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

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

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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

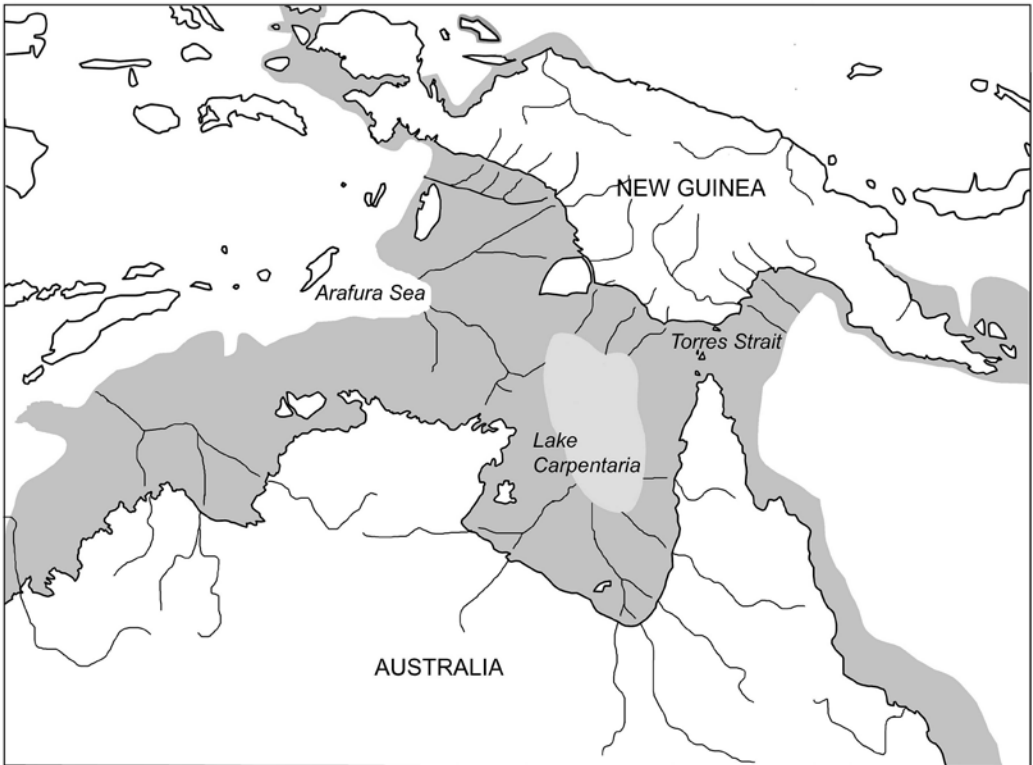


Figure 1. Map of New Guinea and Australia with the extent of land during glacial heights (-150 m) in grey. Modified from Bowman et al. (2010) and Voris (2000).

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*

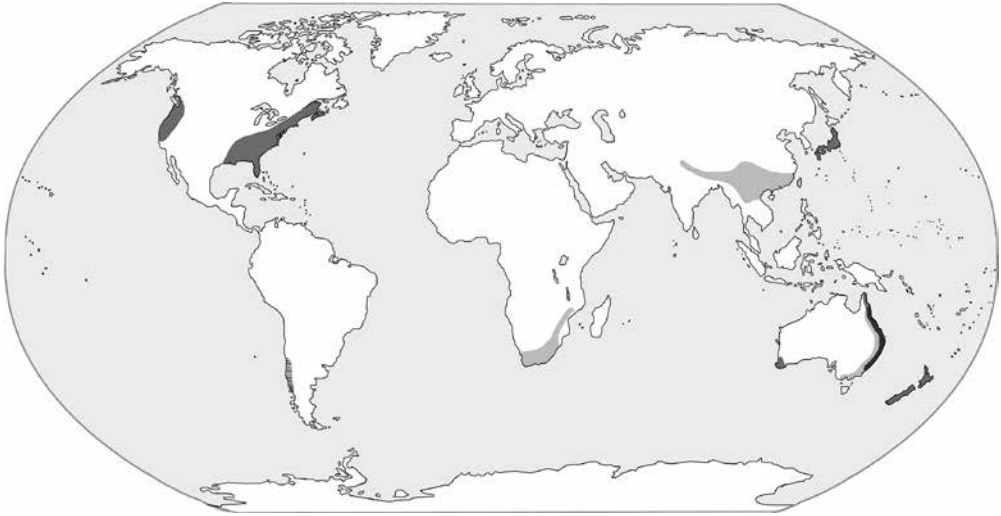


Figure 2. World distribution of the families Synlestidae (pale grey) and Petaluridae (dark grey).

