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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 relationships 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 in New Guinea the result of a single colonization event, i.e. are the Argiolestidae found in 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 is 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 islands 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.

Keywords: dragonfly; biogeography; New Guinea; Papuan Peninsula

Introduction

The Indo-Australian Archipelago (IAA) is a transition zone with flora and fauna of both Asian and Australian origin (Lohman et al., 2011). The islands of the Sunda shelf in the west have been connected to mainland Asia for long periods and are strongly dominated by Asian groups. In the east a land bridge connected New Guinea and adjacent islands for long periods with Australia, resulting in a relatively high proportion of taxa of Australian descent (Lohman et al., 2011). Lying between these areas 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

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flora and fauna from dispersal across intervening sea 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, Riddle, Whittaker, & Brown, 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, the larvae of which 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 (de Bruyn, von Rintelen, von Rintelen, Mather, & Carvalho, 2012; van Tol & Gassmann, 2007). 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, K., Glaubrecht, Schubart, Wessel, & von Rintelen, 2010; von Rintelen, K., von Rintelen, & Glaubrecht, 2007; von Rintelen, T., & Glaubrecht, 2006). 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, Albrecht, Hall, & von Rintelen, 2012). Finally, the New Guinea fauna is largely derived from Asia (e.g. crossing Wallacea and/or the Philippines), but whereas land bridges on the Sahul Shelf permitted exchange with Australia of groups of fishes, shrimps and crayfish (Bowman et al., 2010), it seems to have acted as barrier for taxa with a stricter dependence on running freshwater (Balke, Pons, Ribera, Sagata, & Vogler, 2007; Kalkman & Orr, 2012).

Two available phylogenetic reconstructions for the colonization of New Guinea by freshwater insects show very different patterns. The possibly more than 150 species of *Exocelina* diving beetles on New Guinea resulted from a single colonization event during the late Miocene (approximately 8.2 Ma) and is an example of how such rare events can have a major impact on the fauna (Balke et al., 2007; Balke, Ribera, & Vogler, 2004; Toussaint et al., 2014). A detailed reconstruction of the diversification of the genus *Exocelina* on the island showed that the oldest lineages are found in the central mountain range of New Guinea and that from there repeated colonization of lowland area took place (Toussaint et al., 2014). The other available reconstruction of a group of freshwater insects is that of *Rhantus* diving beetles which were shown to have 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 in New Guinea the result of a single dispersal event, i.e. do the argiolestid species of New Guinea form a monophyletic group?

The larvae of Odonata (dragonflies and damselflies) depend on aquatic habitats for their development. The adult stage is winged and some species fly strongly, allowing them cross oceans and colonize habitats on isolated islands (Troast, Suhling, Jinguji, Sahlén, & Ware, 2016). This

capability, however, is largely restricted to species which breed in standing waters. Species of running water, especially in the tropics, usually have low dispersal capacities (Suhling et al., 2015). With around 6000 described species, Odonata constitute almost 5% of all recorded animal diversity in freshwater habitats (Balian, Segers, Lévèque, & Martens, 2008). The highest species and family diversity is found in the tropics, especially those of America and Asia (Suhling et al., 2015). Due to their size and coloration Odonata receive much attention and therefore their taxonomy and 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. Several large phylogenetic studies, based mainly on molecular data, have been published recently (Bybee, Ogden, Branham, & Whiting, 2008; Carle, Kjer, & May, 2008; Dijkstra et al., 2013; Dijkstra, Kalkman, Dow, Stokvis, & van Tol, 2014; Dumont, Vanfleteren, De Jonckheere, & Weekers, 2005; Dumont, Vierstraete, & Vanfleteren, 2010; Fleck et al., 2008; Hovmöller, Pape, & Kallersjo, 2002; Rehn 2003; Ware, May, & Kjer, 2007). Many of these suffer from poor support of the deeper nodes, so that although the phylogeny within most families is well resolved, 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, Hob, & Kjer, 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., 2013). Nonetheless, the group's age, an increased understanding of the phylogeny and detailed distribution data together offer good opportunities for biogeographic reconstructions, even across 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, the first being the Calopterygidae (Dumont et al., 2005). Argiolestidae contains 117 described and an estimated 30–60 undescribed species (Kalkman & Orr, 2013; Kalkman & Theischinger 2013; Theischinger & Hawking, 2006). The family was included in the Megapodagrionidae until recently (Dijkstra et al., 2014; Kalkman, Choong, C. Y., Orr, A. G., & Schütte, 2010). 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 20 genera in two subfamilies, with the Argiolestinae (16 genera, 90 species) found in Australasia east of Huxley's line and the Podolestinae (four genera, 27 species) in Africa and Southeast Asia west of Huxley's line (Figure 1). Although many species of Argiolestidae occur in poorly explored areas, the ranges

