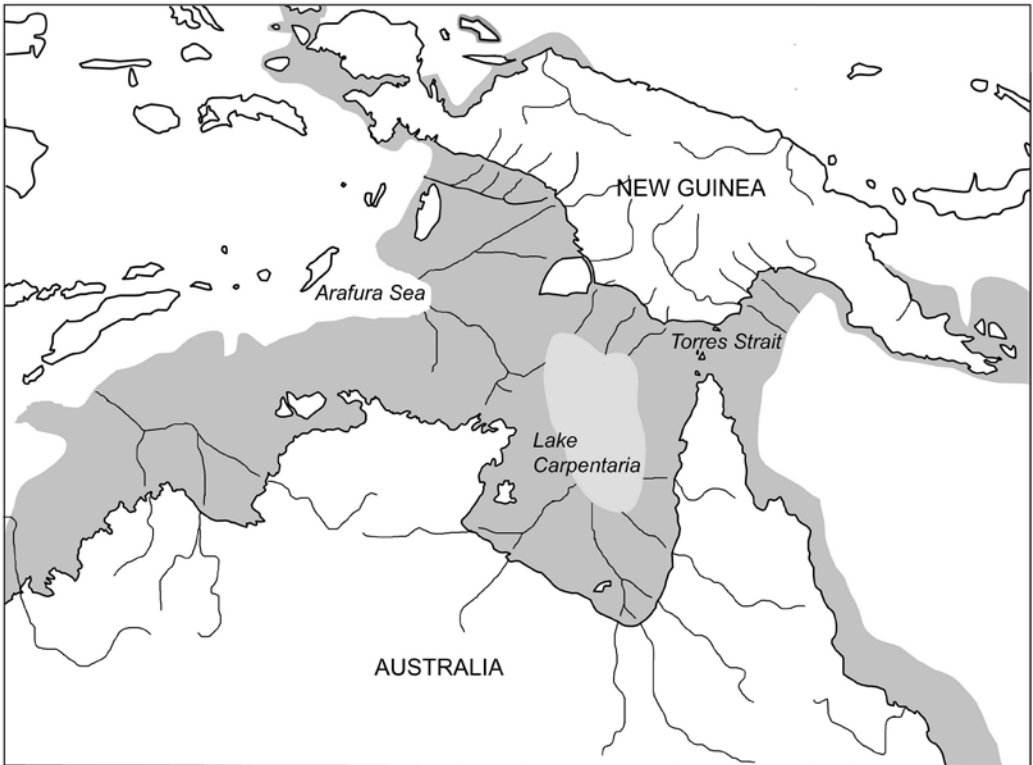


Figure 1. Map of New Guinea and Australia with the extent of land during glacial heights (-150 m) in grey. Modified from Bowman et al. (2010) and Voris (2000).

freshwater faunas of Australia and New Guinea (Allen & Hoese 1980, McGuigan et al. 2000). Based on the distributions of freshwater fishes Unmack (2001) concluded, however, that the area between Australia and New Guinea was probably too arid and, at least for part of the time, Lake Carpentaria too brackish during the Pleistocene glaciations for the exchange of freshwater fishes. He suggested that the disjunct distributions of freshwater fish dated from before the Pleistocene perhaps as early as the Miocene (5.3-23 Ma) and stated that the influences of Plio-Pleistocene events on broad patterns of freshwater fish distributions seemed minimal. The summary of published estimates for the timing of divergence of terrestrial vertebrates based on DNA sequence data between Australia and New Guinea (Macquoen et al. 2010) shows that faunal exchange occurred during sever-

al periods since the late Miocene indicating that a suitable land connection was repeatedly present. It is noteworthy that although exchange of terrestrial vertebrates occurred over a long period, it seems to have been at a lower level during the late Pleistocene despite there being a broad connection between the two areas.

The small number of fresh to brackish water species for which the timing of divergence between Australia and New Guinea has been estimated on the basis of DNA sequence data show mixed results. A late Pleistocene exchange was suggested for the red claw crayfish *Cherax quadricarinatus* (Baker et al. 2008), the giant river prawn *Macrobrachium wallacei* (De Bruyn et al. 2004, De Bruyn & Mather 2007) and melanotaeniid fishes (McGuigan et al. 2000) while work on the pennyfish *Denariusa*

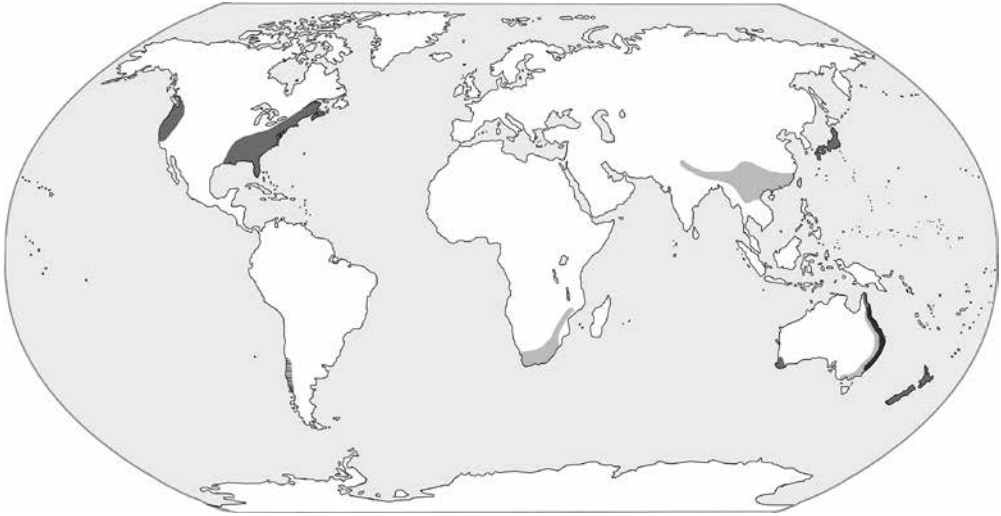


Figure 2. World distribution of the families Synlestidae (pale grey) and Petaluridae (dark grey).

bandata (Cook & Hughes 2010) and *Papuadytes*-diving beetles (Balke et al. 2007) suggest exchange in the mid- and early- Pleistocene and the Miocene, respectively. However some of these studies focus on groups that can survive conditions of high salinity, thus allowing marine dispersal routes, or focus on a single species. They therefore provide limited information on when the divergence took place, knowledge of which is critical to our understanding of the shaping of the freshwater faunas of Australia and New Guinea. The only molecular study which examined a strictly freshwater group, speciose in both Australia and New Guinea, was Balke et al. (2007). This demonstrated that the over 150 species of *Papuadytes* found on New Guinea originated from a single dispersal event around 7 Mya.

Large parts of Australia and southern New Guinea bordering the Arafura Sea and the Torres Strait have a monsoon climate, generally with a high annual rainfall concentrated from November to May, with the remainder of the year experiencing prolonged dry periods (Bowe et al. 2007, Bowman et al. 2010). In their review on the Australian monsoon tropics (AMT), Bowman et al. (2010) showed that the composition of the flora and

fauna in northern Australia is strongly determined by the monsoon climate. This climate probably originated in the region between 40 and 30 Ma (Bowman et al. 2010, and references therein). Over this long period, the region has evolved a fauna adapted to a monsoon climate with regional endemism in the Kimberley area, Arnhem Land and Cape York. The strength of the monsoon and the area to which it extended varied throughout geological time and was partially affected by the progressive aridification of central Australia over the past 20 My which intensified in the past 2-4 My. The impact of the variation in the extent of the monsoon area is well illustrated by the Aru Islands. These islands were connected with mainland New Guinea during the Last Glacial Maximum and long periods thereafter. Fossil records indicate the former presence of open savannah habitats at 20,000 BP but the rainforest belt of mainland New Guinea shifted south and around 14,000 BP rainforest became dominant on the Aru Islands (Hope 2007). Further to the east, the Monsoon climate was probably always more strongly established during the Pleistocene, and there are no indications of the closed canopy tropical forests of Australia and New Guinea having been connected during this period.

Table 1. Number of species and genera in Australia and New Guinea for each of the families/subfamilies considered. The column 'region of occurrence' indicates if a family/subfamily is, within the area considered, limited to Australia, to New Guinea or is found in both areas. The column 'Monophyletic' states if the group is monophyletic and gives the reference on which this is based. The column 'Route to Australian–New Guinean' indicates if a group is presumed to have arrived from Asia (north) or that it is presumed to have been present within the region at the time Australia broke away from Antarctica (south).

	Australia		New Guinea		Monophyletic according to
	Genera	Species	Genera	Species	
Zygoptera					
Lestidae	3	14	2	11	Bybee et al., 2008; Dumont et al., 2010; Fleck et al., 2008
Hemiphlebiidae	1	1	0	0	monotypic
Synlestidae	3	7	0	0	Bybee et al., 2008
Megapodagrionidae	5	22	2	44	Bybee et al., 2008; Kalkman et al., 2010
Chlorocyphidae	0	0	1	1	Bybee et al., 2008; Dumont et al., 2010
Calopterygidae	0	0	1	4	Bybee et al., 2008; Dumont et al., 2005; Dumont et al., 2010
Lestoideidae	2	9	0	0	Bybee et al., 2008; Carle et al., 2008
Isostictidae	7	15	2	17	Bybee et al., 2008; Carle et al., 2008
Platycnemididae	0	0	12	52	Bybee et al., 2008; Gassmann, 2005
Disparoneuridae	1	12	1	31	Bybee et al., 2008; Dumont et al., 2010
Coenagrionidae	13	30	15	88	Bybee et al., 2008; Carle et al., 2008
Platystictidae	0	0	1	14	Bybee et al., 2008; Van Tol et al., 2009
Anisoptera					
Austropteliidae	2	3	0	0	Bybee et al., 2008; Fleck et al., 2008
Aeshninae	6	13	6	21	Bybee et al., 2008; von Ellenrieder, 2002
Brachytroninae	9	37	0	0	No, probably paraphyletic: von Ellenrieder, 2002
Lindeniinae	1	3	1	1	Watson & O'Farrell, 1985; Watson 1991
Gomphinae	7	35	0	0	Watson & O'Farrell, 1985; Watson 1991
Petaluridae	1	5	0	0	Bybee et al., 2008; Fleck et al., 2008
Synthemistidae sensu lato	17	45	1	8	Ware et al., 2007; Ware et al., 2009
Corduliidae sensu stricto	3	11	3	9	Dumont et al., 2010; Fleck et al., 2008; Ware et al., 2007
Macromiidae	1	2	1	9	Dumont et al., 2010; Fleck et al., 2008; Ware et al., 2007
Libellulidae	27	56	33	102	Bybee et al., 2008; Dumont et al., 2010; Fleck et al., 2008; Ware et al., 2007
Total	109	320	85	419	

The column 'route rationale' gives the rationale for the stated route and the reference on which this is based: (1) phylogeny showing dispersal route available; (2) a typical Pangean relict distribution; (3) no known near relatives outside the region; (4) nearest known relatives found in Africa and/or South-America while no likely candidates are present in western Indonesia or in Sundaland; (5) widespread in both Africa and Asia and there having a far higher diversity at both species and genus level, as well as being represented in Australia mainly in the tropical north and east.

Region of occurrence within Australia and New Guinea	Likely route to Australian-New Guinean	Rationale route
shared	Uncertain	
Australian	Present at break away	3: Family confined to SE-Australia (Figure 12)
Australian	Present at break away	2: Figure 2
shared	Present at break away	1: Kalkman et al., unpublished
New Guinean	Arrived from Asia	1: Dijkstra et al., unpublished
New Guinean	Arrived from Asia	1: Dumont et al., 2010
Australian	Present at break away	3: Family confined to East-Australia (Figure 15)
shared	Present at break away	3: Family confined to Australia, New Guinea, Moluccas and New Caledonia
New Guinean	Arrived from Asia	1: Gassmann, 2005
shared	Uncertain	
shared	Arrived from Asia	5: Kalkman et al., 2008
New Guinean	Arrived from Asia	1: Van Tol et al., 2009
Australian	Present at break away	4: von Ellenrieder 2005; Garrison et al., 2006
shared	Arrived from Asia	5: Kalkman et al., 2008
Australian	Present at break away	4: Peters & Theischinger, 2007
shared	Arrived from Asia	5: Kalkman et al., 2008
Australian	Present at break away	4: Watson & O'Farrell, 1985; Watson 1991
Australian	Present at break away	2: Figure 2
shared	Present at break away	4: Ware et al., 2007; Ware et al., 2009
shared	Uncertain	
shared	Arrived from Asia	5: Kalkman et al., 2008
shared	Arrived from Asia	5: Kalkman et al., 2008

Monsoon climates are especially demanding on organisms with an aquatic life cycle. Many stagnant and smaller running waters are ephemeral and desiccate in the dry season, while larger running waters transform into vast muddy floodplains during the wet season. In Australia, the Monsoon climate also results in a landscape dominated by savannah where closed forest is largely absent rendering the area unsuitable for forest-dependent species. The impact of this climate can be observed in the distribution of dragonflies with some families largely absent from monsoon areas. This seems to be determined mainly by the rainfall regime and less by temperature. The strong impact of the monsoon climate on freshwater systems and associated aquatic fauna makes it likely that the AMT acts as a filter or even a barrier to the exchange of aquatic faunas between Australia and New Guinea.

If the climatic conditions and the resulting landscape and habitats within the AMT did form a barrier and restricted exchange in the Pleistocene then one would expect this to have an especially strong impact on the distribution patterns of the freshwater faunas of Australia and New Guinea resulting in (1) limited overlap in species overall, (2) divergence between genera and species dating back to pre-Pleistocene times resulting in most higher taxonomic groups sharing no species or even genera, and (3) shared species to be dominated by eurytopic types adapted to standing water and with high dispersal capacity. These hypotheses are tested here based on the distribution patterns of dragonflies.

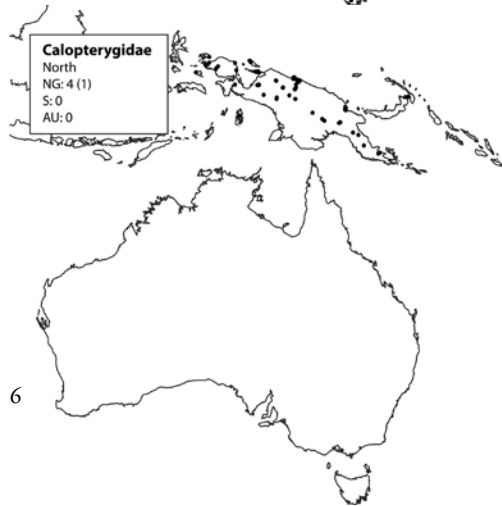
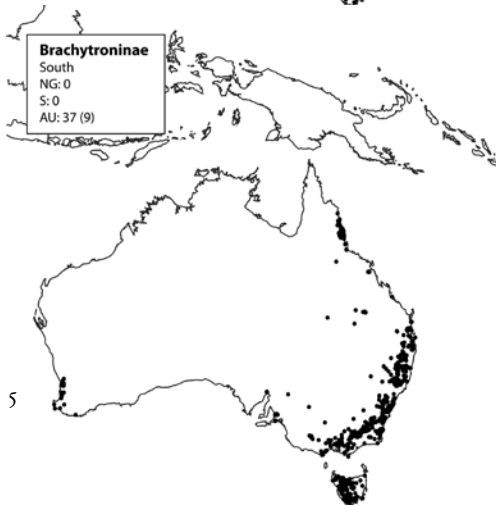
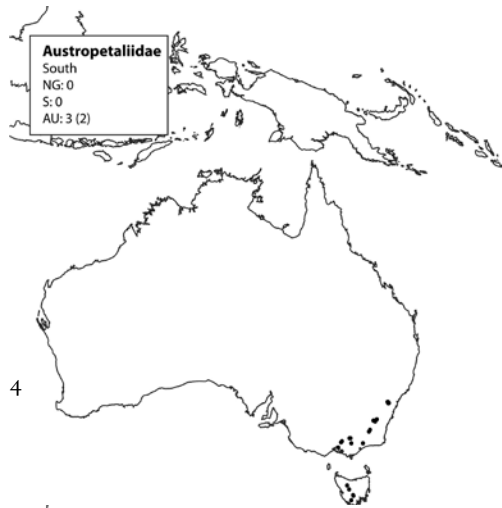
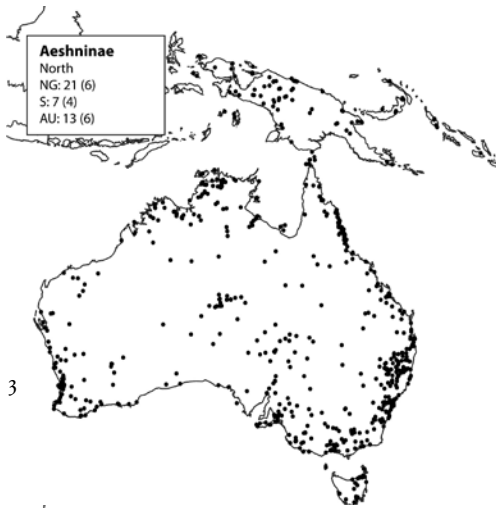
With over 5,700 described species, dragonflies are a relatively small order of aquatic insects (Kalkman et al. 2008). They are among the most ancient of winged insects dating back well into the Permian (Grimaldi & Engel 2005) and the present-day distribution of some families reflects their distribution before the break-up of Pangaea. With very few exceptions larvae of dragonflies live in freshwater habitats. As adults all species are capable of flight, but their dispersal power varies greatly

between families and between species within families.

