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Micro-caddisfly faunas of Australia and the southwest Pacific (Trichoptera, Hydroptilidae)

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Abstract

Today's distributions of faunal groups reflect historic events—geological and evolutionary, as well as dispersals, extinctions and chance events. The extent to which each of these contributed to the hydroptilid faunas of mainland Australia, Tasmania, New Guinea, New Zealand, New Caledonia, Fiji and Vanuatu is explored by comparison of the faunal composition, geology and geography of Australia and these SW Pacific islands. Corroborative evidence is sought from other groups, flora as well as fauna.

Key words: New Zealand, New Guinea, New Caledonia, Vanuatu, Fiji, Tasmania, distributions, biogeography

Introduction

The *Atlas of Trichoptera of the SW Pacific—Australian Region* by Neboiss (1986), is a compendium of mostly genitalic figures taken from original works, accompanied by a key to families. Brief introductions are given for families and for species a set of codes describe broad political, and for Australia, regional, distributions. Whilst preparing for the publication of the "Atlas" Neboiss (1984) published a brief paper listing families, number of species, and % endemism among species for mainland Australia, Tasmania, New Guinea (including West Papua, Papua New Guinea, New Britain, and several Papua New Guinean islands) and "SW Pacific islands". In the last, he combined figures for a number of smaller Pacific islands extending from the west of Wallace's Line, to New Caledonia, Vanuatu (as New Hebrides) and Fiji, but excluding the Moluccas, Sulawesi, and Timor. Here we present, in Table 1, data enabling comparisons between Neboiss' (1984) figures and current estimates: the known fauna of the area at the end of 2012 was close to twice the size in 1984.

Our numbers are indicative only, as in our update, we consider the Australian mainland, Tasmania, New Guinea and of all the smaller islands, only New Caledonia, Fiji and Vanuatu, separately (see Fig. 1). Our data are not definitive. For New Guinea especially, and even for Australia and New Caledonia, many more species are likely to be discovered: for example around 47 undescribed species have been identified in the ecnomid genus *Agmina* Ward & Schefter in New Caledonia, and more are indicated (Espeland & Johanson 2010a).

Aspects of the recent data are remarkable, indicating considerable radiations within some families in the region—for example, in New Caledonia, Helicopsychidae (29 species) and Ecnomidae (28+ spp.); in NZ, Oeconecidae (23 spp.); in Australia, excluding Tasmania, Leptoceridae (170 spp.), Ecnomidae (131 spp.), Hydroptilidae (139 spp.) and Philopotamidae (44 spp.); in New Guinea, Hydropsychidae (38 spp.), and in Fiji, Philopotamidae (27 spp). We focus here on the family Hydroptilidae, the micro-caddisflies, which, with their highly varied feeding behaviour and habitat requirements, wide distributions yet apparently poor dispersal abilities, could serve as a reasonable proxy for the order as a whole. We take a closer look at the components of this family in the region, and speculate on the histories of the various taxa, and the physical factors and historical events and forces that might have shaped the hydroptilid faunas of Australia and these SW Pacific islands. Going full circle, we then seek corroborative evidence among other Trichoptera families, and several other groups of organisms.

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TABLE 1. Trichoptera family representation for Australia (excluding Tasmania), Tasmania, New Guinea and islands of SW Pacific: : *lower figures according to Neboiss (1984), who merged figures for the smaller islands to the east of Wallace's Line, and **upper figures, present day numbers (June 2012), taken from sources below, supplemented by Morse (2012). The numbers in parentheses are modified from Neboiss 1986, since in 1984, the family Psychomyiidae was not recognised for Australia, nor Ecnomidae for New Zealand. *** Espeland & Johanson (2010a). ****Neboiss' (1984) figures for Polycentropodidae included Dipseudopsidae. [1]Data from ABRS (2012) Australian Faunal Directory. [2]Data from Ward (2011). [3]Johanson (unpublished lists). [4]Johanson *et al.* (2011). [5]Johanson & Oláh (2012). Note that Vanuatu and New Caledonia are merged in Neboiss (1986). [Note that several figures tabled by Neboiss (1984) disagree with the numbers of species given by Neboiss in the 1986 *Atlas*]