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					
Austropetaliidae	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.

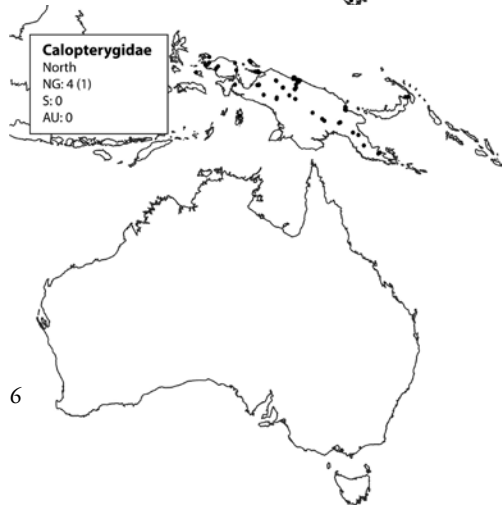
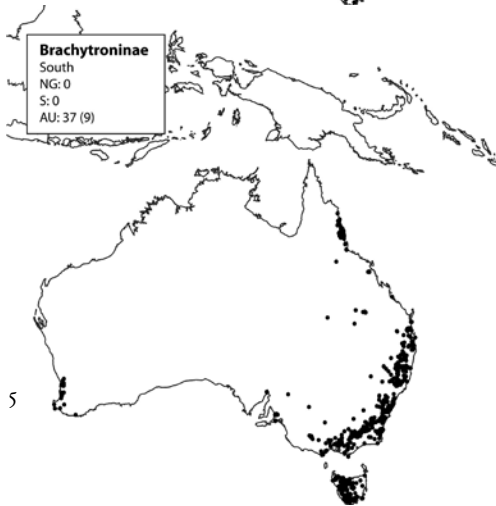
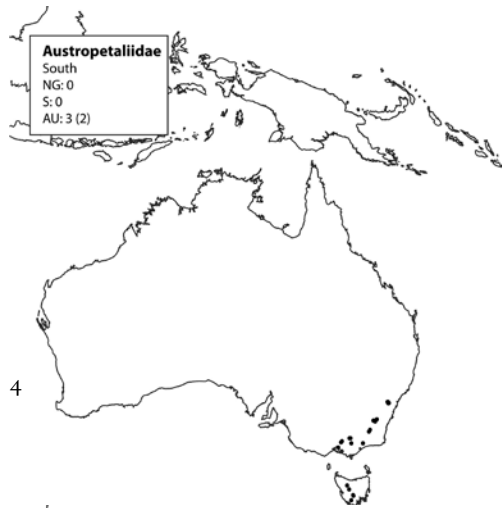
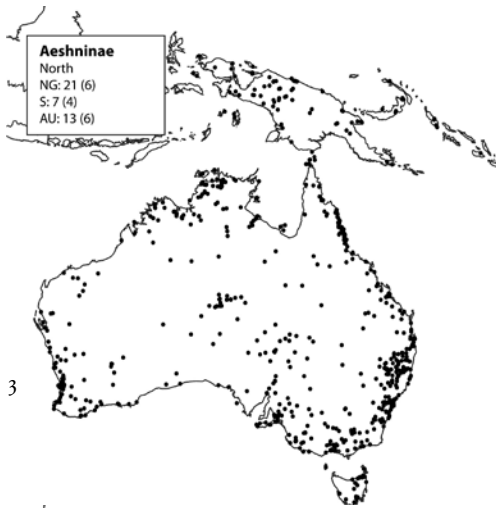
With over 5,700 described species, dragonflies are a relatively small order of aquatic insects (Kalkman et al. 2008). They are among the most ancient of winged insects dating back well into the Permian (Grimaldi & Engel 2005) and the present-day distribution of some families reflects their distribution 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