A total of 678 species of dragonflies are known from Australia and New Guinea, representing approximately 12% of the world fauna. Knowledge of the taxonomy and distribution of Australian and New Guinean dragonflies is generally good and further fieldwork is not expected to result in major changes in the distributions of subfamilies/families involved. It is likely that several dozen species from New Guinea are still to be described. This will increase the percentage of endemic species in New Guinea but is unlikely to significantly alter the currently known distribution of the families and subfamilies. The Australian-Papuan fauna has a high percentage of families of Gondwanan age and at least some of them show a distinct Gondwanan distribution pattern (Theischinger & Watson 1984, Carle 1995, von Ellenrieder & Garrison 2004, von Ellenrieder 2005, Peters & Theischinger 2007). The remainder of the Australian-Papuan dragonfly fauna consist of groups that are likely to have arrived more recently after the region became connected with Asia through island arcs (Liefstinck 1949, Gassmann 2005, Orr & Hämäläinen 2007, van Tol & Gassmann 2007, van Tol et al. 2009).

METHODS

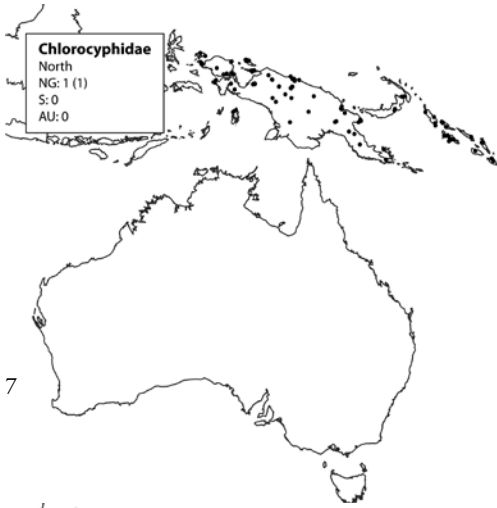
Information on the distribution of the odonate species within the region studied was based largely on the distribution databases of the Australian dragonflies (Theischinger & Endersby 2009) and the Melanesian Odonata Database (Dow & Kalkman, unpublished), which contains information on Malaysia, Indonesia, Papua New Guinea and the Solomon Islands. Using these databases and the checklist provided in Theischinger & Endersby (2009), a checklist for both Australia and New Guinea was compiled. This checklist includes species recorded up to January 2011. The Australian records of *Neurobasis australis* Selys, 1897 and *Rhinocypha tinctoria* Rambur, 1842, which are often included in Australian checklists (e.g. Watson



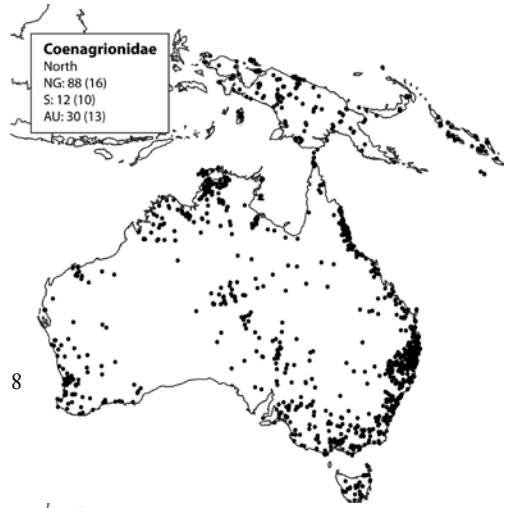
Figs. 3-2.4. Distributions of the 22 considered families/subfamilies of dragonflies within Australia, New Guinea (including Raja Ampat), the Solomons and Aru Islands. The distributions in the later two are shown for reference but are not included in the analysis. The area to the west is shown but the distribution is not mapped for this region. The text box indicates whether the group entered the region from the north or south and gives the number of species and genera (in brackets) in Australia (AU), shared between both regions (s) and in New Guinea (NG). 3: Aeshninae; 4: Austropetaliidae; 5: Brachytroninae; 6: Calopterygidae; 7: Chlorocyphidae; 8: Coenagrionidae; 9: Corduliidae sensu stricto; 10: Disparoneuridae; 11: Gomphinae; 12: Hemiphlebiidae; 13: Isostictidae; 14: Lestidae; 15: Lestoideidae; 16: Libellulidae; 17: Lindeniinae; 18: Macromiidae; 19: Megapodagrionidae; 20: Petaluridae; 21: Platynemididae; 22: Platystictidae; 23: Synlestidae; 24: Synthemistidae sensu lato.

et al. 1991, Theischinger & Hawking 2006), have never been confirmed and are therefore considered to be erroneous (Orr & Hämäläinen 2007). A single male *Diphlebia euphoeoides* Tillyard,

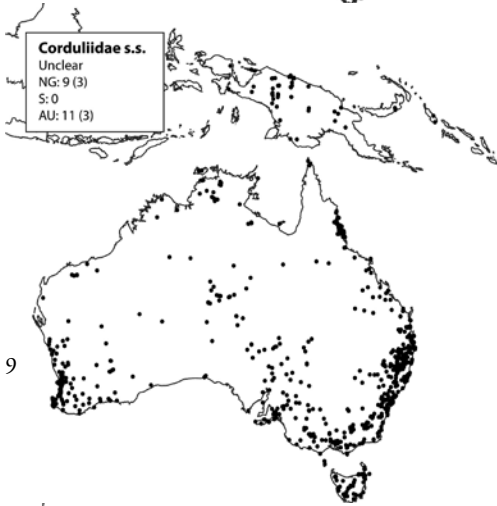
1907 has been recorded from Port Moresby, Papua New Guinea as *D. reinholdi* Foerster, 1910. However, Garrison et al. (2003) showed this record is also erroneous and we removed this species



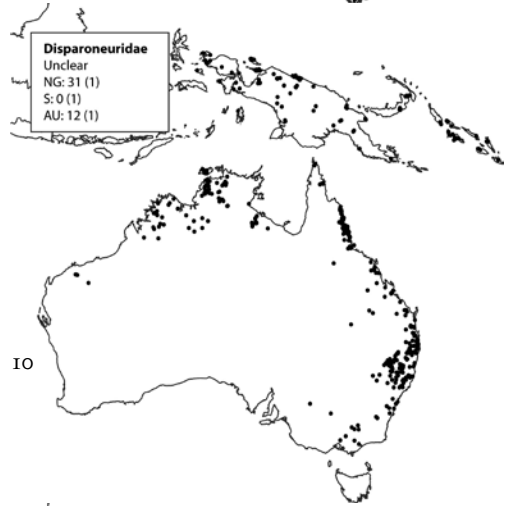
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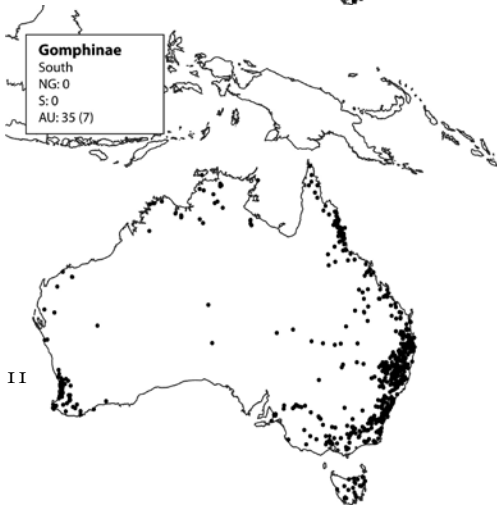
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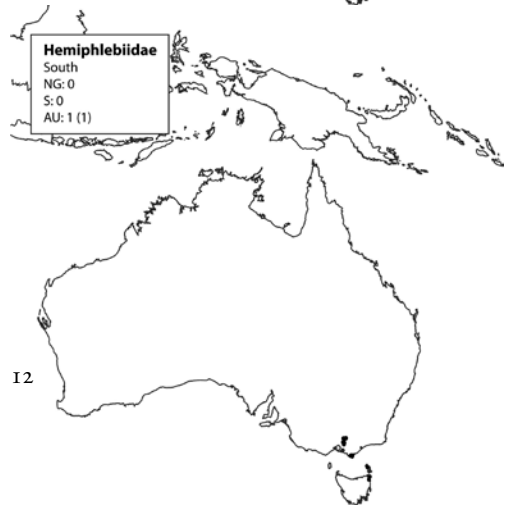
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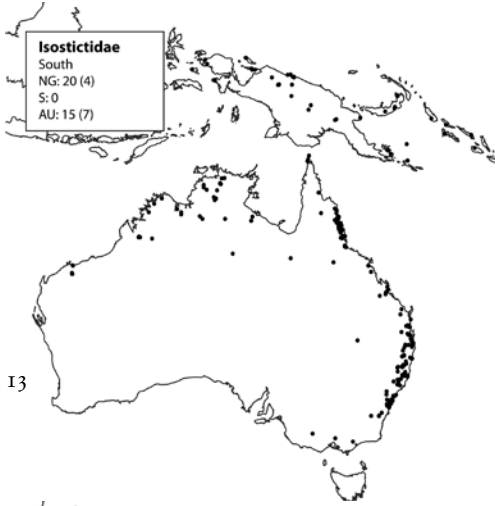
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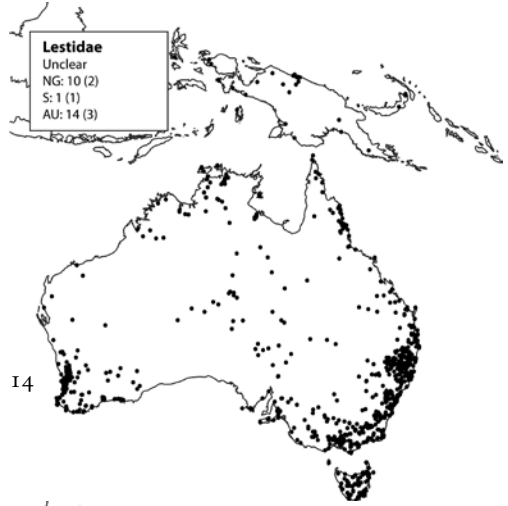
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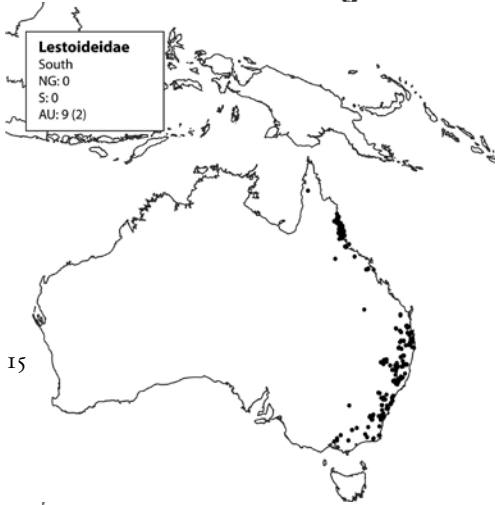
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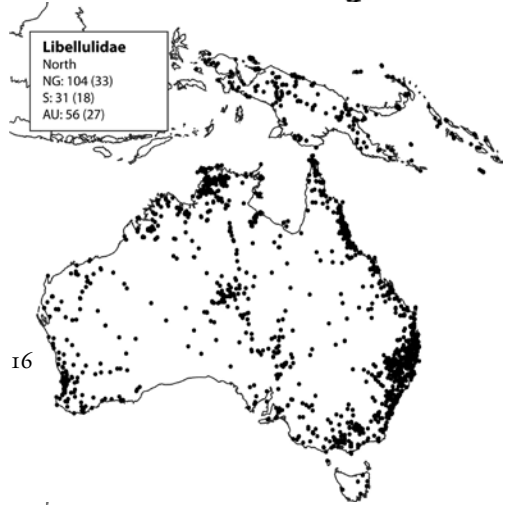
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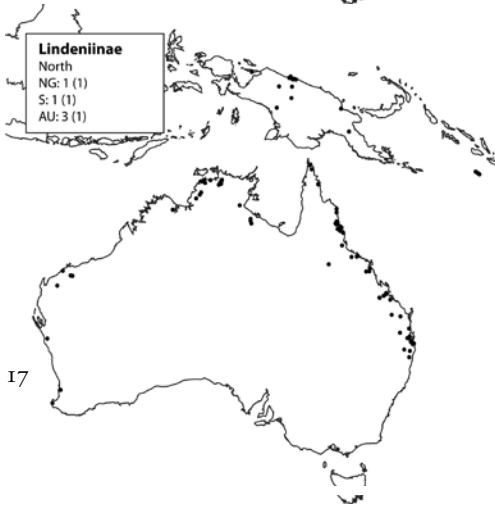
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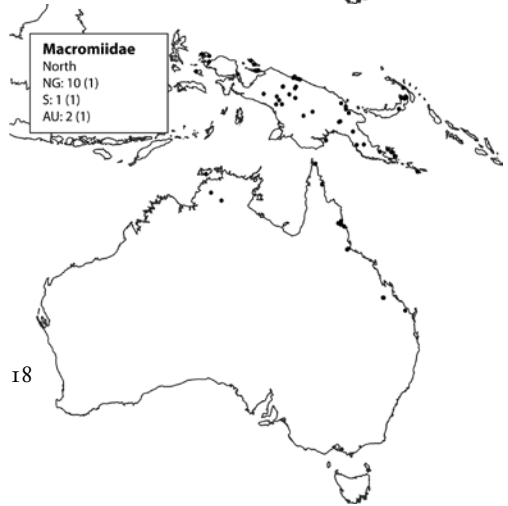
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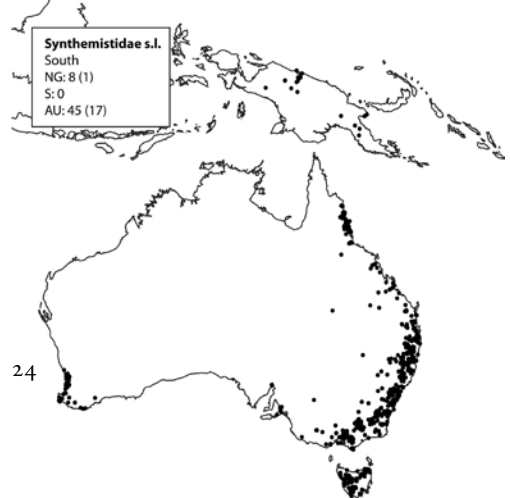
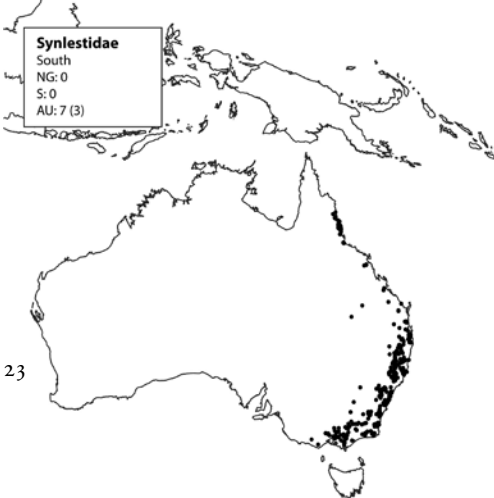
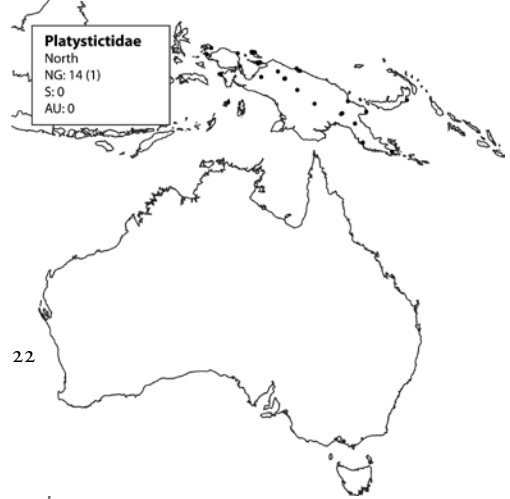
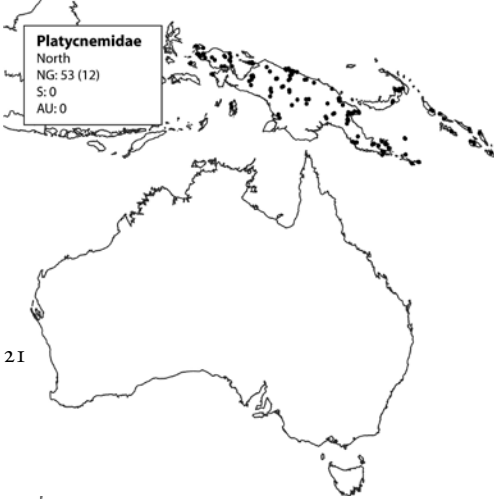
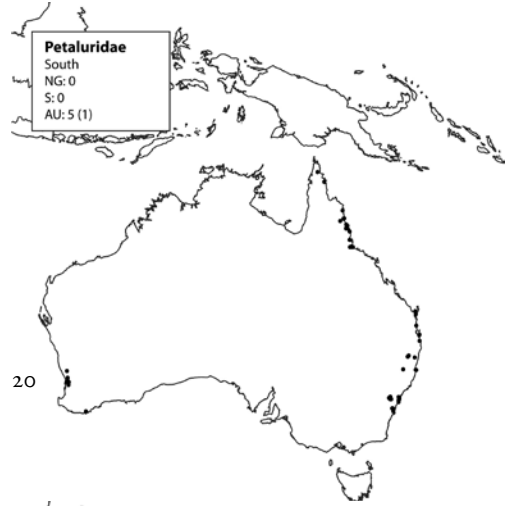
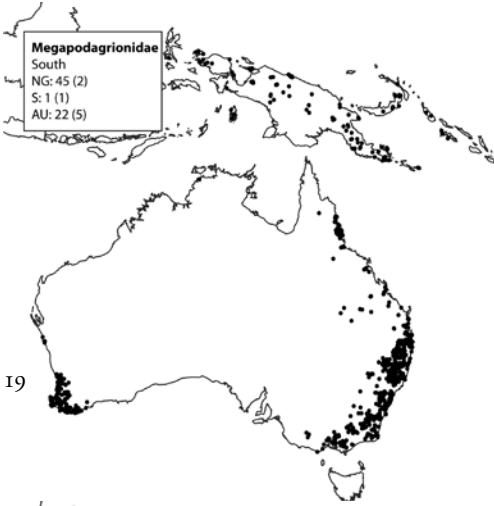
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from the checklist for New Guinea. The Australian *Agriocnemis thoracalis* Sjöstedt, 1917 and *Hemicordulia novaehollandiae* (Selys, 1871) are of uncertain taxonomical status and have been omitted from the list. In this article, Australia is defined as the entire Australian continental shelf territory with the exception of the northernmost islands of the Torres Strait. New Guinea is defined as the territory of the Indonesian provinces of Papua and Papua Barat (West Papua), including the islands to the west of the Bird's Head Peninsula (Misool, Salawati, Batanta, Waigeo) but excluding the island Biak and the territory of Papua New Guinea excepting the Bismarck Archipelago and the island of Bougainville which never have been connected to mainland New Guinea. Although not included in our analysis, the Bismarck Archipelago, Solomon Islands and Biak are included on the distribution maps (fig. 3-24). The higher classifications used in recent publications on Australian dragonflies, notably Theischinger & Hawking (2006) and Theischinger & Endersby (2009), differ from those generally used in world literature, especially in the treatment of family group taxa. This is essentially a matter of splitting versus lumping and generally has little bearing on phylogeny per se. We follow the better known, more conservative family names as used in Kalkman et al. (2008). The exception is the group comprising the Old World representatives of Protoneuridae, which are here placed in the family Disparoneuridae. The New World representatives of this family, including the type genus *Protoneura*, have been shown to belong to the Coenagrionidae and do not seem to be closely related to the Old World Protoneuridae (Carle et al. 2008, Pessacq 2008) necessitating the use of the available family group name, Disparoneuridae. With the exception of Brachytroninae which might be polyphyletic all of the families and subfamilies have shown to be monophyletic (see Table 1). In some cases, clear distributional patterns originating from a different biogeographical history occur at the subfamily, rather than the family level. For this reason, the following subfamilies are discussed separately:

- Aeshnidae is split into Aeshninae and Brachytroninae (sensu Davies & Tobin 1985). The latter group includes those species included in Brachytronidae and Telephlebiidae by Theischinger & Endersby (2009), while the former includes those included in Aeshnidae. The monophyly of Aeshninae is not disputed but the Brachytroninae as here defined are probably a polyphyletic group basal to Aeshninae (Von Ellenrieder 2002).
- Corduliidae together with Synthemistidae is split into Corduliidae sensu stricto and the 'gs1'-clade proposed by Ware et al. (2007). The latter name refers to *Gomphomacromia-Synthemis-Idionyx*, three key genera of this group. The Australian representatives of the 'gs1' clade were placed in Austrocorduliidae, Cordulephyidae, Gomphomacromiidae, Pseudocorduliidae, and Synthemistidae by Theischinger & Endersby (2009). Further study is needed to show if the 'gs1'-clade is indeed monophyletic, in which case it should bear the family name Synthemistidae, as this is the oldest available family group name for this group (Ware in Theischinger & Endersby 2009), and for which reason they are here referred to as Synthemistidae sensu lato. We agree, however, with Theischinger & Endersby (2009) that the different groups within the 'gs1'-clade are morphologically and ecologically distinct and that further study might show that family status for the different groups is warranted.
- Gomphidae is split into Gomphinae and Lindeniinae; both were regarded as full families in Theischinger & Endersby (2009).

Other differences with the family classification as used in Theischinger & Endersby (2009) are:

- Chorismagrionidae with its sole member, *Chorismagrion risi* Morton, 1914 is included in Synlestidae (Bybee et al. 2008).
- Diphlebiidae is included in Lestoideidae (Bybee et al. 2008, Carle et al. 2008). The Southeast Asian genus *Philoganga* is not considered to belong to Lestoideidae (Kalkman et al. 2010).

Based on preliminary DNA-results the Papuan genera *Archboldargia*, *Hylaeargia*, *Papuarugia* and

Palaiargia, formerly placed in Coenagrionidae, are here placed in the Platycnemididae. Conversely, the Papuan species *Thaumatagrion funereum* Liefstinck, 1932 is considered to belong to Coenagrionidae.

For six of the 24 subfamilies/families phylogenies are available showing their area of origin. For the other groups their likely route to Australia and New Guinea was inferred based on their present distribution. Groups were grouped as 'present at break away', e.g., as having been present within Australia at the time it broke away from Antarctica or having evolved afterwards within Australia if they have (1) a typical Pangean relict distribution (fig. 2), (2) no known near relatives outside the region, (3) nearest known relatives found in Africa and/or South-America and no likely candidates present in western Indonesia or in Sundaland. Groups were regarded as having reached the Australian-New Guinean region from Asia ('arrived from Asia') when they are widespread in both Africa and Asia and there exhibit far higher diversity at both species and genus level, as well as being strongly biased towards the northern and eastern tropics within Australia. Three families could not be placed in a group. The proposed grouping largely corresponds with that proposed by Watson (1981). Although several genera probably evolved on New Guinea it is unlikely that any of the subfamilies / families did so. Deduced direction of movement and the sources on which these decisions are based are shown in Table 1.

All 678 species included in the Australian-New Guinean checklist were divided into two habitat categories: running water (lotic) species and still water (lentic) species. Species were classified as 'running water species' when for their reproduction they are strictly dependent on waters that flow at least a part of the year. Those included in the category of 'still water species' breed predominantly in standing waters, although some included species may also facultatively breed in slowly running waters. Information on habitats was

based on Theischinger & Endersby (2009) for the Australian species and on various sources including personal (vjk) field observations for the Papuan species. For Papuan species for which no information was available the designation to habitat type was based on other species of the same genus. In 26 of the 678 species, no habitat association could be determined.

RESULTS

Taken together, Australia and New Guinea are host to 678 dragonfly species belonging to 144 genera. A total of 412 species (82 genera) occur in New Guinea and 320 species (109 genera) are found in Australia (Table 1). Within this area, seven of the 22 families and subfamilies we consider are restricted to Australia, four to New Guinea, while eleven are shared by both regions. The family/subfamily distribution within New Guinea plus Australia, together with a breakdown of total and shared genera and species for each region, is shown for each family/subfamily grouping in figures 3-24. Overall, 50% of families and subfamilies, 33% of genera and 8% of species are shared between Australia and New Guinea (fig. 25). The percentage of Australian, New Guinean or shared species varies strongly from family to family (fig. 26). Of the 11 families/subfamilies occurring in both regions four do not share any species between the regions and four share only one or two species. Of the total 54 shared species 43 belong to just two families (Coenagrionidae and Libellulidae), while another seven belong to Aeshninae. 64% of the 652 Australian-New Guinean species with habitat information are dependent on running water; for Australia and New Guinea this figure is 73 and 67%, respectively. Of the 53 shared species for which habitat information is available only one (2%) is dependent on running water (fig. 27). The difference between the proportion of species dependent on running water for the whole area and that of the shared species is highly significant (χ^2 test = $P < 0.001$).

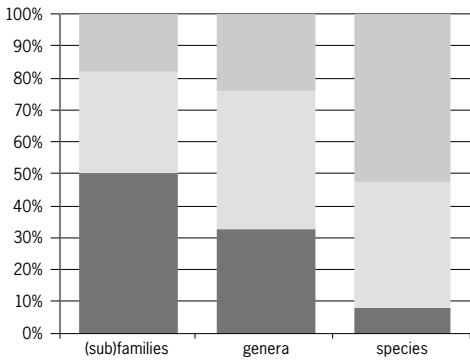


Figure 25. Percentage of families, genera and species limited to Australia, New Guinea or shared.

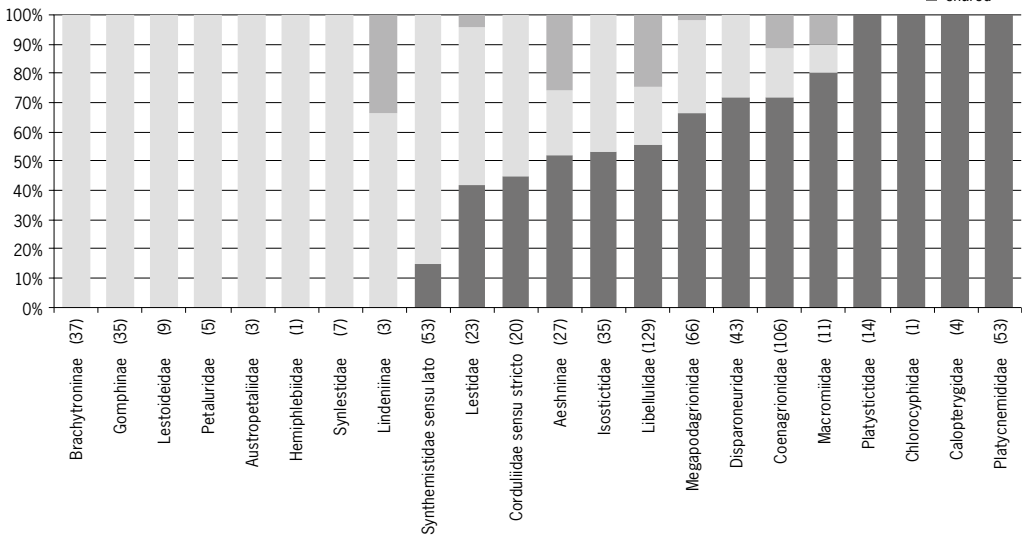


Figure 26. Percentage of Australian, New Guinean or shared species for each of the families/subfamilies considered. The number of species within each family/subfamily is given in brackets.

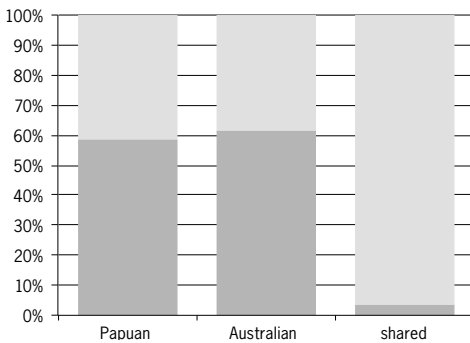


Figure 27. Percentage of dragonfly species associated with either running water or standing water for all New Guinean species, all Australian species and species shared between the regions.

DISCUSSION

The differences in the composition of the dragonfly fauna of New Guinea and Australia are very strongly marked. To the best of our knowledge, there is no other place on earth where the Odonata fauna exhibits such a profound change in composition at the family, genus and species level over such a short distance. Eleven of the 22 families/subfamilies are exclusive to either Australia or New Guinea while another four have no shared species between the two regions. Ten families/subfamilies were probably already present in Australia during its separation from Antarctica of which seven have not colonised New Guinea. Two of these have a mainly temperate distribution (fig. 4, 12) and their absence could be partly due to climatic conditions in much of New Guinea being unsuitable. Although suitable habitat may be available in its high mountain ranges, it is unlikely that a suitable corridor ever existed to allow these cold-adapted species to disperse. The five other families/subfamilies are either found throughout east Australia up to the Queensland Wet Tropics region (fig. 15, 23) or Cape York (fig. 20), are widespread in a large part of Australia as far north as the Queensland Wet tropics (fig. 5) or are widespread in Australia including the Top End and Cape York (fig. 11). In three of these groups, Brachytroninae, Lestoideidae and Synlestidae (fig. 5, 15, 23), their present distribution in the north seems to be constrained by the monsoon climate in northern Australia. The three families/subfamilies present in Australia at the time of its break away from Antarctica that did reach New Guinea (Isostictidae, Megapodagrionidae, Synthemistidae sensu lato) are represented in New Guinea and in Australia by different genera, indicating a long period of separation and divergence. The only exception is the genus *Podopteryx* of which one species *P. selysii* (Foerster, 1899) (Megapodagrionidae) is found in both New Guinea and Australia. Interestingly, this is the only genus of this family that is not dependent on running water as its members breed in phytotelmata (Watson & Dyce 1978).

The faunal turnover between Australia and New Guinea is much stronger than between the Sundaland region directly west of Wallace's line (Borneo, Sumatra, Java, Peninsular Malaysia) and directly east of Wallace's line (Sulawesi, Lesser Sundas, Moluccas, New Guinea) where 15 of the 19 families/subfamilies are shared (Kalkman et al. 2008). Most of the species shared by Australia and New Guinea belong to the Coenagrionidae and Libellulidae. These represent the two largest extant odonate families, with a high proportion of species adapted to standing water and relatively many eurytopic species with a high dispersal potential. These characteristics mean that they are often the dominant families on isolated islands and the first to colonise new habitats. It is therefore no surprise that these, in contrast to other families, have evidently been able to cross from New Guinea to Australia; several of the species of these families are probably able to cross either way even under present conditions. Members of most of the other families have much weaker dispersal powers and it is not surprising that under the present conditions they are unable to cross the barrier of Torres Strait. However during the Pleistocene land bridges were present for long periods. The seemingly lack of exchange of dragonflies between Australia and New Guinea even during these periods can be attributed to either the lack of suitable habitat in the receiving area, the limited dispersal powers of the species under consideration or to protracted climatic conditions rendering the intervening area unsuitable for dispersal. The differences in habitat in the receiving area alone cannot account for the lack of exchange. Despite the obvious differences between the two areas, Australia being a predominantly dry continent and New Guinea being dominated by rain forest, both have habitats which offer suitable conditions for a wide set of species from the other area. On both sides of the present barrier of Torres Strait savannah landscapes with large swamp systems and tropical forest are present (Polhemus & Allen 2007), although the closed canopy rainforest of northern Australia occupies a relatively small area consisting of several isolated patches with limited stream systems.