	Area						
Taxon	Australia (excl. Tasmania)[1]	Tasmania [1]	New Zealand[2]	New Caledonia[3]	Vanuatu[4]	Fiji[5]	New Guinea
Families (2012)	26	23	16	9	8	8	12
after Neboiss 1984*	24	19	15	10			13
Genera**	109	69	48	23	12	12	43
Species**	686	193	256	141	20	67	187
after Neboiss 1984*	318	163	151	33 (in error as 35)			121
Glossosomatidae	20	3	-	-	1	-	6
	5	3	-	-			5
Hydrobiosidae	43	33	81	7	2	3	6
	37	29	67	5			4
Hydroptilidae	139	22	20	60	6	4	73
	92	17	6	2			4
Philopotamidae	44	16	10	7	3	27	17
	10	9	10	7			16
Stenopsychidae	9	-	-	-	-	-	-
	8	-	-	-			-
Dipseudopsidae	1	-	-	-	-	-	3
Ecnomidae	131	10	1	28***	1	-	1
	17	7	1	-			2
Hydropsychidae	31	11	13	28	-	9	38
	22	9	13	6			28
Polycentropodidae****	12	7	6	21	1	3	13
	6	6	7	3			17
Psychomyiidae	2	-	1	-	-	-	1
	-	-	1	-			-
Limnephilidae	2	1	-	-	-	-	-
	3	2	-	-			-
Goeridae	-	-	-	-	-	1	3
	-	-	-	-			-
Lepidostomatidae	-	-	-	-	-	-	3
	-	-	-	-			3
Oeconoesidae	1	1	23	-	-	-	-
	-	1	15	-			-

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TABLE 1. (Continued)

	Area						
Taxon	Australia (excl. Tasmania)[1]	Tasmania [1]	New Zealand[2]	New Caledonia[3]	Vanuatu[4]	Fiji[5]	New Guinea
Plectrotarsidae	5	4	-	-	-	-	-
	2	4	-	-			-
Atriplectididae	2	1	-	-	-	-	-
	1	-	-	-			-
Calamoceratidae	10	1	-	-	-	1	14
	10	1	-	1			8
Kokiriidae	4	3	1	7	-	-	-
	1	3	1	1			-
Leptoceridae	170	33	11	19	-	8	32
	68	30	9	7			32
Odontoceridae	4	1	-	-	-	-	-
	4	-	-	-			-
Philorheithridae	6	11	6	-	-	-	-
	6	9	2	-			-
Antipodoeciidae	1	-	-	-	-	-	-
	1	-	-	-			-
Calocidae	17	5	5	-	-	-	-
	7	5	2	-			-
Chathamiidae	2	-	5	-	-	-	-
	1	-	3	-			-
Conoesucidae + Sericostomatidae	8	19	23	-	-	-	-
	2	17	16	-			-
Helicophidae	4	5	2	18	-	-	-
	2	5	2	-			-
Helicopsychidae	14	2	8	30	-	-	-
	5	2	5	-			-
Tasimiidae	4	4	-	-	-	-	-
	3	4	-	-			-

The Land Masses

Consideration of physical features and geological histories of the land masses of the SW Pacific provides a background, albeit not always stable either physically or in terms of accepted scientific theory. The present day surface areas of each of the targeted components vary greatly, ranging from some 14,760 km^2 for the archipelago of islands that comprises Vanuatu to 7,614,500 km^2 for mainland Australia (SBS 2007; see Table 2). With the exception of Vanuatu, these land areas share aspects of their geological histories, originating as part of the super-continent of Laurasia from which the large land mass of Gondwana separated at about ~215 million years ago (mya). Fragmentation of Gondwana in the late Cretaceous gave rise to the separate land masses of the Australian Region, or their progenitors.

Geological events subsequent to breakup of Gondwana varied between Australia and the smaller islands. Present-day latitudinal ranges and brief descriptors of topography are provided in Table 2. Table 3 gives approximate present day distances between land areas (for most, given as major city to major city, as these are data that are readily available); and Table 4 annotates briefly for each area the geological history (highly simplified) from the late Cretaceous (around 80 to 40 mya) to today, giving estimated time of break away from the Gondwana supercontinent, timing of periods of glaciation, marine incursions, volcanism, and dates of separation from one another. It is important to note that present day latitudes are very different from those experienced in the geological past, as are present day climates (Frakes 1999).

