

***Orthoglymma wangapeka* gen.n., sp.n. (Coleoptera: Carabidae: Broscini): a newly discovered relict from the Buller Terrane, north-western South Island, New Zealand, corroborates a general pattern of Gondwanan endemism**

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Abstract. *Orthoglymma* Liebherr, Marris, Emberson, Syrett & Roig-Juñent **gen.n.** (Coleoptera: Carabidae: Broscini) is described to accommodate the single type species *Orthoglymma wangapeka* Liebherr, Marris, Emberson, Syrett & Roig-Juñent **sp.n.**, known from the Wangapeka Track, Kahurangi National Park, north-western South Island, New Zealand. *Orthoglymma wangapeka* **sp.n.** is analysed cladistically along with a comprehensive array of 42 other broscine generic terminals and four out-group taxa, using information obtained from 73 morphological characters, and placed as adelphotaxon to the remainder of subtribe Nothobroscina, a clade distributed in New Zealand, southern South America and Australia. Based on fossil evidence for Carabidae, the occurrence of *Orthoglymma wangapeka* **sp.n.** on the Buller Terrane, a geological feature once situated on the eastern margin of Gondwana, and early cladistic divergence of *Orthoglymma* from the remaining Nothobroscina, *Orthoglymma wangapeka* **sp.n.** is interpreted as a Gondwanan relict. The New Zealand arthropod fauna is reviewed to identify other taxa in existence at the time of Cretaceous vicariance of New Zealand and Australia. These candidate Gondwanan taxa, all of which are specified using fossil data or molecular divergence-based estimates, are analysed biogeographically. Where phylogenetic hypotheses are available, primordial distributions are optimized using event-based, dispersal-vicariance (DIVA) analysis. The hypothesized Gondwanan-aged taxa demonstrate inordinate fidelity to the Gondwanan-aged geological terranes that constitute the western portions of New Zealand, especially in the South Island. Persistence of these relicts through a hypothesized ‘Oligocene drowning’ event is the most parsimonious explanation for the concentration of Gondwanan relicts in the Nelson, Buller and Fiordland districts of the South Island. Geographic patterns of Gondwanan-aged taxa are compared with distributions of taxa hypothesized to have colonized New Zealand across the Tasman Sea from Australia and New Caledonia, subsequent to Cretaceous vicariance. These post-Gondwanan taxa exhibit very different patterns of distribution and diversification in New Zealand, including: (i) abundant endemism in Northland,

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Unpublished for the purposes of zoological nomenclature (Art. 8.2, ICZN)

and the islands and peninsulas of the North Island; (ii) species geographically restricted to areas underlain by the youngest Rakaia and Pahau geological terranes; and (iii) species exhibiting exceedingly widespread geographic distributions spanning geological terranes of disparate ages.

In relation to the world fauna the austral disjunct insect groups... form a very small fraction, and the pertinent species are, moreover, predominantly very small and inconspicuous creatures which makes it still more easy to overlook their great biogeographic importance.

(Brundin, 1966: 458)

Introduction

The discovery of a previously unknown species allows us to integrate information associated with its evolutionary history into previously proposed hypotheses of phylogenetic relationships. When a species is discovered inhabiting a geological terrane in New Zealand that once comprised an eastern portion of Gondwana, the process of rectifying the novel information becomes especially exciting, given the intense recent interest in the colonization history of New Zealand (King, 2000; Ericson *et al.*, 2001; Cieraad & Lee, 2006; Gibbs, 2006; Campbell & Hutching, 2007). Arguments regarding whether the exceedingly precinctive biota of the southern continents, and especially New Zealand, has been derived via circumantarctic taxic dispersal, or by fragmentation of the supercontinent Gondwana, have swirled since the initial natural history surveys of the region by Joseph Dalton Hooker (reviewed in Brundin, 1966). For the New Zealand biota, this controversy shows no signs of abating (McGlone, 2005; Michaux & Leschen, 2005; Waters & Craw, 2006; Trewick *et al.*, 2007; Goldberg *et al.*, 2008; Boyer & Giribet, 2009; Giribet & Boyer, 2010; Pole *et al.*, 2010). The possibility that Gondwanan-aged relictual taxa have survived in New Zealand since the Cretaceous opening of the Tasman Sea has been argued to depend on the degree to which New Zealand was inundated during Oligocene high sea-level stands: i.e. near inundation leading to Oligocene-aged genetic bottlenecks for terrestrial taxa (Cooper & Cooper, 1995), or total inundation requiring subsequent long-distance dispersal of the entire extant terrestrial biota (Campbell & Hutching, 2007; Landis *et al.*, 2008). Although total inundation has been argued for repeatedly, protagonists of complete drowning invariably equivocate with regard to the possibility that isolated islands persisted throughout New Zealand's voyage from Australia to its present position: e.g. 'All explanations (dispersal or vicariance) seem both possible and plausible at the same time in the south' (McGlone, 2005); 'Biological arguments can be made for the continuous presence of islands' (Campbell & Hutching, 2007: 167); 'Available geological data thus neither

confirm nor reject Oligocene drowning of NZ' (Waters & Craw, 2006: 352); 'we cannot disprove the contention that land existed continuously in the New Zealand region throughout the Cenozoic' (Landis *et al.*, 2008: 193).

We propose an initial return to the first principles of historical biogeography to interpret the occurrence of a newly discovered species of carabid beetle assignable to the tribe Broscini (Roig-Juñent, 2000) known from the Buller Terrane (Wandres & Bradshaw, 2005), situated in the extreme north-western portion of New Zealand's South Island. By first principles we mean a method wherein historical relationships of areas of endemism are interpreted within the phylogenetic frameworks of the various taxa inhabiting those areas (Hennig, 1960; Brundin, 1966; Nelson & Platnick, 1981). Various methods have been used to interpret such data on area relationships, and we propose to use the concordance of phylogenetic relationships that define a taxon-area cladogram with the most well-substantiated geological hypotheses available (McLoughlin, 2001; Sanmartín & Ronquist, 2004; Wandres & Bradshaw, 2005; Wood & Stagpoole, 2007; Michaux, 2009). However, to eliminate circularity in reasoning, whereby biogeographic patterns are proposed as criteria for establishing ages of origin for taxa exhibiting those patterns (Waters & Craw, 2006), we call upon fossil information for the Broscini as well as a variety of other New Zealand arthropod taxa in existence at the time of Gondwanan vicariance. Such fossil data provide minimum ages for taxa of interest, and also form the basis for estimating times of divergence based on molecular sequence data. We demonstrate that the Broscini, as well as numerous other taxa in existence at the time of the Cretaceous opening of the Tasman Sea that isolated New Zealand, display high fidelity to Gondwanan terranes comprising the older portions of New Zealand (Wandres & Bradshaw, 2005). Isolated islands have been hypothesized to have persisted on these terranes during the Oligocene high sea-level stands (Stevens & Suggate, 1978; Kamp, 1986; King, 2000) that preceded the Mio-Pliocene orogeny caused by the transpressive collision of the Challenger and Campbell plates along the Alpine Fault (Campbell & Hutching, 2007). After establishing how Gondwanan taxa could have persisted throughout the history of New Zealand, we examine several examples – including a subsidiary clade of Broscini – that represent instances of trans-Tasman taxic dispersal post-dating Gondwanan vicariance. These taxa exhibit very different patterns of distribution and endemism, including a substantial concentration of diversity in the northern reaches and small isolated islands of the North Island, as well as species precinctive to the isolated mountains and volcanoes of the Eastern Province terranes in the South Island.

Given New Zealand's exceedingly complex geological history, we propose that a multifaceted approach – i.e. establishing phylogenetically-based area relationships, and then determining whether taxa are of the appropriate age to have responded to the geological events implied by those area relationships – is the only means to understand the history of the resident New Zealand biota.

New Zealand's geological development

Testing whether New Zealand's Gondwanan origin is relevant to the evolutionary history of the arthropod taxa that we analyse comparatively here requires an understanding of New Zealand's geological history. The oldest rocks, comprising the Buller and Takaka terranes (Wandres & Bradshaw, 2005) that extend from Nelson to Fiordland, including Stewart Island (Fig. 1), are of latest Cambrian to Devonian age. These terranes formed along the quiet eastern margin of Gondwana, and are composed of sandstones, mudstones and limestones. They were amalgamated by the Devonian, and were episodically intruded by plutonic rocks that can be dated at the earliest from the Late Cambrian to the most active period of magmatic activity associated with subduction along the Gondwanan margin, spanning the Late Jurassic to the Early Cretaceous. During this time New Zealand comprised the margin of Gondwana, with the Challenger Plateau, Campbell Plateau and Marie Byrd Land contiguously forming the continental margin. To the north, the Lord Howe Ridge and New Caledonia comprised the continental margin. The Tutoko Complex granitoids are hypothesized to comprise the foundation of Bounty Island, now isolated on the eastern flanks of the Campbell Plateau (Wandres & Bradshaw, 2005).

The more easterly portions of New Zealand represent successive accretions of island arc-derived and oceanic terranes. The Brook Street Terrane is made up of a Permian island arc emplaced from 245 to 230 Ma. This terrane includes granitoid clasts as young as 170 Ma (Wandres & Bradshaw, 2005). Successive additions of the Murihiku Terrane (a Late Permian to Early Cretaceous sedimentary belt), the Dun Mountain–Maitai Terrane (an Early Permian ophiolite belt) and the Caples Terrane (dated as Early Permian by fossil inclusions) follow. Presently these terranes are greatly in evidence in the South Island, but are greatly reduced or absent in the North Island, a pattern explainable tectonically by models (King, 2000; Wood & Stagpoole, 2007) that configure Cretaceous New Zealand as a broadly triangular continent – Zealandia (Luyendyk, 1995), or subsequently emended to the Latin Zealandia (Leschen *et al.*, 2011) – with the eastern portions of the South Island forming the south-east margin, the eastern half of the North Island comprising the north-eastern margin, and the Buller and Takaka terranes comprising the western margin. Early during New Zealand's 'drifting' from Australia in the Late Cretaceous, immense extensions of the Chatham Rise and Campbell Plateau extended the continent towards the east and south-east, and the Norfolk and Reinga ridges extended it to New Caledonia (Herzer *et al.*, 1997; Campbell & Hutching, 2007; Wood & Stagpoole, 2007).

The Rakaia Terrane, which includes Permian to Early Jurassic sandstones, comprises the largest accretionary unit that currently makes up much of the eastern half of the South Island and portions of inland North Island. The sediments comprising the Rakaia Terrane are proposed to be of Antarctic origin by Wandres & Bradshaw (2005), given that the fossil inclusions are consistent with a high-latitude depositional environment. The Pahau and Waioeka terranes are composed of Late Jurassic to Early Cretaceous sediments, with the youngest in the Pahau Terrane dated to 87 Ma, contemporaneous with the fragmentation of Gondwana via the opening of the Tasman Sea. The Waipapa Terrane, now making up the middle of the North Island, is a heterogeneous assemblage of Permian to Early Cretaceous rocks (Wandres & Bradshaw, 2005). Based on Wood & Stagpoole's (2007) tectonic reconstruction, this terrane would represent some of the leavings from the rotation of the north-eastern margin of the North Island towards the western margin of the North Island – compressing the Caples Terrane – during the major transpressive motion along the Alpine Fault that brought the eastern portions of the South Island (Rakaia and Pahau terranes) into their present configuration (Fig. 1).

