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Running head: Miocene wader from New Zealand

Wading a lost southern connection: Miocene Fossils from New Zealand reveal a new lineage of shorebirds (Charadriiformes) linking Gondwanan avifaunas

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Abstract

An endemic and previously unknown lineage of shorebirds (Charadriiformes: Scolopaci) is described from early Miocene (19–16 million years ago, Ma) deposits of New Zealand (NZ). *Hakawai melvillei* gen. et sp. nov. represents the first Pre-Quaternary record of the clade in NZ and offers the earliest evidence of Australasian breeding for any member of the Scolopaci. *Hakawai melvillei* was a representative of the clade that comprises the South American seedsnipes (Thinocoridae) and the Australian Plains-wanderer (Pedionomidae), and presumed derived features of its postcranial skeleton indicate a sister taxon relationship to Australian pedionomids. Our findings reinforce that terrestrial adaptations in seedsnipes and the Plains-wanderer are convergent as previously proposed, and support an ancestral wading ecology for the clade. Although vicariance events may have contributed to the split between pedionomids and *H. melvillei*, the proposed sister taxon relationship between these taxa indicates that the split of this lineage from thinocorids must have occurred independently from Australia’s and Zealandia’s separation from the rest of Gondwana.

**Key words:** Scolopaci; Pedionomidae, fossil birds, St Bathans Fauna, *Hakawai melvillei*
Introduction

New Zealand (NZ) has long been renowned for having a distinctive terrestrial vertebrate faunal assemblage, characterised by endemic lineages and dominated by birds (Worthy & Holdaway 2002). Early-diverging crown-group representatives of some of the most diverse lineages within extant avian orders, such as songbirds and parrots – for which biogeographic patterns and sequence data support a Gondwanan origin (Ericson et al. 2002; de Kloet & de Kloet 2005) –, have been a part of NZ’s avifauna for more than 20 Ma (Worthy et al. 2010, 2011). The survival of these lineages in NZ can be explained by NZ’s geographic isolation following separation from the rest of Gondwana. The approximate date when isolation would have prevented taxa with low dispersal capabilities from colonising NZ from the rest of Gondwana is now thought to be between 55–52 Ma (Schellart et al. 2006; Worthy et al. 2010). Insights into the evolution, taxonomic diversity, and longevity of endemic lineages of terrestrial vertebrates in NZ are hampered by a poor terrestrial fossil record, with the only pre-Quaternary terrestrial fossils being those from the 19–16 Ma St Bathans Fauna (South Island, Central Otago region) (Worthy et al. 2007, 2008, 2009a,b; 2010a,b, 2011a,b; Jones et al. 2009; Lee et al. 2009; Scofield et al. 2010; Tennyson et al. 2010; Hand et al. 2013).

A small wading bird was briefly reported from the early Miocene St Bathans Fauna (Worthy et al. 2007), representing the only pre-Quaternary record of the charadriiform clade Scolopaci in NZ, and only the second record for Australasia and the Pacific (De Pietri et al. 2015). The suborder Scolopaci is one of the three major clades in the species-rich and ecologically diverse avian order Charadriiformes (waders, gulls, auks, and allies) (Ericson et al. 2003; Paton et al. 2003; Baker et al. 2007). The Scolopaci contain five family-level taxa, which include the painted-snipes (Rostratulidae), jacanas (Jacanidae), seedsnipes (Thinocoridae), the monospecific Plains-wanderer (Pedionomidae), and the diverse radiation
of sandpipers, snipes, and allies (Scolopacidae). Interrelationships among these lineages are well-resolved (Ericson et al. 2003; Paton et al. 2003; Baker et al. 2007; Gibson & Baker 2012), with a basal divergence supporting a seedsnipe/Plains-wanderer clade and a jacana/painted-snipe clade on the one hand, and the large scolopacid radiation on the other.

While the majority of members of the clade containing jacanas, painted-snipes, seedsnipes and the Plains-wanderer currently breed in tropical to temperate areas of the Southern Hemisphere, most species of Scolopacidae breed in boreal, subarctic, and arctic environments in the Northern Hemisphere (Piersma 1996). The explosive radiation of scolopacids is probably linked to climate cooling during the Neogene, and the evolution of grasslands, steppes, and the tundra (e.g. Kraaijeveld & Nieboer 2000; Ballmann 2004). Scolopacids that do breed south of the northern temperate zone include both tropical and temperate residents, such as some species of woodcock (Scolopax) and snipes (Gallinago and Coenocorypha), as well as the Tuamotu sandpiper (Prosobonia parvirostris). The endemic austral snipes (three living species of the genus Coenocorypha), now distributed across NZ’s outlying islands, are the only members of the Scolopaci that currently breed in NZ, and otherwise only long-distance migratory scolopacids that spend the boreal winter in NZ are part of the extant avifauna. Together with some snipes of the genus Gallinago, austral snipes are, however, likely to have evolved from migratory ancestors (Gibson 2010; Gibson & Baker 2012).

The pre-Quaternary Gondwanan fossil record of representatives of the clade Scolopaci is extremely poor, with most fossil representatives known from the Northern Hemisphere (Mlikovsky 2002; Mayr 2009; De Pietri & Mayr 2012). The only record for the Gondwanan lineage represented by the South American seedsnipes and the Australian Plains-wanderer is a pedionomid from the Oligocene of South Australia (De Pietri et al. 2015). It is also worth noting that one of the longest branches in extant charadriiform phylogeny separates the
Plains-wanderer from seedsnipes (Baker et al. 2007; Gibson & Baker 2012), indicating lineage loss over time (e.g. Slack et al. 2007).

Here we describe a species of wading bird representing a hitherto unknown lineage from the early Miocene of NZ, belonging to the Scolopaci and showing close affinities with the Plains-wanderer and seedsnipes, of which no representatives are known from NZ. The fossils here described also offer the earliest unequivocal evidence of Australasian breeding for any member of the Scolopaci, likely indicating that this new taxon was another NZ endemic. This record fills a significant gap in the Gondwanan fossil record of the Scolopaci, and indeed Charadriiformes, and has major implications for understanding Gondwanan phylogeography and the different evolutionary trajectories of Scolopaci in the Northern and Southern Hemispheres.