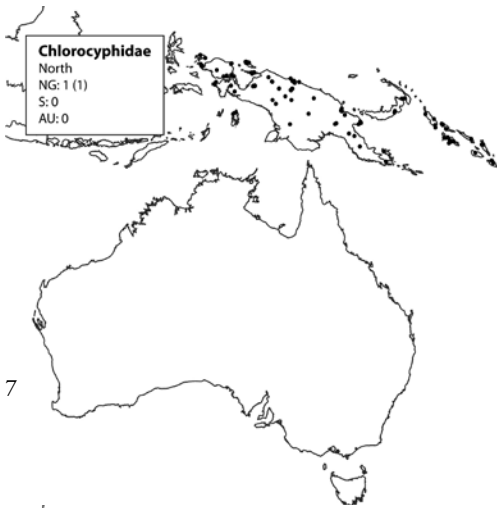
Information on the distribution of the odonate species within the region studied was based largely on the distribution databases of the Australian dragonflies (Theischinger & Endersby 2009) and the Melanesian Odonata Database (Dow & Kalkman, unpublished), which contains information on Malaysia, Indonesia, 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 tincta* Rambur, 1842, which are often included in Australian checklists (e.g. Watson



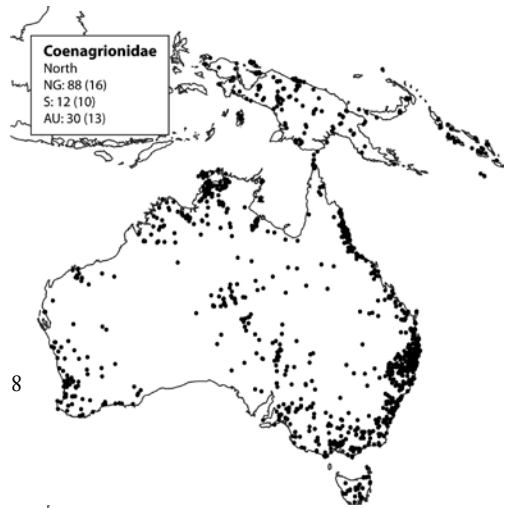
Figs. 3-2.4. Distributions of the 22 considered families/subfamilies of dragonflies within Australia, New Guinea (including Raja Ampat), the Solomons and Aru Islands. The distributions in the later two are shown for reference but are not included in the analysis. The area to the west is shown but the 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,

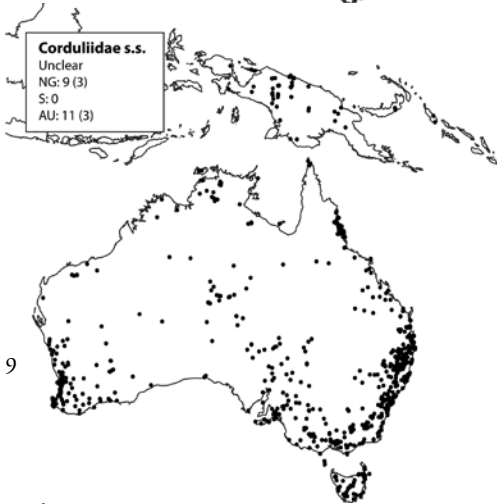
1907 has been recorded from Port Moresby, Papua New Guinea as *D. reinholdi* Foerster, 1910. However, Garrison et al. (2003) showed this record is also erroneous and we removed this species