Subduction-related arc accretion stopped about 100 Ma along the eastern margin of Gondwana, with the geological environment switching to an extensional phase. Initial rifting

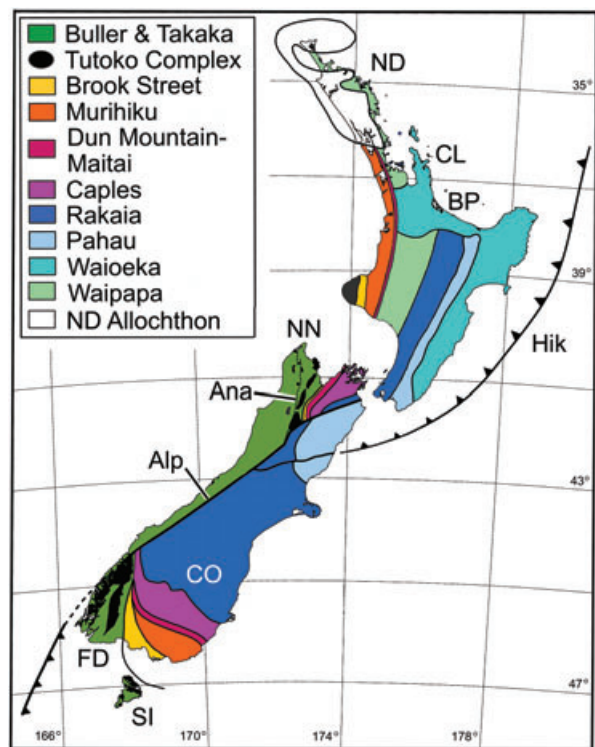


Fig. 1. Distribution of geological terranes comprising New Zealand, based on information from Mortimer (2004), Wandres & Bradshaw (2005) and Campbell & Hutching (2007). Abbreviations include: Alp, Alpine Fault; Ana, Anatoki Fault; BP, Bay of Plenty; CL, Coromandel Peninsula; CO, Central Otago; FD, Fiordland; Hik, Hikurangi subduction zone; ND, Northland; NN, Nelson; SI, Stewart Island.

led to fragmentation of the eastern margin of Gondwana, with isolation of the oldest New Zealand terranes as a result of sea-floor spreading and passive margin subsidence, commencing 84–85 Ma (Laird & Bradshaw, 2004). Any link between the Campbell Plateau and Marie Byrd Land would also have been broken near this time (Wandres & Bradshaw, 2005; Michaux, 2009), effectively isolating these terranes from Antarctica and southern South America. Prior to the change in direction of the Pacific Plate relative to the Australian Plate at 28 Ma (Clague & Dalrymple, 1989), the Buller, Takaka, Brook Street, Murihiku, Dun Mountain–Maitai and Caples terranes formed a cohesive linear series of progressively emplaced terranes. The Buller and Takaka terranes, including Fiordland, comprised a compact assemblage, with the Fiordland Block lying contiguously to the east of the Nelson Block (Wood & Stagpoole, 2007). The Dun Mountain–Maitai Terrane, or Dun Mountain Ophiolite Belt, is associated with the Junction Magnetic Anomaly, with the anomaly assumed to be linear as the Cretaceous starting point for tectonic models (King, 2000; Wood & Stagpoole, 2007). Starting in the Miocene (25 Ma), the relative movement of the Pacific Plate (and then associated Campbell Plateau) against the Australian Plate (including the Challenger Plateau) greatly transformed the proto-New Zealand continent Zealandia, resulting in the present-day configuration of New Zealand (Michaux, 2009). Extensive subduction within the southern half of the North Island resulted in immense crustal thickening (Wood & Stagpoole, 2007). Similarly, transpressive faulting along the length of the South Island resulted in the elevation of the Southern Alps, and vicariance of Fiordland and Stewart Island as well as the southern portions of the Brook Street, Murihiku, Dun Mountain and Caples Terranes from their northern geological sister areas in Nelson and Buller, through the relative southern motion of that margin of the Campbell Plateau. The northern portion of the Caples Terrane (Fig. 1) was dramatically distorted, as this material was emplaced onto the northern margin of the South Island. Also in the Miocene, the Northland Allochthon, a formation comprised of an ophiolite belt associated with the Three Kings subduction system, was emplaced onto the Northland Peninsula (Bradshaw, 2004). This region of the North Island is hypothesized to have been subaerial since the Miocene (Wood & Stagpoole, 2007). Compression to the north is hypothesized to have afforded periodic terrestrial or near-terrestrial connections between New Zealand and New Caledonia along the Reinga and Norfolk ridges (Herzer *et al.*, 1997).

It has been proposed that a Gondwanan origin and subsequent Cretaceous rifting and drifting is irrelevant to the biogeographic history of New Zealand's terrestrial organisms, because Oligocene high sea stands overran all terrestrial habitats (Campbell & Hutching, 2007; Landis *et al.*, 2008). Such a proposal seeks to overturn the relatively long-standing hypothesis that isolated islands serving as Gondwanan refugia persisted in New Zealand throughout the Oligocene (Fleming, 1962; Stevens & Suggate, 1978; Cooper & Cooper, 1995). The locations of these islands were proposed initially based on evaluating patterns of erosional deposition, without the benefit of our present-day understanding of New Zealand's tectonic

evolution (Wood & Stagpoole, 2007). Islands were proposed to have persisted from Central Otago to Stewart Island, in association with coal measures such as the Late Oligocene–Early Miocene Gore Lignite (Ferguson *et al.*, 2010). Fiordland was proposed to have been subaerial with an island including Mount Luxmore (Landis *et al.*, 2008). Other hypothesized islands were proposed for: (i) Nelson, in association with extensive coal deposits (Kamp, 1986); (ii) along the southern margin of Marlborough, currently Nelson Lakes National Park; (iii) in the North Island along the western margin north of Taranaki; (iv) for the area just north of Wellington; and (v) associated with the mountains south-west of the Bay of Plenty, as well as in the Coromandel Peninsula (Stevens & Suggate, 1978). Of these, the Fiordland, Central Otago–Gore Lignite, Nelson and Taranaki islands would have been associated with older Gondwanan terranes. Because of its proposed great size, the Central Otago island would have also been associated with the younger Rakaia Terrane, as would have been the Oligocene island north of Wellington. The Northland island would have bordered the eastern edge of the Northland Allochthon at its northern margin, and would also have included parts of the post-rift Pahau Terrane at its southern margins.

Material and methods

Taxonomic materials

Specimens and species listed in the cladistic analysis of Roig-Juñent (2000) were supplemented by additional taxonomic material representing *Bountya insularis* Townsend (Entomology Research Museum, Lincoln University; LUNZ), *Rawlinius papillatus* Davidson & Ball (Carnegie Museum of Natural History; CMNH) and *Bembidiomorphum convexum* Champion (Museum of Comparative Zoology, Harvard University; MCZ). Character states for taxa included in the prior cladistic analysis were re-examined using specimens deposited in the Cornell University Insect Collection (CUIC).

Laboratory techniques

Dissection techniques for the newly studied material follow Liebherr (2009). All dissections were photographed using a Microoptics (Asheville, NC) macrophotographic apparatus fitted with a Nikon D1X camera body and Infinity K2 lenses, illuminated by a Dyna-Lite 2000DR strobe light with fiberoptic light wands (Union, NJ). Multiple images through different depths of focus were integrated using COMPOSE z5 software (Hadley, 2006).

Cladistic analysis

The original cladistic matrix of Roig-Juñent (2000) was amended based on an examination of male and female specimens of *Bountya insularis*, *Rawlinius papillatus* and *Bembidiomorphum convexum*, by inclusion of the newly described

taxon, and by recombination of the terminal taxon *Microbarypus silvicola* (Roig-Juñent, 2000) as a member of the genus *Bembidiomorphum* Champion (Roig-Juñent *et al.*, 2008). Based on the findings of Maddison *et al.* (1999), two additional out-group taxa – *Blethisa multipunctatus* L. representing Elaphrini, and *Laccocenus ambiguus* Sloane, representing Psydrini sensu stricto – were added to the analysis. Pawson *et al.* (2003) revised the species of *Oregus* Putzeys, doubling the number of known species from two to four. Character states for all four species were used to score the *Oregus* terminal in the matrix.

The cladistic analysis of Roig-Juñent (2000) was based on genus-level terminals. We retain this convention based on the general lack of diversity within many of the genera described in Broscini (11 of the 43 broscine terminals in the analysis represent monotypic genera), and also based on generally monomorphic states for characters across species of the genera, as determined by Roig-Juñent's previous character scoring (Appendix S1). Where character states varied across taxa sampled for this analysis – *Mecodema* Blanchard and *Nothoscacellius* Roig-Juñent – the character states were coded as polymorphic. We found no polymorphic characters defined at the genus level that compromised the monophyly of any of the genus-level terminals.

The 73 characters scored for the cladistic analysis followed Roig-Juñent (2000), with the addition of several character states necessitated by the addition of the several out-groups and the newly described in-group taxon (Appendix S2). Multistate characters were treated both as ordered and as unordered, consistent with Roig-Juñent (2000).

The matrix was composed and edited using WINCLADA (Nixon, 2002), and then analysed initially using the ratchet (Nixon, 1999) by iteratively searching for shortest trees 200 times. These trees were saved and successively analysed using the max* option of NONA (Goloboff, 1993), as well as through the use of TNT (Goloboff *et al.*, 2007). Various options were used in TNT, with the reported results below based on an analysis using sectorial search, the ratchet, drift, tree fusing, random seed 5 and find minimum length 200. For both NONA and TNT, the trees were saved and imported into WINCLADA for viewing and evaluation. Bremer (1994) support was determined by NONA, by finding 2000 suboptimal trees each from one to ten steps longer than the multiple equally parsimonious trees (hold, sub and find* commands), and then calculating support values using the bsupport command.

Biogeographic analysis

The biogeographic analysis focused on two levels of geographic inclusivity. At the broader level, area relationships implicating the Southern Hemisphere continents were evaluated through examination of the taxon-area cladogram derived from the cladistic analysis. Here we find the Broscini of New Zealand do not support a single hierarchical set of area relationships, corroborating New Zealand's checkered history of area relationships with other austral areas, such as southern

South America, Australia and New Caledonia. Therefore, a hierarchical manner of analysis was not pursued for this broader geographic focus.

Geographic distributions of the various broscine genera among the various southern lands follow Roig-Juñent (2000), with the exception that *Percosoma asymmetricum* Fauvel of New Caledonia is better combined with *Percolestus* Sloane (K.W. Will, University of California, Berkeley, personal communication), based on its bisetose maxillary stipes, single supraorbital seta and single lateral pronotal seta. As we have not examined the unique type of *P. asymmetricum*, we do not make that new combination; however, for the purpose of the biogeographic analysis we add New Caledonia to the aggregate distribution of *Percolestus*, and remove it from the aggregate distribution of *Percosoma* Schaum.