Material and methods

Our working hypothesis of relationships between and within the different lineages of the suborder Scolopaci follows Gibson and Baker (2012). Taxonomy and nomenclature is after Dickinson & Remsen (2013), and anatomical terminology follows Baumel and Witmer (1993). All measurements are in mm and were rounded to the nearest 0.1. Commonly used abbreviations: proc, processus; R: right, L: left, d: distal, p: proximal, ML: maximum length, PW: proximal width, DW: distal width, Min.SW: minimal shaft width. Much of the material is fragmentary and therefore measurements are provided for type material only. The fossil specimens are deposited in Canterbury Museum (CM), Christchurch, NZ, and in Museum of New Zealand Te Papa Tongarewa (NMNZ), Wellington, NZ.

Comparative material
Comparative material was sampled from NMNZ; Museum Victoria (NMV), Melbourne, Australia; Natural History Museum Basel (NMB), Switzerland; South Australian Museum (SAM), Adelaide, Australia; and Senckenberg Research Institute (SMF), Frankfurt, Germany.


Additionally, fossil material attributed to an undescribed species of the extinct genus-level taxon *Prosobonia* (Polynesian sandpipers, Scolopacidae) from Henderson Island (Wragg 1995), and the extinct *Coenocorypha neocaledonica* (New Caledonian Snipe; Worthy et al. 2013), were examined.

**Systematic palaeontology**

Class **Aves** Linnaeus, 1758

Order **Charadriiformes** Huxley, 1867

Suborder **Scolopaci** Strauch, 1978; sensu Paton *et al.* (2003)
Referral to this clade is based on the following combination of features: coracoid (Fig. 1C–E; Fig. 2D–E, H) with (1) facies articularis clavicularis ventrodorsally broad; (2) proc. acrocoracoideus ventromedially protruding; (3) foramen nervi supracoracoidei absent. Humerus (Fig. 1I–L; Fig. 2I, K, N, R) with (4) transverse ridge at incisura capitis; (5) tuberculum dorsale proximodistally elongated (except species of Numenius); (6) caudal surface of crista deltopectoralis convex; (7) fossa pneumotricipitalis lacking pneumatic foramina. Tarsometatarsus (Fig. 1O–S; Fig. 2DD, GG, JJ) with (8) tendon of musculus flexor digitorum longus enclosed in bony canal; (9) canal for tendon of musculus flexor digitorum longus situated directly dorsal of sulcus for tendon of m. perforans et perforatus digiti 2 (some scolopacids are an exception; e.g. Arenaria interpres, some species of Tringa and Calidris); (10) fossa metatarsi I present. (1), (2) and (7) are present in most Charadriiformes; (3), (4), (5), (6), (9), and (10) are characteristic of all Scolopaci (see Mayr 2011 and De Pietri & Mayr 2012); features (8), (9), and (10) differentiate Scolopaci from most representatives of Charadrii (plovers and allies), and (3; except Cursorius), (5), (6) and (8) differentiate them from Glareolidae (pratincoles and coursers).

Family incertae sedis

Hakawai melvillei gen. et sp. nov.

(Fig. 1, Fig. 2 A, D, E, H, I, K, N, R, U, X, BB, CC, DD, GG, JJ, LL)

Holotype. Right tarsometatarsus NMNZ S.50806 (ML: 26.3, PW: 3.8, DW: 4.0, Min.SW: 1.5)

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Type locality, stratigraphy, and age. Bed HH4, Manuherikia River, near St Bathans, Central Otago, South Island, NZ (44.907861S, 169.857233E). Located 25.63–25.83 m above the base of lacustrine Bannockburn Formation, Manuherikia Group; Altonian local stage, early Miocene, 19–16 Ma (Schwarzhans et al. 2012). NZ Fossil Record File Number H41/f0095.

Derivation of name. Generic name refers to an unseen and enigmatic “mystery bird” in Māori mythology; gender is feminine. Although recent research shows that Māori from Rakiura (Stewart Island) considered the Coenocorypha snipe’s nocturnal aerial calls to be those of the Hakawai (Miskelly 1987), our choice alludes to a link between the mythical Hakawai and waders of the suborder Scolopaci. Specific name honours NZ-based ornithologist and ecologist David Melville, for his efforts in implementing conservation measures for shorebirds, locally and globally.

Paratypes and measurements. The sites the elements were recovered from are shown in bold (see Schwarzhans et al. 2012 for details). R cranial extremity of scapula NMNZ S.53360 (cranial width: 3.5, W of corpus scapulae: 1.2; HH4); omal extremity of L coracoid NMNZ S.50490 (facies articularis humeralis to proc. acrocoracoideus: 3.6, cotyla scapularis to proc. acrocoracoideus: 4.3, W facies articularis clavicularis: 2.1; HH1a); R coracoid CM 2013.18.785 (ML: 13.3; HH4); pR humerus NMNZ S 43153 (HH1a); dR humerus NMNZ S.50716 (DW: 4.5, dDepth: 2.8; HH4), pR ulna CM 2013.18.195 (PW: 3.4, Min.SW: 1.8; HH1a); dL ulna NMNZ S.53375 (DW: 2.8, Min.SW: 1.7; HH4); L carpometacarpus NMNZ S.53399 (ML: 17.7, PW including proc. extensorius: 3.9, DW: 2.3, width of os metacarpale majus: 1.2; HH4).
Additional referred material. Scapulae: CM 2013.18.1054 (R cranial extremity; HH1a); NMNZ S.43448 (L cranial extremity; immature; HH4); NMNZ S.52801 (L cranial extremity; HH1b); NMNZ S.52755 (R cranial extremity; HH1b). Coracoids: CM 2013.18.781 (R; immature; HH4); NMNZ S.50711 (R; immature; HH2c); CM 2013.18.284 (L omal end; HH1a); NMNZ S.52160 (R omal end; HH1a); NMNZ S.43975 (L lacking sternal end and part of omal end; HH1a); NMNZ S.57903 (R omal end; HH1a); CM 2013.18.114 (R omal end; HH1a); NMNZ S.51871 (L omal end; HH1a); NMNZ S.52771 (L omal end, with procoracoid; HH1b). Humeri: NMNZ S.42416 (pR; Croc site); NMNZ S.50720 (dR; HH4); NMNZ S.52235 (dL; HH1a); NMNZ S.51604 (dL; HH1a); NMNZ S.52548 (dR; HH1a); NMNZ S.52321 (dR; HH4). Ulnae: NMNZ S.52461 (pR; HH1a); NMNZ S.53080 (dR, immature; HH1b); NMNZ S.52629 (dR; HH1a); CM 2013.18.1053 (dR; HH1a); CM 2013.18.1055 (dR; HH1a); CM 2013.18.511 (dL; HH0). Carpometacarpi: NMNZ S.50808 (L; HH4); NMNZ S. 50805 (pR & dR; HH4); CM 2013.18.527 (pR; HH0); NMNZ S. 52108 (pR; HH1a); NMNZ S.51971 (pL; HH1a); NMNZ S.53267 (pL; Mata Creek 5); NMNZ S.51488 (pL; HH1a); NMNZ S.50436 (pR; HH2c); NMNZ S.51371 (pR; HH1a); NMNZ S.53365 (pL; HH4); NMNZ S.53398 (dL, dR; HH4). Tibiotarsus: NMNZ S.50906 (dL, HH4); NMNZ S.52773 (dL, immature; HH1b). Tarsometatarsi: MNZ S.52846 (pL; HH1b); MNZ S.50803 (pL; HH4); MNZ S.52414 (pR; HH1a).

