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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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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

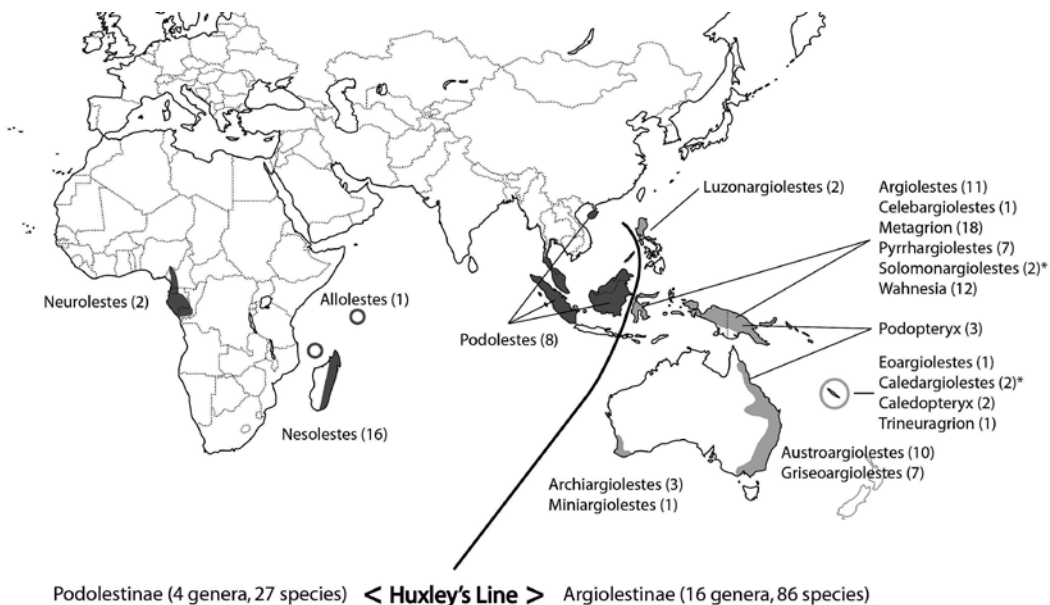


Figure 1. Distribution of Argiolestidae. The number of described species is given between parentheses. No DNA-material was available for the two genera marked with an asterisk.

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 chrysoides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysoides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysoides</i>	(Tillyard)	1913	Orr, A.G.		Australia	Queensland
<i>Austroargiolestes chrysoides</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. & Rando, 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, Tamarau 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.		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.