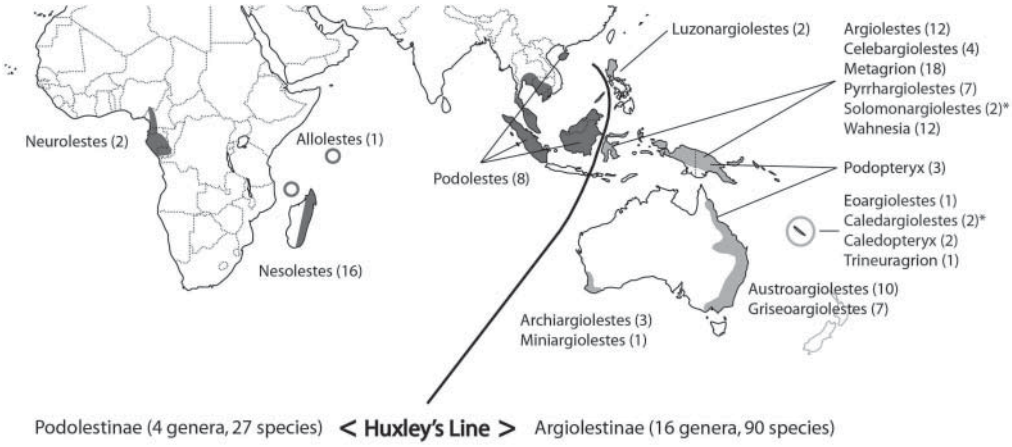

Figure 1. Distribution of Argiolestidae. The number of described species is given in parentheses. No DNA material was available for the two genera marked with an asterisk.

of the genera are considered to be well known (Kalkman & Theischinger, 2013). The family is largely restricted to running waters: most species inhabit seepages or streams, with a few found in rivers. The only genera with a clear preference for standing water 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 exuviae) 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 has flat horizontal caudal gills, a character which is, with the exception of the unrelated genus *Mesopodagrion*, unique to the family.

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 of specimens (see acknowledgments). The DNA material includes 91 samples of over 50 taxa belonging to 18 of the 20 recognized genera (Figure 1, Supplemental Table). With the exception of *Celebargiolestes* all genera with more than three species are represented by samples of at least three different taxa. The genera *Metagrion*, *Nesolestes* and *Wahnesia* are in need of revision and not all material could be identified to species level. No DNA material was available for 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 (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) were amplified using primer combinations developed with Primer3 (Rozen & Skaletsky, 2000). Primer combinations are depicted in Table 1. The 25 µl PCR reaction mixes for 16S contained 2.5 µl of 10 × CoralLoad PCR Buffer (Qiagen), 1 µl of each primer (10 pM), 1.25 U of Taq DNA polymerase (Qiagen), 0.5 µl of dNTPs and 1 µl of DNA template. 5 µl Q-solution (Qiagen) was 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

Table 1. Primer combinations used for amplification of 16SS 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

3730XL sequencer (Applied Biosystems, Carlsbad, California, USA). Taxa were included in the analyses when both 16S and 28S sequences were available. 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, Ann Arbor, MI, USA) and assembled using Bioedit 7.0.9.0 (Hall, T. A., 1999). Geneious Pro 5.6.4 (Biomatters Ltd, Auckland, New Zealand) was used to check 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 listed in the Supplemental Table. 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 (Katoh, Asimenos, & Toh, 2009) under default parameters. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the combined 28S + 16S datasets. ML analyses were run with RAxML (Stamatakis, Hoover, & Rougemont, 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, providing $> 16{,}500$ trees for the consensus after an average standard deviation of split frequencies < 0.01 had been reached. A damselfly belonging to the basal superfamily Lestoidea was selected as representative outgroup (*Lestes virens*, Lestidae) (Figure 2).

RASP (Yu, Harris, & He, 2013) was used for a reconstruction of the ancestral ranges of the genera using the nine regions listed in Figure 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 as the result of RASP preferring scenarios in which the number of dispersal events needed is limited. We therefore choose to discard the outcomes of RASP.

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 antiquity 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 well supported (Figure 2). Figure 3 gives a summary showing only the branches up to genus level.