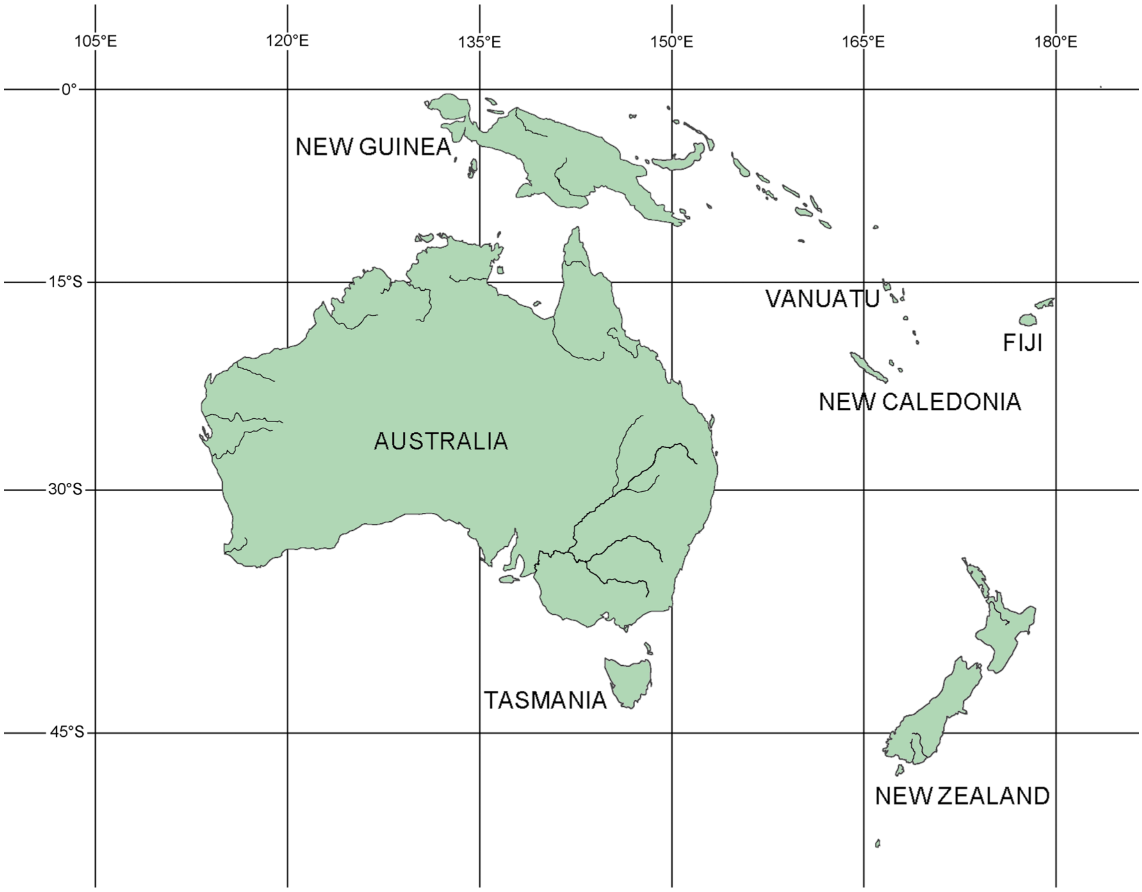

FIGURE 1. Australia and SW Pacific Islands for which new data on representation of Trichoptera groups are given in Table 1.

TABLE 2. Land area, latitudinal range, topography and total numbers of hydroptilid genera and species of Australia and major SW Pacific islands. Data from SBS (2007), Wells (1991), Johanson *et al.* (2011) ABRS (2012) Morse (2012).

	Characteristics			
Area	Area square (km^2)	~Latitude (°S)	Topography	Genera/Species
Vanuatu	14 760	14.7–19.7	mountainous, volcanic	little known 3/6 (+)
New Caledonia	19 000	20.0–22.5	coastal plains, central mountains	6/30 (+~15)
Tasmania	67 800	41.0–43.0	mountainous, central valleys, lakes	well known 6/23
New Zealand	269 057	35.0–47.0	mountainous, volcanic, lakes	well known? 3/20 ?+
New Guinea	786 000	0.0–11.0	mountainous, volcanic, coastal plains	little known 9/65+
Australia (mainland)	7 614 500	11.0-39.0	eastern mountains, flat, much arid	well known 15/146 +
Fiji	18 300	16.0–19.5	mountainous, volcanic	little known 12/67 +

TABLE 3. Approximate closest land distances (kms) to other land areas.

	New Zealand	New Caledonia	Tasmania	New Guinea	Australia	Fiji
Vanuatu	2 220	540	3 100	1 530	1 790	830
New Zealand		1807	1 500	4 120	1 491	1 790
New Caledonia			2 670	1 780	1 270	1 180
Tasmania				3 360	220	3 730
New Guinea					160	2 980
Australia						2 640

TABLE 4. Major geological events and climate affecting Australia and SW Pacific islands. Data from Corbett (2010).