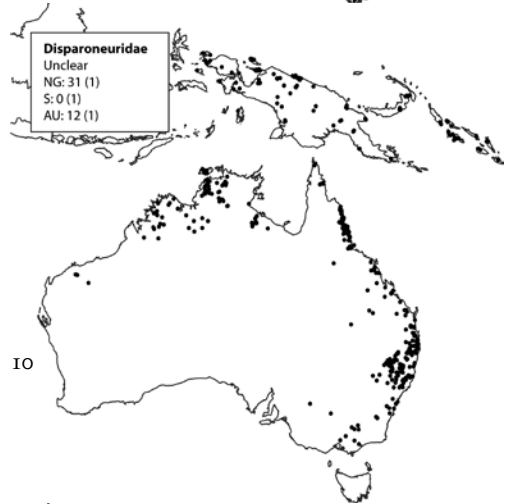
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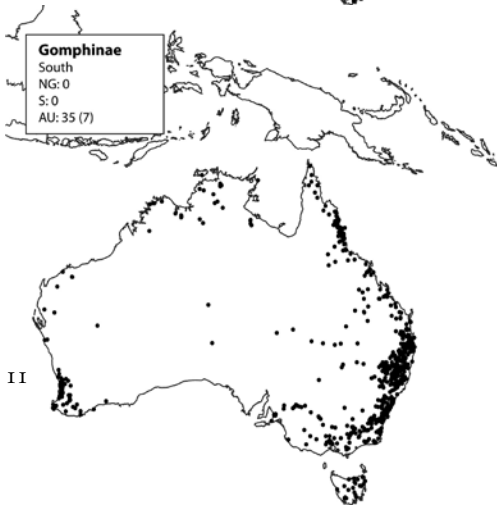
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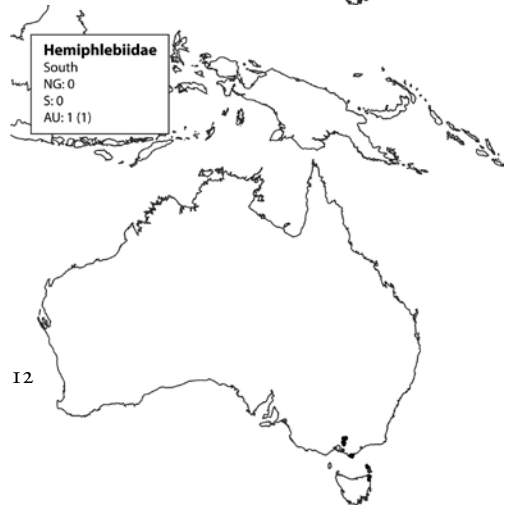
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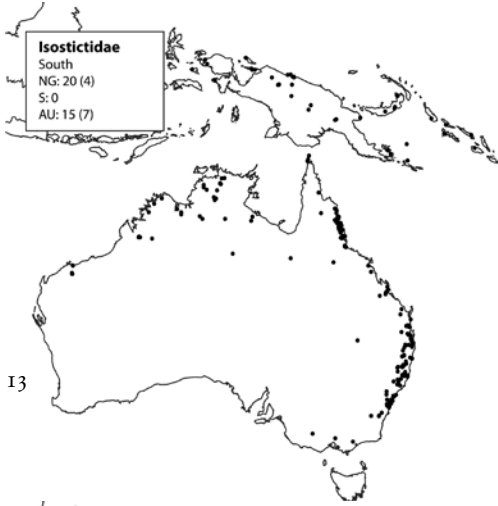
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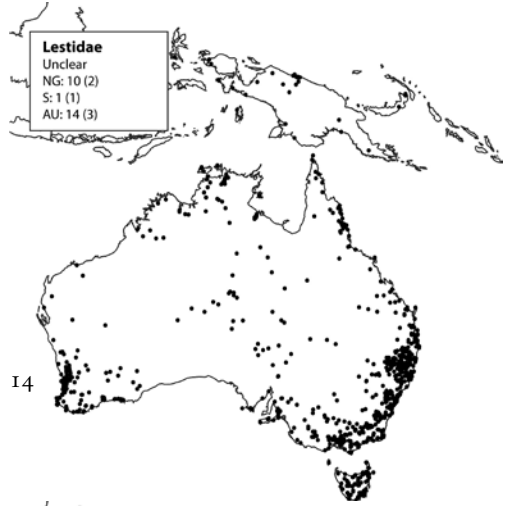
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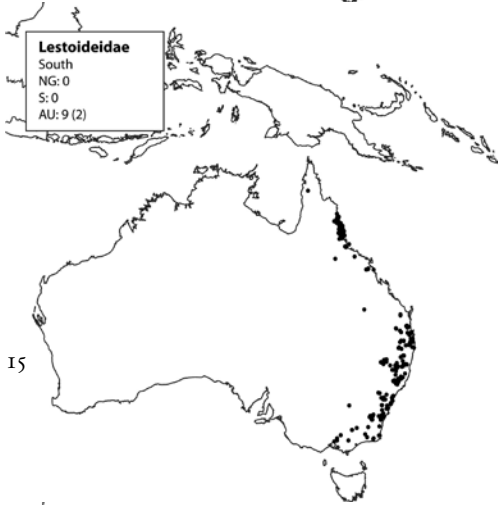
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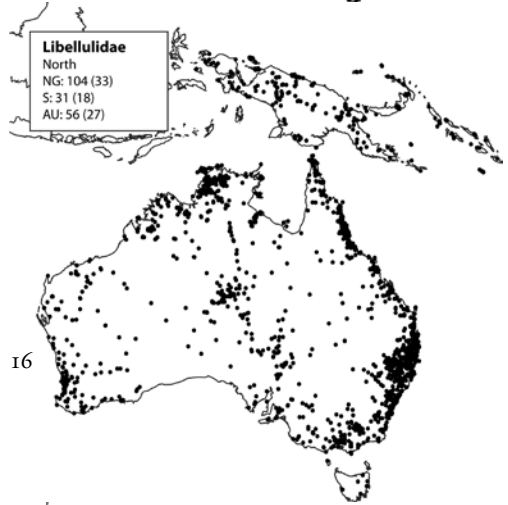
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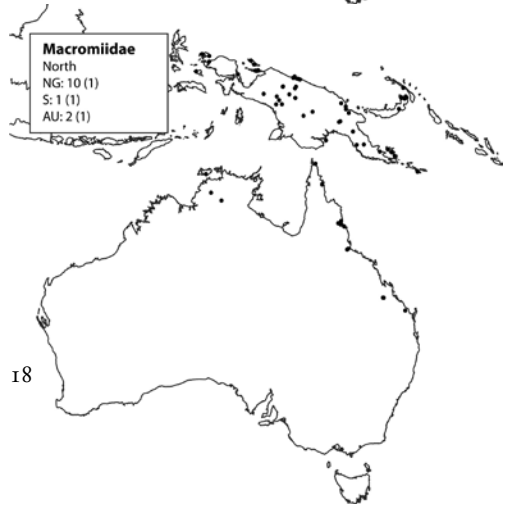