Remarks. Full details of the site locations on Home Hills Station (HH), Central Otago, South Island, New Zealand, and their stratigraphic relationships are given in Schwarzhanst et al. (2012) except one. HH0 is equivalent to FF1 of Lindqvist (1994) and is a fossil stromatolite bed exposed at 44.90359° S, 169.85840° E, Manuherikia River. The fossils were in clay surrounding the stromatolites, New Zealand Fossil Record File (NZ FRF) system administered by the Geoscience Society of New Zealand and GNS Science H41/f059. Two
sites on nearby Dunstanburn Station also yielded fossils: Croc Site, Layer 1 – c.10 cm thick sand and cobble layer, 3.5 m above the base of the Bannockburn Formation, in 3 m north-facing cliff on a small hill on the west side of Mata Creek, Otago, (44.889500° S, 169.837833° E), NZ FRF H41/f84. Mata Creek, Site 5 – 44.88387° S, 169.84113° E, exposure on east side of Mata Creek with stromatolite layer about 30 cm thick with a 10 cm thick conglomerate at its base containing fish and bird fossils; NZ FRF H41/f0118.

The material attributed to *Hakawai melvillei* was collected from the following sites (see Schwarzhans *et al.* 2012): HH4 (type locality), HH1a, and HH1b, with few, mostly single, elements coming from HH0, HH2c, Croc site, and Mata Creek 5. Despite stemming from different sites, this material can be attributed to a single taxon by (1) size, as *H. melvillei* has smaller bones than all other charadriiforms recovered from these localities (i.e. plovers and gulls; Worthy *et al.* 2007), and all elements fall within the range expected for a single species (e.g. Ballmann 2004); and (2) because HH1a, HH1b, and HH4 have yielded comparable elements identical in morphology, attesting to the presence of the same taxon in all these sites.

**Diagnosis.** Small, long-legged wader, displaying the following combination of features (other than those noted above): scapula with (1) round facies articularis humeralis, i.e. nearly equal craniocaudal and dorsoventral width (Fig. 1A); (2) prominent and distinctly globular tuberculum coracoideum, with pronounced notch separating it from facies articularis humeralis (Fig. 1B); (3) acromion with weak cranial projection (Fig. 1A, B); (4) facies articularis clavicularis nearly entirely on dorsal surface of bone (Fig 1A). Coracoid with (5) proc. acrocoracoideus elongated along main axis (Fig. 1C); (6) marked recess below facies articularis clavicularis absent (Fig. 1C, E); (7) cotyla scapularis deep and distinctly round with maximum diameter about half the length of the facies articularis humeralis (Fig. 1D); (8)
shaft elongated in relation to the omal-sternal length of the omal extremity and mediolateral width of the facies articularis sternalis (Fig. 2H; see also De Pietri et al. 2015). Humerus with (9) well-developed dorsal fossa pneumotricipitalis (Fig. 1I); (10) impressio coracobrachialis small and narrow, slightly kidney-shaped (Fig. 1J); (11) condylus ventralis with cranial surface dorsoventrally wide and proximodistally narrow, with reduced distal and cranial projection (Fig. 1K); (12) proc. flexorius projecting markedly ventrally (Fig. 1K, L); (13) proc. supracondylaris dorsalis slightly prominent, subtriangular in shape (Figs. 1K, 2R); (14) fossa musculi brachialis well-developed (Fig. 1K). Ulna with (15) well-defined impressio scapulotricipitis (Fig. 1G); (16) condylus dorsalis ulnaris with caudal margin flaring markedly caudally and with ventral surface very broad craniocaudally (Fig. 1H).

Carpometacarpus with (17) proc. extensorius proportionally narrow and upturned cranially and proximally (Fig. 1M); (18) fovea carpalis caudalis deep (Fig. 1N); (19) ventral facies of os metacarpale minus with well-developed tuberosity proximally (Fig. 1N); (20) os metacarpale minus dorsoventrally broad immediately distal to the fovea carpalis caudalis (i.e. distal to synostosis). Tarsometatarsus with (21) trochlea metatarsi II distinctly proximal to other trochleae (Fig. 1P); (22) in plantar aspect, medial rim of trochlea metatarsi III shorter than lateral one (Figs. 1Q; 2HH); (23) plantar projection on trochlea metatarsi II with notch separating it from the medial surface of the trochlea (Fig. 1S); (24) deep and well-defined pit on proximal and dorsal surface of trochlea metatarsi III (Fig. 1O); (25) fossa metatarsi I well-marked (Fig. 1Q); (26) foramen vasculare distale large (Fig. 1O,Q).