	Characteristics				
Area	Gondwanan	Glaciation	Volcanism	Marine incursion	Aridity
Vanuatu	no	no	5.0–1.6 mya	no	no
New Zealand	Rafted off ~80 mya; from New Caledonia ~20 mya	to present	yes	all or most Oligocene, 25–35 mya	no
New Caledonia	Rafted off ~80 mya; from Australia ~65 mya	no	yes	all or part, 35–60 mya	no
Tasmania	Rafted off ~40 mya; from Australia ~20 mya	to 1.6 mya	58–8 mya	minor sea level rises in Miocene and Pliocene	no
New Guinea	Sunda plate / Australian plate; ~15 mya	yes	yes	parts	no
Australia	Rafted off ~50 mya	yes	yes	centre and south	yes
Fiji	no	no	yes	no	no

Modern mainland Australia is large, stable, continental, and mostly flat and arid (mean annual rainfall of more than one third of the continent is less than 250 mm). A relatively low mountain range, estimated to have been uplifted during the early Palaeozoic, traverses the continent from north to south along the eastern seaboard. From this derive river systems: short rivers and streams flow through the wetter eastern seaboard towards the coast; and on the western side of the range, rivers and streams of slow or intermittent flow, feed either into a single slowly meandering river system that reaches the coast in the mid-south of the continent, or eventually terminate in saline lake systems in central Australia. A further series of small rivers is found in the south-west. Across the far north, larger systems generally produce wide flood plains in the hot monsoon season, the flood plains shrinking during the 7 months of generally dry, cooler weather to leave behind numerous shallow, weedy lakes known as "billabongs". Latitudes of the continent range from the tropics to ~39°S, but only a very small area on the north-east coast can be called truly "tropical", in the sense of having high rainfall that supports rainforest. Overall, Australia has a wide diversity of lentic and lotic habitats more or less around the perimeter. Tasmania, between 41°S and 43°S has a more moderate, island climate, and generally low, but mountainous terrain, numerous small lotic systems, a series of lakes centrally and, in mountain areas, cold moraine lakes.

New Zealand and New Caledonia, together with Lord Howe and Norfolk Islands, are emergent parts of the large Zealandia continent that broke away from Gondwana around 80 mya. In contrast to mainland Australia, modern day New Zealand is wetter overall, mountainous and still tectonically unstable. The large mountain ranges of the South Island are snow covered for much of the year, while the far northern parts of the North Island are subtropical. Debate ranges over whether all or only most of New Zealand was below sea level in the Oligocene (Waters & Craw 2006). Similarly, at least a large part of New Caledonia appears to have been below sea level in Permian interglacial periods. Present day New Caledonia is sub-tropical, has a central range, a generally narrow, very wet coastal strip in the north, and wider, slightly dryer coastal area to the south. An obduction pushed ultramafic rock up over sedimentary rocks of marine and lacustrine origin and subsequent weathering produced the ultrabasic soils that occur over about one third of the island. These soils are thought to have driven evolution of New Caledonia's highly endemic flora. Although among animals levels of endemism appear to vary widely from group to group, generally the island has a highly diverse insect fauna (Cranston 2009). An undoubted influence on the freshwater faunal components are the seasonal spates and often severe flooding (Haase & Bouchet 1998) affecting the numerous streams, river systems, steep falls and cascades.

Present day New Guinea is all but connected to north-eastern Australia through a series of small islands dotting the ~160 km-wide Torres Strait, and a complete land bridge existed until ~10,000 years ago. Only a portion of the island is believed to be Gondwanan in origin, the rest deriving from orogenic activity as the Australian Plate collided with the Eurasian Plate, dated around the Pliocene, some 5.3 to 1.6 mya (Corbett 2012). The island is strongly dissected by mountains and steep valleys and, although entirely within the tropics even has a permanently snow-capped mountain. New Guinea is still tectonically unstable, generally has a very high rainfall, and has abundant smaller and larger stream and river systems; some southern rivers reach the coast through wide deltas. The smaller streams are often bordered by mossy splash zones.