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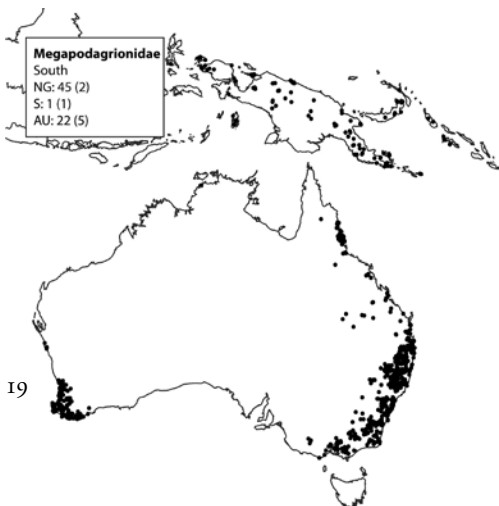
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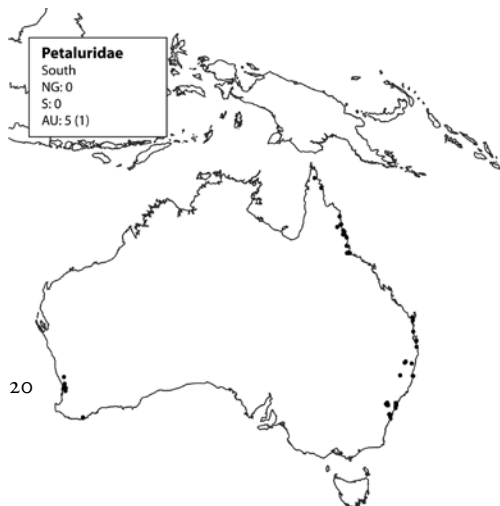
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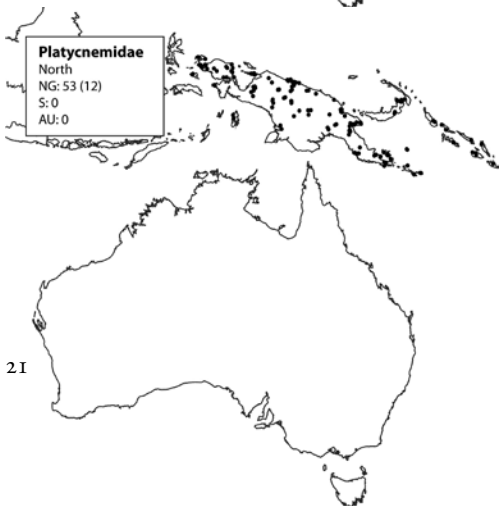
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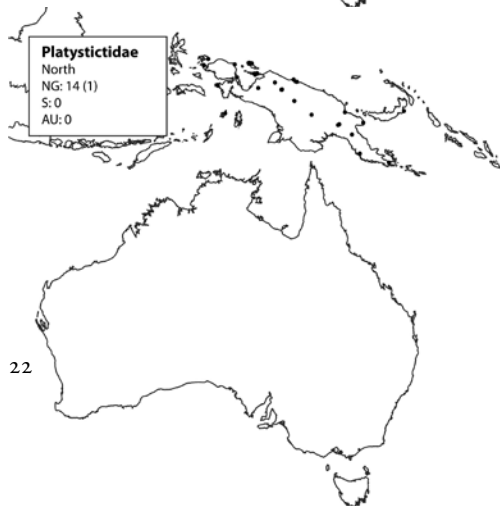
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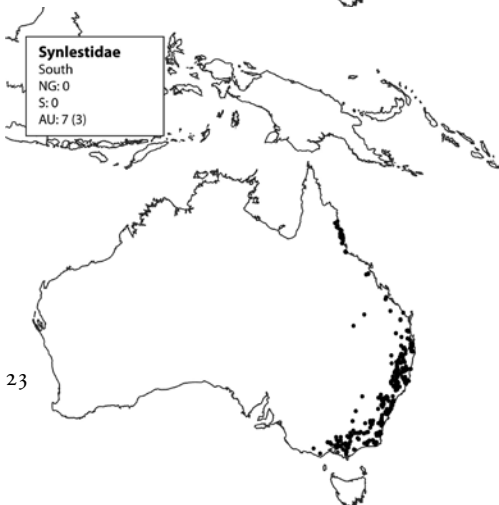
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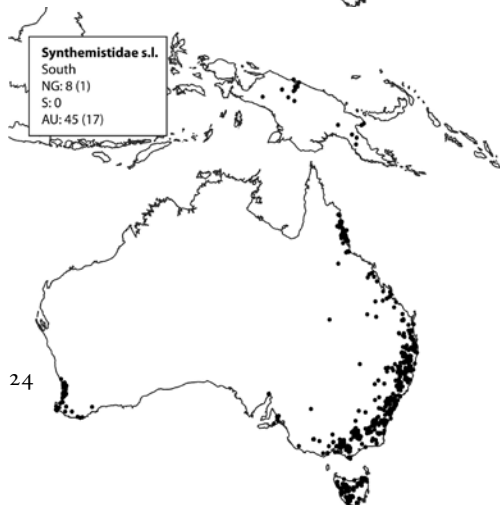
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from the checklist for New Guinea. The Australian *Agriocnemis thoracalis* Sjöstedt, 1917 and *Hemicordulia novaehollandiae* (Selys, 1871) are of uncertain taxonomical status and have been omitted from the list. In this article, Australia is defined 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 'gsi'-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 'gsi' clade were placed in Austrocorduliidae, Cordulephyidae, Gomphomacromiidae, Pseudocorduliidae, and Synthemistidae by Theischinger & Endersby (2009). Further study is needed to show if the 'gsi'-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 'gsi'-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 = $P < 0.001$).