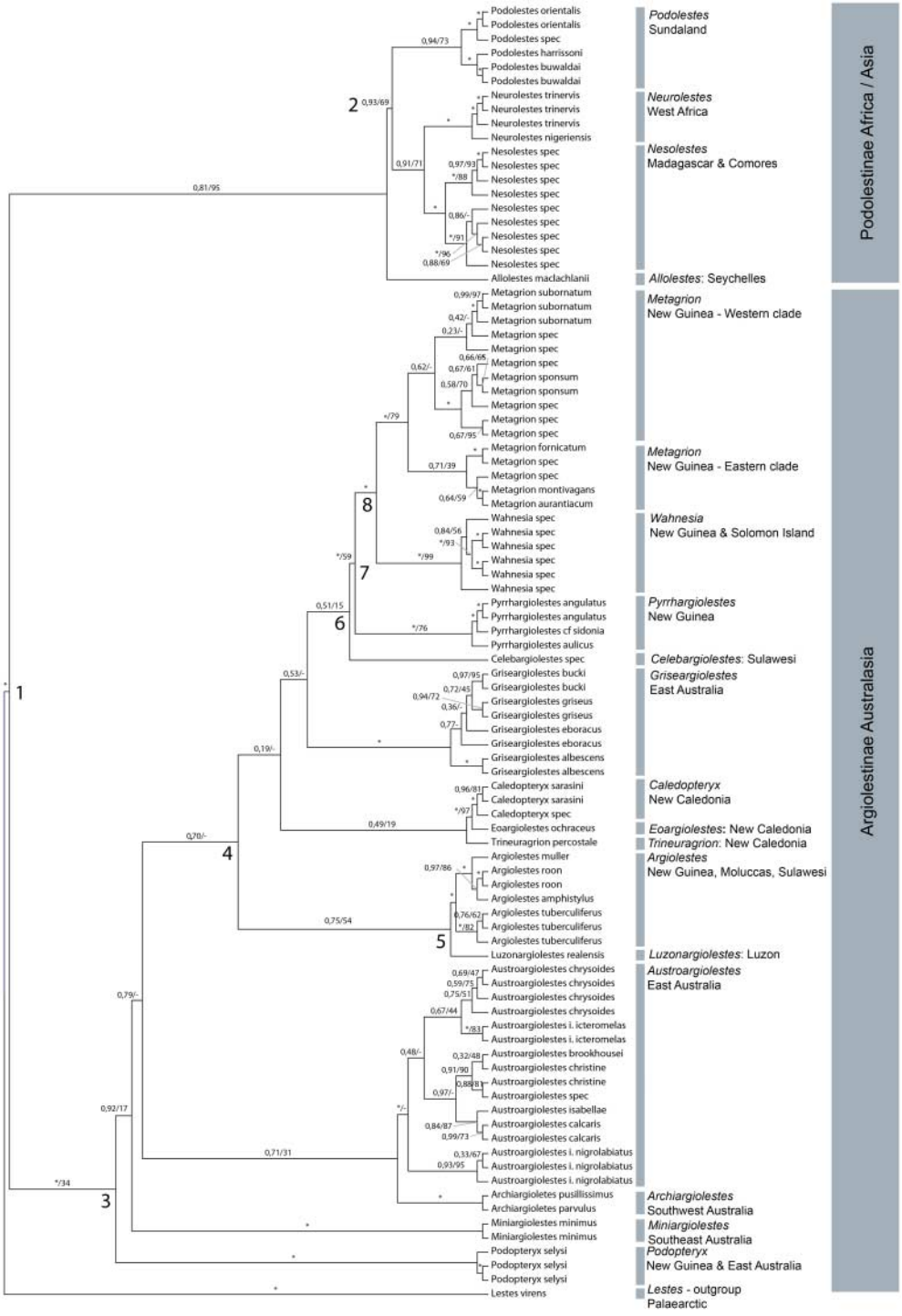

Figure 2. Bayesian consensus tree for Argiolestidae derived from 2033 bp of 16S and 28S with branches proportionally transformed. Bayesian posterior probabilities and maximum likelihood bootstrap supports are given for all interspecific nodes respectively. Those which are 1.00 or 100 are given with an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