A second, more geographically focused level of biogeographic analysis aimed to test the 'Oligocene drowning' hypothesis (Waters & Craw, 2006) – i.e. the total inundation version of the hypothesis – by determining if there is any general pattern of relictualism exhibited by the many arthropod taxa potentially 'on board' New Zealand as it rifted from Australia in the Cretaceous. First we recorded the distributional patterns outside New Zealand for all candidate Gondwanan relicts. As rifting of New Zealand commenced along the eastern margin of Gondwana, New Zealand retained adjacency to both New Caledonia and what is now Queensland to the north, as well as to the Campbell Plateau, Marie Byrd Land, the Antarctic Peninsula and southern South America to the west (Brundin, 1966; Wandres & Bradshaw, 2005). These two sister-area relationships for New Zealand – to Australia and to South America – were sequentially and empirically supported by Hennig (1960) and Brundin (1966). The former Australian area relationship has been termed an eastern Gondwanan pattern (Table 1: MR), and is based on vicariance mediated by the Melanesian Rift (Michaux & Leschen, 2005). Conversely, taxa that exhibit distributions including New Zealand, islands of the Campbell Plateau and southern South America (Table 1: SSA) represent Michaux & Leschen's (2005) western Gondwanan pattern, reflecting the vicariance of New Zealand plus the Campbell Plateau from Marie Byrd Land (Michaux, 2009). Other taxa include representatives in all three areas – Australia, New Zealand and South America – and display the hierarchical southern Gondwanan pattern of area relationships: NZ (Au + SSA) (Crisci *et al.*, 1991; Sanmartín & Ronquist, 2004; Table 1: SGP). The sister groups for several precinctive New Zealand taxa remain obscure or are geographically widespread, making it impossible to assign a biogeographic pattern to these taxa (Table 1: coded '?'). Assuming we have comprehensive knowledge regarding the geographic distributions of the various Gondwanan taxa, New Zealand may be regarded as the panbiogeographic node (Crisci *et al.*, 2003) at which Antarctic and Melanesian tracks intersect (Croizat, 1962: 162, fig. 41A).

For this New Zealand-level, 'Oligocene drowning' analysis, species distributions for candidate Gondwanan taxa (Table 1) were examined relative to their extant presence on either older Gondwanan-aged terranes or on the newer terranes that became

Table 1. Candidate Gondwanan taxa (biogeographic pattern; see text) and numbers of included species occupying terranes categorized as Gondwanan (G) or New Zealand (NZ), or on islands of the Campbell Plateau (CP).

	No. spp. Gondwanan Terranes	No. spp. New Zealand Terranes	No. spp. Campbell Plateau islands	Root	References
Opiliones (Arachnida)					
<i>Neopurcella salmoni</i> (Pettalidae) – MR	1	0	0	G	Boyer & Giribet (2007, 2009)
<i>Aoraki</i> (Pettalidae) – MR	4	6	0	G + NZ	Boyer & Giribet (2007, 2009)
<i>Rakaia</i> (Pettalidae) – MR	8	13	0	G ^a	Boyer & Giribet (2007, 2009)
Sphaerotheriida (Diplopoda)					
<i>Procyliosoma</i> ^b (Procyliosomatidae) – MR	4	3	0	^c	Holloway (1956), Wesener & VandenSpiegel (2009)
Plecoptera (Insecta et seq.)					
<i>Halticoperla</i> (Notonemouridae) – SSA	2	1	0	^c	McLellan (1991), Terry (2003)
<i>Notonemoura</i> (Notonemouridae) – SSA	3	1	0	^c	McLellan (1991), Terry (2003)
Orthoptera					
<i>Deinacrida</i> (Anostostomatidae) – MR	11	11	0	G + NZ	Trewick & Morgan-Richards (2005)
Hemiptera					
<i>Xenophysella</i> + <i>Xenophyes</i> + <i>Oiophysa</i> (Peloriidiidae) – SGP	9	4	0	G	Burkhardt (2009)
<i>Phenacoleachia</i> (Phenacoleachiidae) – SGP	2 ^d	1	1	^c	Gullan & Cook (2002)
<i>Aenicticoris powelli</i> (Enicocephalidae) – MR	1	0	0	G	Woodward (1956), Štys (2008)
<i>Gourlayocoris mirabilis</i> (Enicocephalidae) – MR	1	0	0	G	Woodward (1956), Štys (2008)
<i>Maoristolus</i> (Enicocephalidae) – MR	2	2	0	G + NZ	Woodward (1956), Štys (2008)
<i>Nymphocoris maoricus</i> (Enicocephalidae) – MR	1	0	0	G	Woodward (1956), Štys (2008)
<i>Phthirostenus magnus</i> (Enicocephalidae) – MR	0	0	1	CP	Woodward (1956), Štys (2008)
Coleoptera					
<i>Loxomerus</i> + <i>Taenarthrus</i> (Carabidae) – MR	11	2	4	CP	Johns (1974, 2010), Roig-Juñent (2004)
<i>Erebotrechus infernus</i> (Carabidae) – SGP	1	0	0	G	Townsend (2010)
<i>Kupetrechus</i> (Carabidae) – SGP	3	0	0	G	Townsend (2010)
<i>Metacorneolabium</i> (Staphylinidae) – SGP	7	4	1	G	Thayer (1985)
<i>Chaetosoma</i> + <i>Chaetosomodes</i> (Chaetosomatidae) – SGP	2	3	0	^c	Kobilač (2004), Ewers <i>et al.</i> (2007), Opitz (2010)
<i>Metaxina ornata</i> (Metaxinidae) – SGP	1	1	0	G + NZ	Kobilač (2004), Johnson <i>et al.</i> (2008)
<i>Priasilpha</i> (Priasilphidae) – MR	5	1	1	G + NZ + CP	Leschen & Michaux (2005)
<i>Ostreacryptus clarkae</i> (Cryptophagidae) – SSA	1	0	0	G	Leschen (2001)
<i>Cyclaxyra</i> (Cyclaxyridae) – SSA	1	2	0	G + NZ	Gimmel <i>et al.</i> (2009)
<i>Chalcodrya</i> + <i>Philpottia</i> + <i>Onysius</i> Chalcodryidae – ?	4	3	0	^c	Watt (1974)
Lepidoptera					
<i>Sabatinka</i> s.s. (Micropterigidae) – MR	6	3	0	G	Gibbs (1983, 2010)
<i>Palaeomicra</i> (Micropterigidae) – SGP	8	6	0	G ^a	Gibbs (1983)
<i>Mnesarchaea</i> (Mnesarchaeidae) – ?	11	11	0	G + NZ	Gibbs (1983)
<i>Xanadoses nielsenii</i> (Cecidosidae) – SGP	1	1	0	G + NZ ^e	Hoare & Dugdale (2003)
Mecoptera					
<i>Nannochorista philpotti</i> (Nannochoristidae) – SGP	1	1	0	G + NZ	Pilgrim (1972)
Diptera					
<i>Australosymmerus</i> (Ditomyiidae) – SSA	3	3	0	G + NZ	Munroe (1974)
<i>Starkomyia inexpectata</i> (Sciaroidea) – SSA	0	1	0	NZ	Jaschhof (2004a), Hippa & Vilkamaa (2006)

Table 1. Continued.

	No. spp. Gondwanan Terranes	No. spp. New Zealand Terranes	No. spp. Campbell Plateau islands	Root	References
<i>Anisotricha</i> (Sciaroidea) – SSA	2	0	0	G	Jaschhof (2004b), Hippa & Vilkkamaa (2006)
<i>Insulatricha</i> (Sciaroidea) – SGP	2	2	0	G + NZ	Jaschhof (2004b), Hippa & Vilkkamaa (2006)
<i>Rangomarama</i> [Rangomaramidae (inae)] – SSA	2	4	0	G + NZ	Jaschhof & Didham (2002), Hippa & Vilkkamaa (2006)
<i>Parochlus</i> (incl. <i>Zelandochlus</i>) (Chironomidae) – SGP	10	1	0	G	Brundin (1966), Cranston <i>et al.</i> (2010)
<i>Podochlus</i> (Chironomidae) – SGP	4	3	0	G + NZ	Brundin (1966), Cranston <i>et al.</i> (2010)
Hymenoptera					
<i>Maaminga</i> (Maamingidae) – SGP	1	2	0	G + NZ	Early <i>et al.</i> (2001)
<i>Rotoita basalis</i> (Rotoitidae) – SSA	1	1	0	G + NZ	Bouček & Noyes (1987), Gibson & Huber (2000)

Root area(s) defined by DIVA or by inspection.

^aRoot defined by DIVA either as G only or as G + NZ.

^bFive named subspecific taxa treated as species.

^cCladistic hypothesis required but unavailable for establishing root.

^dUndescribed species known from Stewart Island.

^eTaxon occupies only Gondwanan terranes in the South Island.

subaerial just prior to or after Cretaceous rifting. Based on the above interpretation of terrane ages, and the presently accepted tectonic models (King, 2000; Wood & Stagpoole, 2007), the Buller and Takaka terranes, Tukoko Complex, and Brook Street, Murihiku, Dun Mountain–Maitai and Caples terranes (Fig. 1) were categorized as Gondwanan. Terranes here categorized as New Zealand (meaning they are presumed to have become subaerial later in New Zealand's history, subsequent to New Zealand's vicariance from Gondwana) included the Rakaia, Pahau, Waioeka and Waipapa terranes, plus the Northland Allochthon. A third distributional category – Campbell Plateau – was used to score species found on the isolated islands – Campbell Island, Auckland Islands, etc. – of the Campbell Plateau. For candidate taxa with more than three taxa and a published cladogram, the event-based method of dispersal-vicariance (DIVA) analysis (Ronquist, 1996, 1997) was used to estimate the root distribution of the taxon. DIVA does not necessarily search for a centre of origin, as the geographic distributions of terminal taxa are optimized internally on the taxon-area cladogram. Vicariance events cost nothing, whereas dispersal events have a cost of 1, and the goal is to minimize the cost (Ronquist, 1996). Thus, any number of areas of endemism (in this analysis, from one to three) may be optimized to a cladogram root in an unconstrained DIVA analysis. Given that most Gondwanan taxa reviewed are distributed on mainland New Zealand, our major intent was to test whether presumed relictual taxa originated either on older Gondwanan terranes or on newer post-Gondwanan terranes accreted to a drifting New Zealand. Rooting on the Campbell Plateau, as occurred in only several instances, is interpreted in light of tectonic hypotheses for New Zealand (Wood & Stagpoole, 2007; Michaux, 2009). The null hypothesis to be rejected posits that there is no geographic pattern of relictualism, and therefore taxa will exhibit primordial distributions that may include any

combination of one or more areas. For mainland New Zealand taxa, the critical datum posited by this null hypothesis is the similar numbers of instances of rooting in Gondwanan- versus New Zealand-aged terranes. Asymmetrical deviation from this pattern, whereby candidate relictual taxa exhibit a preponderance of rootings in the older Gondwanan terranes only, suggests the relicts have had a long history in New Zealand, in association with older terranes, consistent with ancestry stemming from New Zealand's contiguity with Gondwana's eastern margin. Such a long history would *by necessity* extend through the hypothesized 'Oligocene drowning' event. The rooting of Gondwanan groups on Gondwanan terranes, regardless of the taxon's participation in the biogeographic pattern (MR, SGP or SSA; Table 1), is also predicted by the paleodistribution of the hypothesized Oligocene islands in Nelson, Fiordland, Southland and Stewart Island, as numerous 'Gondwanan' terranes were compactly arranged at the core of Cretaceous New Zealand (Wood & Stagpoole, 2007; fig. 3, 65 Ma). The subaerial persistence of portions of these Gondwanan fragments as islands throughout the Oligocene would have maintained populations of the resident Gondwanan relictual taxa.