Larger stands of tropical rainforest in Australia are limited to the Australian Wet Tropics in the east of Queensland at about 700 km from New Guinea. Lack of dispersal power is also an unlikely explanation in most cases. This is illustrated by the three tropical rainforest damselfly families (Calopterygidae, Chlorocyphidae and Platynemididae) which failed to colonise Australia but did colonize the Aru Islands during the period when the Aru Islands were transformed from savannah to rainforest (20,000-14,000 BP) prior to their severance from New Guinea. The fact that these groups did reach the Aru Islands but not Australia suggests that their absence in Australia is due not to the limited dispersal powers of these groups but rather to the less favorable climatic conditions and a consequent lack of bridging habitat between New Guinea and Australia. Although there is evidence of some forest present in the zone between Australia and New Guinea during periods of low sea level, these forests were probably relatively dry or deciduous and subjected to a distinct dry season rendering the area unsuitable for species strictly dependent on forest habitats. In addition such conditions would result in relatively few permanent standing and smaller running waters. Under these conditions, larger rivers would be strongly seasonal with a low water table in the dry period and turning into large, muddy floodplains in the wet season, especially so on the Arafura Shelf where the low gradients would have resulted in slow currents. Furthermore, a majority of rivers originating from both Australia and New Guinea would have run to the intermittently brackish Lake Carpentaria which would have constituted another barrier to dispersal for all species of running water and, at times, most species of standing water. The presence of this obstacle might explain in particular the low proportion of running water species shared between New Guinea and Australia.

It is remarkable that the AMT seems to have formed a barrier not only for those families, which are generally poorly represented in the monsoon-dominated region (e.g., Megapodagrionidae,

Brachytroninae), but also for families that are well represented such as Gomphinae (not present in New Guinea), Isostictidae (no shared genera) and Disparoneuridae (no shared species). It is also noteworthy that among running water groups, the three families/subfamilies, which have crossed the barrier in a known direction (Megapodagrionidae, Isostictidae, Synthemistidae), all originated in Australia, possibly indicating a dispersal event in the relatively distant past when circumstances for dispersal were better, before the present Asian derived elements of the New Guinea fauna had become established.

The patterns described here for dragonflies are consistent with an absence of exchange during the Pleistocene glacial as has already been suggested for freshwater fish (Unmack 2001) and has been shown for *Papuadytes*-diving beetles (Balke et al. 2007) and is a strong indication that the largely savannah dominated AMT have formed a robust barrier to the exchange of freshwater biota between Australia and New Guinea. The fact that those families/subfamilies associated with running water that did cross are represented in the two areas by different genera is seen as an indication that this barrier has operated at least throughout the Pleistocene. The largely congruent results for freshwater fish and for dragonflies based on distribution patterns and *Papuadytes*-diving beetles based on molecular data make it likely that the same patterns apply to most strictly freshwater groups found in these areas.

ACKNOWLEDGEMENTS

We thank Ian Endersby and Günther Theischinger for allowing us the use of their database of Australian dragonflies without which this work would not have been possible. We thank Steve Richards, Peter van Welzen, Gunther Theischinger and Jan van Tol for comments that substantially improved this work. This study was made possible due to a grant of the Schure-Beijerinck-Popping Fonds of the KNAW.

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7. OUT OF AUSTRALIA: THE ARGIOLESTIDAE REVEAL THE MELANESIAN ARC SYSTEM AND EAST PAPUA COMPOSITE TERRANE AS POSSIBLE ANCIENT DISPERSAL ROUTES TO THE INDO-AUSTRALIAN ARCHIPELAGO (ODONATA, ARGIOLESTIDAE)

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Citation: Kalkman, V.J., K.-D.B. Dijkstra, R.A. Dow, F.R. Stokvis & J. van Tol 2013. Out of Australia: the Argiolestidae reveal the Melanesian Arc System and East Papua Composite Terrane as possible ancient dispersal routes to the Indo-Australian archipelago (Odonata, Argiolestidae). – PhD-thesis, Naturalis Biodiversity Center, Leiden.

Information on the origin of distribution patterns shown by freshwater invertebrates in the Indo-Australian Archipelago is poor. Here we present a molecular based hypothesis of the phylogenetic relationship of Argiolestidae, a family of damselflies found throughout the tropical parts of the Eastern Hemisphere. We use this to address the following questions: (1) did Argiolestidae colonize Wallacea and the Philippines from the Eurasian or from the Australian continent?; (2) is the presence of Argiolestidae on New Guinea the result of a single colonization event, i.e. are the Argiolestidae found on New Guinea monophyletic? The results show that clades occurring in the Philippines, Wallacea and New Guinea all originate from Australian ancestors. Representatives in Sundaland are most closely related to African genera and failed to reach the Philippines and Wallacea. The presence of Argiolestidae north of Australia was the result of at least three colonization events from Australia to areas that presently compose New Guinea and probably a fourth from Australia to Sulawesi. The two most diverse lineages found north of Australia show different distribution patterns. One reaching north as far as Luzon, presumably facilitated by Late Oligocene to Miocene island arcs (Melanesian Arc System). The other clade shows a diversification of two genera and numerous species in the eastern tail of New Guinea, an area largely corresponding with the East Papuan Composite Terrane (EPCT) followed by the expansion of one genus into the rest of New Guinea. The EPCT's importance as source area for the New Guinean fauna has been suggested on the basis of distribution patterns, but we present the first evidence based on phylogeny reconstruction of strong diversification on this formerly isolated landmass.

INTRODUCTION

The Indo-Australian Archipelago (IAA) is a mixture zone of flora and fauna of Asian and Australian descent (Lohman et al. 2011). The islands of the Sunda shelf in the west have for long periods

been connected to mainland Asia and are strongly dominated by Asian groups. In the east a land bridge connected New Guinea and adjacent island for long periods with Australia, resulting in a relatively high proportion of taxa of Australian descent (Lohman et al. 2011). In between are the

islands of Wallacea (Sulawesi, Lesser Sunda Islands, Moluccas) and the Philippines, most of which have never been connected to Asia or Australia and received their flora and fauna from overseas dispersal or, in some cases, from drifting continental fragments. The species composition of these islands is determined by the dispersal capacity of the species, the islands' sub-aerial history and the opportunities they offer for speciation and survival (Lomolino et al. 2010). These factors must have played out differently for different taxonomic groups and it is unlikely that a single pattern describing the faunistic and floristic transition between Asia and Australia can be found. Nonetheless common patterns should occur in groups with similar dispersal capacities and ecological requirements. The present paper focuses on damselflies, whose larvae require freshwater habitats. It seems likely that this dependence restricted their dispersal into Wallacea and the Philippines. The distribution patterns of several groups of freshwater invertebrates in the IAA have been described in detail, but biogeographic reconstructions based on molecular data are still rare (van Tol & Gassmann 2007, De Bruyn et al. 2012). Most studies focus on crustaceans or molluscs (see De Bruyn et al. 2012 for a review) with relatively many studying the diversification in ancient lakes in Sulawesi (Von Rintelen et al. 2006, 2007, 2010). Phylogenies describing the colonization of the Philippines, Wallacea and New Guinea by freshwater invertebrates show that there is huge variation in the timing and direction of colonization events, making it difficult to describe the relative importance of the various dispersal routes. Common patterns found are summarized in De Bruyn et al. (2012) and include repeated colonization of the Philippines from Borneo and Sulawesi, colonization of Sulawesi mainly by dispersal from the west with a small portion of groups with an eastern origin which might have arrived by terrane drifting (De Bruyn et al. 2012, Stelbrink et al. 2012). Finally, the New Guinea fauna is largely derived from Asia (e.g. crossing Wallacea and/or the Philippines), but where the landbridges on the Sahul Shelf allowed for a

exchange with Australia of groups of fishes, shrimps and crayfish (Bowman et al. 2010), this is not true for taxa strictly dependent on running freshwater (Balke et al. 2007, Kalkman & Theischinger 2013).

Two available phylogenetic reconstructions for the colonization of New Guinea by freshwater insects show very different patterns. The possibly over 150 species of *Exocelina* diving beetles on New Guinea resulted from a single colonization event and is an example of how such rare events can have a major impact on the fauna (Balke et al. 2004, 2007). *Rhantus* diving beetles dispersed east from Eurasia, resulting in about 25 closely related species in Australasia and Oceania, with one species originating in the New Guinean highlands and subsequently establishing itself from New Zealand to Portugal (Balke et al. 2009).

Here we present a phylogeny of Argiolestidae, an Eastern Hemisphere damselfly family, in order to answer the following two questions:

- (1) Did Argiolestidae colonize Wallacea and the Philippines from the Asian continent or from the Australian continent?
- (2) Is the presence of Argiolestidae on New Guinea the result of a single dispersal event, i.e., do the species of New Guinea form a monophyletic group?

The larvae of Odonata (dragonflies and damselflies) strictly depend on aquatic habitats for their development. The adult stage is winged and some species fly well, allowing them to colonize habitats on isolated islands. This capability, however, is largely restricted to species of standing waters. Species of running water, especially in the tropics, usually have low dispersal capacities (Kalkman et al. 2008). With almost 6,000 described species Odonata constitute almost 5% of the animal diversity in freshwater (Balian et al. 2008). The highest species and family diversity is found in the tropics, especially those of America and Asia (Dijkstra et al. 2013a, Kalkman et al. 2008). Due to their size and coloration Odonata receive much attention and therefore their taxonomy and

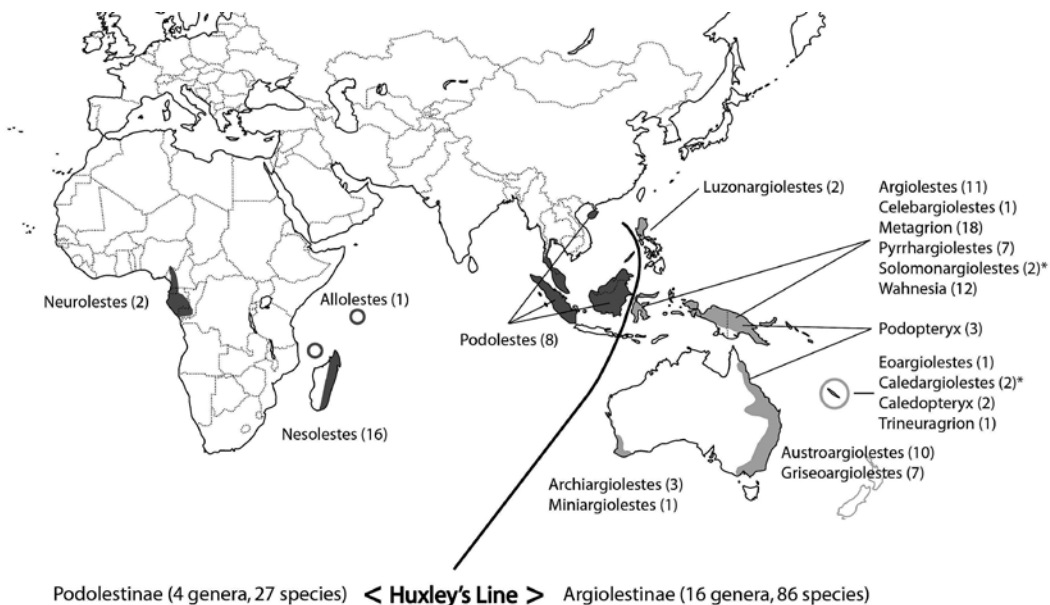


Figure 1. Distribution of Argiolestidae. The number of described species is given between parentheses. No DNA-material was available for the two genera marked with an asterisk.

distribution are relatively well known. This makes odonates one of the few groups of freshwater invertebrates, and one of very few insect orders, for which it is possible to reconstruct the phylogeny and biogeography within the coming decades. Several large phylogenetic studies, based mainly on molecular data, have been published recently (Hovmöller et al. 2002, Rehn 2003, Dumont et al. 2005, Ware et al. 2007, Fleck et al. 2008, Bybee et al. 2008, Carle et al. 2008, Dumont et al. 2010, Dijkstra et al. 2013a, Dijkstra et al. 2013b). Many of these suffer from poor support of the deeper nodes, so that the phylogeny within the families is well-resolved but the relationships between them remain obscure. This is partly due to their great age with nearly all extant families known from the Mesozoic onwards and most probably originating in the Jurassic period (Dumont et al. 2005, Grimaldi & Engel 2005, Ware et al. 2008). Furthermore, dating phylogenies is difficult as the identification of fossils is generally based on wing venation, which is often

a poor indicator of taxonomic affinity (Dijkstra et al. 2013a). Nonetheless, the group's age, phylogenetic progress and detailed distribution data offer good opportunities for biogeographic reconstructions, also on longer time scales.

The current paper is only the second in which a nearly complete phylogenetic and biogeographic reconstruction of a damselfly family is presented after the Calopterygidae (Dumont et al. 2005). Argiolestidae contains 113 described and an estimated 40-80 undescribed species. The family was included in the Megapodagrionidae until recently (Kalkman et al. 2010, Dijkstra et al. 2013a). Argiolestidae in the present sense is confined to the Eastern Hemisphere with the majority of species restricted to tropical or subtropical regions. A recent revision (Kalkman & Theischinger 2013) recognized twenty genera in two subfamilies, with the Argiolestinae (16 genera, 86 species) found in Australasia east of Huxley's line and the Podolestinae (4 genera,

27 species) in Africa and Southeast Asia west of Huxley's line (fig. 1). Although many species of Argiolestidae occur in poorly explored areas, the ranges of the genera are considered to be well known (Kalkman & Theischinger 2013). The family is almost restricted to running waters: most species inhabit seepages or streams, with a few found in rivers. The only exceptions are the Southeast Asian *Podolestes*, found mainly in swamps, and *Podopteryx*, of which probably all species breed in phytotelmata (plant-held waters). All species inhabit forest habitats with the exception of some Australian species found in more open alpine marshland. A larva (or larval skin) and wingtip enclosed together in Baltic amber of Eocene age is the only fossil that can indisputably be attributed to Argiolestidae (Bechly & Wichard 2008). The larva shows flat horizontal caudal gills, which is an apomorphy of the family, but a more precise identification is impossible.

MATERIAL AND METHODS

Taxon selection

The study relies on collections assembled in recent years at Naturalis Biodiversity Center, Leiden, The Netherlands (formerly National Museum of Natural History) by the authors, supplemented with donations (see acknowledgements). The DNA-material includes 91 samples of over fifty taxa belonging to 18 of the 20 recognized genera (table 1, fig. 1). All genera with more than three species are represented by samples of at least three different taxa. The genera *Metagrion*, *Nesolestes* and *Wabnesia* are in need of revision and not all material could be identified to species level. No DNA-material was available of two genera: *Solomonargiolestes*, of which only three old specimens are known, and *Caledargiolestes*. The latter is considered on morphological characters the sister genus of *Caledopteryx*. Both are endemic to New Caledonia and share a unique character of the genital ligula (apical lobes with numerous minute spines). *Solomonargiolestes* is not discussed as its position is unknown.

DNA extraction and amplification

Genomic DNA was extracted from one or two legs per specimen using the Qiagen DNeasy Blood & Tissue Kit. Elution was performed in 100 µl elution buffer. Fragments of the nuclear 28S rRNA gene (1346-1532 bp) and the mitochondrial 16S rRNA (522-542 bp) were amplified using primer combinations developed with Primer3 (Rozen & Skaletsky 2000). Primer combinations are depicted in Table 2. The 25 µl PCR reaction mixes for 16S contained 2.5 µl of 10 × CoralLoad PCR Buffer (Qiagen, USA), 1 µl of each primer (10 pM), 1.25 U of Taq DNA Polymerase (Qiagen, USA), 0.5 µl of dNTP's and 1 µl of DNA template. 5 µl Q-solution (Qiagen, USA) was added to the reaction mix for 28S. The amplification protocol consisted of 3 min at 94°C followed by 40 to 50 cycles of 15 s at 94°C, 30 s at 60°C to 35°C and 40 s at 72°C, and a final 5 min at 72°C. Direct sequencing was performed at MacroGen Europe on an ABI 3730XL sequencer. COI was available for only 62 of the 91 samples and missing for some key samples and has therefore been discarded in the analyses.