Differs from all examined species of Scolopacidae in (2), (4), (16), (18), (20), (23), (26), and from most scolopacids in (1), (3), (8), (12), (13), (14), (17), (21). Characters (9) and (16) were present in members of Thinocoridae; characters (2), (4), (6), (8), (24), (26) were found in Pedionomus torquatus; and (1), (7), (11), (19), (20), (22), (23) in both thinocorids and P. torquatus (See figure S2). Character (7) is also present in Rostratulidae, and (16), (19), (21),
(22) in Rostratulidae and Jacanidae. *Hakawai melvillei* differs from members of Rostratulidae and Jacanidae in (5), (6), (8), (9), (10), (12), (13), (14), (23), (24); character (26) is also present in this clade, but the foramen is much larger and situated in a very deep and wide groove, which is a derived trait for species in Jacanidae and Rostratulidae (see also Mayr (2011))

**Description and comparisons.** Although the scapula and coracoid are about the size of the Red-necked Stint *Calidris ruficollis*, one of the smallest scolopacids, overall proportions across different postcranial elements suggest *Hakawai melvillei* was larger than previously reported (Worthy *et al.* 2007), and about the size of a male Plains-wanderer (Table 1).

*Pedionomus torquatus* displays pronounced sexual dimorphism, with females being larger than males (Baker-Gabb 1996). All elements except the tarsometatarsus (Fig. 3R–W) agree in size and proportions with those of *Pedionomus torquatus*, whereas those of scolopacids and thinocorids are markedly different (Table 1). Elements of the pectoral girdle and wing display features that most closely match the condition in the corresponding elements of *P. torquatus* and thinocorids (Fig. 2).

The facies articularis humeralis is round and distinctly offset, ventrolaterally, from the cranial extremity of the scapula (Fig. 1A, B). The tuberculum coracoideum is prominent and globular. Other than in *P. torquatus* (Fig. 2B) and seedsnipes, this feature is also present in species of *Gallinago, Scolopax* and *Coenocorypha*, but unlike these taxa, the tuberculum coracoideum is distinctly separated from the facies articularis humeralis by a notch (Fig. 2A). Unlike in several of the examined scolopacids (Fig. 2C), the acromion is rounded and lacks the marked dorsocranial projection. The facies articularis clavicularis is robust and more dorsally rather than laterally positioned compared to that of the examined scolopacids and thinocorids, but resembling *P. torquatus* (Fig. 2B). The facies articularis clavicularis of the...
coracoid has nearly the same breadth throughout its dorsoventral extent (Fig. 2D), as in *P. torquatus*. In other examined taxa, the dorsal section is more elongated in the omal-sternal direction than the ventral section. Also as in *P. torquatus*, a well-developed recess under the facies articularis clavicularis is absent (Fig. 1C; De Pietri et al. 2015). Unlike in pedionomids, the sulcus m. supracoracoidei is more deeply excavated. The cotyla scapularis is round and deep, with a maximum diameter of about half the length of the facies articularis humeralis (Fig. 1D).

At the proximal end of the humerus, a dorsal fossa pneumotricipitalis is well developed (Fig. 1I, 2K). This fossa is absent in *P. torquatus*, whereas the condition is variable within Scolopacidae (Mayr 2011) (Fig. 2M). In *H. melvillei* (Fig. 2K), this fossa is much deeper and dorsoventrally wide, approaching the condition in thinocorids (Fig. 2L). The shape of the caput humeri (Fig. 1J; Fig. 2I) resembles that of thinocorids (Fig. 2J), but much of its caudal surface is worn in one of the specimens (NMNZ S.42416; Fig. 2K). A markedly proximally protruding caput humeri was considered a derived similarity of thinocorids and *P. torquatus* (Olson & Steadman 1981), but it occurs to some degree in certain scolopacids, and is as such not a distinguishing character. The distal end closely matches that of *Thinocorus rumicivorus* (Fig. 2N). The fossa musculi brachialis is as deep as that of *T. orbignyianus*. Similar to seedsnipes (except *T. orbignyianus*) and *P. torquatus*, the cranial surface of the condylus ventralis is not markedly globular and distally protruding compared to that of scolopacids (Fig. 1K, Fig. 2O), being wider ventrodorsally and narrower proximodistally (Fig. 1K, Fig. 3I). The cranial-most surface of the proc. supracondylaris dorsalis becomes gradually wider proximally, and is subtriangular in shape (Fig. 1L, Fig. 2R).

The ulna is similar to that of *T. rumicivorus* and *P. torquatus*, differing primarily in the presence of a better defined impressio scapulotricipitis at the proximal end (Fig. 1G). The tuberculum carpale is less cranially protruding compared to that of *P. torquatus* and most
scolopacids (Fig. 2U–W). As in thinocorids, the caudal margin of the condylus dorsalis ulnaris flares markedly caudally, and the ventral surface is craniocaudally very broad (Fig. 1H, Fig. 2U, V). As in thinocorids (Fig. 2Y), the proc. extensorius of the carpometacarpus (Fig. 2X) is proportionally narrow and upturned cranially and proximally. The fovea carpalis caudalis (Fig. 1N, 2BB) is deep but less so than in *P. torquatus*. At the proximal end of the os metacarpale minus there is a well-developed tuberosity ventrally for ligamental attachment (Fig. 1N, 2BB). This tubercle is also present in thinocorids and *P. torquatus*, albeit less pronounced (Fig. 2AA). In *H. melvillei, P. torquatus*, and thinocorids, the os metacarpale minus is, proximally and immediately distal to the fovea carpalis caudalis, noticeably broad dorventrally, whereas scolopacids lack the pronounced dorsal flare (Fig. 2AA). At the distal end, the cranial projection of the dorsal facet of the facies articularis digitalis major (Fig. 1M) is globular in shape, and identical to that of *P. torquatus*.

The distal end of the tibiotarsus is only partially preserved (Fig. 2CC). The tubercle lateral to the pons supratendineus for the attachment of lig. meniscotibiale intertarsi is better developed than in most of the other examined scolopacids, being absent in thinocorids and very well developed in *P. torquatus*. The pons supratendineus is proximodistally wide and the tuberositas retinaculum extensoris is elongated and ridge-like. In *P. torquatus* this tuberositas is mediolaterally broader and slightly longer proximodistally. The condylus lateralis is not as laterally projecting as that of *T. rumicivorus*. Both the epicondylus lateralis and the depressio epicondylaris lateralis are well developed.