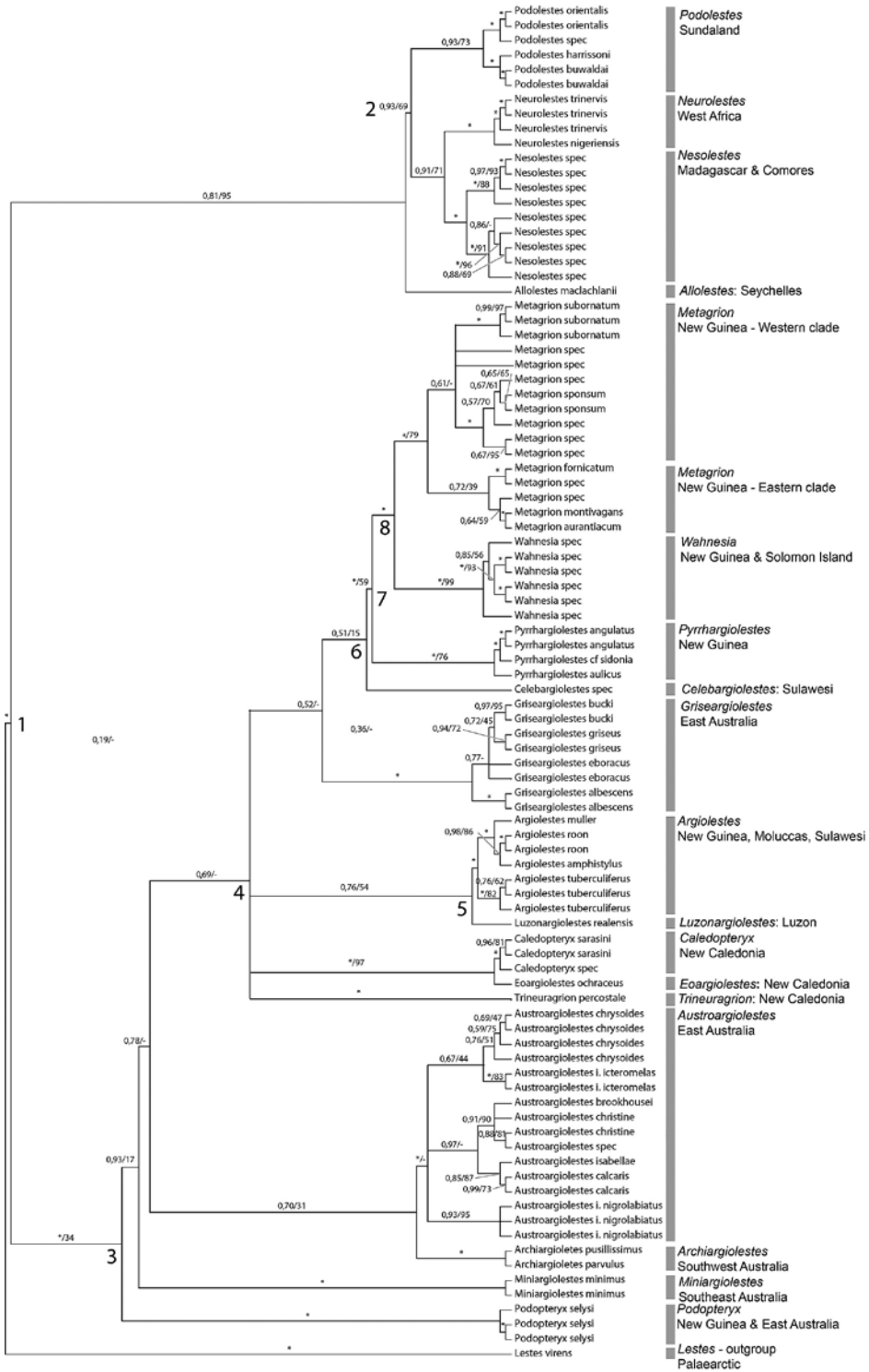
Distribution data

Kalkman & Theischinger (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.



Podolestinae Afrika / Asia

Argiolestinae Australasia

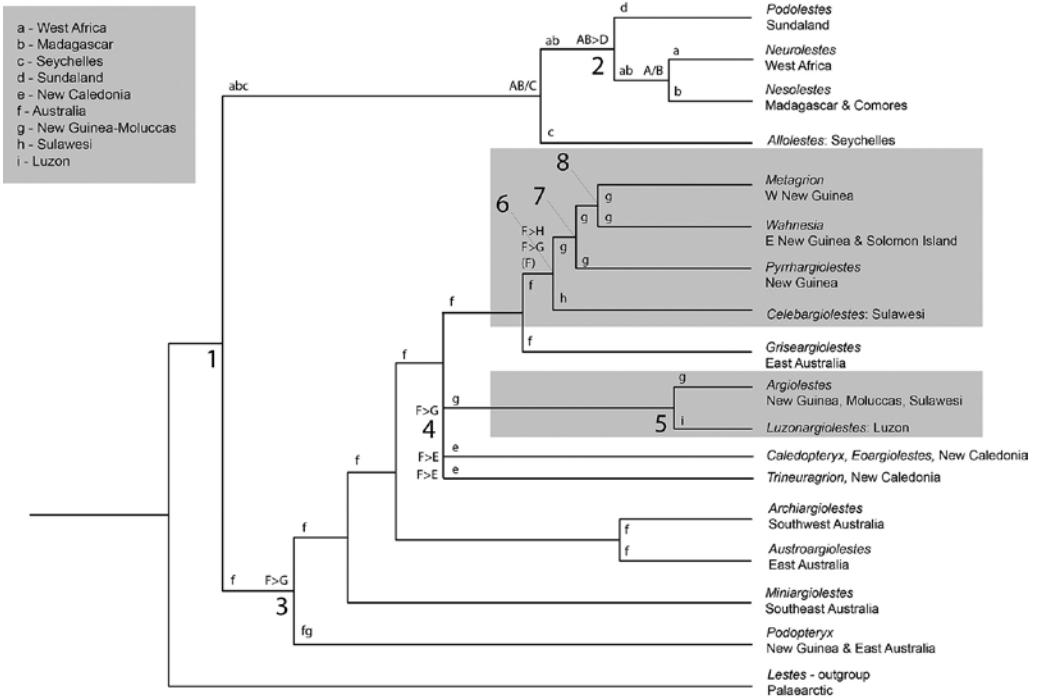


Figure 3. Summary of the phylogeny of argiolepid genera and biogeographic hypothesis. The distribution of each clade is given in lower case letters (see legend in box). The processes thought to be responsible for divergence are given in bold with the upper case letters referring to the recognized areas 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