Fiji constitutes an archipelago of 332 volcanic islands with a land mass area corresponding to that of New Caledonia. The area of the 4 islands of Viti Levu, Vanua Levu, Taveuni Island and Kadavu Island is equivalent to 92% of Fiji's total land area. Most of the islands are covered by rainforest and have a mean yearly temperature of around 25°C (Neall & Trewick 2008). A large number of permanent streams and rivers drain the interior highlands of the larger islands, providing suitable and diverse habitats for various aquatic insect groups. Permanent freshwater habitats on the islands are possibly of Miocene age, since Strandberg and Johanson (2011) argued from molecular data that a monophyletic group of *Apsilochorema* caddisflies (Hydrobiosidae) from Fiji separated from the Vanuatuan sister species about 16 million years ago (mean age). This time corresponds with the age of the earliest available land, dated to Middle Miocene (Neall & Trewick 2008). Espeland and Johanson (2010b) found that Fijian hydropsychid caddisflies form a monophyletic sister group to a monophyletic New Caledonian clade that separated during Middle Oligocene, approximately 29.5 million years ago (mean age), well ahead of the supposed existence of terrestrial Fijian land.

Vanuatu has a more recent history than all the above land areas, dating from 5 to 1.6 mya—it is an archipelago of small tropical volcanic islands developed along a subduction zone between the Australian and Pacific Plates.

Faunal Comparisons—Hydroptilidae

The Trichoptera fauna, including Hydroptilidae, of mainland Australia, Tasmania, New Zealand, Fiji and New Caledonia are reasonably well known. Little is known of the New Guinea fauna, or, possibly, the fauna of Vanuatu. For each of the land areas hydroptilid genera and number of described species recorded are given in Table 5 (derived from the Australian Faunal Directory (ABRS 2012) and World Trichoptera List (Morse 2012)). Separate figures for Australia and Tasmania are given, and for New Caledonia and Fiji an estimated number of unpublished species is given in parentheses (derived from studies underway by Wells & Johanson).

Overall, there appears to be a paucity of hydroptilid genera in New Zealand for which only 3 genera and 20 species are recorded: *Oxyethira* Eaton (4 spp.), *Paroxyethira* Mosely (15 spp.) and *Xuthotrichia* Mosely (1 sp.). Australia and New Zealand share the genera *Oxyethira* and *Xuthotrichia*, but no species. *Paroxyethira* is known only from New Zealand (15 spp.) and New Caledonia (10 spp.). New Caledonia has one endemic genus, *Caledonotrichia* Sykora and Australia several, *Maydenoptila* Neboiss, *Orphninotrichia* Mosely and *Austratrichia* Wells, *Acanthotrichia* Wells and *Mulgravia* Wells—although the last 3 are possibly the result of excessive splitting, the species possibly being referrable to *Hellyethira* Neboiss. Finally, in Australia *Orthotrichia* Eaton is highly diverse (51 spp.) and *Hellyethira* reasonably so (28 spp.) and, while *Orthotrichia* will probably be found to be similarly rich in New Guinea (26 spp.), only 4 species of *Hellyethira* are known at present from there (10 species are described from SE Asia and Japan (Morse 2012)). One species of *Hellyethira* is recorded from New Caledonia and this species and the only species of *Hydroptila* Auct. recorded for the island are common species in eastern Australia; Wells (1995) suggested that both may have been introduced to New Caledonia in early days of European settlement, in fresh water transferred during traffic between the 2 areas. Three genera are known from Fiji: *Orthotrichia*, *Hydroptila* and *Orphninotrichia*. The species have not yet been described formally.

In development of hypotheses of origins of hydroptilid taxa in the SW Pacific region, consideration of the distribution of various genera within Australia is informative (see Table 6). Of endemic Australian hydroptilid taxa, only *Maydenoptila* occurs in the south-west, where there is one species; and *Orphninotrichia* is found only in the east, with one species known from the "Top End", 2 in Tasmania, and 1 in Fiji. *Orthotrichia* is the most diverse genus and the majority of species are found across the north, none in the south-west and again only 2 species in Tasmania. Curiously, *Tricholeiochiton* Kloet & Hincks, with 11 species scattered worldwide (Morse 2012)—Europe, Brazil, SE Asia and Australia—has 5 species in northern Australia, and a single one in south-western Tasmania (Wells 1998). The distribution of *Jabitrichia* Wells is also a puzzle: northern Australia (Wells 1990), West Malaysia (O'Connor & Ashe 1992) and western Africa (Marlier 1965; Kjaerandsen & Andersen 2002). Are *Tricholeiochiton* and *Jabitrichia* relictual genera that were more widespread before the breakup of the Laurasian land mass?

TABLE 5. Figures for hydroptilid genera and species in Australia, New Guinea and islands of the SW Pacific; *endemic genera, **possibly introduced accidentally. Figures are taken from Wells (1991), Johanson et al. (2011), ABRS (2012), Morse (2012) and Wells & Johanson (2014, 2015).