Conversely, rooting predominantly in younger New Zealand terranes would suggest a lack of early colonization of the older terranes, perhaps consistent with post-Gondwanan dispersal-based colonization, or removal of colonists from older terranes via Oligocene drowning contemporaneous with survival on younger terrane-based islands. In either instance, biogeographic data would appear unreliable as the basis for inferring long-term residence in presently occupied areas, as the Gondwanan-aged taxa would have retained sufficient dispersal abilities to allow them to colonize new areas. Where species numbers were few enough, or distributions simple enough, we estimated primordial distribution by inspection. We report taxa that lack phylogenetic hypotheses, and therefore are

ambiguous for this analysis, in the hopes that they might attract cladistic attention.

Determining whether a taxon was of Gondwanan in age (Table 1) was accomplished in two ways, both dependent on the presence of suitable fossils. Phylogenetic analysis establishes hierarchically arranged sets of sister taxa, and the availability of a fossil representing a taxon's sister group can establish a minimum age for the in-group taxon of interest (Hennig, 1966; Grimaldi & Engel, 2005). The literature was searched for arthropod taxa exhibiting high levels of endemism in New Zealand (precinctive genera and families), and also for fossils representing out-groups to those taxa (Appendix S3). This direct approach is also necessary for establishing our second category of Gondwanan candidates: those taxa for which phylogenetic relationships have been analysed using molecular sequence data (DNA, RNA and mtDNA), and for which divergence estimates of New Zealand taxa have been published. For these taxa, ages for New Zealand clades based on parametric rate-smoothing estimates (Giribet & Boyer, 2010), and other Bayesian methods (Cranston *et al.*, 2010), were substituted for direct fossil-age estimation. As for the direct approach, the availability of reliably dated fossils is essential.

Results and discussion

Cladistic analysis of Broscini

The initial cladistic analysis using WINCLADA (200 iterations of the ratchet at default settings) resulted in 66 trees of 326 steps in length. The strict consensus of these trees collapsed eight nodes and resulted in a tree of 343 steps (Fig. 2). Submitting these 66 trees to the max* command of NONA – and reducing the polymorphic coding of WINCLADA to ambiguous states – resulted in 96 trees of 326 steps in length. Examining these in WINCLADA and thereby restoring the polymorphic character codings resulted in 72 best trees of 326 steps in length (Appendix S1), and the same strict consensus (Fig. 2). Submitting the matrix to TNT, using the parameters presented above, resulted in a best score of 326 steps being hit 96 times, with 624 777 336 rearrangements examined, and 90 best trees retained. Examining these trees using WINCLADA (keeping the best trees and deleting the suboptimal trees) resulted in 70 trees, the consensus of which was identical to Fig. 2.

Phylogenetic relationships among the broscine taxa in this analysis are very similar to those reported previously based on the earlier matrix for Broscini, with no resolved relationship on the 240-tree strict consensus of the prior analysis (Roig-Juñent, 2000) deviating by more than one node from the present strict consensus cladogram (Fig. 2). *Broscus* Panzer is no longer posited to be the sister group to *Craspedonotus* Schauman, and instead unresolvedly subtends a clade including *Chaetobroscus* Semenov and five other Holarctic genera. The basal dichotomy between Holarctic and austral Broscini is retained. In support of the synonymization of *Microbarypus* Roig-Juñent with *Bembidiomorphum* Champion (Roig-Juñent

et al., 2008), the type species of the genus, *B. convexum*, is placed as sister species to *Bembidiomorphum silvicola* (Roig-Juñent). The two species can be diagnosed by differences in the male aedeagal median lobe, the apex of which is nearly parallel-sided in *B. convexum* males, versus expanded in *B. silvicola* (Roig-Juñent, 2000: figs 225–226). Also, the bursa copulatrix of *B. convexum* females exhibits an accessory gland that is absent in females of *B. silvicola* (Roig-Juñent, 2000: fig. 227). Moreover, the spermatheca of *B. convexum* females is elongate and laterally curved apically, not broad and truncate as in females of *B. silvicola*.

The newly described New Zealand relictual taxon, *Orthoglymma wangapeka* sp.n., is placed as the adelphotaxon to the remaining taxa comprising the austral subtribe Nothobroscina (Fig. 2). All phylogenetic relationships within Nothobroscina remain identical with those in Roig-Juñent (2000). The earliest divergent position of *Orthoglymma wangapeka* sp.n. in this clade is supported by the symplesiomorphic retention of a narrowed left-lateral margin to the ninth male abdominal tergite (Fig. 3E), a state shared with all other Broscini save the nothobroscine clade subtended by *Diglymma* Sharp. Monophyly of Nothobroscina plus Baripina is supported by synapomorphies (Appendix S2) of characters 54 (state 2, median lobe, basal orifice completely closed; Fig. 3B) and 55 (state 1, median lobe dorsal surface sclerotized; Fig. 3B). Monophyly of the subtribe Nothobroscina is supported by synapomorphous characters: 12 (state 1, two deep and rounded foveae laterad mentum tooth; Fig. 4A); 59 (state 2, sclerite X of internal sac broad with a median constriction, three apical points and without lateroapical projections; Fig. 3B, D); 60 (state 1, internal sac sclerite Y present; Fig. 3B, D); 61 (state 2, internal sac apical plate composed of free spiculae and central tooth; Fig. 3B); 63 (state 2, rami of gonocoxite IX long; Fig. 4F); 65 (state 2, accessory gland of bursa copulatrix medial, far from spermatheca; Fig. 4E); 67 (state 1, bursal sclerite at base of common oviduct present; Fig. 4E); 72 (state 1, vaginal apophysis present; Fig. 4E); and 73 (state 2, helminthoid sclerite broad and short; Fig. 4E). Of these synapomorphous transformations at the base of Nothobroscina, only characters 12 and 67 subsequently reverse within the subtribal in-group (as reported by Roig-Juñent, 2000).

Inclusion of all pertinent character-state data for *Bountya insularis*, via the availability of specimens representing both sexes, enhances resolution within the Creobiina. *Bountya* Townsend is placed as the adelphotaxon to the clade subtended by *Promecoderus brunnicornis* Dejean + *Acallistus* Sharp (Fig. 2: node ϵ). Additionally, *Cascellius* Curtis and *Creobius eydouxi* Guérin-Ménéville are resolved as successive adelphotaxa of the unresolved node subtending four other sections of *Promecoderus* Dejean plus *Anheterus* Putzeys.

Biogeographic analysis of Broscini

Based on this cladistic analysis, the New Zealand broscine fauna comprises three sets of taxa. *Orthoglymma* and *Diglymma* adjacently and successively diverge at and above the

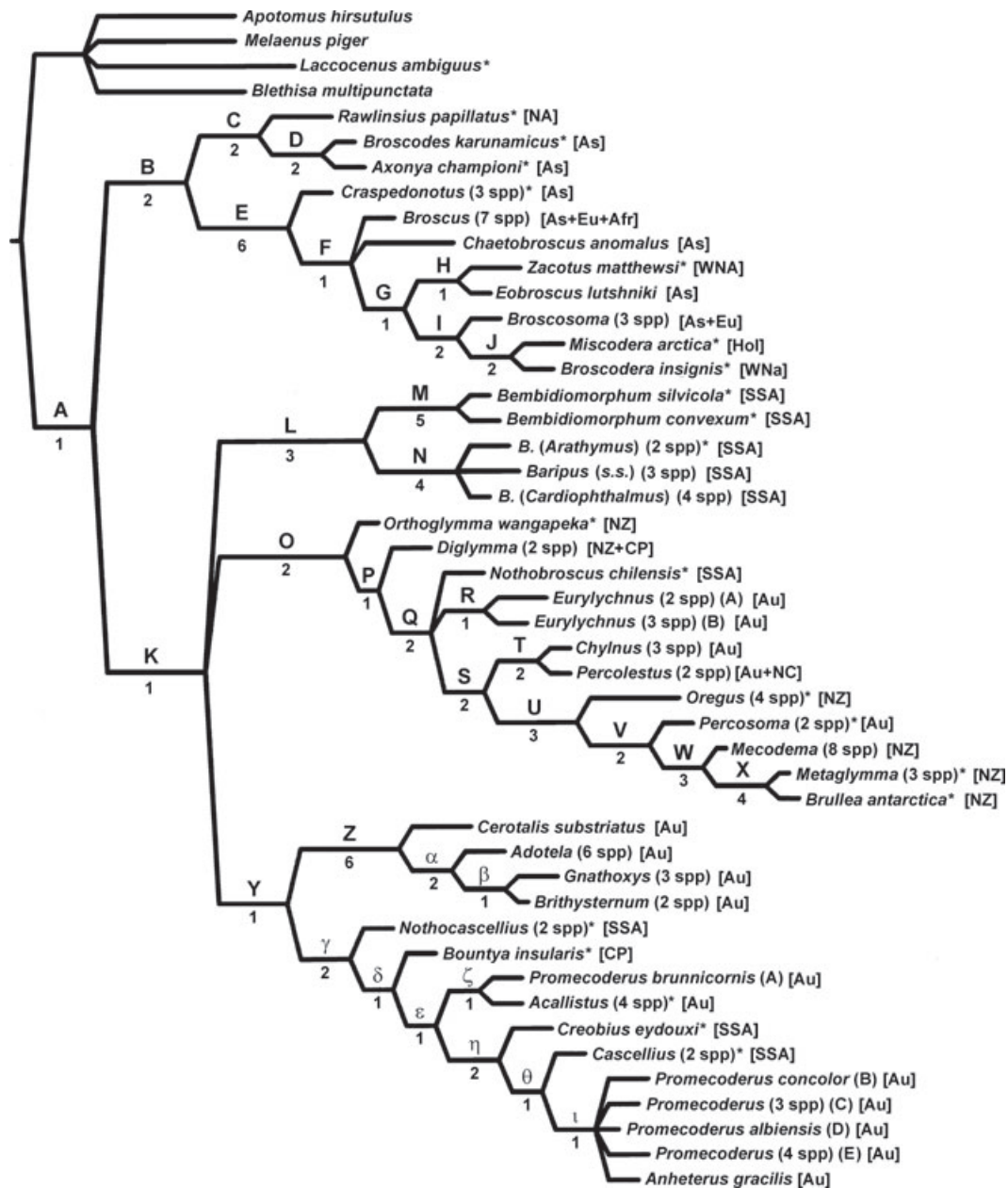


Fig. 2. Strict consensus cladogram for Broscini (A) and four out-group taxa showing geographic distributions of terminals. Numbers of species-level taxa examined for character scoring in parentheses. *Generic-level terminals for which all described taxa were examined over the course of character scoring. Bremer support values are indicated below each cladogram edge. Subtribal taxa include Axonyina (edge C), Broscina (edge E), Baripina (edge L), Nothobroscina (Edge O) and Creobiina (edge Y). Areas of geographic distribution include: Africa, (Afr), Asia (As), Australia including Tasmania (Au), Campbell Plateau (CP), Europe (Eu), Holarctic (Hol), New Caledonia (NC), New Zealand (NZ), North America (NA), southern South America (SSA) and western North America (WNA).