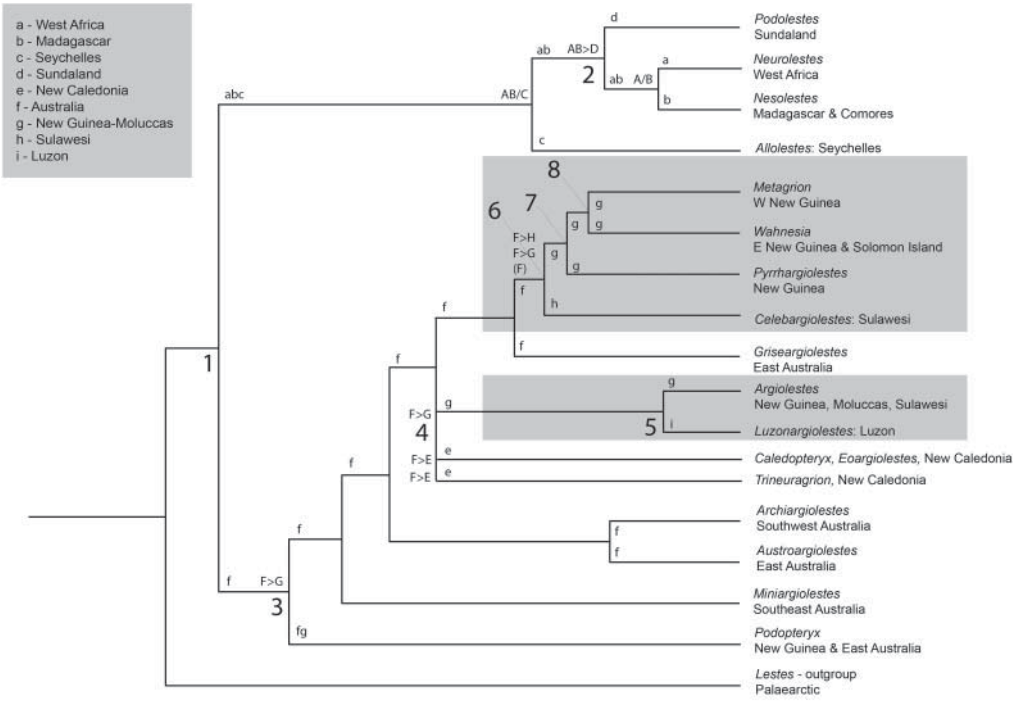

Figure 3. Summary of the phylogeny of argiolestid genera and biogeographic hypothesis. The distribution of each clade is given in lower case letters (regions represented listed upper left). The processes thought to be responsible for divergence are given in upper case letters which refer to the recognized areas of distribution with an 'arrow' (>) indicating dispersal between region (either active or passive), a right slash indicating fragmentation between regions, and parentheses indicating 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 is mainly focused are highlighted in grey. The upper grey box corresponds to the PWM group (Figure 5) and the lower grey box corresponds to the *Argiolestes-Luzonargiolestes* group (Figure 4).

The one major difference between the two 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. The clades on which the discussion mainly focuses (see node 5 and 7 in Figure 2) are reasonably well resolved with a Bayesian posterior probability/maximum likelihood bootstrap support of 0.76/54 and 1/59, respectively.

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 rifting of Africa, India and Madagascar (node 1 in Figures 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, Brandis, Ng, Yeo, & Schubart, 2009; de Bruyn, Wilson, & Mather, 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 sides of the Makassar Strait have different habitat preferences (streams versus swamps) suggesting that it is the barrier itself and not the competition with other argiolestid genera 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 presumed phytotelm breeding *Podopteryx* species are endemic to New Guinea and the Aru Islands, while one is found in New Guinea and northeastern Australia. Presumably ancestors of the genus colonized New Guinea and subsequently diversified, with one species (*P. selysii*) crossing the Torres Strait back to Australia. This is the only species and genus of Argiolestidae shared by New Guinea and Australia despite there having been a broad land connection for much of the Pleistocene (Voris, 2000). The absence of exchange across this land bridge is marked in most dragonflies: the seasonal drought associated with the monsoon climate probably acted as a filter allowing passage only of species breeding in standing water, including phytotelmata (Kalkman & Orr, 2012). A similarly limited exchange has been noted for freshwater fish and some groups of aquatic beetles (Balke et al., 2007; Unmack, 2001), although exchange may have been more common for aquatic groups that are salt tolerant or less dependent on running water (Balke, 1995; Macqueen, Seddon, Austin, Hamilton, & Goldizen, 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 four species, all of which mutually exclusive geographical ranges (Kalkman, 2016) (Figure 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