	Number of species in genera in corresponding areas						
Genera	Australia / Tasmania	New Guinea	New Zealand	Tasmania	New Caledonia	Vanuatu	Fiji
Chrysotrichia	1	3	-	-	-	-	-
Scelotrichia	1	4	-	-	-	-	-
Niuginitrichia	-	13	-	-	-	-	-
Maydenoptila	8*	-	-	3*	-	-	-
Caledonotrichia	-	-	-	-	11	-	-
Hydroptila	9	11	-	4	1**	3	1
Acritoptila	5	-	-	-	12	-	-
Austratrichia	1*	-	-	-	-	-	-
Hellyethira	28	4	-	5	1**	-	-
Xuthotrichia	1	-	1	-	-	-	-
Jabitrichia	1	-	-	-	-	-	-
Acanthotrichia	1*	-	-	-	-	-	-
Missitrichia	-	1	-	-	-	-	-
Mulgravia	2*	-	-	-	-	-	-
Oxyethira	14	2	4	6	26	2	1
Paroxyethira	-	-	15	-	10	-	-
Tricholeiochiton	6	-	-	1	-	-	-
Orphninotrichia	20*	-	-	2*	-	-	1
Ugandatrichia	-	1	-	-	-	-	-
Orthotrichia	51	26	-	2	-	1	1
Total genera	15	8	3	6	6	3	4
Total species	149	65	20	23	61	6	4

Distributions of the respectively endemic *Caledonotrichia* (New Caledonia) and *Maydenoptila* (Australia, including Tasmania) suggest vicariance, with derivation from austral stock following fragmentation of the Gondwanan supercontinent. These 2 genera exhibit stactobiine features and may be closest to other austral, rather than Oriental, stactobiines. Alternatively, the 2 share a more recent ancestor, the New Caledonian genus being derived by vicariance following a more recent dispersal from Australia. The hydroptiline genera, *Paroxyethira* and *Orphninotrichia* could also have originated from Gondwanan stock. Possible relationships between these 2 genera and *Tricholeiochiton* warrant exploration, too—intromittant organs of all 3 are usually closely similar, resembling those seen in *Orthotrichia* species.

Not distinguished in the data in Tables 5 and 6 are the 3 subgenera of *Oxyethira* that occur in the region: *Dampfitichia* Mosely in New Guinea, northern Australia, New Caledonia and Vanuatu; *Pacificotrichia* Kelley in New Caledonia; and *Trichoglene* Neboiss, in Australia, Tasmania, New Zealand New Caledonia and Vanuatu. If Kelley's (1984) hypothesis is correct—namely that subgenus *Trichoglene* is sister group to all other *Oxyethira* subgenera—then that group may also be in the older Gondwanan category. Subgenus *Pacificotrichia* Kelley is found in New Caledonia, Vanuatu and Fiji (Kelley 1989) but Kelley suggested that it is most closely related to *Dampfitrichia*, which would rule out any older Gondwanan connections, instead suggesting more recent dispersals from the Oriental Region.

TABLE 6. Figures for hydroptilid genera and species in Australia and Australian ”regions”. Data from ABRS (2012).

	Australian ”regions”						
Genera	all ”regions”	north-west	”Top End”	north-east	south-east	Tasmania	south-west
Chrysotrichia	1	-	-	1	-	-	-
Scelotrichia	1	-	-	1	-	-	-
Maydenoptila	8	-	-	2	5	3	1
Hydroptila	9	1	1	5	5	2	1
Acritoptila	5	-	-	3	-	-	2
Austratrichia	1	-	-	-	1	-	-
Hellyethira	28	9	9	13	8	5	2
Xuthotrichia	1	-	-	1	1	-	-
Jabitrichia	1	-	1	1	-	-	-
Acanthotrichia	1	-	-	1	1	-	-
Mulgravia	2	-	-	1	1	-	-
Oxyethira	14	1	4	5	1	5	2
Tricholeiochiton	6	4	4	1	-	1	-
Orphninotrichia	20	-	1	6	7	2	-
Orthotrichia	51	12	18	24	17	2	-
Total genera	15	5	7	14	9	7	5
Total species	149	27	38	65	45	20	7

The hydroptilid fauna of Vanuatu as known at present is consistent with it being derived by dispersals, *Orthotrichia, Hydroptila* and *Oxyethira (Dampfitrichia)* probably from New Guinea, *Oxyethira (Trichoglene)* possibly from New Caledonia or even New Zealand.