Phylogenetic analyses

Sequences were edited with Sequencher 4.10.1 (Gene Codes Corporation) and assembled using Bioedit 7.0.9.0 (Hall 1999). Geneious Pro 5.6.4 (Biomatters Ltd) was used for stop codons (Drummond et al. 2011). All sequence data and additional geographic data are deposited at GenBank. In addition, COI sequence data of 62 samples as well as photographs of the specimens were uploaded to the Barcode of Life Data System (BOLD, Ratnasingham & Hebert 2007). GenBank accession numbers are included are listed in Table 1. The sequences included 2033 base pairs while the number of unique sites was 635 for 28S and 452 for 16S.

Multiple sequence alignments were performed using MAFFT (Kato et al. 2002, 2005, 2009) under default parameters. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the combined 28S+16S datasets.

Table 1. Specimens used in molecular phylogenetic analyses. All belong to Argiolestidae with the exception of *Lestes virens* (Lestidae). For all specimens: Repository = RMNH except: *Neurolestes trinervis* Dijkstra, K.-D.B. & Schuette, K. 2008 = RMNH/ZMUH; *Wahnesia* spec Polhemus, D.A. 2003 = BPBM; *Wahnesia* spec Polhemus, D.A. 2002 = BPBM; *Wahnesia* spec Polhemus, D.A. 2002 = BPBM.

Name new	Authority	Year	Collector	Year	Country	Location
<i>Allolestes macdahlani</i>	Selys	1869	Gerlach, J.	2008	Seychelles	Mahe
<i>Archiargiolestes parvulus</i>	(Watson)	1977	Taylor, J.	2010	Australia	Western Australia
<i>Archiargiolestes pusillissimus</i>	(Kennedy)	1925	Taylor, J.	2009	Australia	Western Australia
<i>Argiolestes amphistylus</i>	Lieftinck	1949	Kalkman, V.J.	2006	Indonesia	Papua Province, Borneo
<i>Argiolestes muller</i>	Kalkman, Richards & Polhemus	2010	Kalkman, V.J.	2009	Papua New Guinea	Western Province, Muller Range
<i>Argiolestes roon</i>	Kalkman, Richards & Polhemus	2010	Polhemus, D.A.	2008	Indonesia	West Papua Province, Roon Island
<i>Argiolestes roon</i>	Kalkman, Richards & Polhemus	2010	Kaize, J.	2009	Indonesia	West Papua Province, Mioswaar Island
<i>Argiolestes tuberculiferus</i>	Michalski & O'Farrell	2010	O'Farrell	2003-2004	Papua New Guinea	Simbu Province
<i>Argiolestes tuberculiferus</i>	Michalski & O'Farrell	2010	O'Farrell	2004	Papua New Guinea	Simbu Province
<i>Argiolestes tuberculiferus</i>	Michalski & O'Farrell	2010	Richards, S.	2010	Papua New Guinea	mainland
<i>Austroargiolestes alpinus</i>	Tillyard	1913	Kalkman, V.J.	2011	Australia	Cathedral Rock NP
<i>Austroargiolestes brookhousei</i>	Theischinger & O'Farrell	1986	Theischinger, G. & Mueller, L.	1997	Australia	Barrington Tops
<i>Austroargiolestes calcaris</i>	(Fraser)	1958	Kalkman, V.J.	2012	Australia	New South Wales
<i>Austroargiolestes calcaris</i>	(Fraser)	1958	Kalkman, V.J.	2012	Australia	New South Wales
<i>Austroargiolestes christine</i>	Theischinger & O'Farrell	1986	Kalkman, V.J.	2011	Australia	Barrington Tops
<i>Austroargiolestes christine</i>	Theischinger & O'Farrell	1986	Kalkman, V.J.	2011	Australia	Barrington Tops
<i>Austroargiolestes chrysooides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysooides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysooides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysooides</i>	(Tillyard)	1913	Kalkman, V.J.	2011	Australia	Queensland
<i>Austroargiolestes icteromelas</i>	(Selys)	1862	Kalkman, V.J.	2011	Australia	New South Wales
<i>Austroargiolestes icteromelas</i>	Theischinger & O'Farrell	1986	Dijkstra K.-D.B. & Kalkman, V.J.	2002	Australia	New South Wales
<i>nigrolabiatus</i>	(Selys)	1862	Kalkman, V.J.	2011	Australia	New South Wales
<i>Austroargiolestes icteromelas</i>	Theischinger & O'Farrell	1986	Kalkman, V.J.	2011	Australia	New South Wales
<i>Austroargiolestes icteromelas</i>	Theischinger & O'Farrell	1986	Kalkman, V.J.	2011	Australia	New South Wales
<i>nigrolabiatus</i>	Theischinger & O'Farrell	1986	Kalkman, V.J.	2009	Australia	Queensland

Table 1. Continued

Name new	Authority	Year	Collector	Year	Country	Location
<i>Austroargiolestes isabellae</i>	Theischinger & O'Farrell	1986	Dijkstra K.-D.B. & Kalkman, V.J.	2002	Australia	New South Wales
<i>Caledopteryx sarasini</i>	(Ris)	1915	Marinov, M. & Richards, S.	2010	New Caledonia	Grand Terre
<i>Caledopteryx sarasini</i>	(Ris)	1915	Marinov, M. & Richards, S.	2010	New Caledonia	Grand Terre
<i>Caledopteryx</i> spec			Marinov, M.	2009	New Caledonia	South Province
<i>Cetebergiolestes</i> spec			Gunther, A. & Randow, F.	1994	Indonesia	Sulawesi
<i>Eoargiolestes ochraceus</i>	Montrouzier	1864	Marinov, M.	2009	New Caledonia	mainland
<i>Griseargiolestes albescens</i>	(Tillyard)	1913	Kalkman, V.J.	2011	Australia	Queensland
<i>Griseargiolestes albescens</i>	(Tillyard)	1913	Kalkman, V.J.	2011	Australia	Queensland
<i>Griseargiolestes bucki</i>	Theischinger	1998	Kalkman, V.J.	2011	Australia	New South Wales
<i>Griseargiolestes bucki</i>	Theischinger	1998	Kalkman, V.J.	2011	Australia	New South Wales
<i>Griseargiolestes eboracus</i>	(Tillyard)	1913	Kalkman, V.J.	2011	Australia	New South Wales
<i>Griseargiolestes eboracus</i>	(Tillyard)	1913	Kalkman, V.J.	2011	Australia	New South Wales
<i>Griseargiolestes griseus</i>	(Selys)	1862	Kalkman, V.J.	2012	Australia	New South Wales
<i>Griseargiolestes griseus</i>	(Selys)	1862	Kalkman, V.J.	2012	Australia	New South Wales
<i>Lestes vitrens</i>	(Charpentier)	1825			Europe	
<i>Luconargiolestes balazarae</i>	(Gapud & Recuenco)	2001	Nazareno, C.M.	1997	Philippines	Luzon
<i>Metagrion aunnaticum</i>	(Ris)	1898	Gassmann, D.	1997	Papua New Guinea	East New Britain Province
<i>Metagrion formicatum</i>	(Theischinger & Richards)	2007	Oppel, S.	2004	Papua New Guinea	Simbu province
<i>Metagrion montivagans</i>	(Förster)	1900	Gassmann, D.	1997	Papua New Guinea	Morobe province, Huon Peninsula
<i>Metagrion</i> spec			Richards, S.	2009	Papua New Guinea	Mainland
<i>Metagrion</i> spec			Kalkman, V.J.	2009	Papua New Guinea	Western Province, Muller Range
<i>Metagrion</i> spec			Kalkman, V.J.	2009	Papua New Guinea	Western Province, Muller Range
<i>Metagrion</i> spec			Oppel, S.	2004	Papua New Guinea	Simbu province
<i>Metagrion</i> spec			Richards, S.	2009	Papua New Guinea	Mainland
<i>Metagrion</i> spec			Ammer, M.	2008	Indonesia	West Papua Province, Tamrau Mts.
<i>Metagrion</i> spec			Richards, S.	2011	Papua New Guinea	Mainland
<i>Metagrion sponsum</i>	Lieftinck	1956	Kalkman, V.J.	2006	Indonesia	Papua, Borne
<i>Metagrion</i> species			Kaize, J.	2009	Indonesia	Papua Barat, Mioswaar Island
<i>Metagrion sponsum</i>	Lieftinck	1956	Kalkman, V.J.	2008	Indonesia	Papua, Lelambo
<i>Metagrion subornatum</i>	Lieftinck	1935	Kalkman, V.J.	2006	Indonesia	Papua, Abepura

<i>Metagrion subornatum</i>	Lieftinck	1935	Kalkman, V.J.	2006	Indonesia	Papua, Japen Island
<i>Metagrion subornatum</i>	Lieftinck	1935	Kalkman, V.J.	2006	Indonesia	Papua, Japen Island
<i>Miniargiolestes minimus</i>	(Tillyard)	1908	Taylor, J.	2010	Australia	Western Australia
<i>Miniargiolestes minimus</i>	(Tillyard)	1908	Taylor, J.	2010	Australia	Western Australia
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Amboavola
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Andasibe
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Andasibe
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Apasy
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Apasy
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Apasy
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Sainte Luce
<i>Nesolestes spec</i>			Schuetter, K.	200?	Madagascar	Tolongoina
<i>Neurolestes nigeriensis</i>	Gambles	1970	Parr, M.J.	2005	Madagascar	Obudu Plareau
<i>Neurolestes trimerus</i>	(Selys)	1885	Dijkstra, K.-D.B., Mézière, N. & Vanappelghem, C.	2010	Nigeria	Haut-Ogooué
<i>Neurolestes trimerus</i>	(Selys)	1885	Mézière, N. & Vanappelghem, C.	2010	Gabon	Haut-Ogooué
<i>Neurolestes trimerus</i>	(Selys)	1885	Mézière, N. & Vanappelghem, C.	2010	Gabon	Haut-Ogooué
<i>Neurolestes trimerus</i>	(Selys)	1885	Dijkstra, K.-D.B. & Schuetter, K.	2008	Cameroon	Southwest Province
<i>Podolestes buwaldai</i>	Lieftinck	1940	Dow, R.A.	2009	Malaysia	Pahang
<i>Podolestes buwaldai</i>	Lieftinck	1940	Dow, R.A.	2009	Malaysia	Pahang
<i>Podolestes harrissoni</i>	Lieftinck	1953	Dow, R.A.	2010	Malaysia	Sarawak
<i>Podolestes orientalis</i>	Selys	1862	Dow, R.A.	2010	Malaysia	Sarawak
<i>Podolestes orientalis</i>	Selys	1862	Dow, R.A.	2009	Malaysia	Sarawak
<i>Podolestes spec</i>			Makbun, N.	2008	Thailand	Nakhon Sawan
<i>Podopteryx selysi</i>	(Förster)	1899	Theischinger, G. & Mueller, L.	1997	Australia	Queensland
<i>Podopteryx selysi</i>	(Förster)	1899	Richards, S.	2009	Papua New Guinea	West Sepik Province
<i>Podopteryx selysi</i>	(Förster)	1899	Richards, S.	2010	Papua New Guinea	West Sepik Province
<i>Pyrrhargiolestes angulatus</i>	(Theischinger & Richards)	2007	Oppel, S.	2003	Papua New Guinea	Chimbu
<i>Pyrrhargiolestes angulatus</i>	(Theischinger & Richards)	2007	Oppel, S.	2004	Papua New Guinea	Chimbu
<i>Pyrrhargiolestes aulicus</i>	(Lieftinck)	1949	Richards, S.	2009	Papua New Guinea	mainland
<i>Pyrrhargiolestes cf sidonia</i>	(Martin)	1909	Richards, S.	2004	Papua New Guinea	mainland
<i>Trineuragrion percostale</i>	Ris	1915	Martinov, M.	2009	New Caledonia	South Province
<i>Wahnesia spec</i>			Polhemus, D.A.	2003	Papua New Guinea	Milne Bay Province
<i>Wahnesia spec</i>			Polhemus, D.A.	2002	Papua New Guinea	Milne Bay Province
<i>Wahnesia spec</i>			Polhemus, D.A.	2002	Papua New Guinea	Milne Bay Province
<i>Wahnesia spec</i>			Richards, S.	2002	Papua New Guinea	mainland
<i>Wahnesia spec</i>			Gassmann, D.	1997	Papua New Guinea	Morobe Province
<i>Wahnesia spec</i>			Gassmann, D.	1997	Papua New Guinea	Morobe Province

Table 2. Primer combinations used for amplification of 16S and 28S.

Primer name	Target	Direction	Sequence (5' to 3')
ODO_28S_f2_2	28S	F	CCCGGCCGGGTCCCCGACGGT
ODO_28S_r2_p3	28S	R	TTACACACTCCTTAGCGGATTC
ODO_28S_f3	28S	F	ACCATGAAAGGTGTTGGTTG
ODO_28S_r3_p3	28S	R	ATCTCCCTGCGAGAGGATTC
ODO_12852F	16S	F	AGAAACCGACCTGGCTTAAA
ODO_13393R	16S	R	CGCCTGTTTATCAAAAACAT

ML analyses were run with RA×ML (Stamatakis et al. 2008) using a Gamma model of rate heterogeneity. For the BI, the best-fitting nucleotide substitution model for each of the individual fragments was assessed using hierarchical likelihood ratio tests in MrModeltest 2.3 (Nylander 2004). For all partitions a General Time Reversal (GTR+I+G) model (nst=6) with a proportion of invariable sites and a gamma distribution for rates across sites (rates=invgamma) was selected. For each dataset two independent Monte Carlo Markov Chain simulations were run in MrBayes 3.2.1 (Huelsenbeck & Ronquist 2001) with four chains, for 10,000,000 generations and a sample frequency of 500 at a temperature of 0.05. A damselfly belonging to the basal superfamily Lestoidea was selected as representative outgroup (*Lestes virens*, Lestidae).

RASP (Yu et al. 2013) was used for a reconstruction of the ancestral ranges of the genera using the nine regions listed in fig. 3 as possible areas of distribution. RASP favored a scenario in which early dispersion resulted in a common ancestor occurring throughout most of the region under study with subsequent vicariance events leading to the distribution as observed today. This scenario is deemed unlikely and is regarded the result of

RASP preferring scenario's in which the number of dispersal events needed is limited. We therefore choose to discard the outcomes of RASP and present a reconstruction of the ancestral ranges based on common sense.

We refrained from molecular dating as no suitable fossils are available for calibration and simply applying a standard diversification rate of, for instance, insects, is problematic due to the presumed old age of the group. Calibration based on geological events would introduce circularity to our biogeographic reasoning.