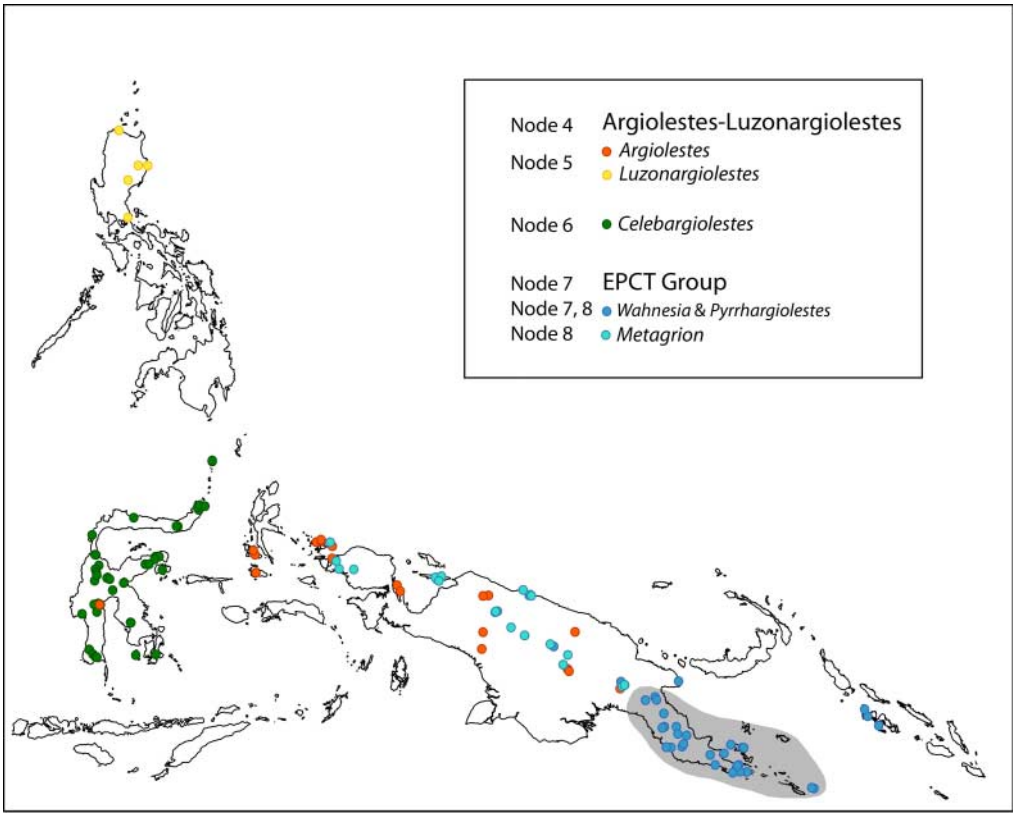

Figure 4. Distribution of three of the four lineages that colonized the eastern part of the Malay Archipelago: (1) *Celebargiolestes*, confined to Sulawesi and adjacent islands; (2) *Argiolestes-Luzonargiolestes*, the western two-thirds of New Guinea, northern Moluccas, Sulawesi and Luzon; (3) PWM group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

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 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 us to distinguish between dispersal or vicariance, although the allopatry of the four species suggest a relative recent arrival of the genus.

The main diversity of Argiolestidae in 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. While *Metagrion* occurs throughout most of the island (Figure 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

inferred by some authors to have formed around 60 Ma by the accretion of several sub-terranes 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 (Davies, Perembo, Winn, & Kengermar, 1997; Davies, Winn, & Kengemar, 1996; Hill & Hall, 2003; Pigram & Davies, 1987; Polhemus, D. A. & Polhemus, 2004). Based on distribution patterns the EPCT has been recognized as an important center of endemism for various groups of aquatic Heteroptera and Coleoptera. This center of endemism was linked to its history as a separate landmass, although no phylogenetic support was provided (Polhemus, D. A., 2011; Polhemus, D. A. & Polhemus, 1998, 2004; Polhemus, J. T. & Polhemus, 2002). A plausible scenario for the PWM group is that an ancestor reached the EPCT when it still was a separate island, which subsequently radiated to the 60–80 species presently included in 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 (Figure 5). *Metagrion* (node 8 in Figure 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 analysis 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 amalgamated with other parts of New Guinea. While we find that the PWM group colonized New Guinea from east (EPCT) to west, Toussaint et al. (2014) in their reconstruction of *Exocelina* found that colonization went from the main body of New Guinea in