common ancestor of the Nothobroscina (Fig. 2: edge O), with the lineage subsequently divergent in southern South America, Australia, New Caledonia and, three nodes away, again in New Zealand. Secondly, *Bountya insularis* is isolated as a New Zealand relict within the otherwise Australian plus southern South American Creobiina (Fig. 2), a relationship recognized since Townsend (1971) described the taxon. Thirdly,

a paraphyletic grouping comprises the second set of New Zealand nothobroscine taxa *Oregus*, *Mecodema*, *Metaglymma* Bates and *Brullea* Castelnau. These four genera exhibit close relationships with genera distributed in Australia and New Caledonia, with the Australian *Percosoma* being a member of the clade including the four New Zealand genera, with this clade's sister group – the sister genera *Chylnus* Sloane

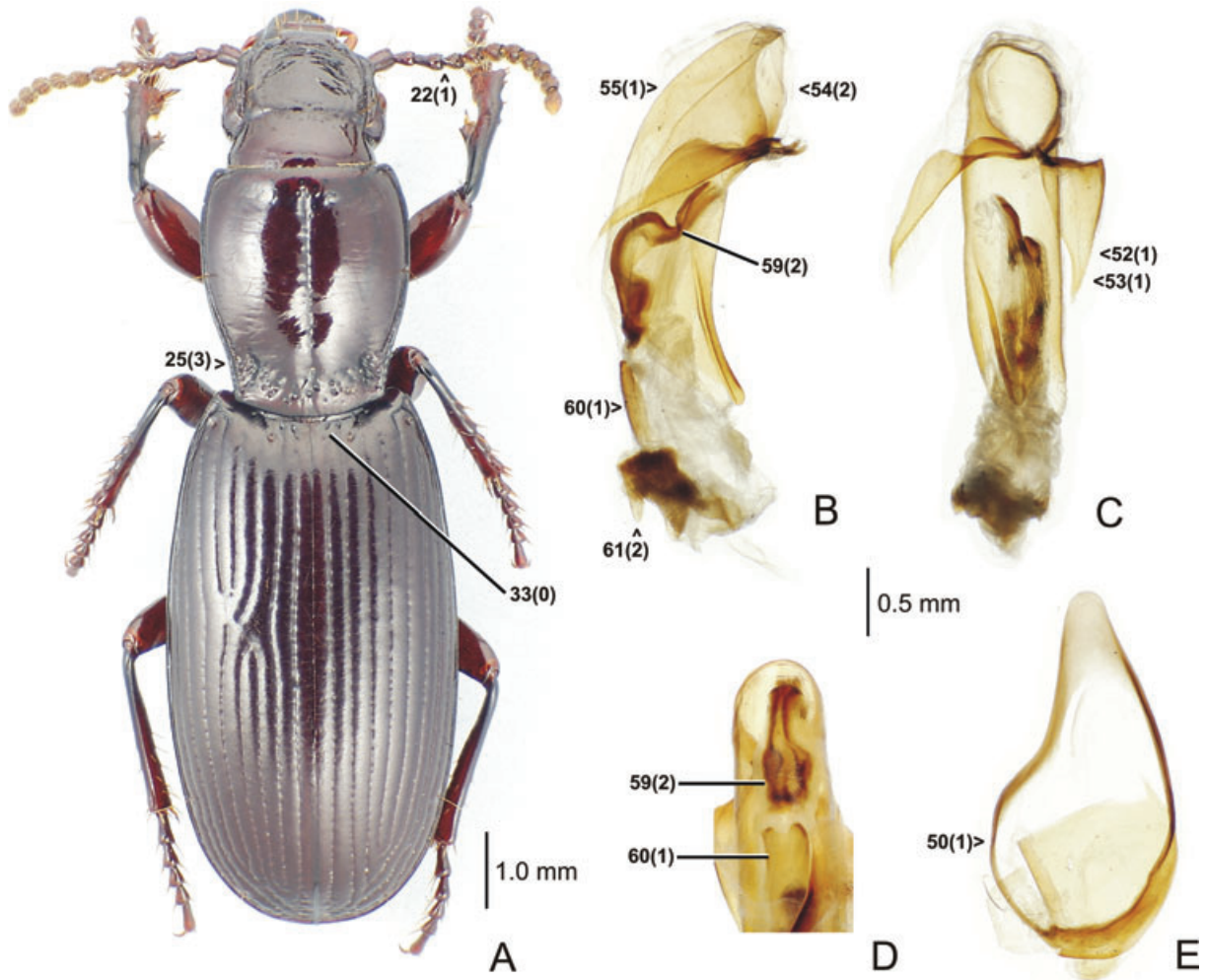


Fig. 3. *Orthoglymma wangapeka* sp.n. (A) Male paratype, dorsal view. (B) Male aedeagal median lobe and associated parameres, right lateral view. (C) Male aedeagal median lobe and associated parameres, ventral view. (D) Male median lobe base, dorsal view. (E) male ring sclerite, modified tergite IX (Deuve, 1993), dorsal view. Characters and (states) treated in text and in Appendix S2. Scale bars: 1.0 mm (A); 0.5 mm (B–E).

and *Percolestus*—distributed in Australia and New Caledonia. We propose that the first two instances represent New Zealand's inclusion in an Antarctic, or Campbell Plateau, track that implicates the three areas of New Zealand, southern South America and Australia, along with an implicit primitive cosmopolitan presence in Antarctica. The paraphyletic grouping subtended by *Oregus* is proposed as a post-Gondwanan evolving lineage that exhibits trans-Tasman relationships, with the inclusion of *Percosoma* indicating a biogeographic ebb and flow of broscines across the Norfolk-Reinga Ridge system that also connected New Caledonia with New Zealand.

The overall division of Broscini into Holarctic and austral assemblages (Fig. 2: edge K) has been proposed to represent an ancient amphitropical relationship, supporting the evolution of the many southern taxa on an evolving and fragmenting Gondwana (Roig-Juñent, 2000). Fossil evidence for Carabidae support a Mesozoic origin of Broscini, based on a fossil assignable to Harpalinae reported from Upper Cretaceous

Turonian-aged deposits of South Kazakhstan (Ponomarenko, 1992). Phylogenetic placement of Broscini as an out-group, not closely related, to Harpalinae (Maddison *et al.*, 1999: figs 6–7) necessitates the tribe's origin well before the Turonian. These fossil data are consistent with molecular sequence data supporting a Cretaceous origin of the subfamily Harpalinae (Ober, 2002). In this instance, then, an amphitropical biogeographic pattern and fossil and molecular data agree, supporting the existence of taxa attributable to Broscini from a time well before New Zealand's vicariance from Gondwana.

The distributions of species-level (and thus in aggregate, generic-level) taxa within each of the groupings of New Zealand taxa can be used to support assignment to either an Antarctic or trans-Tasman track. *Orthoglymma wangapeka* sp.n. is resident on the Buller Terrane, with the type locality situated on the Karamea Batholith of the Tuhua Intrusive Group, a pluton of Devonian age (Suggate *et al.*, 1978). Thus, the origin of this taxon is presently interpreted to

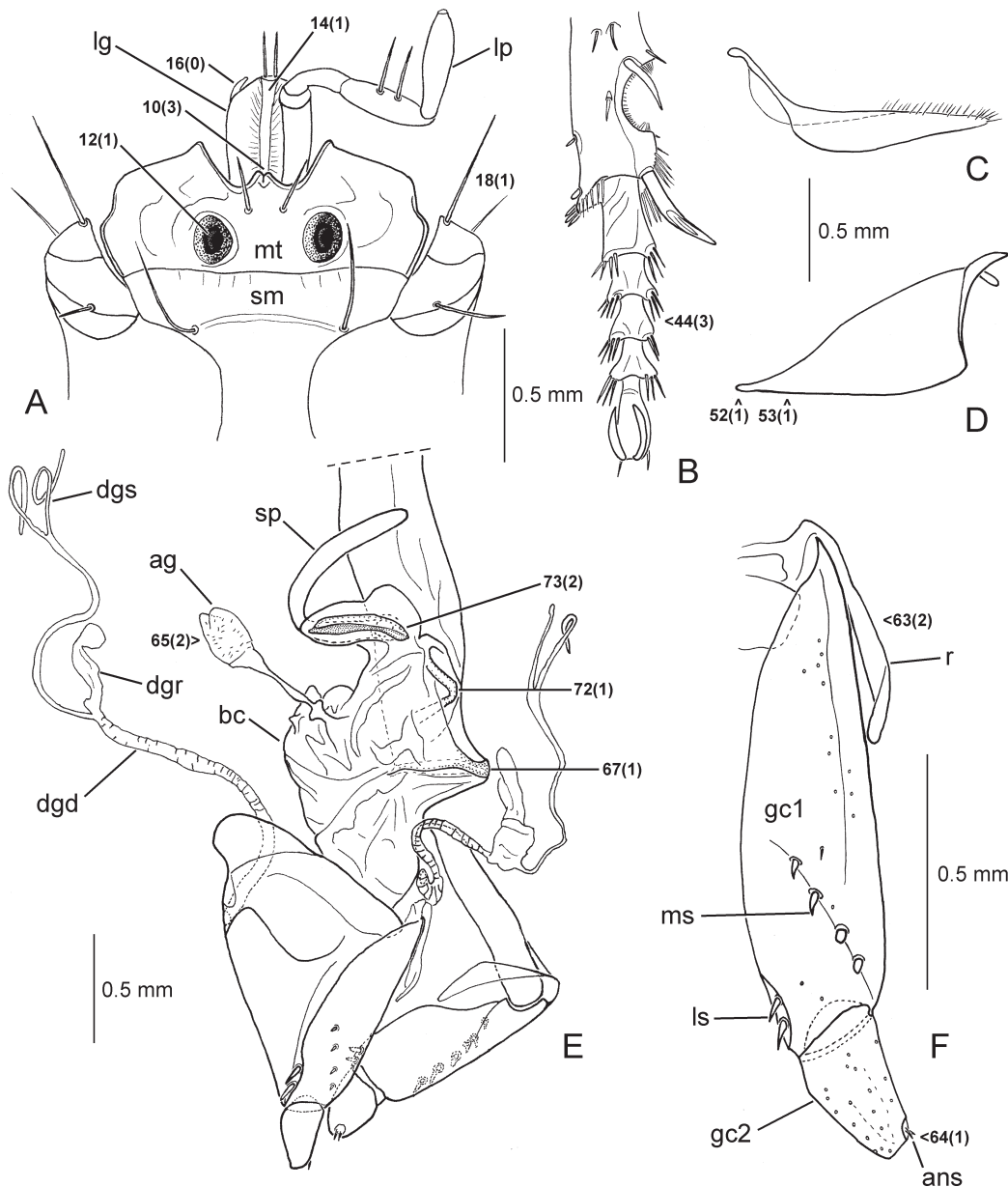


Fig. 4. *Orthoglymma wangapeka* *sp.n.* (A) Ventral mouthparts including mentum, submentum, ligula and labial palps. (B) Apex of left male protibia and five protarsomeres, ventral view. (C) Right male paramere, right view. (D) Left male paramere, left view. (E) Female gonocoxae and reproductive tract, ventral view. (F) Right gonocoxa, ventral view. Abbreviations include: ag, accessory gland; ans, apical nematiform setae of gonocoxite 2; bc, bursa copulatrix; dgd, defensive gland duct; dgr, defensive gland reservoir; dgs, defensive gland secretory ductules; gc1 and gc2, basal and apical gonocoxites 1 and 2; lg, ligula; lp, labial palp; ls, lateral setae of gonocoxite 1; ms, medial setae of gonocoxite 1; mt, mentum; sm, submentum; r, ramus; sp, spermatheca. Characters and (states) are described in the text and in Appendix S2. Scale bars: 0.5 mm.