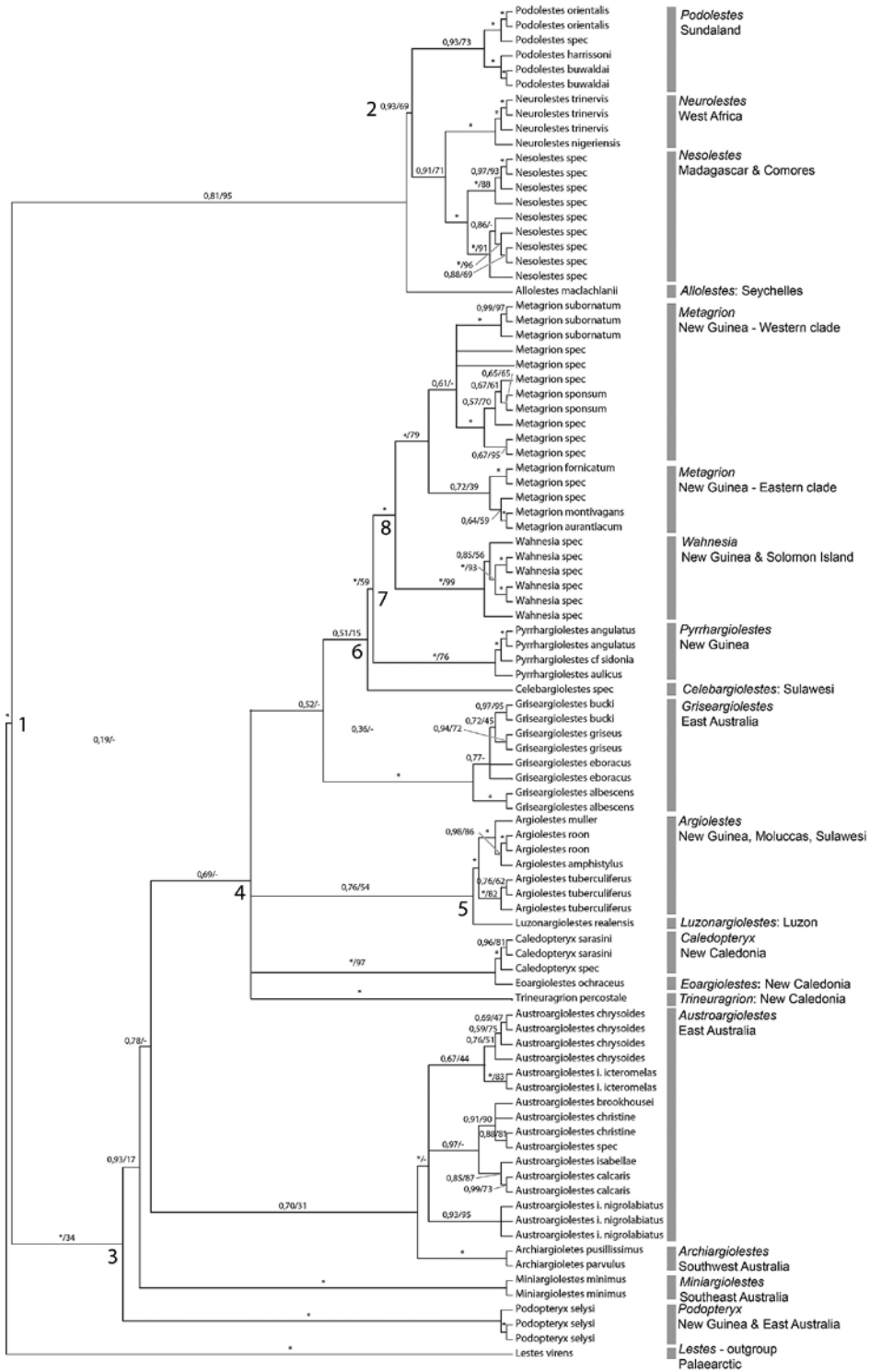
Distribution data

Kalkman & Theislinger (2013) presented dot maps of the distribution of the genera based on both published and unpublished records. The main sources for these maps and the maps published here are the Australian Odonata Database, the Malesian Odonata Database and the Odonata Database of Africa.

RESULTS

Final maximum likelihood and Bayesian trees have very similar topologies with most clades

Figure 2. Bayesian consensus tree for Argiolestidae derived from 2033 bp of 16S and 28S with branches proportionally transformed. Bayesian posterior probabilities and maximum likelihood bootstrap supports are given for all interspecific nodes respectively. Those which are 1.00 or 100 are given with an asterisk. Branches with a Bayesian posterior probability below 0.50 are collapsed. Region of occurrence is given on right. Locality and specimen details are provided in Table 1. Numbered nodes are discussed in the text and are identical to figure 3.



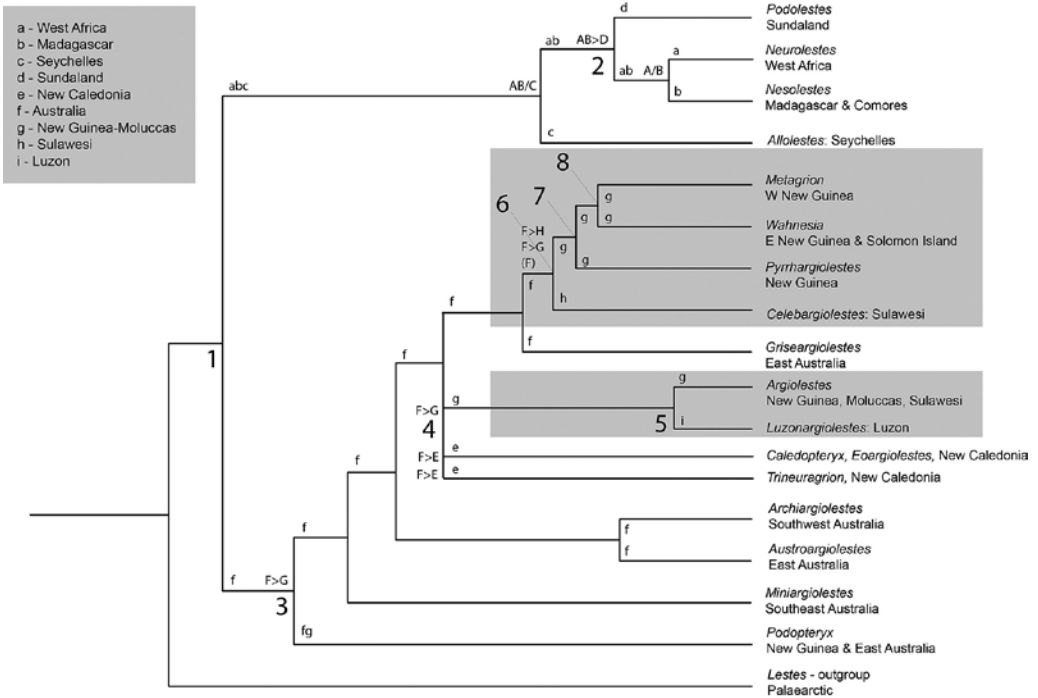


Figure 3. Summary of the phylogeny of argiolepid genera and biogeographic hypothesis. The distribution of each clade is given in lower case letters (see legend in box). The processes thought to be responsible for divergence are given in bold with the upper case letters referring to the recognized areas of distribution. An arrow (>) indicates dispersal between region (either active or passive), a dash indicates fragmentation between regions and parentheses refers to extinction. Speciation within the recognized areas is not indicated. Numbered nodes are discussed in the text and identical to figure 2. The two groups on which the discussion mainly focuses are highlighted in grey.

well supported (fig. 2). Figure 3 gives a summary showing only the branches up to genus level. The one major difference between both analyses is that the origin of the clade of *Austroargiolestes*/*Archiargiolestes* is placed between that of *Griseargiolestes* and *Celebargiolestes* in the maximum likelihood analyses. The phylogeny is well resolved except for a polytomy including clades from New Caledonia, New Guinea to the Philippines and the Australian *Griseargiolestes*. These clades themselves are well supported but due to the polytomy the order in which these groups split off remains unclear. Both the Bayesian analyses and the maximum likelihood retrieve the two subfamilies and the 18 included genera as monophyletic,

corresponding with the revision by Kalkman & Theischinger (2013). For most genera unique morphological characters are available, allowing the placement of species not included in the molecular analysis.

DISCUSSION

The origin of Malesian lineages

The distribution of the two subfamilies best matches a Gondwanan origin in which the group evolved in the region Australia-Antarctica-Africa when these continents were still connected, followed by a split between the Podolestinae

(presently found in Africa and Asia) and Argiolestinae (Australasia) induced by the northward drift of Africa, India and Madagascar (node 1 in fig. 2 and 3). Trans-oceanic dispersal between Africa and Australia would account for the same pattern and cannot be ruled out, as dating of the phylogeny is not possible due to the lack of calibration points. Dispersal between Africa and Australia has been suggested for several groups, including insects (allodapine bees), to explain the divergence between African and Australian taxa after continental breakup (Chenoweth & Schwarz 2011). The tree indicates that the presence of the family in the Philippines, eastern Indonesia and New Guinea results from colonization from Australia and not Asia. The Asian *Podolestes* is the sister genus of the African genera and must have arrived either by drift on the Indian plate or by an overland route after Africa connected with Eurasia (node 2), as has also been suggested for the family Platystictidae (van Tol 2009). The dispersal of possibly Gondwanan derived taxa from India after it docked with the Asian mainland into Sundaland followed by radiation across Sundaland has been suggested for various groups of freshwater crabs and the giant river prawn (*Macrobrachium rosenbergii*) (Klaus et al. 2009, de Bruyn et al. 2004). The fossil larva in Baltic amber indicates that the conditions in northern Europe were favorable for the Argiolestidae during the Eocene (Bechly & Wichard 2008) and thus an expansion from Africa over Europe and Asia is also a possibility. Both subfamilies of Argiolestidae nearly meet, with Argiolestinae found in Sulawesi (genus *Celebargiolestes*) and Podolestinae in Borneo (genus *Podolestes*) separated by less than 150 km of sea. Since their last common ancestor these groups have dispersed across the distance of Asia, Africa and Australia including the IAA. Interestingly, they failed to cross the Makassar Strait although this seems a relatively small barrier. The genera living on the opposite sites of the Makassar Strait have different habitat preferences (streams versus swamps) suggesting that it is the barrier itself and not the competition by congeners that prevented them from crossing.

The role of the Melanesian Arc System and the East Papua Composite Terrane

The presence of Argiolestinae beyond Australia is probably the result of one range expansion to Sulawesi (*Celebargiolestes*, node 6), one or two to New Caledonia and three to areas presently part of New Guinea (*Podopteryx*, *Argiolestes-Luzonargiolestes*, PWM-group, nodes 3, 4, 6, respectively). Two *Podopteryx* species are endemic to New Guinea and the Aru Islands, while one is found in New Guinea and north-eastern Australia. Presumably ancestors of the genus colonized New Guinea and subsequently diversified, with one species (*P. selysi*) crossing the Torres Strait back to Australia. This is the only species and even genus of Argiolestidae shared by New Guinea and Australia despite a broad land connection for much of the Pleistocene (Voris 2000). The absence of exchange across this landbridge is apparent in all dragonflies: the seasonal drought associated with the monsoon climate acted as a filter allowing passage only of species breeding in standing (i.e. less stable) water (Kalkman & Orr 2012). A similarly limited exchange has been noted for freshwater fish and some groups of aquatic beetles (Unmack 2001, Balke et al. 2007), although exchange may have been more common for aquatic groups that are salt tolerant or less dependent on running water (Balke 1995, Macqueen et al. 2010). *Podopteryx* is the only genus of the subfamily Argiolestinae not depending on running water, which might explain its unique distribution.

The results are unclear about the origin of *Celebargiolestes* (node 6), a genus widespread on Sulawesi with one described and several closely related undescribed species, all of which have allopatric ranges (fig. 4). The genus groups with low support with a clade of three Papuan genera whose origin lies in the east of New Guinea (the PWM-group discussed below). A scenario where the common ancestor colonized areas presently included in the east of New Guinea and from there Sulawesi (or the other way round) seems unlikely as the group is largely absent in between. The alternative is that they share an extinct

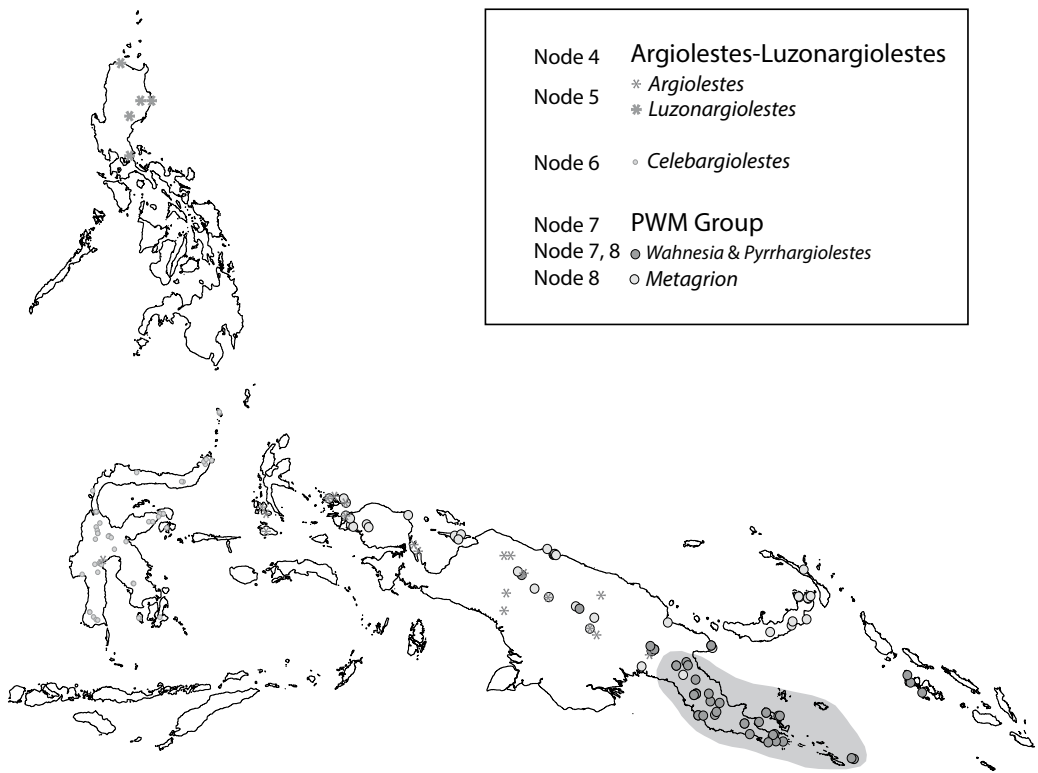


Figure. 4. Distribution of three of the four lineages that colonized the eastern part of the Malay Archipelago: (1) *Celebargiolestes*, confined to Sulawesi and adjacent islands; (2) *Argiolestes-Luzonargiolestes*, the western two-thirds of New Guinea, northern Moluccas, Sulawesi and Luzon; (3) PWM-group (*Pyrrhargiolestes*, *Wahnesia*, *Metagrion*), with two genera largely confined to the East Papuan Composite Terrane and one genus found in the western two-thirds of New Guinea (see also fig. 5). The grey shading indicates the extent of the East Papuan Composite Terrane (EPCT).

common ancestor, which was found in the north of Australia and whose descendants, during separate events, colonized the eastern parts of New Guinea and Sulawesi. A meta-analysis of divergence dates of 20 different taxonomical groups occurring in Sulawesi showed that the majority of these postdate relevant tectonic vicariant events, suggesting that they arrived on Sulawesi by dispersal, whereas only 20% of the analyzed taxa showed divergence dates old enough to allow for the possibility of tectonic dispersal (Stelbrink et al. 2012). In the case of *Celebargiolestes* the current phylogeny does not allow to distinguish between dispersal or vicariance, although the allopatric ranges of the species suggest a relative recent arrival of the genus.