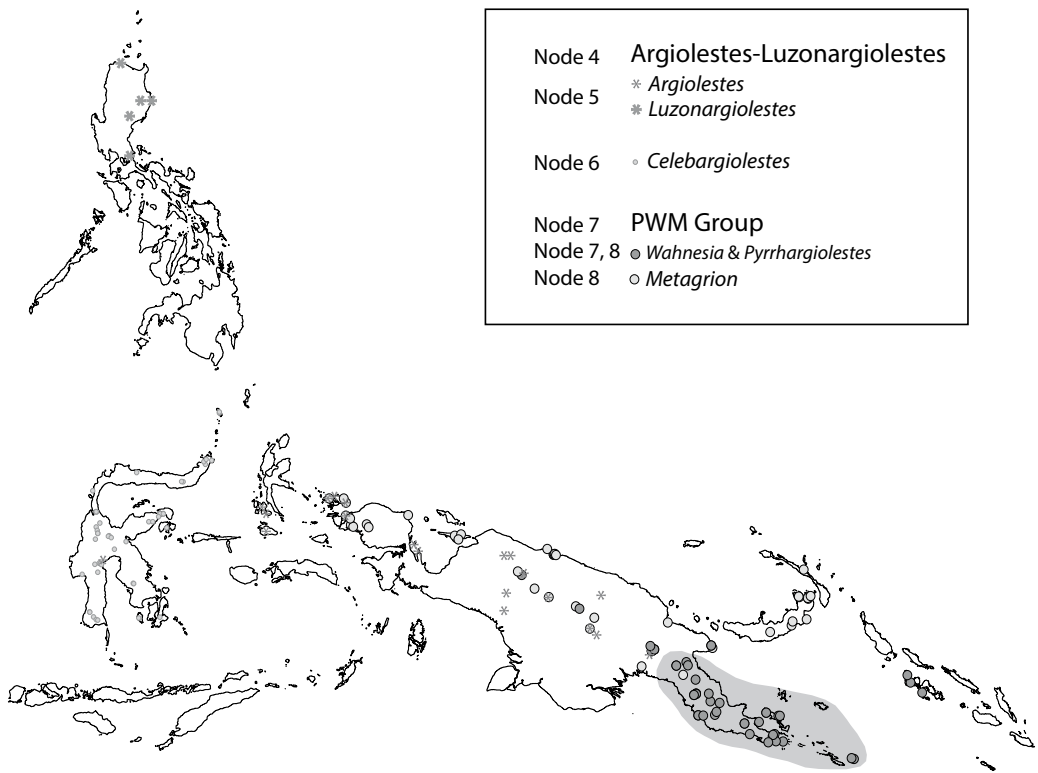


Figure. 4. Distribution of three of the four lineages that colonized the eastern part of the Malay Archipelago: (1) *Celebargiolestes*, confined to Sulawesi and adjacent islands; (2) *Argiolestes-Luzonargiolestes*, the western two-thirds of New Guinea, northern Moluccas, Sulawesi and Luzon; (3) PWM-group (*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

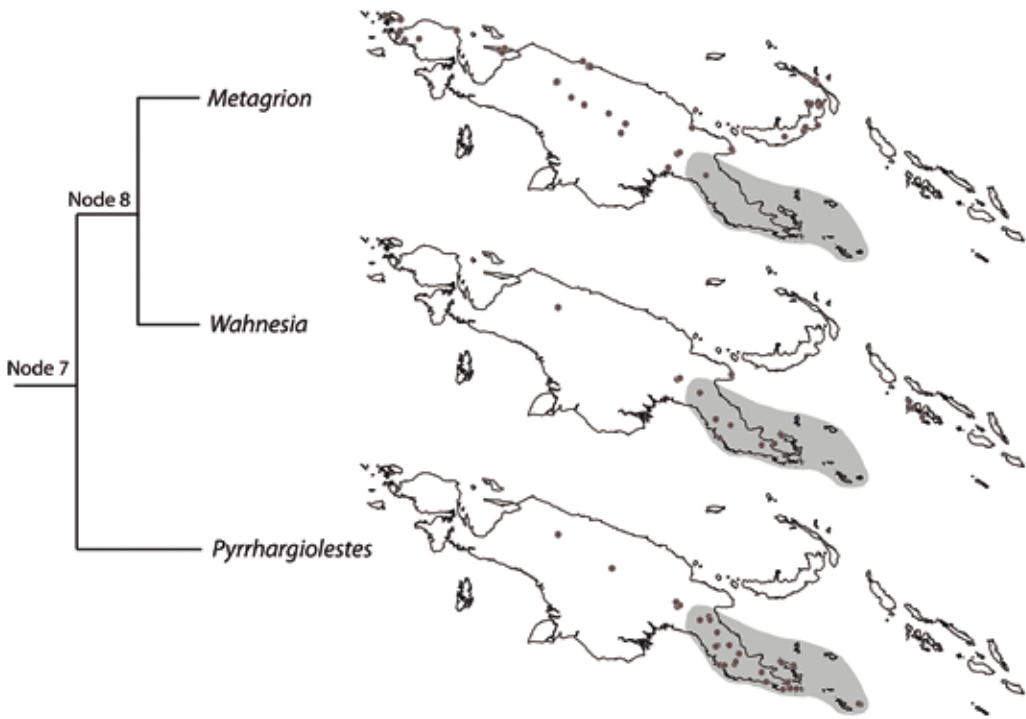


Figure. 5. Distribution of the three genera whose origin is supposed to be linked to the East Papuan Composite Terrane (EPCT; grey shading). The distributions of both *Pyrrhargiolestes* and *Wahnesia* suggest that these evolved when the EPCT formed a separate island.

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.

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