In size and proportions the tarsometatarsus resembles that of *P. torquatus* and is very much unlike the proportionally shorter and stouter tarsometatarsus of thinocorids (Fig. 2FF). As in nearly all members of Scolopaci, the tendon of musculus flexor digitorum longus is enclosed in bony canal, which is medially positioned in the hypotarsus. The crista lateralis hypotarsi is dorsoplantarly short and projects markedly laterally (Fig. 2LL). In plantar view

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(Fig. 1Q), the hypotarsus closely resembles that of thinocorids, *P. torquatus*, and species of *Numenius* in being proximodistally shorter than that of most scolopacids. The proximal end of the hypotarsus differs from that of species of *Gallinago*, *Coenocorypha*, *Limnodromus*, and *Scolopax*, in that in these, the crista medialis hypotarsi almost completely encloses the sulcus for the tendon of m. perforans et perforates digit 2, and there is more than one bony canal for the tendons of the extensor muscles of the foot. The trochlea metatarsi II (Fig. 1P) at the distal end is more proximally situated than that of most scolopacids, resembling thinocorids (Fig. 2FF) and *P. torquatus*, albeit this condition is also present in species of *Limnodromus* and *Gallinago*. In *H. melvillei*, the medial rim of the trochlea metatarsi III plantarly is very short compared to the lateral one (Fig. 1Q; Fig. 2GG), which it does not reach proximally (Fig. 2II). This asymmetry was absent in all examined scolopacids but, as in *H. melvillei*, is very pronounced in thinocorids (Fig. 2HH). The plantar projecting flange on trochlea metatarsi II (in distal view) makes a notch with the medial surface of the trochlea (Fig. 1S) – this condition is present in thinocorids and *P. torquatus* and is absent in the examined scolopacids (Fig. 2KK). A fossa metatarsi I is well marked (Fig. 1Q). The round pit on the proximal and dorsal surface of trochlea metatarsi III resembles that of *P. torquatus*, and is much deeper than in all other examined taxa (Fig. 1O). The foramen vasculare distale is larger than that found in scolopacids and seedsnipes (Fig. 1Q), and resembles that of *P. torquatus*.

**Ontogenetic stage of osteologically immature individuals**

Bone surface texture is a useful indicator of skeletal maturity in modern and fossil birds, provided the studied taxa undergo similar growth patterns (Tumarkin-Deratzian *et al.* 2006). Most (but not all) neornithine birds are considered to obtain postcranial skeletal maturity within the first year of life (Padian *et al.* 2010); they can however reach adult size as early as
the time of fledging, i.e. before becoming osteologically mature (Tumarkin-Deratzian et al. 2006; Watanabe & Matsuoka 2013). Although few skeletal ontogenetic studies have been conducted for neognathous birds, congruence in patterns of surface texture and age classes across diverse taxa (ducks, geese, cranes, herons, gulls; Gotfredsen 1997, Serjeantson 1998, Tumarkin-Deratzian et al. 2006, Watanabe & Matsuoka 2013) suggests results may be largely applicable to taxa within Neognathae (Tumarkin-Deratzian et al. 2006).

Two coracoids (CM 2013.18.781; NMNZ S.50711) of *H. melvillei* (Fig. 2H) show a striated, rough surface, with longitudinal ridges, deep grooves, and transverse struts (Fig. 2H). This texture is consistent with an early juvenile or late chick stage, i.e. before fledging and before functionally mature plumage is obtained (Watanabe & Matsuoka 2013). Striations in the osseous surface of bones tend to be absent in immature but adult-sized (i.e. sub-adult) individuals (Tumarkin-Deratzian et al. 2006). Osteological detail of structures and muscle attachment scars not observable in detail at chick stage become progressively evident from fledging to the adult stage. Because of this, much detail is lacking in the sternal end of both juvenile coracoids of *H. melvillei*, and although some features of the omal end are recognisable (cotyla scapularis, facies articularis humeralis), the facies articularis clavicularis, the proc. acrocoracoideus, and the medial surface of the bone are poorly developed (Fig. 2H). Scapula NMNZ S.43448 (Fig. 2A) and ulna NMNZ S.53080 are of adult size but are not yet fully skeletally mature (sub-adult sensu Tumarkin-Deratzian et al. 2006). These elements still show some porosity in the texture of the shaft, and well-defined longitudinal lines still remain (Fig. 2A). All these observations provide unequivocal evidence that *H. melvillei* was breeding in the vicinity of palaeolake Manuherikia in the early Miocene.

**Discussion**
Hakawai melvillei gen. et. sp. nov. represents a unique and distinct lineage within Scolopaci, with close affinities to the clade encompassing thinocorids and pedionomids. The overall similarity in morphology to members of this clade is evident in all examined elements of the postcranial skeleton, particularly the scapula, coracoid, humerus, and tarsometatarsus. While several distinctive postcranial features (characters 1, 7, 11, 19, 20, 22, 23 in Diagnosis) are present in both thinocorids and pedionomids, some (2, 4, 6, 8, 24, 26) appear to be shared only by *H. melvillei* and *Pedionomus torquatus*. Despite there being a relatively high proportion of characters that exhibit homoplasy within Scolopaci, especially in Scolopacidae, the unique combination of features present in seedsnipes, the Plains-wanderer, and *H. melvillei* (Fig. 3) is not replicated in any lineage within Scolopacidae, and represents strong evidence for a link between these taxa. Despite the overall derived morphology of the Plains-wanderer compared to other Scolopaci (Bock & Mc Evey 1969; Olson & Steadman 1981), we propose a sister taxon relationship between *H. melvillei* and *P. torquatus* based on presumably derived features retained in both lineages (Fig. 3).