have been associated with the Western Province of New Zealand (Wandres & Bradshaw, 2005) on the Challenger Plate. The cladistically adjacent *Diglymma* comprises five species: *Diglymma castigatum* Broun, precinctive to the Snares Islands of the Campbell Plateau; two others [*Diglymma marginale* Broun and *Diglymma seclusum* (Johns)], restricted to the Buller and Takaka terranes of western New Zealand; *Diglymma obtusum* (Broun), distributed predominantly on Gondwanan

terranes in the south, but with a northern distributional limit on the extreme southern margin of the Rakaia Terrane near Dunedin; and lastly, *Diglymma clivinoides* (Castelnau), distributed broadly on the Rakaia and Pahau terranes in Canterbury, South Island, as well as the southern reaches of the North Island (Townsend, 1971; Laroche & Larivière, 2001, 2007; Johns, 2007). A cladistic hypothesis for *Diglymma* will establish whether the lineage's common ancestor was restricted

to a Gondwanan terrane, but the occurrences of *Orthoglymma wangapeka* sp.n. plus four of the five *Diglymma* spp. on Gondwanan terranes point towards the assignment of these taxa to the Antarctic track. The precinctive occurrence of the creobiine *Bountya insularis* on the Bounty Islands, without any relatives in New Zealand, but with adjacent relatives in southern South America and Australia, supports the assignment of *Bountya* to the Antarctic track. The relatively early divergent cladistic position of *Bountya* amongst the Creobiina also supports its relatively early origin (Fig. 2).

Species classified in the other four cladistically subordinate New Zealand nothobroschine genera (Fig. 2) tend to occur predominantly on eastern, or younger, New Zealand terranes. For example, the three species of *Metaglymma* all occur on the eastern parts of the South Island overlying the Rakaia Terrane, although the distribution of *Metaglymma tibiale* (Castelnau) extends southwards into Southland (Larochelle & Larivière, 2001), onto what we score as Gondwanan terranes (Fig. 1; Caples and Dun Mountain–Maitai). *Brullea antarctica* Castelnau exhibits psammophilous habits, with individuals found on sea beaches of both east and west coasts of both islands. For *Oregus* spp., all taxa occur in areas underlain by the Rakaia or Pahau terranes, although the widespread *Oregus aereus* (White) also occurs on the older Gondwanan terranes (Larochelle & Larivière, 2001; Pawson et al., 2003). The phylogenetic hypothesis proposed for *Oregus* (Pawson et al., 2003) roots on the Rakaia Terrane, as that area houses the two earliest diverging species, *Oregus crypticulus* Pawson and *Oregus septentrionalis* Pawson.

The fourth genus in this trans-Tasman suite represents a major radiation of New Zealand Carabidae. *Mecodema* has undergone diversification, resulting in 70 presently known specific and subspecific taxa (Britton, 1949; Larochelle & Larivière, 2001, 2007; Seldon & Leschen, 2011). The aggregate generic distribution includes all of the arbitrary mainland areas of Crosby et al. (1976) as well as the Three Kings Islands to the north, the Chatham Islands to the east and the Snares Islands to the south of New Zealand.

Biogeography of Gondwanan taxa

Having proposed *Orthoglymma wangapeka* sp.n. as a biogeographic relict that primordially occupied the Gondwanan-aged Buller Terrane, and persisted through the ‘Oligocene drowning’, the question of whether other taxa might exhibit the same biogeographic pattern of relictualism is raised. Based on the area relationships of *Orthoglymma* and *Diglymma* relative to southern South American and Australian nothobroschine taxa, these two New Zealand nothobroschines can be considered to represent New Zealand in the southern Gondwanan biogeographic pattern: i.e. NZ (Au + SSA) (Sanmartín & Ronquist, 2004) in the set of area relationships recognized first by Brundin (1966). Based on our review, 14 other New Zealand arthropod taxa can be shown to exhibit the southern Gondwanan pattern (Table 1: SGP). Of these 14 taxa, phylogenetic information can place the origin for seven in

a Gondwanan terrane. The root areas for taxon-area cladograms of five taxa include both Gondwanan and New Zealand terranes, and we lack cladistic information for two putative Gondwanan-aged taxa, precluding assignment of a biogeographic root.

We have documented 13 New Zealand arthropod taxa of Gondwanan age with the cladistically closest relatives in New Caledonia or Australia. Further general area relationships are diverse or remain obscure; however, the closest relationship of areas across the Melanesian Rift allows the assignment of these taxa to the MR pattern (Table 1). As demonstrated by Chambers et al. (2001), phylogenetic relationships involving taxa occupying New Zealand, New Caledonia and Australia may be of disparate ages, with some very recent and putatively requiring dispersal along an intermittently emergent Norfolk Ridge (Herzer et al., 1997). Nevertheless, all of the examples we have listed for the Melanesian Rift vicariance pattern are supported by the fossil record or molecular sequence divergence estimates, which are consistent with a Mesozoic origin of the taxa in New Zealand (Appendix S3). Of these 13 taxa, six are unambiguously rooted biogeographically on Gondwanan terranes, and three are ambiguous biogeographically, as the root of their taxon-area cladograms include both Gondwanan and New Zealand terranes. Three other taxa include species precinctive to the islands of the Campbell Plateau: the migadopine carabid beetles of the genus *Loxomerus* (Johns, 2010), *Priasilpha aucklandicus* Leschen, Lawrence & Šlipiński (Priasilphidae) (Leschen & Michaux, 2005) and *Phthiricostenus magnus* (Woodward) (Enicocephalidae) (Štys, 2008). Based on cladistic relationships for *Priasilpha*, the root areas of the cladogram may include Gondwanan, New Zealand or Campbell Plateau areas, although diversification in *Priasilpha* has centered on the Gondwanan terranes, with a clade of five species arrayed allopatrically along the west coast of New Zealand’s South Island (Leschen & Michaux, 2005). We lack a phylogenetic hypothesis for the final taxon exhibiting the Melanesian Rift pattern, the giant pill-millipedes (Procyliosomatidae) (Holloway, 1956; Wesener & VandenSpiegel, 2009), although again more taxa are found in areas we assigned as being Gondwanan rather than in younger terranes assigned to an isolated New Zealand (Table 1).

Jeannel (1938, 1942) included the migadopine carabid beetles as one of his primary examples of diversification facilitated via the geographic fragmentation of Gondwana. Using cladistic analysis, Roig-Juñent (2004) proposed that the New Zealand migadopines consituted three lineages: a *Loxomerus* lineage [i.e. species placed both in *Loxomerus* Chaudoir and *Taenarthrus* Broun by Johns (2010)], the mainland New Zealand species *Amarotypus edwardsii* Bates and the monotypic *Calathosoma* Jeannel from the Auckland Islands. These three lineages were hypothesized to be paraphyletic relative to *Stichonotus* Sloane of Australia, thereby leading to the assignment of this group to the trans-Tasman pattern (Table 1). Analysing Roig-Juñent’s (2004) phylogenetic hypothesis using DIVA places the geographic root of this trans-Tasman clade on the Campbell Plateau. If we adopt Michaux’s (2009) geological reconstruction, whereby the Campbell and Challenger plateaux

were separated broadly by the Campbell Rift until Late Oligocene–Early Miocene impingement led to the development of the Alpine Fault and Miocene–Pliocene orogeny of the Southern Alps (Campbell & Hutching, 2007), then abundant phylogenesis – including radiation of *Taenarthrus* on the South Island (Johns, 2010), origins of *Amarotypus edwardsii* in New Zealand and dispersal of its recently described relatives to Australia (Baehr, 2009), as well as the independent dispersal of the ancestor of *Stichonotus* to Australia – must have occurred after 25 Ma. Johns (2010) presented shared characters restricted to both *Loxomerus* (setose female gonocoxae with a very small apical coxite; Johns, 1974: figs 8, 9) and *Taenarthrus* (male aedeagal median lobe strongly bent; Johns, 2010: figs 18–21), suggesting that Roig-Juñent's (2004) synonymy of *Taenarthrus* under *Loxomerus* requires re-evaluation. In any event, the many recently described taxa (Baehr, 2009; Johns, 2010) indicate the need for an updated, taxonomically comprehensive cladistic analysis for this group.

The third biogeographic pattern – the southern South American pattern (Table 1: SSA) – represents the second of the two Antarctic biogeographic patterns proposed by Brundin (1966). For these taxa, species are recorded from New Zealand and Patagonia, with a Mesozoic occurrence in areas of Antarctica, e.g. Marie Byrd Land, being implicit. Of the eight arthropod taxa we record that exhibit this pattern, two exhibit a biogeographic root in Gondwanan terranes, three are associated ambiguously with both Gondwana and younger New Zealand terranes, and one – *Starkomyia inexpectata* Jaschhof (Sciaroidea) – is known only from the young Waipapa Terrane (Table 1). *Starkomyia inexpectata* was described from a single holotype collected in Tongariro National Park, Taupo District, the North Island (Jaschhof, 2004a). The type specimen was found in *Nothofagus/podocarp* forest, 4 km from the type locality of *Insulatricha hippai* Jaschhof (2004b) (Sciaroidea), a species also distributed in the Buller District (Buller and Takaka terranes) of the South Island. Based on the predominant findings that Gondwanan-aged taxa occupy Gondwanan terranes, we predict that *S. inexpectata* or an undescribed congener will also be found in *Nothofagus/podocarp* forest on Gondwanan terranes of Nelson or Buller districts, in the South Island.

We have included two other New Zealand taxa with area relations to Patagonia – both Notonemouridae (Plecoptera) – the origin of which cannot be assigned to Gondwanan or New Zealand terranes because rooted phylogenetic hypotheses are not available (Table 1). These taxa were chosen for exposition based on their earliest divergence, among Notonemouridae, in the worldwide analysis of Terry (2003). However, Terry includes only a single species in each genus in his analysis. McCulloch *et al.* (2010) proposed that divergence within *Halticoperla* McLellan & Winterbourn was mediated by Pleistocene-aged, glacially mediated vicariance of populations in the South Island, but their study did not include the North Island species *Halticoperla gibbsi* McLellan (1991), and the network joining the South Island population samples was not out-group rooted. Analysing divergence among the

New Zealand taxa, as well as their relationships with extra-New Zealand taxa [based on Terry (2003), this would entail the South American species of *Neofulla* Claassen], is required to elucidate the time and place of origin for New Zealand Notonemouridae.