Thus, while some distributions in the region can be explained best by postulating origins on the Gondwanan supercontinent or as having derived by vicariance subsequent to separation of the land masses, others are best explained by colonisation from the Oriental Region. In this category are 3 stactobiines *Niuginitrichia*, *Scelotrichia* and *Chrysotrichia* in New Guinea, the latter 2 also in the "Wet Tropics" of north-eastern Australia; *Orthotrichia* in New Guinea and Australia, but not further eastwards; and species in the *Oxyethira* subgenus *Dampfitrichia* that are widespread in SE Asia and occur in New Guinea, northern Australia, and New Caledonia. These hypotheses of origins of hydroptilids in the SW Pacific region all could benefit from testing with molecular data.

Faunal Comparisons—Other Trichoptera Families

At a broader level among Trichoptera, the situation is similar: data on distributions of other families (Table 1) support older austral relationships for some groups, and more recent Oriental and Australia-New Zealand-New Caledonia relationships for others. A feature to be noted for Trichoptera in the region is that at family level endemism is low—only Australia has 2 endemic families, Antipodoecidae (although apparently this family is likely to be suppressed in synonymy) and Plectrotarsidae. Given that fossils attributed to Plectrotarsidae have been found in the Northern Hemisphere (Sukatsheva & Jarzembowski 2001) that family may be relictual.

Family diversity is greatest in Australia. Notably, a number of families are absent from New Guinea: Limnephilidae, Oeconecidae, Plectrotarsidae, Odontoceridae, Philorheithridae, Stenopsychidae, [Antipodoecidae], Calocidae, Chathamiidae, Conoesucidae, Helicophidae, Helicopsychidae and Tasimiidae. These are generally considered to be of Gondwanan origin or derived from Gondwanan groups (Neboiss 1986). Two basically Northern Hemisphere families are present in the region: Goeridae in New Guinea and Fiji, and Lepidostomatidae in Vanuatu.

Family diversity attenuates as one goes further eastwards from Australia. Calocidae, Chathamiidae and Conoesucidae occur only in Australia and New Zealand. Helicophidae are found in Australia, New Zealand and New Caledonia as well as in South America. Conoesucidae are recorded only from Australia and New Zealand; a study by Johanson *et al.* (2009) found evidence for post-Zealandia-separation dispersal events between Australia and New Zealand, but the authors were undecided on direction of dispersals—for many groups it appears dispersal may have occurred in both directions.

Within some families, diversification is quite extensive as noted above. Endemism, too, is high at both genus and species levels (Table 7). Among the 27 hydrobiosid genera in the region, only *Apsilochorema* Ulmer is not endemic to a particular SW Pacific land mass (does this reflect excessive splitting?). Hydrobiosids are also found in southern South America, but only few in the Northern Hemisphere; and fossils attributed to Hydrobiosidae have been found in the Northern Hemisphere (Mey 1998). *Apsilochorema* is a widely distributed Northern and Southern Hemisphere genus, but according to Strandberg and Johanson (2011) originated on the Australian continent, dispersing to the Oriental Region about 28 mya, from where representatives dispersed to SW Pacific islands 16 mya and later. A separate lineage dispersed to New Caledonia directly from the Australian mainland about 15 mya.

TABLE 7. Figures for all described Trichoptera and estimates of % endemism in areas of the SW Pacific. Knowledge of the diversity in Vanuatu is considered insufficient. Data are taken from ABRS (2012), Espeland & Johanson (2007, 2010a,b, 2008, 2011), Johanson (2007, 2011), Johanson & Keijsner (2008), Johanson & Ward (2009), Malm & Johanson (2007, 2008a,b), Morse (2012), Ward (2011) and Wells & Johanson (2014, 2015).

	Taxon numbers (% endemism)		
Land mass	Families	Genera	Species
Vanuatu	8 (0)	12 (0)	20 (100)
New Caledonia	9 (0)	23 (35)	178 (98)
Tasmania	23 (0)	69 (15)	194 (61)
New Zealand	16 (0)	48 (73)	256 (99)
New Guinea	12 (0)	43 (?)	187 (?)
Australia excl. Tasmania	26 (0.04)	109 (52)	686 (90)
Fiji	8 (0)	12 (0)	67 (100)