The absence of several traits that are possibly derived for scolopacids, indicate that *H. melvillei* was not a representative of this lineage, contrary to previous reports (Worthy *et al.* 2007), and therefore preclude it from being closely related to the endemic austral snipes (species of *Coenocorypha*). Late Oligocene-early Miocene (ca. 24–20.5 Ma) scolopacids from Europe already possessed a combination of features characteristic of extant scolopacids (De Pietri & Mayr 2012), and resembled early-diverging taxa such as *Numenius* and *Limosa*. Given the biogeographic, phylogenetic, and boreal breeding patterns of extant scolopacids (Piersma 1996; Gibson 2010; Gibson & Baker 2012), it is likely that members of the crown group did not arrive in Australasia until after shifts in non-breeding ranges (in response to climate cooling during the Neogene) prompted the onset of long distance migration (Louchart 2009). Response to geographic and environmental changes from the early to mid-Cenozoic
has therefore contributed to the different evolutionary trajectories for Scolopaci in the
Northern and Southern Hemispheres. High endemism resulted from geographical isolation in
Australia and NZ, while crown-group scolopacids breeding in the Northern Hemisphere
formed a Neogene radiation characterised by migratory behaviour.

In the absence of terrestrial predators, several endemic NZ birds have become flightless
(Tennyson & Martinson 2007), but there is still little indication that the St Bathans Fauna
possessed a high proportion of flightless birds (Worthy et al. 2007; Worthy et al. 2009b;
Tennyson et al. 2007). Morphology and limb proportions do not suggest that *Hakawai*
*melvillei* was flightless or possessed diminished flight capabilities. The morphology of the
humerus, carpometacarpus, and ulna, which closely matches that of seedsnipes (Fig. 3), may
indicate that *H. melvillei* was a better flier than the extant Plains-wanderer, which is a
notoriously poor flier (e.g. De Pietri *et al.* 2015). However, the presence of osteologically
immature individuals at chick or near fledging stage demonstrates that *H. melvillei* bred in
Zealandia, which supports it having been an insular, endemic taxon nonetheless.

The proportionally elongated and gracile tarsometatarsus, which resembles that of wading
scolopacids (also in the arrangement of the hypotarsal canals), is unlike the stouter
tarsometatarsi of seedsnipes, the Plains-wanderer, and species of *Coenocorypha* (austral
snipes), all of which inhabit terrestrial environments. This likely indicates that *H. melvillei*
was a littoral zone feeder, which is supported also by its abundance in these lacustrine fossil
sites. The terrestrial adaptations of *P. torquatus* and seedsnipes were proposed to be
convergent for both taxa (De Pietri *et al.* 2015), which is further substantiated by the wading
habits of *H. melvillei*. We propose that wading was likely to have been the ancestral ecology
of the clade, as suggested by the wading habits of other Scolopaci (Scolopacidae,
Rostratulidae, and Jacanidae).
Combined knowledge of present and extinct NZ groups points to long-term conservatism in its distinctive and endemic fauna, at least from the mid-Cenozoic onwards. Nevertheless, because of the absence of temporal data for terrestrial faunas for the Cenozoic of NZ, it is not possible to determine when *H. melvillei* went extinct or for how long after the early Miocene its lineage was a part of NZ’s fauna. Vulnerability after the Oligocene bottleneck, i.e. the reduction of land area as a result of eustatic sea-level rise and associated niche diversity loss during the late Oligocene and earliest Miocene, and the climatic fluctuations that reduced opportunity for refugia after the middle Miocene, have been listed as contributing factors to floral turnover and faunal changes during the Cenozoic (but see Tennyson 2010), leading to the disappearance of many taxa, including crocodilians and tropical birds (Cooper & Cooper 1995; Worthy *et al.* 2007; Pole 2008; 2014; Jones *et al.* 2009; Reichgelt *et al.* 2015).

Pedionomids and *Hakawai melvillei* were part of the ancestral radiation of a lineage that, similar to sphenodontids (Jones *et al.* 2009), may have been more widespread in the past, but only managed to survive locally in Australasian landmasses (Olson & Steadman 1981). *H. melvillei* fills an important gap in the fossil record of the Charadriiformes in the Southern Hemisphere, and demonstrates that, as proposed for passerines and parrots, the splits between seedsnipes, pedionomids and *H. melvillei* are to some degree likely to be associated with the breakup of Gondwana and the resulting isolation of landmasses that prevented gene flow among the ancestors of these lineages during the period 55–35 Ma (Fig. 4) (Schellart *et al.* 2006; Selvatti *et al.* 2015). Nevertheless, contrary to biogeographic models proposed for passerines (e.g. Ericson *et al.* 2003; Selvatti *et al.* 2015), vicariance alone probably does not explain these patterns, as the proposed sister taxon relationship between pedionomids and *H. melvillei* indicates that the split of this lineage from the seedsnipe-lineage must have occurred independently from Zealandia’s separation from the rest of Gondwana (Fig. 4). Due to the incomplete nature of the fossil record, this phylogeographic pattern could as well reflect
differential extinctions in post-Gondwana landmasses. We note that this less parsimonious scenario is not supported by the available data. A parallel among other vertebrate groups might be found in the divergence of Australasia’s endemic mystacinid bats (the extinct *Icarops* lineage in Australia and surviving *Mystacina* lineage in NZ (Hand *et al.* 2013) from ancestral noctilionoids 51–41 Ma (Teeling *et al.* 2005) in East Gondwana before its final fragmentation (Gunnell *et al.* 2014).

**Acknowledgements**

We are grateful to K Roberts, P Horton, and G Mayr for access to comparative material. We thank Lynx Editions for permission to use the images in figure 4. We are grateful to the landowners A and E Johnstone of Home Hills Station and J and T Enright, Dunstanburn Station, Southern Lakes Holdings Ltd, for access to sites, and to J Worthy for sorting the material. We also thank G. Gully and B. Choo for their assistance with preparing figures. This work was funded by grants from the Australian Research Council DP0770660 to S Hand *et al.* and DP120100486 to TH Worthy *et al.*

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Table and figure captions

Table 1. Comparative measurements of selected postcranial elements of the Plains-wanderer Pedionomus torquatus, Hakawai melvillei sp. nov., the Least Seedsnipe Thinocorus rumicivorus, and the Sharp-tailed Sandpiper Calidris acuminata. Both female (left) and male (right) individuals of P. torquatus were measured. Measurements of H. melvillei were obtained from type material only. Abbreviations: csc, cotyla scapularis; fah, facies articularis humeralis; DW, distal width; ML, maximum length; MSW, minimum shaft width; pac, processus acrocoracoideus; PW, proximal width. All measurements are in mm.