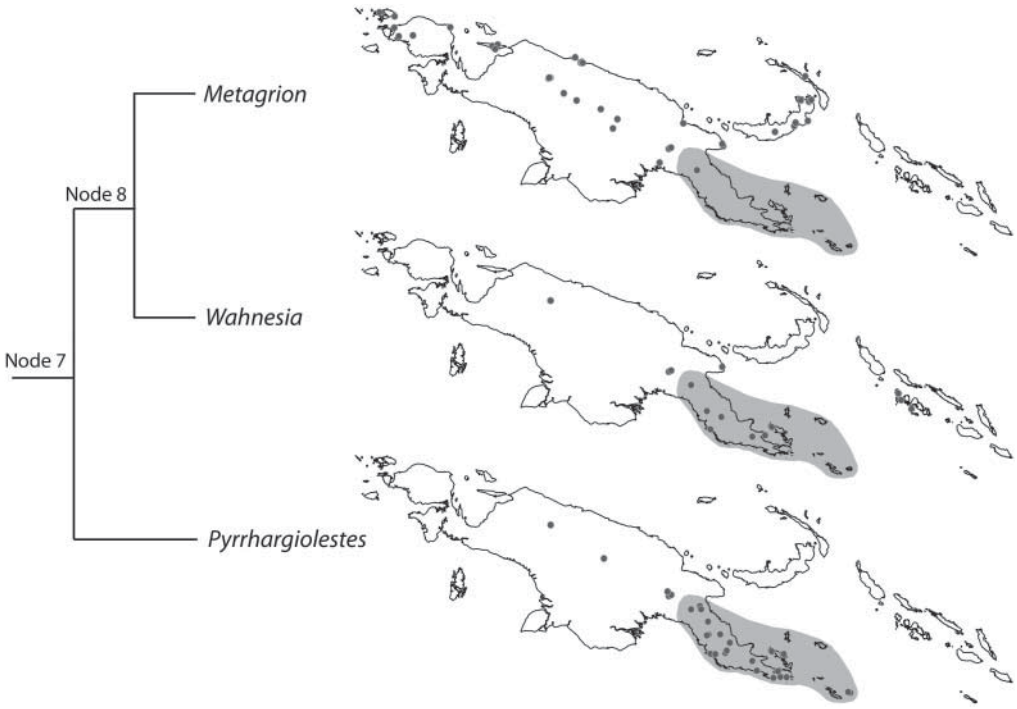

Figure 5. Distribution of the three genera whose origin is supposed to be linked to the East Papuan Composite Terrane (EPCT; grey shading). The distributions of both *Pyrrhargiolestes* and *Wahnesia* suggest that these evolved when the EPCT formed a separate island.

the west to the EPCT (named Papuan Peninsula in their paper) in the east. This does not mean that one of the scenarios is incorrect but merely shows that different groups have different histories and that reconstructions of numerous groups are needed to determine the relative importance of the different patterns for the present-day distribution patterns.

The other lineage, which makes up a large part of the argiolestine diversity of New Guinea, has a completely different distribution (Figure 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, D. A., 1995; Polhemus, J. T. & Polhemus, 1987). Molecular studies confirm this recurrent pattern in birds (Jønsson, Irestedt, Bowie, Christidis, & Fjeldså, 2011), mammals (Heaney, Walsh Jr, & Peterson, 2005; Jansa, Barker, & Heaney, 2006; Steppan, Zawadski, & Heaney, 2003) and the myrtle family (Ladiges, Udovicic, & Nelson, 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 (Hall, 2002; Hill & Hall, 2003; Kroenke, 1984; with summaries in Polhemus, D. A., 2007; van Tol & Gassmann, 2007). The islands that today make up the northern Moluccas were north of mainland New Guinea 30 Ma; directly east of them was a series of islands that are now part of northern New Guinea, and directly west a series of islands that now forms 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 following millions of years the distance between the northern Moluccas and the eastern Philippines extended, while the eastern islands fused with New Guinea, where they are currently recognizable as a series of mountains chains (e.g. the Cyclops, Foja and Adelbert Mountains). 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, they 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 (Platycnemididae) 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 *Wahnesia* from expanding west.

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Supplemental data

Supplemental data for this article can be accessed https://doi.org/10.1080/13887890.2017.1402825. Specimens used in molecular phylogenetic analyses with GenBank Accession numbers for 16S and 28S. All belong to Argiolestidae with the exception of *Lestes virens* (Lestidae).

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