Discussion

These findings are supported by data from diverse faunal groups (*e.g.* passerine birds, Raikow & Bledsoe 2000; select terrestrial insect groups, Austin *et al.* 2004; freshwater shrimps, Page *et al.* 2005) and floral groups (*e.g.* daisy genus *Abrotanella*, Swenson & Bremer 1997; Crisp *et al.* 1999; Hill *et al.* 1999; *Nothofagus*, Cook & Crisp 2005). However, for these and other groups the picture seems to be far from clear cut. Giribet & Boyer (2010) studying short range soil-dwelling invertebrates concluded that some ancient groups have persisted on New Zealand since its break from Gondwana, and Krosch *et al.* (2011) studying orthocladiine chironomid midges found evidence for a mix of "disjunct clades of potential Gondwanan origin" as well as groups that appear to be derived from more recent dispersals from Australia to New Zealand, and also in the reverse direction.

A further complication is the gradually accumulating evidence for both New Zealand and New Caledonia being fully submerged for some time around 23 mya, post break away of Zealandia from Gondwana (Landis *et al.* 2008; Espeland & Murienne 2011). Espeland and Murienne (2011) and Espeland and Johanson (2010b) suggest that the high diversity of particular taxa in New Caledonia is a result of "evolutionary radiation" into unoccupied territories following recolonisation, and this could also apply to New Zealand, but note the low diversity of Hydroptilidae in New Zealand.

Another aspect is that among Trichoptera certain trophic groups have radiated extensively in New Caledonia. For example, a high diversity of Helicopsychidae, a group that lives by scraping epilithos from the upper surfaces of rock, could be attributable to their gastropod-like case form (sometimes a smooth, low-relief cone) being well adapted to withstanding the severe floods and spates that seem to sweep the streams clear of some components of the invertebrate faunas (Haase & Bouchet 1998); rather similarly, some of the species of the hydroptilid genus *Caledonotrichia* have dome-shaped case that they attach to the upper surface of rocks and from which they, too, probably graze on epilithos. In Australia, diversification of leptocerids has involved groups such as *Triplectides, Triaenodes* and *Oecetis* that are common in slower lotic to lentic waters. Among these, larvae of *Triaenodes* and *Triplectides* are shredders or opportunistic feeders. However, a number of the highly diverse and speciose groups in the region are predatory: these include Hydrobiosidae, Ecnomidae and, among Leptoceridae, *Oecetis*. For example, the ecnomid genus *Agmina* Ward & Schefter appears to be extraordinarily speciose in New Caledonia, with some 74 to 80 identified species (over 47 yet to be described), a radiation that Espeland and Johanson (2010a) attribute to the diversity among the ultramafic substrates and the elongate shape of the island providing separation of streams and rivers. The radiation of the endemic stactobiine genus, *Niuginitrichia*, in New Guinea could be correlated with the prevalence of mossy splash zones associated with waterfalls and mossy seepages.

In terms of overall representation of hydroptilids in the region, what factors are likely to have contributed to presence or absence? One cannot assume that all land areas had an equal opportunity to share the groups prior to fragmentation of Gondwana. The greater representation of genera in Australia is probably attributable, in part at least, to its stability, greater total land area and latitudinal span, together providing diverse, but generally moderate, climatic conditions and habitats into which groups can radiate—were the progenitors of austral groups already warm adapted? For Australia, aridity and marine incursions have undoubtedly played their part in causing extinctions and driving speciation, as well as distance from other land masses. Chance may also have had an effect on dispersal and/or establishment. Factors such as prevailing winds—in recent times wind systems have been the south westerlies produced by anti-cyclonic patterns moving across southern Australia towards New Zealand; the easterly trade winds blowing from the islands towards northern Australia and New Guinea; and in the summer months, strong, erratic cyclones and storms developing in the western Pacific and areas to the north-east, north and north-west of Australia, causing violent winds that could carry insects in many directions. The so-called "southerly busters" are known to carry insects from Australia to New Zealand from time to time (Fox 1978). Establishment, though, is no doubt a chancy event and of Australian insects carried to New Zealand, probably few have established.

Finally, we can speculate on why the New Zealand hydroptilid fauna is so depauperate compared with, for example, the much smaller island of New Caledonia. If, as seems likely, all or most of New Zealand and New Caledonia were inundated in interglacial periods post fragmentation of Gondwana (Landis *et al.* 2008), it is unlikely that any austral groups survived on either island. It seems probable that post-inundation exchanges between Australia and New Caledonia, between New Caledonia and New Zealand, and Australia and New Zealand provided the progenitors of present day hydroptilid faunas of these land masses, but do not provide satisfactory explanations for all groups.

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