Figure 1. Type material of Hakawai melvillei gen. et sp. nov. Right scapula NMNZ S.53360 in lateral (A) and medial (B) views. Left coracoid NMNZ S.50490 in dorsal (C), dorsolateral (D), and ventral (E) views. Right ulna CM 2013.18.195 in ventral (F) and dorsal (G) views. Left ulna NMNZ S.53375 in dorsal view (H). Right humerus NMNZ S.43153 in caudal (I) and cranial (J) views. Distal right humerus NMNZ S.50716 in cranial (K) and caudal (L) views. Left carpometacarpus NMNZ S.53399 in ventral (M) and caudal (N) views. Right tarsometatarsus NMNZ S.50806 (holotype) in dorsal (O), medial (P), plantar (Q), proximal
(R), and distal (S) views. Abbreviations: acr, acromion; cdp, crista deltopectoralis; cdu, condylus dorsalis ulnaris; cdv, condylus ventralis; cih, cristae intermediae hypotarsi; cmh, crista medialis hypotarsi; csc, cotyla scapularis; ctd, cotyla dorsalis; ctv, cotyla ventralis; dfp, dorsal fossa pneumotricipitalis; epv, epicondylus ventralis; fac, facies articularis clavicularis; fah, facies articularis humeralis; fcc, fovea carpalis caudalis; fdl, canal for tendon of musculus flexor digitorum longus; fdm, facies articularis digitalis major; fic, fossa infracotylar is dorsalis; fml, fossa metatarsi; fmb, fossa m. brachialis; fos, fossa; fpm, fossa parahypotarsalis medialis; icb, impressio coracobrachialis; fvd, foramen vasculare distale; ist, impressio scapulotricipitis; m&l tr. met III, medial and lateral rims of trochlea metatarsi III; pex, proc. extensorius; pp2, sulcus for tendon of m. perforans et perforatus digit 2; ppr, plantar projection; prf, proc. flexorius; psd, proc. supracondylaris dorsalis; sht, sulcus humerotricipitalis; tbc, tuberculum coracoideum; tbd, tuberculum dorsale; tcp, tuberculum carpale; tmII, trochlea metatarsi II; tmIII; trochlea metatarsi III; trd, transverse ridge; tub, tubercle. Scale bars equal 2 mm, except OQ, which equal 5 mm.

**Figure 2.** Selected elements of *Hakawai melvillei* gen. et sp. nov. (A, D, E, H, I, K, N, R, U, X, BB, CC, DD, GG, JJ, LL) in comparison to extant taxa in Scolopaci, illustrating differences in the features discussed. Right scapula of *H. melvillei* NMNZ S.53360 (A), *Pedionomus torquatus* (B), and *Calidris acuminata* (C). Left coracoid of *H. melvillei* NMNZ S.50490 (D, E), *Thinocorus rumicivorus* (F), and *Calidris canutus* (G). Right coracoid of *H. melvillei* CM 2013.18.785, immature individual (H). Right proximal humerus of *H. melvillei* NMNZ S.42416 (I, K), *T. rumicivorus* (J, L) and *Gallinago hardwickii* (M). Distal right humerus of *H. melvillei* NMNZ S.50716 (N, R), *T. rumicivorus* (O, S), *G. hardwickii* (P, T), and *Calidris acuminata* (Q). Distal left ulna of *H. melvillei* NMNZ S.53375 (U), *T. rumicivorus* (V), and *Limosa lapponica* (W). Left carpometacarpus of *H. melvillei* NMNZ
S.53399 (X, BB), *T. rumicivorus* (Y, AA), *C. acuminata* (Z). Distal left tibiotarsus of *H. melvillei* NMNZ S.50906 (CC). Right tarsometatarsus of *H. melvillei* NMNZ S.50806 (holotype) (DD, GG, JJ, LL), *Calidris canutus* (EE, MM), *T. rumicivorus* (EE, HH, NN), *G. hardwickii* (II), and *Limos a lapponica* (KK). Abbreviations: acr, acromion; cdl, condyles lateralis; cdu, condylus dorsalis ulnaris; cdv, condylus ventralis; cph, caput humeri; csc, cotyla scapularis; dfp, dorsal fossa pneumotricipitalis; dom, dorsal flare at os metacarpale minus; fac, facies articularis clavicularis; fah, facies articularis humeralis; fdl, canal for tendon of musculus flexor digitorum longus; fdm, facies articularis digitalis major; fmb, fossa m. brachialis; m&l tr. met III, medial and lateral rims of trochlea metatarsi III; not, notch; pex, proc. extensorius; ppr, plantar projection; prf, proc. flexorius; psd, proc. supracondylaris dorsalis; pst, pons supratendineus; tbc, tuberculum coracoideum; tcp, tuberculum carpale; tmII, trochlea metatarsi II; tre, tuberositas retinaculum extensoris; tub, tubercle. Scale bars equal 2 mm, except M, P, Q, T, W–Z, EGG, which equal 5 mm.

**Figure 3.** Postcranial elements of *Hakawai melvillei* gen. et sp. nov. (A, C, E, H, K, N, P, R, T, V, X) in comparison to *Pedionomus torquatus* (B, D, F, I, L, O0, Q, S, U, W, Y) and *Thinocorus rumicivorus* (G, J, M). Illustrated characters (see Diagnosis for character description) (1), (7), (11), (20), (23), (24) are shared with members of Thinocoridae and *P. torquatus*. Characters (2), (4), (6), (8), (25), (27) are interpreted as presumably derived for *P. torquatus* and *H. melvillei*. Note the proportionally more elongate tarsometatarsus of *H. melvillei* compared to the Plains-wanderer. Abbreviations: cdv, condylus ventralis; csc, cotyla scapularis; dom, dorsal flare at os metacarpale minus; fac, facies articularis clavicularis; fah, facies articularis humeralis; m&l tr. met III, medial and lateral rims of trochlea metatarsi III; pit, rounded depression on dorsal surface of trochlea metatarsi III; ppr, plantar projection; rec,
recess below facies articularis clavicularis (absent); shf, shaft; tbc, tuberculum coracoideum; tmII, trochlea metatarsi II. Not to scale.