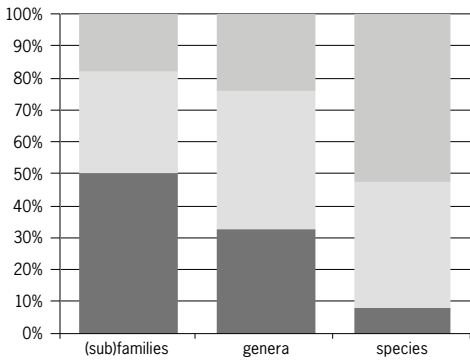


Figure 25. Percentage of families, genera and species limited to Australia, New Guinea or shared.

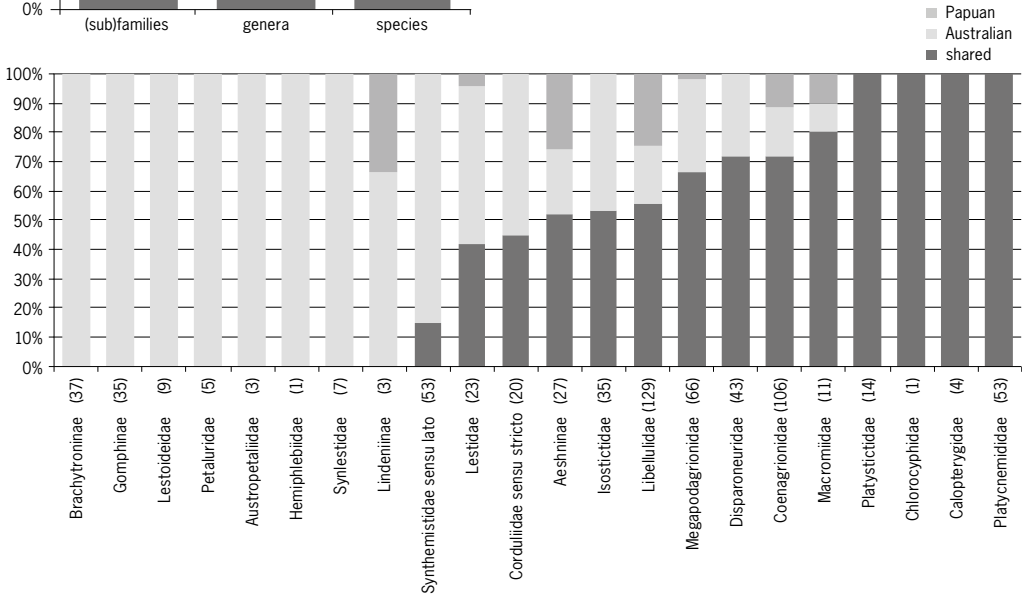


Figure 26. Percentage of Australian, New Guinean or shared species for each of the families/subfamilies considered. The number of species within each family/subfamily is given in brackets.

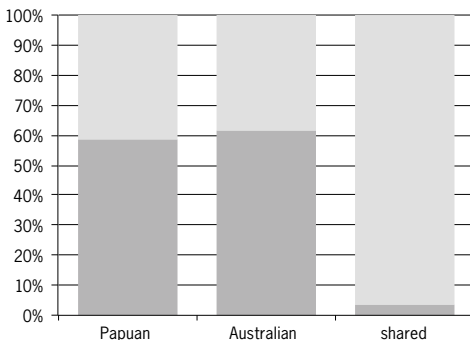


Figure 27. Percentage of dragonfly species associated with either running water or standing water for all New Guinean species, all Australian species and species shared between the regions.

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.

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