Surviving 'Oligocene drowning'

Given that there is an asymmetrical bias towards Gondwanan terranes as the place of earliest diversification for Gondwanan-aged New Zealand arthropods, we focus on two signature New Zealand insect groups (weta and micropterigid moths) to explore generalities regarding how these ancient lineages might have survived Oligocene high sea-level stands (Landis *et al.*, 2008). The weta (Orthoptera: Anostostomatidae) represent an ancient lineage that has diversified into a wide range of habitats in New Zealand. The taxon is probably of Jurassic age, based on the Upper Jurassic occurrence of a fossil left wing fragment from Port Waikato, Auckland District, the North Island, described as *Notohagla maurii* Johns (Grant-Mackie *et al.*, 1996). *Notohagla* comprises a taxon of the Prophalangopsidae, with the proposed cladistic relationship Anostostomatidae [Prophalangopsidae (Haglidae + Gryllidae)] supporting the mid-Mesozoic age of the weta assemblage (Grant-Mackie *et al.*, 1996). Based on molecular sequence data, the weta genera *Deinacrida* White plus *Hemideina* Walker comprise a monophylum, although the genera are mutually paraphyletic based on a neighbour-joining analysis of mitochondrial cytochrome *c* oxidase subunit I (mtCOI) data (Trewick & Morgan-Richards, 2005). For *Deinacrida* alone, Trewick & Morgan-Richards (2005) used a two-gene (mtDNA plus 12S rDNA) maximum likelihood analysis to estimate divergence times based on pairwise genetic distances, assuming Brower's (1994) 2% divergence per Myr, despite Brower proposing this divergence rate only for estimating speciation times among very closely related species. By this model-based molecular clock, they estimated the earliest divergence among *Deinacrida* at 17 Ma: i.e. post-Oligocene. However, they included no species of *Hemideina* placed phylogenetically within *Deinacrida* by mtCOI, nor more distantly related tusked wetas or ground wetas in the divergence analysis. Taking an alternative biogeographic approach, the distributions of three *Deinacrida* clades – I, IV and VI + *Hemideina broughi* (Buller) (Trewick & Morgan-Richards, 2005: figs 5, 8) – are sympatric in north-west Nelson, South Island. This area corresponds to the South Taranaki Graben, a fault structure with which Kamp (1986) associated several uninundated Oligocene plateaux based on coal isorank values. If ancestral representatives of these three weta lineages were in place prior to Oligocene high sea-level stands, such islands would have supported their continued local persistence.

The origin of the zeuglopteran moth family Micropterigidae can be dated to Lower Cretaceous based on fossils in Lebanese amber (Whalley, 1977, 1978). There are three lineages in New Zealand, of which two have diversified extensively; *Sabatınca* s.s. Walker and *Palaeomicra* Meyrick (Gibbs,

1983). The six species of *Sabatinca* are distributed such that all have populations surviving on what we have categorized as Gondwanan terranes, with three of these species restricted there: *Sabatinca incongruella* Walker and *Sabatinca heighwayi* Philpott restricted to Nelson and Buller districts, and *Sabatinca* 'sp.n. fiordland' to Fiordland. The two Nelson/Buller species are member taxa of different branches of the cladogram, and thus their primordial sympatric distribution delimited by an Oligocene-aged Nelson Island would explain most parsimoniously the subsequent range expansions and allopatric speciation undergone by the group. Given that Fiordland was adjacent to Nelson in the Oligocene (Wood & Stagpoole, 2007), the present-day geographic isolation of the Fiordland species – the adelphotaxon to *S. heighwayi* – may have been mediated through movement of the Alpine Fault (e.g. Heads, 1998). Conversely, vicariance could be younger, for example being mediated via Pleistocene glaciation (McCulloch *et al.*, 2010). *Palaeomicra* includes nine species, three of which are endemic to Gondwanan terranes, five of which are widespread and *Palaeomicra aenea* (Hudson), which is restricted to lands comprising the younger Pahau Terrane: i.e. the east coast of the South Island from Kaikoura south to the Banks Peninsula and Mount Somers. DIVA optimizes the root of Gibbs' (1983) *Palaeomicra* cladogram to either Gondwanan or Gondwanan + New Zealand terranes (Table 1).

Post-Gondwanan trans-Tasman taxa

Diverse radiations of New Zealand taxa have been investigated with regard to their biogeographic origins. Trans-Tasman relationships have been shown to represent disparate ages of origin, with origins of groups such as the Pettalidae (Opiliones) (Boyer & Giribet, 2007, 2009; Giribet & Boyer, 2010, Table 1) and crateristigmomorph centipedes (Edgecombe & Giribet, 2008) being dated prior to Cretaceous vicariance of New Zealand from Australia. Conversely, other radiations are dated to much later times, necessitating the arrival of their New Zealand ancestors via dispersal. As with the New Zealand broscine genera *Oregus*, *Mecodema*, *Metaglymma* and *Brullea* (Fig. 2), these putative later arrivals exhibit paraphyly versus Australian taxa. For example, New Zealand's cicadas comprise two clades: one sister to a New Caledonian clade and the second sister to an Australian clade (Arensburger *et al.*, 2004). Estimates of divergence place the arrival of each New Zealand clade during the Miocene. New Zealand stick insects (Phasmatodea: Lanceocercata) comprise two independent clades, both nested within a biogeographically paraphyletic radiation of New Caledonian stick insects (Buckley *et al.*, 2010a). Bayesian divergence estimates place the origin of the common ancestor of the New Caledonian adelphotaxon at 34 Ma (24–46 Ma), potentially corroborating the initial radiation of the more speciose New Zealand clade as being contemporaneous with the maximal Oligocene submergence of the continent. However, if Oligocene drowning constrained primordial distributions of New Zealand stick insects, their present-day distributions do not reflect such a constraint as most species are

widespread geographically (Buckley *et al.*, 2009, 2010b). This can be explained by enhanced dispersal propensities for these insects, or alternatively by positing a post-Oligocene arrival of the group in New Zealand consistent with the younger end of the range of the Bayesian divergence estimate. Enhanced dispersal propensity has been demonstrated for *Niveaphasma annulata* (Hutton), as this species was divided into a number of glacial refugia during the Pleistocene, and then dispersed from those refugia to establish zones of secondary contact (O'Neill *et al.*, 2009).

Distributional data alone can provide compelling evidence for post-Gondwanan times of arrival into New Zealand for groups with trans-Tasman relationships. As for the Gondwanan-aged taxa, we focus on two signature New Zealand taxa to demonstrate biogeographic patterns for these later arrivals. The ghost moths, Hepialidae, comprise a radiation of 27 species, many of which are distributed across all ages of terranes (Dugdale, 1994). As for the stick insects and cicadas, the New Zealand hepialid taxa do not constitute a monophyletic group, instead being multiply paraphyletic relative to Australian taxa (Brown *et al.*, 1999). DIVA analysis of the current phylogenetic hypothesis (Brown *et al.*, 1999) indicates that both Gondwanan plus New Zealand terranes constituted the ancestral area. Moreover, the adelphotaxon to the remainder of all New Zealand taxa – *Aenetus virescens* Doubleday – is distributed on younger terranes of the North Island. A late arrival for the hepialid radiation is corroborated by molecular divergence data: Brown *et al.* (1999) estimated the age of origin for the well-sampled genus *Wiseana* at only 1–1.5 Ma. As moths classified in this genus are grass feeders and dominant members of grassland communities in the rain shadow of the New Zealand Southern Alps, their evolutionary history would appear to be tied to the Pliocene orogeny of those mountains.

The endemic New Zealand marine caddis fly family Chathamidae (Riek, 1976; Ward, 1995) constitutes a second group of special interest. Among species in this group are included endemics on the Chatham Islands (*Chathamia brevipennis* Tillyard), Kermadec Islands (*Philaninus fasciatus* Riek), and on the North Island and adjacent islands, including Great Island in the Three Kings group (*Philaninus mataua* Ward). The adelphotaxon to Chathamidae remains ambiguous, with the group alternately placed: (i) within Sericostomatoidea; (ii) as sister to the Australian Calocidae (Kjer *et al.*, 2002); or (iii) as the adelphotaxon to Leptocercidae plus Molannidae (Johanson & Malm, 2010). Therefore a molecularly based time of divergence cannot yet be hypothesized. Nevertheless, the occupation of marine habitats coupled with geographically peripheral distributions heavily skewed towards the occupation of New Zealand's North Island and adjacent offshore islands is consistent with a later, post-Gondwanan arrival. This peripheral pattern of endemism is much like that exhibited by the *Mecodema curvidens* group (Seldon & Leschen, 2011), supporting our contention that *Mecodema* species constitute a lineage resulting from the trans-Tasman colonization of New Zealand long after the Gondwanan origin of *Orthoglymma wangapeka* sp.n.

Zoogeographic conclusions

Based on our analysis of biogeographic patterns, including area relationships to other southern lands and also occupation of Gondwanan-aged terranes in New Zealand, we propose that three broscine genera have Gondwanan origins: (i) *Orthoglymma*; (ii) *Bountyia*; and (iii) *Diglymma*. *Orthoglymma* is restricted to Gondwanan terranes of mainland New Zealand, whereas *Bountyia* is endemic to the isolated Bounty Island group of the Campbell Plateau. *Diglymma* species predominantly occupy Gondwanan terranes of mainland New Zealand, although one species is endemic to isolated islands of the Campbell Plateau. All three diverged cladistically very early within their respective monophyla.

As demonstrated for Chironomidae (Brundin, 1966), Gondwanan-aged relicts are well represented in New Zealand, where they exhibit concentrated diversity on Gondwanan-aged terranes. Analysing the available phylogenetic data using dispersal vicariance analysis also indicates primordial distributions for the ancestors of many of these taxa on Gondwanan terranes. Given the evidence of Oligocene submergence for much of New Zealand, this common relictual pattern may represent a biogeographic constraint during the evolutionary history of Gondwanan-aged groups, with temporal persistence facilitated by a limited number of subaerial islands. The Nelson area is proposed as one such island, consistent with the existence of *Orthoglymma wangapeka* *sp.n.*, with overlapping distributions of several weta clades (Trewick & Morgan-Richards, 2005), and with the presence of multiple representatives of other exceedingly ancient and sedentary groups (Table 1), such as Pettalidae (Boyer & Giribet, 2007) and Micropterigidae (Gibbs, 1983).

Conversely, the ages of eastern Gondwanan, i.e. Melanesian Rift area relationships (Michaux & Leschen, 2005) that implicate Australian, New Caledonian and New Zealand taxa, appear much less constrained. The oldest Melanesian Rift vicariants exhibit fidelity to Gondwanan terranes similar to that observed for Gondwanan-aged taxa assignable to a southern, Antarctic or western Gondwanan track. Post-Gondwanan aged taxa do not exhibit such fidelity; moreover, they display abundant diversification on peripheral habitat islands, such as the barrier islands of the north, or the Banks and Otago peninsulas of the south (Pawson *et al.*, 2003; Seldon & Leschen, 2011). These suites of later arriving taxa may also exhibit paraphyly relative to Australian or New Caledonian groups (Brown *et al.*, 1999; Arensburger *et al.*, 2004; Buckley *et al.*, 2010a).