The main diversity of Argiolestidae on New Guinea consists of two lineages, the ancestors of which colonized the island from Australia, resulting in two strikingly different distributional patterns (nodes 4, 6). The monophyletic group consisting of *Pyrrhargiolestes*, *Wahnesia* and *Metagrion* (PWM-group) is confined to New Guinea and surrounding islands with one species occurring in the Solomons. Whilst *Metagrion* occurs throughout most of the island (fig. 4), the distribution of *Wahnesia* and *Pyrrhargiolestes* (node 7) is concentrated in eastern New Guinea in an area largely corresponding with the East Papuan Composite Terrane (EPCT). This terrane is by some authors inferred to have formed around 60 Ma by the accretion of several sub-terrane

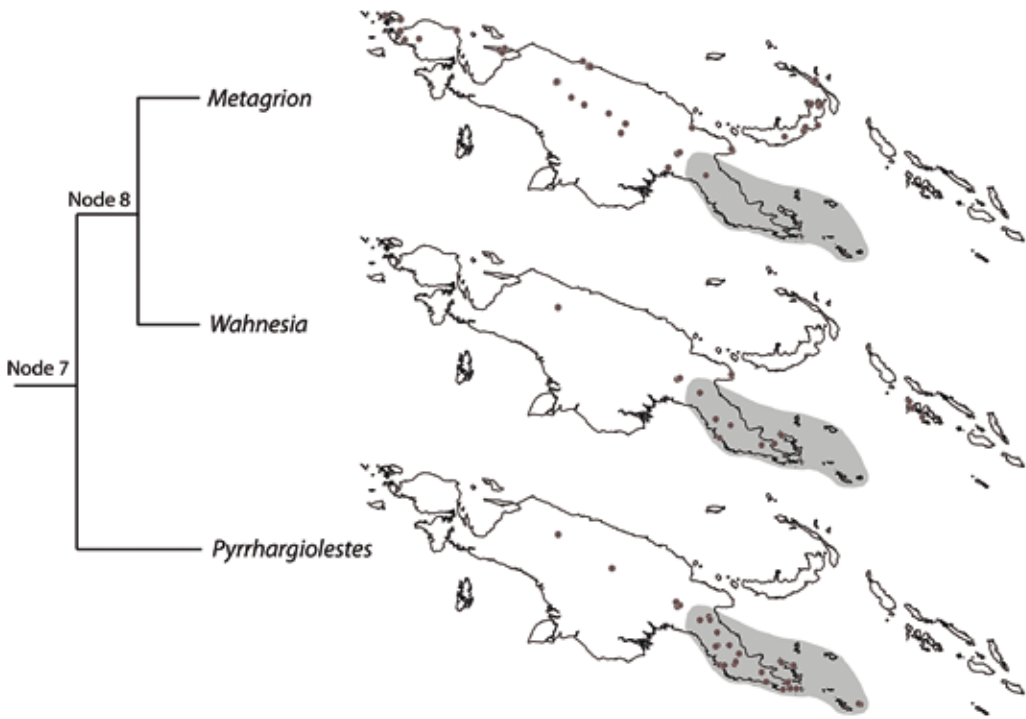


Figure. 5. Distribution of the three genera whose origin is supposed to be linked to the East Papuan Composite Terrane (EPCT; grey shading). The distributions of both *Pyrrhargiolestes* and *Wahnesia* suggest that these evolved when the EPCT formed a separate island.

and is believed to have existed as a separate island for at least 25 Ma before suturing on mainland New Guinea at 28–22 Ma (Pigram & Davies 1987, Davies et al. 1996, Davies et al. 1997, Hill & Hall 2003, Polhemus & Polhemus 2004). Based on distribution patterns the EPCT has been recognized as an important centre of endemism for various groups of aquatic Heteroptera and Coleoptera. This centre of endemism was linked to its history as a separate landmass although no phylogenetic support was provided (Polhemus & Polhemus 1998, 2002, 2004, Polhemus 2011). A plausible scenario for the PWM-group is that an ancestor reached the EPCT when it still formed a separate island, which subsequently radiated to the 60 to 80 species presently forming the three genera.

Species of *Wahnesia* and *Pyrrhargiolestes* largely failed to colonize the main island of New Guinea, with only two of the 19 described species and none of the undescribed species found more than 100 km outside the EPCT (fig. 5). *Metagrion* (node 8 in fig. 3) consists of two clades of which one is found in the western part of the EPCT and the adjacent Huon Peninsula and Bismarck Archipelago (the *Metagrion* PNG-group of Kalkman & Theischinger 2013). The other clade is found throughout New Guinea except the EPCT. This pattern suggests that a range expansion from the EPCT into New Guinea led to the rise of one of the most species-rich genera of damselflies currently found on New Guinea. Our molecular analyses gives support to the idea that the EPCT has been

an important source area for the fauna of New Guinea, although a dated phylogeny is needed in order to determine if this diversification took place before or after it docked to New Guinea.

The other lineage, which makes up a large part of the argiolestine diversity of New Guinea, has a completely different distribution (fig. 4). It consists of two genera, of which *Luzonargiolestes* is restricted to the northern Philippine island of Luzon, and *Argiolestes* is found on Sulawesi (one species), the northern Moluccas (two species) and New Guinea (seven species). The occurrence of related species or genera on New Guinea and the Philippines, often including the northern Moluccas and sometimes Sulawesi, has been noted for several groups including aquatic bugs (Polhemus & Polhemus 1987, Polhemus 1995). Molecular studies confirm this recurrent pattern in birds (Jønsson et al. 2011), mammals (Steppan et al. 2003, Heaney et al. 2005, Jansa et al. 2006) and the myrtle family (Ladiges et al. 2003). Its origin is believed to lie in a series of arc systems, which during the Late Oligocene to Miocene (25 to 10 Ma) provided a pathway between the Philippine and Indonesian archipelagoes (Kroenke 1984, Hall, 2002, Hill & Hall, 2003, with summaries in Polhemus 2007, van Tol & Gassmann 2007). The islands that today make up the northern Moluccas were north of mainland New Guinea 30 Ma, with directly east of them a series of islands that are now part of northern New Guinea, and directly west a series of islands that now form the eastern Philippines. This island arc rotated clockwise so that by 15 Ma the northern Moluccas were close to the northwest of New Guinea, while some of the islands east of it moved south towards the northern margin of New Guinea and the eastern Philippines drifted northwards. In the next millions of years the distance between the northern Moluccas and the eastern Philippines grew, while the eastern islands docked with New Guinea, where they are currently recognizable as a northern mountain chain. The tectonic reconstruction suggests that for millions of years this arc formed a semi-continuous series of

islands. Assuming that most of these were above sea-level, these may have served as stepping stones allowing faunal exchange between the Philippines and New Guinea. Taxa with limited dispersal capacity, unable to hop between islands, may still have been transported gradually by the rotating movement of the island arc: *Argiolestes* and *Luzonargiolestes* seem to be an example of this. There are various other groups of dragonflies that show close links between New Guinea and the Philippines and the Oligocene-Miocene arc systems might have played a major role in their biogeography as well. Examples include the *Rhinocypha tincta*-group (Chlorocyphidae), *Diplacina* (Libellulidae), the *Drepanosticta lymetta*-group (Platystictidae), the subfamily Idiocnemidinae (Platynemididae) and possibly *Neurobasis* (Calopterygidae) (Gassmann 2005, Orr & Hämäläinen 2007, van Tol 2007, van Tol & Gassmann 2007). It is interesting to note that the genus *Argiolestes* failed to colonize the EPCT, which suggests that at the time that the EPCT sutured with New Guinea most appropriate niches were already occupied, preventing *Argiolestes* from expanding east and *Pyrrhargiolestes* and *Wabnesia* from expanding west.

ACKNOWLEDGEMENTS

Specimens and DNA samples were received from Dirk Gassmann, Andre Gunther, René Hoess, Milen Marinov, Henk van Mastrigt, John Michalski, Steffen Oppel, Steve Richards, Kay Schütte and Jan Taylor. Fieldwork in Australia and New Guinea was made possible due to grants from the Uyttenboogaart-Eliassen Foundation and Schure-Beijerinck-Popping Fund (KNAW).

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Part 4

Nederlandse samenvatting en curriculum vitae

SAMENVATTING EN LEESWIJZER

DE VERWANTSCHAPPEN EN BIOGEOGRAFIE VAN JUFFERS (ODONATA), MET SPECIALE AANDACHT VOOR DE ARGIOLESTIDAE

Leeswijzer

Tijdens de start van dit project in 2006 werd de familienaam Megapodagrionidae gebruikt voor een groep van 260 soorten behorende tot 39 verschillende genera. Al snel bleek dat het nodig was de familie op te delen in meerdere families. De betekenis van de naam Megapodagrionidae is daardoor in de loop van het project veranderd. In deze samenvatting wordt met Megapodagrionidae *sensu lato* de groep aangeduid zoals die was op het moment dat de studie begon. Bij de nieuwe indeling ging de naam Megapodagrionidae over op een relatief kleine groep (3 genera, 29 soorten) van Zuid-Amerikaanse soorten die in deze samenvatting wordt aangeduid als Megapodagrionidae *sensu stricto*.

DIVERSITEIT EN BESCHERMING

Hoofdstuk 1.

De mondiale diversiteit van libellen

Kalkman, V.J., V. Clausnitzer, K.-D.B. Dijkstra, A.G. Orr, D.R. Paulson & J. van Tol 2008. Global diversity of dragonflies (Odonata) in freshwater. – *Hydrobiologia* 595: 351-363.

Dit hoofdstuk is oorspronkelijk geschreven voor de Freshwater Animal Diversity Assessment (FADA) en is gepubliceerd in een meer dan 600 pagina's dik overzicht van de mondiale diversiteit van zoetwaterdieren en -planten (Balian et al. 2008). Het artikel geeft een korte samenvatting van de levenswijze van libellen en hun diversiteit en bevat een beschrijving van de belangrijkste verspreidingspatronen per biogeografische regio (Palearctisch gebied, Nearctische gebied, Neotropisch gebied, Afrotropisch gebied, Oriëntaals gebied, Australaziatisch gebied, Pacifisch gebied, Antarc-tisch gebied). Centraal in het hoofdstuk staat een

tabel met daarin per familie en per biogeografische regio het aantal beschreven soorten en genera. In totaal waren er ten tijde van de publicatie 5.680 soorten, verdeeld over 642 genera bekend. Hiermee zijn libellen ten opzichte van veel andere insectengroepen relatief soortenarm. De grootste diversiteit aan libellen is aanwezig in de tropen, waarbij opvalt dat de tropen van Amerika en Azië bijna twee maal zo rijk zijn als die van Afrika. Een belangrijke reden daarvoor is de reductie van het tropisch regenwoud in Afrika tijdens de glacialen. Opvallend is voorts het sterke verschil in diversiteit tussen Europa en Noord-Amerika, iets wat grotendeels veroorzaakt wordt door de sterke negatieve invloed die IJstijden op Europa hebben gehad. Per regio hebben de auteurs een schatting gemaakt van het aantal nog onbeschreven soorten (1085-1425 in totaal). Sinds 1970 worden er gemiddeld 38 soorten per jaar beschreven. Naar schatting zal tegen 2030 meer dan 95% van de libellen beschreven zijn.

Hoofdstuk 2.

De mondiale beschermingsstatus van libellen

Clausnitzer, V., V.J. Kalkman, M. Ram, B. Collen, J.E.M. Baillie, M. Bedjanič, W.R.T. Darwall, K.-D.B. Dijkstra, R. Dow, J. Hawking, H. Karube, E. Malikova, D. Paulson, K. Schütte, F. Suhling, R. Villanueva, N. von Ellenrieder & K. Wilson 2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. – *Biological Conservation* 142: 1864-1869.

De in 1992 gesloten Convention on Biological Diversity (CBD) streefde naar een significante reductie van het verlies aan biodiversiteit in 2010. De doelstelling van de CBD was heel duidelijk, minder duidelijk was hoe deze gemeten moest worden. Om hier verandering in aan te brengen is de International Union for the Conservation of Nature (IUCN) in 2007 begonnen met het opzetten van een meetnet voor de wereldwijde biodiversiteit. Libellen zijn een van de groepen die deel uit maken van deze Red List Species Index.

Voor 1500 random geselecteerd libellensoorten (26 procent van het totaal) werd de mondiale status bepaald op basis van IUCN-criteria. Dit is gedaan door een groep van twaalf internationale specialisten en werd gecoördineerd door de voorzitters van de IUCN dragonfly specialist group (Viola Clausnitzer, Vincent Kalkman) in samenwerking met de Zoological Society of London en IUCN. Ongeveer 10 procent van de 1500 beoordeelde soorten bleek bedreigd te zijn. Relatief veel bedreigde soorten komen voor op eilanden in de Filipijnen, Indonesië en op Sri Lanka, allemaal plaatsen met veel soorten met kleine verspreidingsgebieden en een hoge bevolkingsdichtheid. Daarnaast bleken veel soorten in Australië bedreigd door de gevolgen van klimaatverandering. Uit een vergelijking tussen de biotoopvoorkeur van bedreigde en niet-bedreigde soorten bleek dat soorten van stromend water sterker bedreigd zijn dan die van stilstaand water. Dit kan deels verklaard worden doordat soorten van stilstaand water over het algemeen een grotere verspreiding hebben en vaak beter in staat zijn nieuwe biotopen te (her)koloniseren. De resultaten worden beïnvloed door het hoge aantal soorten waarvan te weinig informatie beschikbaar is om een reële inschatting van hun status te geven (35 procent). Het gaat daarbij vooral om soorten van tropisch regenwoud die voorkomen in slecht onderzochte regio's (bijvoorbeeld Madagaskar) of om soorten die zich moeilijk laten vangen.

TAXONOMIE EN FYLOGENIE

Hoofdstuk 3.

De taxonomie van Megapodagrionidae met nadruk op de larven

Kalkman, V.J., C.Y. Choong, A.G. Orr & K. Schütte 2010. Remarks on the taxonomy of Megapodagrionidae with emphasis on the larval gills (Odonata). – International Journal of Odonatology 13: 119-135.

Het werk aan dit proefschrift richtte zich oorspronkelijk op de taxonomie en biogeografie van

de Megapodagrionidae *sensu lato*. Taxonomie richt zich grofweg op twee zaken: (1) het goed beschrijven van de soorten zodat deze voor andere herkenbaar zijn en (2) het indelen van soorten in groepen die een weergave zijn van hun onderlinge verwantschap. Bij dat laatste wordt gestreefd naar monofyletische groepen (alle soorten die afstammen van een gedeelde voorouder). Lange tijd werd gedacht dat de vleugeladering van libellen betrouwbare informatie geeft over de verwantschap en veel soorten van de Megapodagrionidae *sensu lato* waren oorspronkelijk in deze familie geplaatst op basis van vleugeladering. Bij de start van de werkzaamheden aan dit proefschrift was het al duidelijk dat de gebruikte indeling niet klopte en dat de groep een bewerking moest ondergaan. Het aantal soorten in de familie en hun diversiteit in uiterlijke kenmerken was echter zo groot dat niemand een idee had hoe de groep moest worden ingedeeld of zelfs maar wist waar te beginnen. Omdat de kenmerken van de volwassen exemplaren geen nieuw inzicht gaven werden de larven bestudeerd. Daarvoor hebben we een overzicht gemaakt van alle literatuur waarin larven van soorten behorende tot de Megapodagrionidae *sensu lato* beschreven worden. De larven van juffers hebben kieuwen aan het achterlijf die vaak per familie verschillen en daarom inzicht geven in hun verwantschap. Met behulp van de vorm van deze kieuwen komt het artikel tot een indeling in vier groepen, Long-legged megapods (de huidige Megapodagrionidae *sensu stricto*), de Fan megapods (nu Argiolestidae), Tube megapods (de huidige Philosinidae) en de Balloonmegapods. De variatie in de vorm van de kieuwen bleek overeen te komen met de aanwezigheid van stekels op de ligula (de functionele penis). Hierdoor werd het mogelijk de vorm van de kieuwen te voorspellen van genera waarvan de larve niet bekend was. Van de Long-legged, de Tube en de Fan megapods werd in het artikel vastgesteld dat ze monofyletisch zijn, terwijl dit voor de Balloon megapods niet kon worden aangetoond. Het artikel heeft geleid tot een toename in de interesse in de larven van Megapodagrionidae en vanaf 2010 zijn van acht genera de larven voor het eerst beschreven (*Allopodagrion*, *Heteropoda-*

grion, *Mesagrion*, *Nesolestes*, *Philosina*, *Podolestes*, *Pseudolestes*, *Trineuragrion*). Met uitzondering van de zeer aberrante *Pseudolestes mirabilis* bleken de in dit artikel gedane voorspellingen over de vorm van de kieuwen bij de op dat moment nog niet beschreven genera correct. De moleculaire fylogenie gepresenteerd in hoofdstuk 7 komt goed overeen met de indeling op basis van larven.

Hoofdstuk 4.

Revisie van de genera van Argiolestidae

Kalkman, V.J. & G. Theischinger 2013. Generic revision of Argiolestidae (Odonata), with four new genera. – International Journal of Odonatology 16: 1-52.