**Figure 4.** Proposed Gondwanan diversification of the lineage from which the South American seedsnipes (Thinocoridae), the Australian Plains-wanderer (Pedionomidae), and NZ’s *Hakawai melvillei* gen. et sp. nov. originated. Continents are shown in their current position. The possibility of trans-Tasman dispersal between Australia and NZ is indicated by a dotted arrow and a question mark. However, there is no evidence of a common ancestor of *H. melvillei* and pedionomids in Australia, and Oligocene pedionomids already shared derived traits with *Pedionomus torquatus* (De Pietri *et al.* 2015) that are absent in *H. melvillei*. We propose instead that both lineages have common ancestry in East Gondwana before its final fragmentation, and became independently isolated following complete separation of NZ and Australia from the rest of Gondwana. Insets: A, Phylogeny of Scolopaci (Gibson & Baker 2010), showing the proposed sister taxon relationship between *H. melvillei* and pedionomids; B, position of continents at 55 Ma (Lawver & Gahagan 2003). Bird images reproduced with permission of HBW Alive (Baker-Gabb DJ. 1996; Fjeldså J. 1996)
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III, medial and lateral rims of trochlea metatarsi III; pex, proc. extensorius; pp2, sulcus for tendon of m. perforans et perforatus digiti 2; ppr, plantar projection; prf, proc. flexorius; psd, proc. supracondylaris dorsalis; sht, sulcus humerotricipitalis; tbc, tuberculum coracoideum; tbd, tuberculum dorsale; tcp, tuberculum carpale; tmII, trochlea metatarsi II; tmIII; trochlea metatarsi III; trd, transverse ridge; tub, tubercle. Scale bars equal 2 mm, except O–Q, which equal 5 mm.

278x431mm (300 x 300 DPI)
Selected elements of Hakawai melvillei gen. et sp. nov. (A, D, E, H, I, K, N, R, U, X, BB, CC, DD, GG, JJ, LL) in comparison to extant taxa in Scolopaci, illustrating differences in the features discussed. Right scapula of H. melvillei NMNZ S.53360 (A), Pedionomus torquatus (B), and Calidris acuminata (C). Left coracoid of H. melvillei NMNZ S.50490 (D, E), Thinocorus rumicivorus (F), and Calidris canutus (G). Right coracoid of H. melvillei CM 2013.18.785, immature individual (H). Right proximal humerus of H. melvillei NMNZ S.42416 (I, K), T. rumicivorus (J, L) and Gallinago hardwickii (M). Distal right humerus of H. melvillei NMNZ S.50716 (N, R), T. rumicivorus (O, S), G. hardwickii (P, T), and Calidris acuminata (Q). Distal left ulna of H. melvillei NMNZ S.53375 (U), T. rumicivorus (V), and Limosa lapponica (W). Left carpometacarpus of H. melvillei NMNZ S.53399 (X, BB), T. rumicivorus (Y, AA), C. acuminata (Z). Distal left tibiotarsus of H. melvillei NMNZ S.50906 (CC). Right tarsometatarsus of H. melvillei NMNZ S.50806 (holotype) (DD, GG, JJ, LL), Calidris canutus (EE, MM), T. rumicivorus (EE, HH, NN), G. hardwickii (II), and Limosa lapponica (KK).

Abbreviations: acr, acromion; cdll, condyles lateralis; cdv, condylus dorsalis ulnaris; cdv, condylus ventralis; cph, caput humeri; csc, cotyla scapularis; dfp, dorsal fossa pneumotricipitalis; dom, dorsal flare at os
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269x403mm (300 x 300 DPI)
Postcranial elements of Hakawai melvillei gen. et sp. nov. (A, C, E, H, K, N, P, R, T, V, X) in comparison to Pedionomus torquatus (B, D, F, I, L, O0, Q, S, U, W, Y) and Thinocorus rumicivorus (G, J, M). Illustrated characters (see Diagnosis for character description) (1), (7), (11), (20), (23), (24) are shared with members of Thinocoridae and P. torquatus. Characters (2), (4), (6), (8), (25), (27) are interpreted as presumably derived for P. torquatus and H. melvillei. Note the proportionally more elongate tarsometatarsus of H. melvillei compared to the Plains-wanderer. Abbreviations: cdv, condylus ventralis; csc, cotyla scapularis; dom, dorsal flare at os metacarpale minus; fac, facies articularis clavicularis; fah, facies articularis humeralis; m&l tr. met III, medial and lateral rims of trochlea metatarsi III; pit, rounded depression on dorsal surface of trochlea metatarsi III; ppr, plantar projection; rec, recess below facies articularis clavicularis (absent); shf, shaft; tbc, tuberculum coracoideum; tmII, trochlea metatarsi II. Not to scale.

233x303mm (300 x 300 DPI)
Proposed Gondwanan diversification of the lineage from which the South American seedsnipes (Thinocoridae), the Australian Plains-wanderer (Pedionomidae), and NZ’s Hakawai melvillei gen. et sp. nov. originated. Continents are shown in their current position. The possibility of trans-Tasman dispersal between Australia and NZ is indicated by a dotted arrow and a question mark. However, there is no evidence of a common ancestor of H. melvillei and pedionomids in Australia, and Oligocene pedionomids already shared derived traits with Pedionomus torquatus (De Pietri et al. 2015) that are absent in H. melvillei. We propose instead that both lineages have common ancestry in East Gondwana before its final fragmentation, and became independently isolated following complete separation of NZ and Australia from the rest of Gondwana. Insets: A, Phylogeny of Scolopaci (Gibson & Baker 2010), showing the proposed sister taxon relationship between H. melvillei and pedionomids; B, position of continents at 55 Ma (Lawver & Gahagan 2003). Bird images reproduced with permission of HBW Alive (Baker-Gabb DJ. 1996; Fjeldså J. 1996) 167x102mm (300 x 300 DPI)
### Coracid

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### Scapula

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### Carpometacarpus

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### Tarsometatarsus

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*Coracoid CM 2013.18.785 is a juvenile (see Results section) with omal end sternal ends not fully defined. The maximum length of an adult individual is therefore likely to be greater.

Shaft width of an adult individual (MNZ S. 52771) is also noted. Proportions (Fig. 2H) indicate the coracoid of *H. melvillei* is elongated in omal-sternal direction, as that of the *P. torquatus* and unlike that of thinocorids and scolopacids (De Pietri et al. 2015).