Taxonomy

Orthoglymma *gen.n.*

Type species. *Orthoglymma wangapeka* *sp.n.*

Generic diagnosis. The deep paramedial mentum foveae (Fig. 4A) characterizing this genus are also characteristic of

the genera *Broscofera* Lindroth, *Diglymma*, *Nothobrosclus* Roig-Juñent & Ball, *Eurylychnus* Bates, *Chylinus* and *Percolestus*. The presence of distinct punctures across the pronotal base diagnoses this new taxon from all other genera of Broscini, with the possible exception of *Broscofera*, which is characterized by much more shallow indented punctures sparsely distributed across the pronotal base. *Orthoglymma* can be differentiated from *Broscofera* by numerous characters, including: (i) the male aedeagal sclerite X without apicolateral projections versus with projections; (ii) an incomplete temporal ridge behind the eye, with the ridge present only posteriorly near the pronotum (complete in *Broscofera*); (iii) presence of two submentum setae (Fig. 4A); six submentum setae in *Broscofera*; (iv) absence of flight wings and fusion of metepimeron to metepisternum; (v) isolation of an obsolete parascutellar striole from the first elytral stria (parascutellar striole better developed and joined to stria 1 in *Broscofera*); and (vi) absence of articuloetae on male tarsomeres (Fig. 4B) (present on both pro- and mesotarsi of *Broscofera*).

Generic description. Body narrow, elongate, the pronotum cordate (Fig. 3A); head with single posterior supraorbital seta in small pit dorsomedial to hind margin of eye; vertex with distinct, minutely punctate transverse groove; antennomeres 1–3 glabrous, with exception of large seta on outer surface of antennomere 1, and apical ring of setae on antennomere 3, segment 4 setose in apical half, segments 5–11 setose throughout. Mandible with scrobal seta present. Mentum tooth minutely bifid (Fig. 4A); glossal sclerite of ligula apically bisetose, the ventral surface medially carinate, paraglossae evident, moderately elongate. Pronotum elongate, basally constricted; laterobasal depressions and median base covered with distinct punctures, pronotal disc smoothly convex each side; a single lateral seta each side of pronotum, pronotal hind angles glabrous. Elytra with parascutellar seta in base of third interval; no dorsal elytral setae present; three lateral elytral setae, one at acute humeral angle, two widely separated in apical quarter of elytral length; elytral margin convex subapically, elytral plica represented by an internal ridge. Abdominal ventrites minutely punctured in lateral reaches, visible ventrites 3–5 broadly and shallowly depressed laterally.

Male genitalia (Figs 3B–E, 4C, D). Ring sclerite (modified tergite IX; Deuve, 1993) with sclerotized ring complete but with apical margin narrowed on left side (Fig. 3E). Median lobe with dorsal surface sclerotized, basal orifice completely closed dorsally (Fig. 3B). Internal sac with sclerites X and Y present; sclerite X medially constricted and bent, broad apically, lacking lateroapical projections (Fig. 3B, D); apical plate with median tooth (Fig. 3B). Right paramere narrowly styloid, ventral edge setose in apical half (Fig. 4C); left paramere triangular, narrowed and only slightly extended apically (Fig. 4D).

Female ovipositor and reproductive tract (Fig. 4E, F). Rami of gonocoxite long but not distinctly sclerotized nor melanized (Fig. 4F). Basal gonocoxite with two longitudinal rows of

ensiform setae, a lateral row of two setae, and a medial row of between four and six setae (Fig. 4E, F); apical gonocoxite broadly trapezoidal, two nematiform setae present in sensory furrow at lateroapical angle. Spermatheca present, situated dorsad a well-developed helminthoid sclerite and entering bursa copulatrix independent of common oviduct (Fig. 4E); bursal wall with sclerotized fold basad of the helminthoid sclerite; accessory gland entering bursa copulatrix far from spermatheca, and without basal sclerite; area near juncture of common oviduct and bursa sclerotized.

Etymology. The neuter generic epithet *Orthoglymma* is a compounding of the Greek words *orthos*, i.e. straight or right, and *glymma*, an engraved or carved figure.

Key to subtribes and genera of New Zealand Broscini

This key is modified from Roig-Juñent (2000), and includes some characters used by Britton (1949) and Larochelle & Larivière (2007) in order to accommodate the newly described taxon. Differentiating the two subtribes Creobiina and Nothobroscina, as done in the initial couplet, can rest on the configuration of the mentum tooth and glossal sclerite in currently known taxa; however, the genitalic characters are provided to ensure adequate information for tribal diagnosis should additional novel taxa be discovered.

- 1. Mentum tooth bifid, glossal sclerite with two setae (Fig. 4A); basal orifice of median lobe completely closed dorsally (Fig. 3B); internal sac of aedeagus with sclerites X and Y; female reproductive track with helminthoid sclerite (Fig. 4E) (subtribe Nothobroscina; Roig-Juñent, 2000)–2
 - Mentum tooth simple, glossal sclerite with four apical setae; basal orifice of median lobe completely or partially open dorsally; internal sac of aedeagus without sclerites X and Y; female reproductive tract without helminthoid sclerite (subtribe Creobiina; Jeannel, 1941) *Bounty* Townsend
- 2. Each side of head with single, plurisetose supraorbital puncture; external apex of foretibia expanded; elytra with row of setiferous punctures in seventh interval 3
 - Each side of head with one or more supraorbital punctures, each bearing a single seta; external apex of foretibia not expanded; elytra without row of setiferous punctures on seventh interval 5
- 3. Foretibia narrow, with expansion at apex; middle and hind tibiae not curved and expanded, with few punctures on outer surface 4
 - Foretibia broad, markedly expanded at apex; middle and hind tibiae curved and greatly expanded at apex, very punctulate on the outer surface *Brullea* Castelnau
- 4. Antennomeres 2–10 lacking pubescence except for apical ring of setae; fifth visible abdominal ventrite with between six and 20 setiferous punctures across width of segment *Metaglymma* Bates

- Antennomeres 3–5 glabrous except for apical ring of setae, antennomeres 6–11 pubescent throughout length, at least along sides; fifth visible abdominal ventrite with between two and six setiferous punctures (rarely without setae) *Mecodema* Blanchard
- 5. Head with one supraorbital seta; mentum with two deep paramedial foveae (Fig. 4A); base of maxillary stipes bisetose 6
 - Head with two supraorbital setae; mentum broadly and shallowly depressed paramedially, lacking deep paramedial foveae; base of maxillary stipes trisetose *Oregus* Putzeys
- 6. Pronotal base smooth, linear laterobasal depressions present each side immediately mesad basolateral margin; basal two male protarsomeres with adhesive articuloetae on ventral surface *Diglymma* Sharp
 - Pronotal base distinctly punctate, both in the laterobasal depressions as well as medially (Fig. 3A); all male protarsomeres glabrous medioventrally (Fig. 4B) *Orthoglymma* **gen.n.**

***Orthoglymma wangapeka* sp.n.**

Type material. Holotype female pinned: NEW ZEALAND NN/Wangapeka Track/172°17'E 41°23'S/21 xii 1999/R.R. Scott/under logs/HOLOTYPES/*Orthoglymma/wangapeka* Liebherr, Marris, Emberson/Syrett & Roig-Juñent/2010 (red label) (LUNZ). Paratypes, same locality as holotype, 10 xii 2008 (Marris, Emberson, Liebherr & Syrett) (CUIC, one female; LUNZ, one male; NZAC, one female).

Diagnosis. Individuals of this species are readily discerned from all other New Zealand Broscini by the distinctly punctate pronotal base, presence of a single posterior supraorbital seta, a single lateral pronotal seta, deep paramedial foveae on the mentum, and a depressed elytral base that is laterally extended to acutely angulate humeri; body length 12.0–13.2 mm.

Description. In addition to characters mentioned in the generic diagnosis and description, body coloration dark castaneus with piceous cast; vertex with deep, sinuous supraorbital grooves each side, and shallowly wrinkled frontal grooves, but the surface smooth and shiny, microsculpture lacking; eyes very small and convex, diameter subequal to length of third antennomere; pronotal disc covered with very shallow transverse mesh microsculpture, partially obscured by minute micropunctures that cover surface; elytral intervals moderately convex, the medial striae indistinctly punctate, and lateral striae more punctate; elytral surface covered with distinct isodiametric mesh microsculpture.

Asymmetrical variation. Three of the four specimens exhibit asymmetrical variation in the configuration of elytral striae 3

and 4. The male paratype (Fig. 3A) has striae 3 and 4 irregularly fused to each other on the left elytron, with each stria broken near elytral midlength, whereas stria 3 and 4 are not joined on the right elytron. One female paratype has striae 3 and 4 fused, and therefore broken longitudinally, near the apical third on the left elytron (much as in the male), but striae 3 and 4 are apically united on the right near their juncture with fused striae 5 + 6. The second female paratype has striae 3 and 4 united apically on the left elytron, but free all the way to their respective junctures with the fused striae 5 + 6 on the right. The female holotype is the only symmetrical individual in these regards, with striae 3 and 4 apically united, both sides, just anterad of their juncture with apically fused striae 5 + 6.

Distribution. This species is known only from the valley of the Little Wanganui River at 580 m a.s.l., Nelson District, New Zealand.

Habitat. Three individuals of this species collected in 2008 were found in *Nothofagus* forest, under a log and rocks. The ground surface was covered with abundant decayed humus; however, granitic rocks comprise the foundation for this vegetative surface, and there were numerous voids among the granite rocks and boulders that line the valley floor along the river. The holotype was collected in manuka (*Leptospermum scoparium* J.R. & G. Forster) scrub immediately adjacent to the closed canopy *Nothofagus* forest.

Etymology. The species epithet is taken from the Wangapeka Track, extending from the west coast eastwards up the Little Wanganui River to Little Wanganui Saddle, and then continuing eastwards via the Taipo and Karamea rivers to Wangapeka Saddle, and continuing eastwards down the Wangapeka River. The epithet is to be treated as a noun in apposition.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2011.00569.x

Appendix S1. Data matrix and associated text file modified from NONA (Goloboff, 1993).

Appendix S2. Descriptions of characters and states for 73 morphological characters.

Appendix S3. Criteria by which the ages of origin of New Zealand Gondwanan taxa were determined.

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Acknowledgements

Institutional curators supplying taxonomic materials for the cladistic analysis are gratefully acknowledged: Robert L. Davidson, Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A.; Philip D. Perkins, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. The senior author wishes to thank the College of Agriculture and Life Sciences, Cornell University, for sabbatical support, and the Bio-Protection and Ecology Division, Lincoln University, for hosting the sabbatical leave. We thank Kipling W. Will for information regarding the type of *Percosoma asymmetricum*, and David Seldon for sharing prepublication data on *Mecodema*. We acknowledge the help and cooperation of the New Zealand Department of Conservation staff in providing the low-impact collecting permit: CA-17982-FAU. Finally, and most importantly, we acknowledge Dr R.R. Eric Scott who collected the initial specimen of *Orthoglymma wangapeka* *sp.n.*, and then saw it safely to the Entomology Research Museum, Lincoln University, even though his wife Margaret fell badly on the Wangapeka Track, breaking her arm, thereby necessitating an arduous traverse of the remainder of the track before emergency medical treatment.

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Accepted 10 March 2011