In dit hoofdstuk wordt een overzicht gegeven van de genera van de Argiolestidae. Deze familie maakte voorheen deel uit van de Megapodagrionidae *sensu lato*. Op basis van de kenmerken van de larven (Hoofdstuk 4) en de moleculaire analyse (Hoofdstuk 8) waren we tot de conclusie gekomen dat deze groep in een eigen familie geplaatst moest worden. Per genus bevat het hoofdstuk een overzicht van de karakteristieke kenmerken, informatie over herkenning, biotoop en verspreiding. Dit is geïllustreerd met foto's van de ligula (de functionele penis) gemaakt met een elektronen microscoop, veldfoto's van de adulten, foto's van een selectie van biotopen en kaarten van de verspreiding. Op basis van vormkenmerken zijn we gekomen tot een indeling in twintig genera. Vier worden in het artikel voor het eerst beschreven en twee, gesynomiseerde en in vergetelheid geraakte genera, worden in ere hersteld. De nieuw beschreven genera betreffen *Eoargiolestes* (Nieuw-Caledonië), *Luzonargiolestes* (Filippijnen), *Solomonargiolestes* (Bougainville en Solomon eilanden) en *Pyrrhargiolestes* (Nieuw-Guinea). Op basis van details in de ligula wordt de familie in twee subfamilies verdeeld: de Argiolestinae van de Australaziatische regio en de Podolestinae van Afrika en Zuidoost Azië. Informatie over de biotoop is van bijna alle soorten oppervlakkig of geheel afwezig. Over het algemeen kan gesteld worden dat ze voorkomen in

bos bij beekjes en soms bij rivieren, hoewel enkele Australische soorten te vinden zijn in meer open alpiene gebieden en enkele Aziatische soorten in moerasbos. Een markante uitzondering is *Podopteryx* waarvan de larven in met water gevulde boomholtes leven. Het is opmerkelijk dat een geslacht afkomstig uit een aan stromend water gebonden familie op zo'n extreem type van stilstaand water overstapt.

Hoofdstuk 5.

Een moleculaire stamboom van juffers

Dijkstra, K.-D.B., V.J. Kalkman, R.A. Dow, F.R. Stokvis & J. van Tol 2013. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). – Systematic Entomology, DOI: 10.1111/syen.12035

In dit hoofdstuk wordt een reconstructie van de verwantschappen van de juffers gepresenteerd. Uit de meer dan 5.000 van libellen beschikbare DNA-monsters is een selectie gemaakt van 356 monsters behorende tot 298 soorten en 184 genera. Daaronder bevinden zich vertegenwoordigers van alle voorheen in gebruik zijnde families met uitzondering van Hemiphlebiidae. De analyses zijn gebaseerd op drie stukken DNA (COI, 16S en 28S) die bij elkaar circa 2530-2730 basenparen lang zijn. De gegevens zijn op drie verschillende manieren geanalyseerd: Bayesian, Maximum Likelihood en Maximum Parsimony. Dit zijn drie methoden die elk op een verschillende manier de verschillen en overeenkomsten in basenparen beoordelen om zo te komen tot een inschatting van de onderlinge verwantschap. De uitkomsten van deze verschillende methoden kwamen sterk overeen waardoor meer zekerheid verkregen werd over de accuraatheid van de reconstructie. De door ons voorgestelde stamboom komt in grote lijnen overeen met eerdere gepubliceerde reconstructies. Eerdere reconstructies waren echter gebaseerd op uiterlijke kenmerken (morfologie) of waren gebaseerd op een geringere en vooral minder evenwichtige selectie van soorten. De door ons gemaakt stam-

boom is daarom vermoedelijk beter en betrouwbaarder. Op basis van de nieuwe gegevens moet de indeling in families worden aangepast. Ten opzichte van de oude indeling worden twee families opgeheven en worden maar liefst elf families toegevoegd hetgeen neerkomt op een uitbreiding van 18 naar 27 families. Ongeveer twintig procent van de juffers verandert hierdoor van familie. Daarnaast wordt een groot aantal genera opgeheven of in ere hersteld en worden meer dan tachtig soorten aan een andere genus toebedeeld. De uitbreiding van het aantal families komt door het opsplitsen van de voormalige families Amphipterygidae en Megapodagrionidae in respectievelijk vijf en acht families. Deze laatste groep wordt opgedeeld in de volgende acht families: Argiolestidae, Heteragrionidae, Hypolestidae, Megapodagrionidae, Philogeniidae, Philosinidae, Pseudolestidae en Thaumatonneuridae. Daarnaast zijn er nog tien genera die eerder tot Megapodagrionidae *sensu stricto* werden gerekend die we momenteel onplaatsbaar achten. Dit zijn allemaal kleine, voornamelijk tropische genera (gemiddeld minder dan vier soorten)

waarvoor in de toekomst mogelijk nog zeven nieuwe families gecreëerd moeten (1: *Amanipodagrion*; 2: *Dimeragrion*, *Heteropodagrion*, *Mesagrion*; 3: *Mesopodagrion*; 4: *Priscagrion*, *Sinocnemis*; 5: *Protolestes*; 6: *Tatocnemis*; 7: *Sciotropis*).

BIOGEOGRAFIE

Hoofdstuk 6.

Het Australische moessongebied als barrière voor dispersie tussen Australië en Nieuw-Guinea

Kalkman, V.J. & A.G. Orr 2012. The Australian monsoon tropics as a barrier for exchange of dragonflies (Insecta: Odonata) between New Guinea and Australia. – *Hydrobiologia* 693: 55-70

Nieuw-Guinea heeft biologen altijd gefascineerd. Het eiland is een van de laatste onontdekte en moeilijk bereisbare wildernissen en heeft een rijke en zeer karakteristieke flora en fauna. Dat laatste

wordt veroorzaakt doordat Nieuw-Guinea een eiland is waar de evolutie kans kreeg om tot geheel eigen eindproducten te komen. De zee tussen Nieuw-Guinea en Australië is ondiep en is tussen Queensland en Nieuw-Guinea slechts 150 km breed en tussen Noordelijk Territorium en Nieuw-Guinea 400 km breed. Gedurende lange perioden in het Pleistoceen was de zeespiegel veel lager en waren Nieuw-Guinea en Australië verbonden door een brede strook land. Tijdens die perioden vormde Nieuw-Guinea het meest noordelijke stukje van Australië. Het is verrassend dat er in die periode relatief weinig uitwisseling tussen beide gebieden is geweest. In dit artikel laten we zien dat de verschillen tussen Australië and Nieuw-Guinea bij libellen heel sterk zijn. Zo delen beide gebieden slechts 50% van de families and subfamilies, slechts 33% van de genera en 8% van de soorten. Nergens anders zijn zulke sterke verschillen te vinden tussen aan elkaar grenzende eilanden of continenten. Deze grote verschillen kunnen slechts deels verklaard worden door het verschil in biotopen tussen in beide deelgebieden. Zowel Australië als Nieuw-Guinea hebben grote oppervlakten met boomsavanne en beide hebben ook tropisch regenwoud, hoewel dat in Australië nu een relatief klein oppervlak beslaat. Het gebrek aan uitwisseling in de periode dat het tussenliggende gebied droog lag wordt vermoedelijk vooral veroorzaakt door het moesson-klimaat in deze regio. Kleine, permanente stromende wateren waren daardoor in het tussenliggende gebied afwezig en zoet water was grotendeels beperkt tot moerassen die grotendeels uitdroogden in de droge tijd en rivieren die in de natte tijd enorm in omvang toenamen. Van de 652 soorten die in Australië en/of Nieuw-Guinea voorkomen is 64% gebonden aan stromend water. Daarentegen heeft slechts één van de 53 soorten die in beide gebieden voorkomt een strikte binding met stromend water. Dit is een verdere aanwijzing dat het moesson-klimaat de uitwisseling tussen Australië en Nieuw-Guinea via de Pleistocene landverbinding heeft belemmerd. Het is echter opvallend dat niet alleen het aantal gedeelde soorten laag is, maar ook heel veel genera of zelfs families slechts in een van beide deel-

gebieden aanwezig zijn. Voorbeelden daarvan zijn Gomphinae, die wijd verspreid voorkomen in noordelijk Australië maar ontbreken in Nieuw-Guinea, en de familie Isostictidae, die in beide deelgebieden voorkomt maar geen gedeelde genera heeft. Dit suggereert dat de scheiding tussen beide gebieden verder terug gaat dan het Pleistoceen. Het moesson-klimaat in Noord Australië en zuid Nieuw-Guinea is waarschijnlijk al 30 miljoen jaar geleden ontstaan en mogelijk heeft het klimaat dus niet alleen in het Pleistoceen een barrière gevormd maar gaat de invloed veel verder terug.

Hoofdstuk 7.

Het belang van de Melanesische eilandenboog en het Oost Papua Microcontinent voor de biogeografie van een aquatisch insectengroep

Kalkman, V.J., K.-D.B. Dijkstra, R.A. Dow, F.R. Stokvis & J. van Tol (submitted). Out of Australia: the Argiolestidae reveal the Melanesian Arc System and East Papua Composite Terrane as possible ancient dispersal routes to the Indo-Australian Archipelago (Odonata, Argiolestidae).

In dit hoofdstuk wordt een reconstructie van de verwantschap van de Argiolestidae gepresenteerd op basis waarvan een schets wordt gegeven van de vermoedelijke geschiedenis van de groep in het gebied ten noorden van Australië. De reconstructie van de verwantschappen is gebaseerd op 91 DNA-monsters van 18 van de 20 bekende genera. Voor de analyse is gebruik gemaakt van de genen 16S en 28S (2033 basenparen in totaal). De stamboom die daaruit komt laat zich lezen als een geschiedenis van de familie waarbij aftakkingen te zien zijn als het moment waarop de voorouders van twee groepen van elkaar gescheiden raakten. Zo'n afsplitsing kan binnen een gebied plaatsvinden (bijvoorbeeld als een groep een andere biotoopvoorkeur ontwikkelt) of kan optreden doordat twee groepen fysiek gescheiden raken (bijvoorbeeld als door verdroging een stuk tussenliggend bos verdwijnt). De bestudeerde familie valt uiteen in twee subfamilies waarvan één voorkomt in Afrika en Zuidoost Azië

(subfamilie Podolestinae), terwijl de andere te vinden is in Australazië inclusief de Filippijnen (subfamilie Argiolestinae). Dit patroon doet vermoeden dat de familie ontstaan is in Gondwana, een megacontinent bestaande uit Zuid-Amerika, Afrika, India, Antarctica en Australië, en dat de afsplitsing van de subfamilie Podolestinae terug gaat op het wegrijven van Afrika en India, ongeveer 130 Ma geleden (Ma = miljoen jaar). De diversiteit van de subfamilie Argiolestinae ten noorden van Australië bestaat voornamelijk uit twee groepen die onafhankelijk van elkaar Nieuw-Guinea hebben bereikt. De huidige verspreiding van een van deze groepen (*Argiolestes-Luzonargiolestes*) is vermoedelijk terug te voeren op het bestaan van enkele eilandbogen die tijdens het late Oligoceen tot het Mioceen (25 tot 10 Ma) als een snoer van eilanden tussen Nieuw-Guinea en de Filippijnen hebben gelegen. Dit snoer van eilanden lag c. 30 Ma ten noorden van Nieuw-Guinea en is sindsdien met de klok mee gedraaid, waardoor eilanden die eerst in de buurt van Nieuw-Guinea lagen nu het oosten van de Filippijnen vormen. Veel dier- en plantengroepen zijn beperkt tot Nieuw-Guinea, de Molukken en de Filippijnen, een verspreidingspatroon wat is terug te voeren op deze eilandboog. De verspreiding van *Argiolestes-Luzonargiolestes* is mogelijk ook op deze wijze ontstaan. De andere groep heeft zijn ontstaan te danken aan de East Papua Composite Terrane (EPCT). Dit is een microcontinent dat vermoedelijk vanaf 60 My (miljoen jaar geleden) geleden ten oosten van het huidige Nieuw-Guinea werd gevormd en pas 25 My geleden tegen Nieuw-Guinea is aangeschoven, waarvan het nu de oostpunt vormt. De stamboom laat zien dat de EPCT eenmalig is gekoloniseerd vanaf Australië waarna speciatie (soortvorming) heeft geresulteerd in het ontstaan van een groot aantal soorten verdeeld over enkele genera. De voorouder van een van die genera heeft vervolgens de overstap gemaakt naar de andere delen van Nieuw-Guinea wat geresulteerd heeft in het ontstaan van een nieuw genus waarvan de soorten voorkomen op de westelijke twee-derde van Nieuw-Guinea. Het was al bekend dat verschillende dier- en plantengroepen

grotendeels beperkt zijn tot het gebied wat behoort tot de EPCT en er werd vermoed dat deze groepen ontstaan waren voordat de EPCT smolt met Nieuw-Guinea. De in dit artikel gepresenteerde stamboom is een eerste onderbouwde aanwijzing dat de EPCT inderdaad een belangrijke bron voor de fauna van Nieuw-Guinea is geweest.

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Vincent Kalkman was born on 9 August 1974 in Hilversum where he finished secondary school in 1996 (HAVO, Comenius College). During his years in secondary school he became member of the Dutch youth organisation for nature study (NJN) which had an important influence on his life. During these years he developed a broad interest in nature with much attention going to birds and plants. He started the study Environmental Technology and Nature management at the Saxion University in Deventer in 1992 and graduated in June 1996 (Ing.). In the same year he was one of the founders of the Dutch dragonfly mapping scheme, serving as editor of the newsletter and in later years as chair. He was one of the founders of the Dutch Dragonfly Association (1997) and chaired this organization during its first years. In the same period he was part of the editorial board (K.-D.B. Dijkstra, V.J. Kalkman, R. Ketelaar and M. van der Weide) of the the book 'De Nederlandse Libellen' which was eventually published in 2002. After his study he moved to Oegstgeest and during these years he started to focus on the dragonflies of Turkey as there was still much to discover in that country while travel was inexpensive. This led to an intensive co-operation with Gert-Jan van Pelt resulting in a series of publication in the period 2001-2006 on dragonflies of Southwest Asia including a checklist, a key to the species and a distribution atlas. Vincent has worked for the European Invertebrate Survey (EIS) since 1997, dividing his time between consultancy projects for NGO's and governmental organizations and supporting volunteer based research projects. Larger international projects he coordinated for EIS include the Red List of Dragonflies for the European Union (2010) and the European atlas

of dragonflies (scheduled for 2014). From 2005 on he became involved in the work of the IUCN dragonfly specialist group being chair in the years 2007-2009 during which several large projects were completed such as the Sampled Red List, an effort of IUCN and the Zoological Society of London to produce a global biodiversity indicator capable of measuring the goals of Convention on Biological Diversity. The finding of a new species of the enigmatic Papuan damselfly genus *Archboldargia* in the collection of the Zoological Museum Amsterdam in 2005 triggered his interested in the dragonflies of New Guinea and brought him in contact with Henk van Mastrigt resulting in 2006 in his first of three collecting trips to New Guinea and a series of papers on this fauna including a field guide to the damselflies of New Guinea together with Bert Orr. He started to consider doing a PhD on tropical dragonflies in 2004 and from 2006 on he devoted much of his spare time to this project. On the suggestion of Jan van Tol the subject of this work became the damselfly family Megapodagrionidae, a choice which in hindsight seems overambitious but which turned out well. In 2012 the Naturalis Biodiversity Center financially supported the project which in early 2013 resulted in the project being completed.

The mixture of travelling and field work had always a great appeal and led to fieldwork in most European countries and a series of trips to Turkey. In the last decade most field time was spent in the tropics with collections or observation made in Australia (2003, 2009, 2011, 2012), Brunei (2003, 2004), China (2005), India (2000), Indonesia (2006, 2008), Malaysia (2002, 2004), Mexico (2009), Namibia (2007), Papua New Guinea (2009), Philippines (2004), South Africa (2007), Thailand (2001). Publications include over 20 science citation indexed papers and another 40 peer-reviewed papers and numerous book chapters and official IUCN-reports. Many of these publications were the result of international co-operations which were often initiated or coordinated by Vincent and resulted in joined publication with over a hundred authors from over twenty countries.

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ACKNOWLEDGEMENTS

During my dragonfly years I have been fortunate to work together with many odonatologist in the world and these co-operations were always both fruitful and pleasant. The collegiality and friendship among odonatologist is one of the many reasons that make working on dragonflies so attractive. My gratitude therefore goes to the odonatological community. A special mention is needed for Albert Orr, Stephen Richards and Gunther Theischinger for their co-operation both in the field and while working on publications. Their shared interest in the dragonfly fauna of

New Guinea has strongly contributed to my motivation to work on the biogeography of the Papuan region. My fellow workers on damselflies and dragonflies at Naturalis – KD Dijkstra, Rory Dow, Dirk Gassmann, Matti Hämäläinen, Yvonne van Nierop, Frank Stokvis and Jan van Tol – all strongly contributed to the projects I worked on. I am grateful for their help and proud to be member of this productive team. KD Dijkstra and Marcel Wasscher are thanked not only for being my paranimfs but especially for being my odonatological companions and friends for the past twenty years.

